The Journal of Experimental Biology **198**, 61–69 (1995)
Printed in Great Britain © The Company of Biologists Limited 1995

PHYSIOLOGY AND BEHAVIOUR OF FREE-SWIMMING ATLANTIC COD (*GADUS MORHUA*) FACING FLUCTUATING SALINITY AND OXYGENATION CONDITIONS

G. CLAIREAUX[1], D. M. WEBBER[1], S. R. KERR[2] AND R. G. BOUTILIER[3]

[1]*Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1,* [2]*Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada B2Y 4A2* and [3]*Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK*

Accepted 15 August 1994

Summary

1. Atlantic cod (*Gadus morhua* L.) acclimated to a temperature of 5 ˚C and 30 ‰ salinity were equipped with ultrasonic transmitters which allowed continuous monitoring of their heart rate and their position in the water column. Fish were placed in a 125 m^3 tower tank which permitted various environmentally relevant modifications of the salinity and oxygenation conditions. Cod physiological and behavioural responses were followed in parallel to the environmental manipulations. Some of the experimental conditions studied in the tower tank were also reproduced in a swimming respirometer where fish oxygen consumption and heart rate were monitored at various levels of activity.

2. Lowering salinity from 30 to 26 ‰ did not change resting oxygen consumption, but increased active oxygen consumption.

3. Lowering salinity from 30 to 26 ‰ increased heart rate over the whole range of swimming speeds except at maximum speed.

4. Lowering oxygen tension to 9 kPa decreased oxygen consumption over the whole range of swimming speeds and decreased resting heart rate.

5. Low salinity did not significantly affect the relationship between heart rate and oxygen consumption.

6. Low oxygen levels decreased the oxygen transported per heart beat.

7. In the tower tank, bursts of activity were associated with tachycardias.

8. In uniform conditions, fish swam more deeply during the day than at night.

9. After an exploratory period of approximately 6 h, fish chose to remain in a low-salinity upper layer of the tank. Thereafter, high salinities were avoided. Fish tended to select low salinities if a choice was provided.

10. Fish generally avoided zones of low oxygen (<9 kPa) but continued voluntarily to enter regions with values as low as 3.0 kPa for short excursions or if food was offered.

Key words: salinity, oxygen, halocline, chemocline, depth, heart rate, oxygen consumption, exercise, ultrasonic transmitter, cod, *Gadus morhua.*

Introduction

In the preceding paper (Claireaux *et al.* 1995), we reported the effects of variations in water temperature on the physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua* L.). In heterogeneous temperature fields, cod appear to ‘track’ the water temperatures to which they were previously acclimated. Moreover, acute temperature changes of less than a few degrees Celsius can lead to marked changes in metabolic rate, which may be counterproductive to further activity or foraging. In order to understand more extensively the various interactions existing between the fish and its physico-chemical environment, and so to have a broader view of the processes that regulate the distribution and migratory patterns of cod, the repercussions of fluctuating salinity and oxygenation conditions also had to be addressed. In nature, cod seldom encounter changes in environmental conditions which require full-scale physiological regulatory mechanisms. It follows that, in most instances, the full scope of these response mechanisms will not be the prime determinant of fish behaviour. Typically, Atlantic cod are faced with environmental perturbations which are well below the resistance threshold. Thus, in optimizing their position in the water column, cod take into account factors such as the presence of prey or predators, hierarchical organisation within the school, their own biological and nutritional status and other environmental cues such as depth and bottom structure. In the present experiment, we examine the effects of variations in water salinity and oxygenation in a further attempt to understand the sensitivity with which cod perceive their physico-chemical environment.

Atlantic cod acclimated to a temperature of 5 ˚C and a salinity of 30 ‰ were equipped with ultrasonic transmitters which allowed the continuous monitoring of their vertical movements and heart rate. Fish were then placed in a 125 m^3 tower tank in which various environmentally relevant fluctuations in the salinity and oxygenation conditions were replicated. The physiological and behavioural responses of cod were followed in parallel to the environmental manipulations. To evaluate the impact of the water physico-chemical characteristics on their metabolism, some of the experimental conditions studied in the tower tank were also reproduced in a swimming respirometer where fish oxygen consumption and heart rate could be monitored at various levels of activity.

Materials and methods

The fish holding and instrumentation procedures, the oxygen consumption measurement method, the ultrasonic transmitters and the computerized data acquisition system were as described in the accompanying paper (Claireaux *et al.* 1995).

Swim-tunnel respirometry

The respirometry measurements presented here used the same individuals as were tested by Claireaux *et al.* (1995). Following the temperature experiments, and after an overnight recovery period at their temperature and salinity of acclimation (i.e. 5 ˚C and 30‰), the water salinity in the respirometer was quickly reduced (<30 min) to 26 ‰. Fish oxygen consumption ($\dot{M}_{O_2}$) and heart rate (*f*H) were then measured during an exercise sequence similar to the one previously described (i.e. at 7, 18, 27, 37, 48 and 57 cm s^{-1}). At the end of the swimming trial, water salinity was returned to 30 ‰ and the fish were allowed to recover. The next day, the effect of a decrease in water oxygenation level from full saturation (17.9 kPa) down to 9.0 kPa was then tested according to the same swimming protocol. To induce hypoxia, water flowed through a gas-exchange column bubbled with nitrogen before reaching the respirometer. $\dot{M}_{O_2}$ and *f*H recorded during swimming in the respirometer were expressed as mean ± standard error of the mean (S.E.M.) and were compared with their value at the lowest water speed (reference condition) to assess the statistical significance of any changes (unpaired Student's *t*-test; $P<0.05$).

Tower tank

The experimental conditions (water supply, lighting, number of fish) in the tower tank were identical to those described previously (Claireaux *et al.* 1995).

Adjustments in salinity and the stratification of the water column were achieved by flowing known volumes of full-strength or diluted sea water through inlets placed at various depths in the tank. Water temperature was controlled using two titanium heat-exchange coils immersed at different levels in the tank. Water oxygen content was controlled using an H-shaped 'airlift' immersed in the tank. This device, made of 10 cm diameter polyvinylchloride pipe, consisted of two 6 m long vertical sections connected at the top by a 0.5 m horizontal piece. When air or nitrogen was bubbled into one of the 'legs' of the H, the upward movement of the bubbles in the pipe caused a suction effect and caused water to ascend. When it reached the top of the pipe, the newly equilibrated water flowed through the horizontal portion and returned to its initial layer *via* the second vertical section. The intensity of the bubbling was adjusted to regulate the water flow in the airlift and to avoid mixing with adjacent water layers. Oxygen, salinity and temperature profiles of the water column were made periodically using YSI meters, models 57 DO and 33 SCT, respectively.

Results

Swim-tunnel respirometry

The respirometry experiments described here were conducted as part of the experimental series described in the preceding paper (Claireaux *et al.* 1995) and thus concern the same individual cod (see Materials and methods). The relationships between heart rate (*f*H), oxygen consumption ($\dot{M}_{O_2}$) and swimming speed established in reference conditions (i.e. a temperature of 5 ˚C, a salinity of 30 ‰) are presented in Fig. 1A. Fig. 1B shows the same relationships following an abrupt (within 30 min) decrease in water salinity from 30 to 26 ‰. When compared with reference conditions, similar $\dot{M}_{O_2}$ values were measured in resting fish (7 cm s^{-1}) exposed to dilute sea water, although the mean *f*H was higher, 22.1±0.6 beats min^{-1} in reference conditions and 24.0±0.5 beats min^{-1} in low-salinity water. During the subsequent exercise period, the metabolic responses observed in both salinity conditions (Fig. 1A,B) were of comparable amplitude. Furthermore, as in the reference conditions, no significant changes in mean heart rate were observed during exercise in low-salinity water.

When cod were exposed to decreased water oxygen tension ($P\text{w}_{O_2}$=9 kPa), a bradycardia was observed, as fish resting *f*H dropped from 22.1±0.6 beats min^{-1} in reference conditions to 19.9±0.8 beats min^{-1} in the lower-oxygen environment. Simultaneously, their resting $\dot{M}_{O_2}$ decreased from 26.8±2.1 μmol min^{-1} kg^{-1} in normoxia to 19.5±0.9 μmol min^{-1} kg^{-1} in hypoxia. During exercise, however, $\dot{M}_{O_2}$ did not change noticeably with increasing water velocity, but *f*H rose significantly, reaching 25.8±1.2 beats min^{-1} at 57 cm s^{-1}.

When these *f*H and $\dot{M}_{O_2}$ data were plotted irrespective of the swimming speed at which they were measured, more interesting features were observed. Following exposure to diluted sea water (Fig. 2), no significant changes in the relationship between the two variables were observed, suggesting that a 4 ‰ fluctuation in the water salinity had no major physiological consequences for the animal. In hypoxic conditions, however, we noticed a downward shift of the regression line (Fig. 3). This deviation, presumably related to an overall decrease in the scope of the aerobic metabolism, suggested that fish were operating on new bioenergetic bases in order to satisfy their energetic requirements.

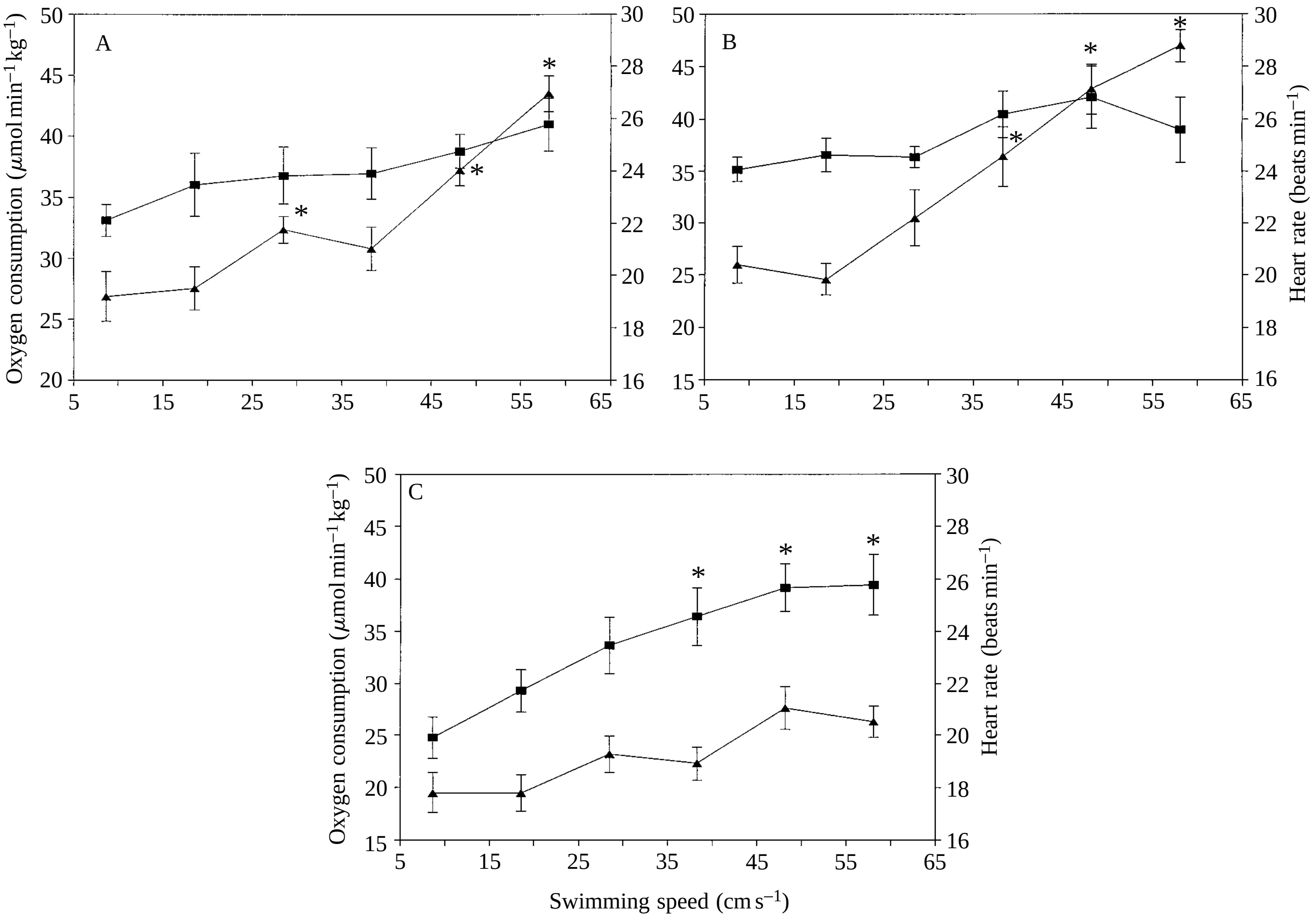

Fig. 1. Mean (± S.E.M.) oxygen consumption (triangles) and heart rate (squares) of cod swimming at speeds ranging from 7 to 57 cm s^{-1} ($N=5$). In A, fish were exercised at their acclimation temperature and salinity (i.e. 5 °C and 30 ‰). In B, water salinity in the respirometer was dropped to 26 ‰ within 30 min prior to the swimming trial. In C, water oxygenation level was dropped from saturation to 9.0 kPa within 30 min prior to the exercise sequence. Asterisks indicate a significant difference from resting values ($P<0.05$).

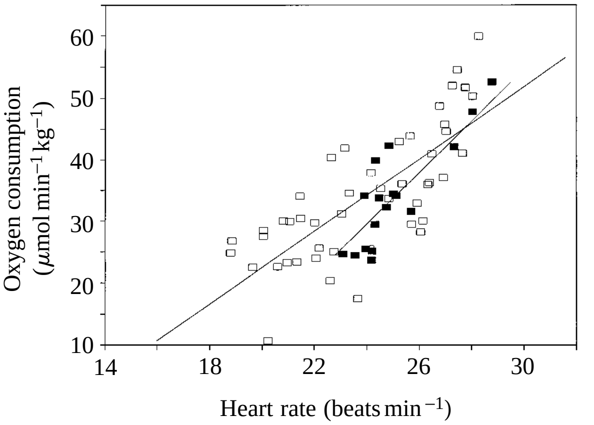

Fig. 2. Oxygen consumption *versus* heart rate relationship in 5.0 °C, 30 ‰ acclimated cod, at 30 ‰ (open squares) and following a drop in the water salinity to 26 ‰ (filled squares). Data are plotted irrespective of the fish swimming speed. 30 ‰, $\dot{M}\mathrm{O}_2=2.98f\mathrm{H}-37.34$, $r=0.76$; 26 ‰, $\dot{M}\mathrm{O}_2=4.60f\mathrm{H}-81.20$, $r=0.66$.

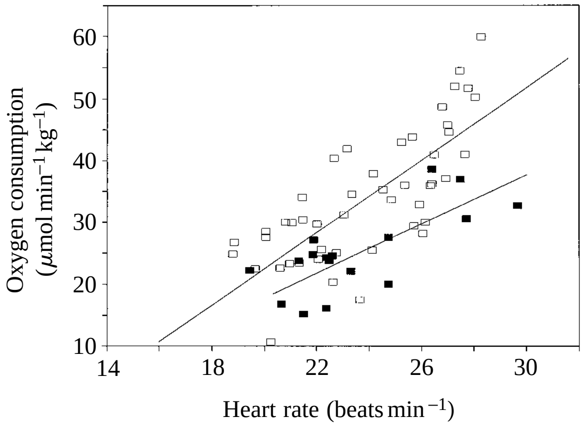

Fig. 3. Oxygen consumption *versus* heart rate relationship in 5.0 °C, 30 ‰ acclimated cod, in fully aerated water (open squares) and following a drop in the water oxygenation level to 9.0 kPa (filled squares). Data are plotted irrespective of the fish swimming speed. Normoxia, $\dot{M}\mathrm{O}_2=2.98f\mathrm{H}-37.34$, $r=0.76$; hypoxia, $\dot{M}\mathrm{O}_2=1.45f\mathrm{H}-9.10$, $r=0.85$.

Telemetry

Following a 24 h post-surgery recovery period, Atlantic cod, acclimated to 5 ˚C and 30 ‰ salinity, were placed in the tower tank and their vertical movements and heart rate were monitored from their ultrasonic tags for 3 days. During this period, water temperature and salinity conditions remained homogeneous across the tank (5 ˚C, 30 ‰). On the fourth day, diluted sea water was slowly added at the top of the tank, resulting in a layering of the water column which was completed after 2 days. Fig. 4A shows the behavioural and metabolic responses recorded from one fish during the second day of this stratification procedure. As during the previous 4 days, this animal spent the dark hours at the bottom of the tank (9.5–10.5 m). After daybreak (06:30–06:45 h), however, a marked change in the animal's behaviour was observed. Instead of patrolling the bottom 1 m of the tank, the cod undertook periodic and rapid excursions into the upper layers of the water column. Ultimately (between 12:00 and 15:00 h), presumably after having become accustomed to their new environmental conditions, all fish present in the tank voluntarily moved into the low-salinity upper half of the tower. Moreover, from then on cod were never observed at salinities above 27 ‰, excluding their feeding period (see Figs 7 and 8).

After a week, the reverse experiment was conducted as the water column was homogenized over a 2 day period by flowing full-strength sea water into the bottom of the tank. Fig. 4B shows the behavioural response of the individual previously followed (Fig. 4A). As high-salinity layers rose in the tower tank, this animal, togather with the rest of the school, moved up into increasingly shallower water, presumably to avoid being exposed to the higher-salinity water mass.

Heart rate recordings made during these two experiments also displayed intriguing features. Irrespective of the environmental conditions faced by the animal, daytime was

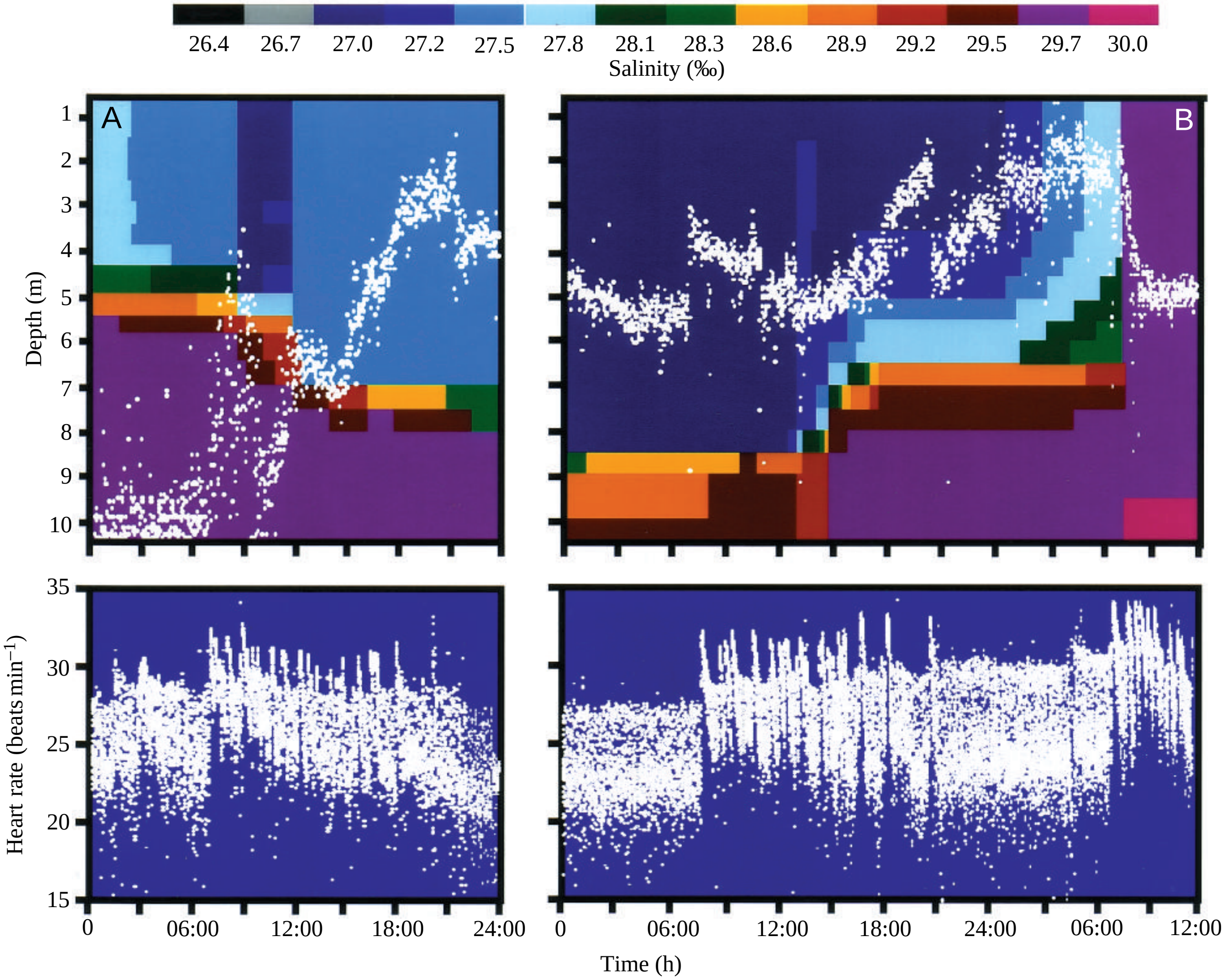

Fig. 4. Depth and heart rate of a 5.0 ˚C, 30 ‰ acclimated Atlantic cod facing fluctuating salinities. The water salinity is given by the colour codes at the top of the figure. (A) Stratification of the water column by introducing diluted sea water at the top of the tank. (B) Homogenisation of the water column by introducing full-strength sea water at the bottom of the tank. During this experiment, the data acquisition system scanned each tag for 30 s. Every heart beat recorded during each of these scanning periods is reported on the graph (lower panels). However, only the mean depths calculated from each 30 s interval were plotted here (for details, see Materials and methods in Claireaux *et al.* 1995).

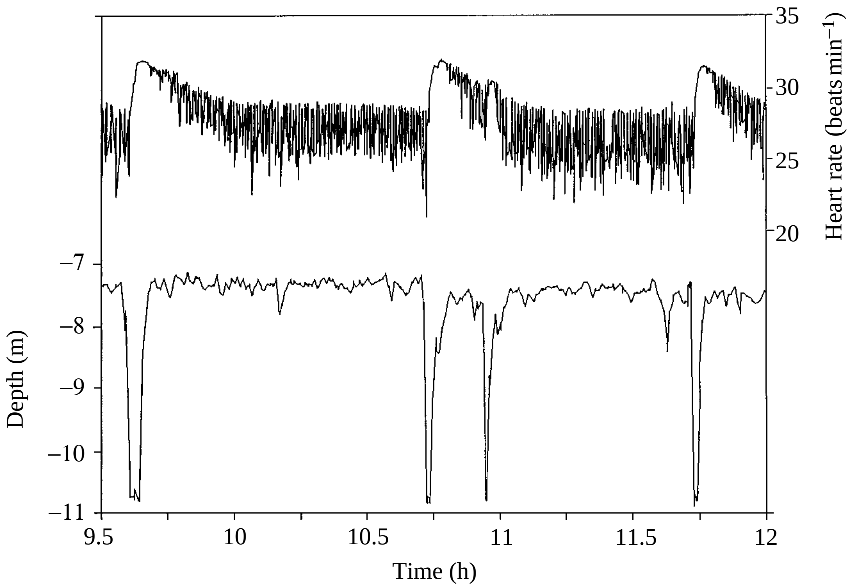

Fig. 5. Example of the relationship between heart rate and swimming activity in a free-ranging Atlantic cod.

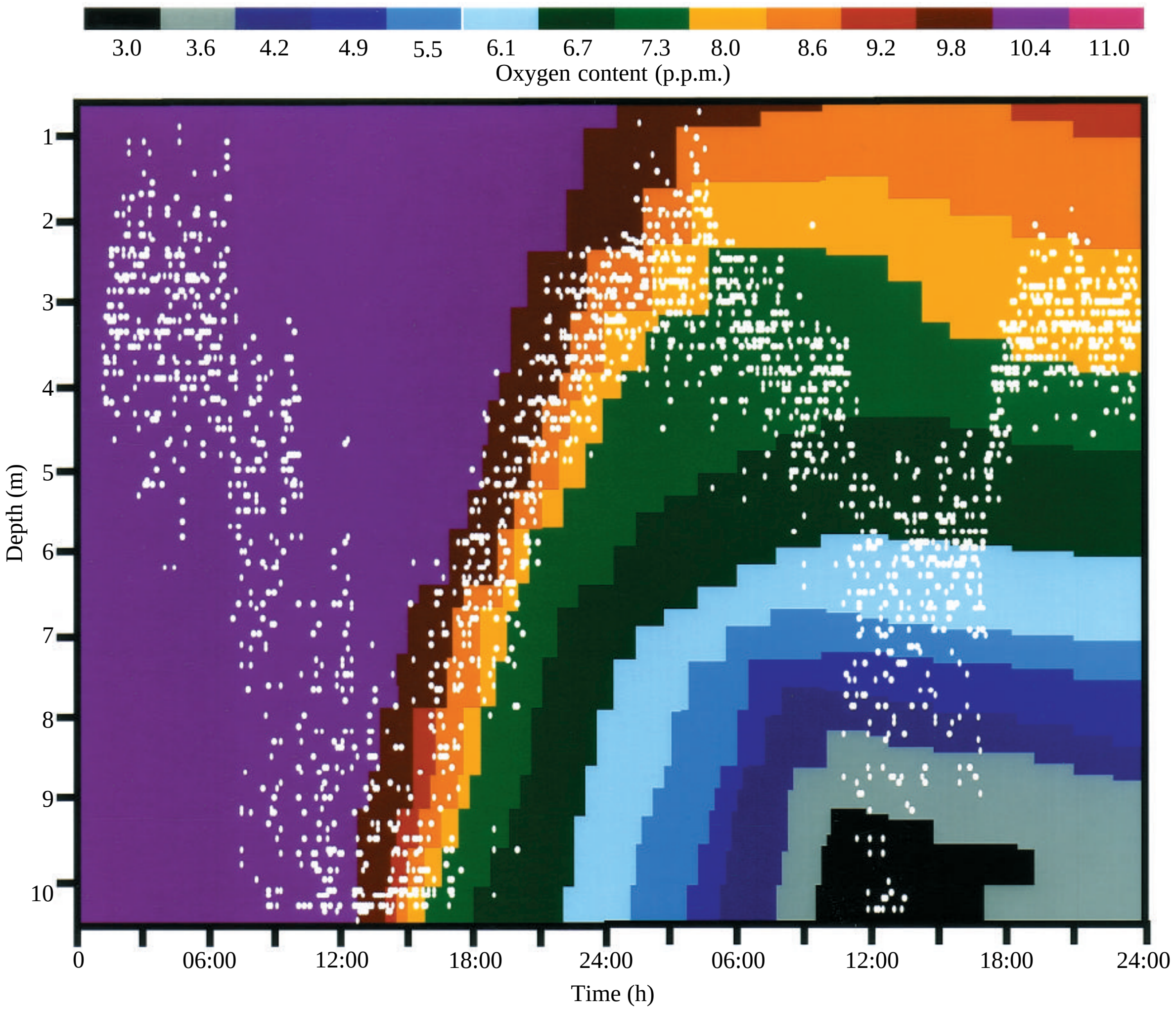

Fig. 6. Effect of an expanding hypoxic layer at the bottom of the tank (starting at 13:00 h) on the behaviour of the Atlantic cod. The water oxygen content is given by the colour codes at the top of the figure. Note that, under these conditions, the range in oxygen content from 3.0 to 11.0 p.p.m. corresponds to a range in partial pressures from 4.4 to 16.2 kPa. Note the reduction in the amplitude of the vertical migration at day 2.

always associated with sudden, short-lived periods of tachycardia. These cardiac events were never observed during the night and occurred at increasing frequency during periods of environmental perturbations. During stable conditions, in contrast, their frequency of occurrence diminished irrespective of the exact nature of the conditions imposed. For example, before and after the stratification of the water column (Fig. 4A), spikes in the fish heart beat occurred approximately 5–10 times per day. During the stratification procedure (Fig. 4A), or as the water column was being homogenized (Fig. 4B), these brief episodes of tachycardia were observed on approximately 20 occasions per day.

To determine the cause of the alterations in the cardiac rhythm, we examined the vertical movements of the fish and their heart rate on a more appropriate time scale (Fig. 5). It then emerged that each distinguishable cardiac event was associated with a sudden burst in cod activity. Indeed, each time the animal initiated a ‘round-trip’ to the bottom of the tank, a slight, short-lived bradycardia was observed, followed by a more prolonged tachycardia. Although the leisurely shuttle down and up the tank usually occupied less than 2–3 min, 5–6 min was needed for the heart rate to recover. Interestingly, these periods of relatively higher heartbeat frequency were also characterized by little or no beat-to-beat variability in the heart rate. The animal response depicted in Fig. 5 was selected because it displayed the most obvious cardiac responses. However, although less clear-cut, these features were observed in several other fish, including those monitored during the temperature experiments (Claireaux *et al.* 1995).

Fig. 6 shows the behavioural response recorded from one fish monitored when the water oxygen partial pressure ($P\mathrm{w}_{\mathrm{O_2}}$) was reduced over a 2 day period. During the first 12 h, the fish followed the daily cycle it had conformed to during the preceding days, i.e. swimming into shallower waters at night and into deeper water layers during the day. However, as $P\mathrm{w}_{\mathrm{O_2}}$ started to decrease at the bottom of the tank, an alteration of fish behaviour was observed, the animal initiating its upward migration 3–4 h earlier than usual. On the next day, the downward migration associated with daybreak still occurred, but its amplitude was then greatly reduced as the fish avoided being exposed to hypoxic water (i.e. $P\mathrm{w}_{\mathrm{O_2}}<5.0$ p.p.m.). All the animals ($N=12$) present in the tank at the time displayed the same behaviour. During the following days, fish were occasionally observed swimming through the less-oxygenated water layers. However, these incursions were transitory and animals always returned to the normoxic layers within 2–3 min.

These quick intrusions into ‘inauspicious’ waters were frequently observed during feeding periods (Figs 7 and 8). Fig. 7 illustrates how the introduction of food at the bottom of the tank impacts on cod behaviour. The water column was stratified in salinity and, before food was introduced into the tank, the fish occupied the upper half of the tower (salinity >27 ‰). As soon as the animals perceived the presence of food at the bottom, they immediately moved into the high-salinity layer and remained there for as long as food could be found (45 min). When no more food was available, fish eventually returned above the ‘chemocline’ (in this case a halocline) symbolised by the shaded area. When the bottom layer was made hypoxic, the feeding behaviour changed again, illustrating the great accuracy of the fish’s perception of its environment (Fig. 8). Following the addition of food, fish moved from their initial position down to the vicinity of the chemocline and from there made swift ‘round-trips’ to the bottom and back of the tank to grab food. When all the food was eaten, the fish swam away from the chemocline and eventually returned to their original depth. Note that the values presented in Figs 7 and 8 are the averaged depth measured over 30 s at 2 min intervals. In the case of Fig. 8, fish shuttle-trips

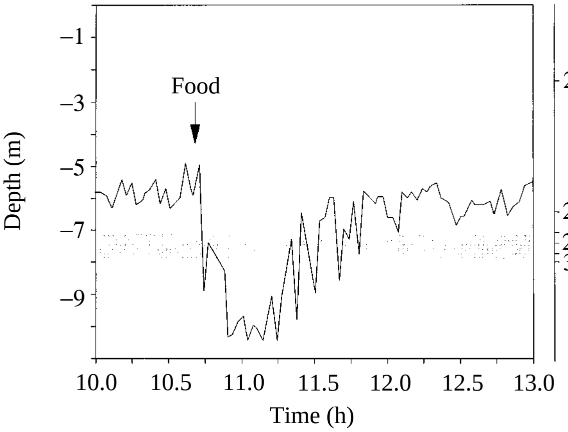

Fig. 7. Impact of a layered water column on the feeding behaviour of an Atlantic cod. Food was introduced into the bottom of the tank. The water salinity is given at the right of the figure. The shaded area outlines the position of the halocline. During this experiment, the data acquisition system only stored the averaged depth measured over each of the 30 s scanning periods.

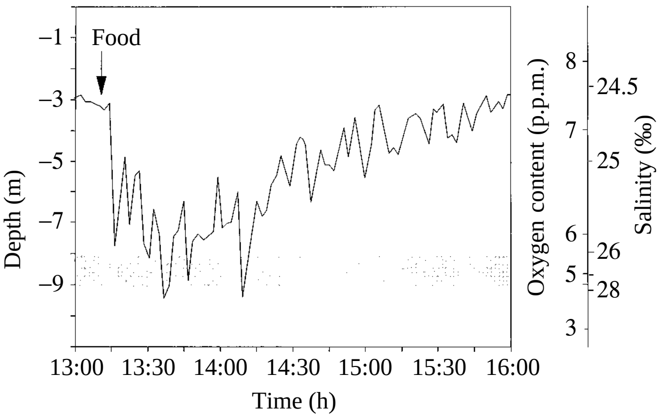

Fig. 8. Impact of a layered water column on the feeding behaviour of an Atlantic cod. Food was introduced into the bottom of the tank. The water salinity and oxygen content are given at the right of the figure. The shaded area outlines the position of the chemocline. During this experiment, the data acquisition system only stored the averaged depth measured over each of the 30 s scanning period.

below the transition zone were so fast that we could not precisely individualize each of them.

Discussion

We first examined, in a swim-tunnel respirometer, certain aspects of the physiology of the Atlantic cod in situations of changing salinity or oxygenation. The results showed that, whereas a 4 ‰ decrease in water salinity had no major impact on the fish metabolic and cardiac performances, a reduction in ambient oxygenation level from saturation to 9.0 kPa induced significant physiological readjustments.

Apart from some initial differences in the resting heart rate immediately following exposure to diluted sea water, no additional discrepancies between the two salinity treatments were observed in the relationships connecting f_H, $\dot{M}_{O_2}$ and swimming speed (Figs 1A,B and 2). While many studies have investigated the changes in oxygen consumption in fish acclimated to various salinities, very few have actually examined the impact of acute salinity changes on the metabolic rate. Davenport and Vahl (1979) studied, in the euryhaline species *Blennius pholis*, the effect of salinity fluctuation in the range 0–34 ‰ at tidal periodicity. They found that $\dot{M}_{O_2}$ increased at low and rising salinities but dropped back to routine level at high or falling salinities. These authors also reported no significant changes in the heart rate of blenny during these salinity oscillations. Atlantic cod is also considered to be a euryhaline fish (Odense *et al.* 1966; Fletcher, 1978*a*,*b*). For example, Dutil *et al.* (1992) showed that cod directly exposed to ambient salinities as low as 7 ‰ do not experience severe osmoregulatory disturbances, even during the first 24 h in diluted sea water. Similarly, Claireaux and Dutil (1992) showed that acclimation of cod to salinities ranging from 28 to 7 ‰ had no repercussion on their ability to tolerate low oxygen levels. In the present study, the lack of any significant cardiac and metabolic perturbations following a 4 ‰ decrease in ambient salinity may relate to this osmo-and iono-regulatory ability. However, as only heart rate was measured, conclusions concerning the cardiac responses at rest, and also during swimming, must be treated carefully. Priede and Tytler (1977) showed that the range of possible $\dot{M}_{O_2}$ values for a given heart rate was very large in cod, substantiating the statement by Randall (1968) that, in fish, the stroke volume can vary extensively, giving a wide range of cardiac output for any given heart rate. This is illustrated by the fact that, in the respirometer, f_H changed little with increasing swimming speed (Fig. 1A,B), whereas in the tower tank, increased activity was accompanied by marked changes in f_H (Fig. 5).

When cod were exposed to hypoxic conditions, significant metabolic and cardiac adjustments occurred, resulting in the decline of both f_H and $\dot{M}_{O_2}$ in resting conditions and in the amplitude of the metabolic response during swimming (Fig. 1A,C). In contrast, the tachycardia observed during exercise in hypoxic water was more pronounced, f_H measured at high swimming speed reaching the level recorded under normoxic conditions. This resulted in a downward shift of the f_H *versus* $\dot{M}_{O_2}$ relationship (Fig. 3). As in many other species (Randall and Daxboeck, 1984; Taylor, 1985), the hypoxic bradycardia in cod occurs with essentially no change in cardiac output (Fritsche and Nilsson, 1989) owing to a simultaneous increase in the stroke volume of the heart. According to Randall (1982), these cardiac adjustments promote lamellar recruitment in situations of limited oxygen availability. It is generally accepted that the metabolic response of fish exposed to low oxygen levels can be partitioned into two phases. In moderate hypoxia, adjustments in the fish respiration and circulation allow the oxygen consumption to be sustained (regulatory phase), whereas under more severe hypoxic conditions $\dot{M}_{O_2}$ decreases (conforming phase). The threshold between these two phases is species-specific. Our data suggest that, in Atlantic cod, modification of the metabolic rate according to the amount of oxygen available may take place at P_{WO_2} as high as 9 kPa (Figs 1C, 3). Sundnes (1957) reported 8.0 kPa to be the P_{WO_2} below which $\dot{M}_{O_2}$ became dependent upon water oxygen content. Saunders (1963) also reported that the oxygen consumption of small cod (1.14 kg) tended to decrease in situations of decreasing ambient oxygen content. In larger individuals (2.33 kg), however, $\dot{M}_{O_2}$ was apparently maintained constant over the range of P_{WO_2} tested (3–10 p.p.m.). To explain this difference in the metabolic response with size, Saunders drew a parallel between the observed changes in metabolic rate and the fact that the increase in the respiratory volume was from 7 to 27 l h^{-1} (threefold) in small fish and from 18 to 90 l h^{-1} (fivefold) in large fish. Conversely, Claireaux and Dutil (1992) reported no significant changes in the concentrations of lactate, pyruvate and glucose measured in the white muscle, the liver and the heart of cod exposed to mild hypoxia (8.0 kPa) for 6 h.

Our objective in comparing swim-tunnel respirometry experiments with observations made on free-swimming animals was to characterize the potential ties existing between the physiological and behavioural processes taking place in cod. For example, even though the environmental conditions tested in the tower tank were well within the range of the perturbations ordinarily experienced by cod, they nevertheless induced marked behavioural responses. This is a clear example where inferences about the behavioural response of free-ranging animals facing a given set of ambient conditions based only on their physiological ability to endure these conditions could be very misleading. For instance, the data presented in Fig. 2 and the studies by Odense *et al.* (1966), Fletcher (1978*a*,*b*) and Dutil *et al.* (1992) indicate that Atlantic cod can withstand a wide range of ambient salinities. It might therefore be tempting to conclude that, in the range 30–7 ‰, water salinity has no major impact on the distribution of this species in its natural environment. Similarly, it could easily be concluded from our respirometry data and from the study by Claireaux and Dutil (1992) that ambient oxygen level is not a predominant environmental factor influencing cod distribution and migration patterns. However, the telemetry experiments clearly reveal that this is not the case and that, as for temperature (Claireaux *et al.* 1995), small changes in salinity or oxygenation levels are meaningful when trying to understand cod behaviour.

When a low-salinity water layer was made available to the fish, they all moved into it and were then reluctant to leave. When full-strength sea water was then added to the tank, fish distribution was altered again as they tried to escape from the approaching higher-salinity water mass. However, if food was introduced into the high-salinity layer, fish did not hesitate to dive in to feed, but they always returned to the low-salinity layer soon afterwards. Numerous reasons can be proposed to explain the behavioural choices made by cod, but the extent of their osmoregulatory ability is clearly not one of them. Likewise, the marked behavioural response we observed as hypoxia developed at the bottom of the tank was probably not directly driven by any sort of *physiological requirements* related to respiration. Indeed, Jobling (1988) mentioned 1.7 p.p.m. as being the limit below which cod asphyxiate. The lowest level measured at day 1 of the hypoxia experiments was still above 6.0 p.p.m. (Fig. 6). It seems probable that, in these environmental conditions, the need to meet respiratory criteria was higher in the fish's priority list and thus weighed more heavily than other factors in determining certain aspects of their daily behaviour (e.g. the amplitude of their daily vertical migration or feeding behaviour). Schurmann and Steffensen (1992) also described interactions between the behaviour of cod and the oxygenation conditions in their environment. They showed that, as the amount of oxygen available decreased, cod tended to select colder environments (i.e. behavioural hypothermia), increasing their chance of survival by reducing their metabolic rate.

Several workers have tried to relate marine fish abundance with the physico-chemical properties of the surrounding water and found no reproducible patterns (Jean, 1964; Scott, 1982; Tremblay and Sinclair, 1985; Perry and Neilson, 1988; Smith *et al.* 1991). Our data suggest that, when establishing correlations between distribution patterns and environmental factors, one should also take into account the various options available to the fish at the time. In some instances, fish may simply be constrained into choosing the lesser of two evils.

Most estimates of energy expenditures in wild fish have been made by extrapolating laboratory measurements of metabolic rate to the field situation. However, as pointed out by Lucas *et al.* (1991), in order to formulate a bioenergetic model which fits with field estimates, information concerning short-term changes in the metabolic rate are essential. The heart rate recordings presented in Figs 4 and 5 exemplify this necessity for Atlantic cod. Indeed, in addition to the problem already discussed of the loose relationship between heart rate and cardiac output in fish, the data reported in Figs 4 and 5 show that the heart rate of a free-ranging animal, and presumably its metabolic rate, can be extremely variable (Figs 2 and 3). Overlooking the relevance of such short-term oscillations will inevitably result in an underestimation of the true energy expenditure of the fish. In this example, the beat-to-beat variability was related to swimming activity and confirmed the existence of a daily cycle in the fish movements. Sureau and Lagardère (1991) reported similar peaks in the heart rate of sole *Solea solea* in relation to activity, although in this case they mainly occurred at night. Such short-term cardiac adjustments with bursts of animal activity were also observed in pike *Esox lucius* by Lucas *et al.* (1991).

Great caution must be taken when extrapolating laboratory measurements to the field, since different time scales necessarily apply. Priede (1985) discussed the problem of choosing the most appropriate time scale when measuring metabolic processes. Priede argued that fluctuations in oxygen uptake at the gill are regulated on a time-base of about a minute and that the immediate energetic objective of a fish is simply to regulate its metabolism on a minute-by-minute basis. Accordingly, the most significant changes in the heart rate of our telemetered cod occurred within a time frame of 5–6 min and they were the result of periods of fish activity which lasted no longer than 2–3 min.

In conclusion, the present study, together with that of Claireaux *et al.* (1995), indicates that the distribution and movements of Atlantic cod are determined by complex interactions, behavioural and physiological, between the animal and its environment. The studies also clearly illustrate that such interactions cannot be satisfactorily described if only the physiological regulatory ability of this species is taken into account. These data also shed new light on the growing amount of information concerning the heterogeneity of cod distribution (Jean, 1964; Scott, 1982; Tremblay and Sinclair, 1985; Perry and Neilson, 1988; Smith *et al.* 1991), the variability of its migratory patterns (Rose and Leggett, 1988*a,b*, 1989), the genetic variation throughout its range (Mork *et al.* 1985) and the cyclic variations in its abundance (Sutcliffe *et al.* 1983; Koslow 1984; Koslow *et al.* 1987). Obviously, cod are exquisitely sensitive to their surroundings, and it follows that the productivity of their stocks will reflect these sensitivities.

We are indebted to Todd Bishop for his technical assistance and to Norval Balch and the staff of the Aquatron (Dalhousie University, Halifax) for providing us with exemplary working conditions. We also thank VEMCO Engineering Ltd for their excellent heart rate and depth transmitters. Funding for this research has been provided by OPEN, one of the fifteen Network of Centres of Excellence supported by the Government of Canada, to S.R.K. and R.G.B.

References

CLAIREAUX, G. AND DUTIL, J.-D. (1992). Physiological response of the Atlantic cod *Gadus morhua* to hypoxia at various environmental salinities. *J. exp. Biol.* **163**, 97–118.

CLAIREAUX, G., WEBBER, D. M., KERR, S. R. AND BOUTILIER, R. G. (1995). Physiology and behaviour of free-swimming Atlantic cod *Gadus morhua* facing fluctuating temperature conditions. *J. exp. Biol.* **198**, 49–60.

DAVENPORT, J. AND VAHL, O. (1979). Response of the fish *Blennius pholis* to fluctuating salinities. *Mar. Ecol. Prog. Ser.* **1**, 101–107.

DUTIL, J.-D., MUNRO, J., AUDET, C. AND BESNER, M. (1992). Seasonal variation in the physiological response of the Atlantic cod *Gadus morhua* to low salinity. *Can. J. Fish. aquat. Sci.* **49**, 1149–1156.

FLETCHER, C. R. (1978*a*). Osmotic and ionic regulation in the cod *Gadus callaria*. I. Water balance. *J. comp. Physiol.* **124**, 149–155.

FLETCHER, C. R. (1978*b*). Osmotic and ionic regulation in the cod *Gadus callaria*. II. Salt balance. *J. comp. Physiol.* **124**, 157–168.

FRITSCHE, R. AND NILSSON, S. (1989). Cardiovascular responses to hypoxia in the Atlantic cod, *Gadus morhua*. *Exp. Biol.* **48**, 153–160.

JEAN, Y. (1964). Seasonal distribution of cod (*Gadus morhua* L.) along the Canadian Atlantic coast in relation to water temperature. *J. Fish. Res. Bd Can.* **21**, 429–460.

JOBLING, M. (1988). A review of the physiological and nutritional energetics of the cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. *Aquaculture* **70**, 1–19.

KOSLOW, J. A. (1984). Recruitment patterns in Northwest Atlantic fish stocks. *Can. J. Fish. aquat. Sci.* **41**, 1722–1729.

KOSLOW, J. A., THOMPSON, K. R. AND SILVERT, W. (1987). Recruitment to Northwest Atlantic cod, *Gadus morhua* and haddock, *Melanogrammus aeglefinus*, stocks: influence of stock size and climate. *Can. J. Fish. aquat. Sci.* **44**, 26–39.

LUCAS, M. C., PRIEDE, I. G., AMSTRONG, J. D., GINDY, A. N. Z. AND DE VERA, L. (1991). Direct measurements of metabolism, activity and feeding behaviour of pike, *Esox lucius* L., in the wild, by the use of heart rate telemetry *J. Fish Biol.* **39**, 325–345.

MORK, J., RYMAN, N., GUNNAR, S., UTTER, F. AND SUNDNES, G. (1985). Genetic variation in Atlantic cod (*Gadus morhua*) throughout its range. *Can. J. Fish. aquat. Sci.* **42**, 1580–1587.

ODENSE, P., BORDELEAU, A. AND GUILBAULT, R. (1966). Tolerance level of cod *Gadus morhua* to low salinity. *J. Fish. Res. Bd Can.* **23**, 1465–1467.

PERRY, R. I. AND NEILSON, J. D. (1988). Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. *Mar. Ecol. Prog. Ser.* **49**, 199–214.

PRIEDE, I. G. (1985). Metabolic scope in fish. In *Fish Energetics New Perspectives* (ed. P. Tytler and P. Calow), pp. 33–64. London: Croom Helm.

PRIEDE, I. G. AND TYTLER, P. (1977). Heart rate as a measure of metabolic rate in teleost fishes; *Salmo gairdneri*, *Salmo trutta* and *Gadus morhua*. *J. Fish Biol.* **10**, 231–242.

RANDALL, D. J. (1968). Functional morphology in the heart of fish. *Am. Zool.* **8**, 179–190.

RANDALL, D. J. (1982). The control of respiration and circulation in fish during exercise and hypoxia. *J. exp. Biol.* **100**, 275–288.

RANDALL, D. J. AND DAXBOECK, C. (1984). Oxygen and carbon dioxide transfer across fish gills. In *Fish Physiology*, vol. XA (ed. W. Hoar and D. J. Randall), pp. 263–314. Orlando: Academic Press.

ROSE, G. A. AND LEGGETT, W. C. (1988*a*). Atmosphere–ocean coupling in the northern Gulf of St. Lawrence: frequency-dependent wind-forced variations in nearshore sea temperatures and currents. *Can. J. Fish. aquat. Sci.* **45**, 1222–1233.

ROSE, G. A. AND LEGGETT, W. C. (1988*b*). Atmosphere–ocean coupling and Atlantic cod migrations: effects of wind-forced variations in sea temperatures and currents on nearshore distributions and catch rates of *Gadus morhua*. *Can. J. Fish. aquat. Sci.* **45**, 1234–1243.

ROSE, G. A. AND LEGGETT, W. C. (1989). Interactive effects of geophysically-forced sea temperatures and prey abundances on mesoscale coastal distributions of marine predator, Atlantic cod *Gadus morhua*. *Can. J. Fish. aquat. Sci.* **46**, 1904–1913.

SAUNDERS, R. L. (1963). Respiration of Atlantic cod. *J. Fish. Res. Bd Can.* **20**, 373–386.

SCHURMANN, H. AND STEFFENSEN, J. F. (1992). Lethal oxygen levels at different temperature and the preferred temperature during hypoxia of the Atlantic cod *Gadus morhua* L. *J. Fish Biol.* **41**, 927–934.

SCOTT, J. S. (1982). Depth, temperature and salinity preferences of common fishes of the scotian shelf. *J. Northw. Atl. Fish. Sci.* **3**, 29–39.

SMITH, S. J., PERRY, R. I. AND FANNING, L. P. (1991). Relationship between water mass characteristics and estimates of fish population abundance from trawl surveys. *Env. Monit. Assess.* **17**, 227–245.

SUNDNES, G. (1957). Notes on the energy metabolism of cod (*Gadus callaria* L.) and coalfish (*Gadus virens* L.) in relation to body size. *Fiskeridirektoratets Skrifter, Serie Havundersokelser* **6**, 1–10.

SUREAU, D. AND LAGARDERE, J.-P. (1991). Coupling of heart rate and locomotor activity in sole, *solea solea* (L.) and bass, *Dicentrarchus labrax* (L.), in their natural environment by using ultrasonic telemetry. *J. Fish Biol.* **38**, 399–405.

SUTCLIFFE, W. H., LOUCKS, H. R., DRINKWATER, K. F. AND COOTE, A. R. (1983). Nutrient flux onto the Labrador shelf from Hudson Strait and its biological consequenses. *Can. J. Fish. aquat. Sci.* **40**, 1692–1701.

TAYLOR, E. W. (1985). Control and co-ordination of gill ventilation and perfusion. In *Physiological Adaptations of Marine Animals* (ed. M. S. Laverack), pp. 123–161. Cambridge: The Company of Biologists Limited.

TREMBLAY, M. J. AND SINCLAIR, M. (1985). Gulf of St Lawrence cod: age-specific geographic distributions and environmental occurances from 1971–1981. *Can. Tech. Rep. Fish. aquat. Sci.* **1387**, pp. 43.