

In situ investigations on the respiration and behaviour of the eelpout *Zoarces viviparus* under short-term hypoxia

P. Fischer¹, K. Rademacher², U. Kils²

¹ Limnologisches Institut, Universität Konstanz, Mainaustraße 212, W-7750 Konstanz 1, Germany

² Institut für Meereskunde Kiel, Universität Kiel, Düsternbrookerweg 20, W-2300 Kiel 1, Germany

ABSTRACT: Respiration and activity of eelpouts *Zoarces viviparus* L. were measured in an underwater respiration chamber in Kiel Bay (Germany) under short-term hypoxia. Respiration and swimming activity both declined almost continuously with decreasing oxygen saturation. Oxygen consumption dropped from an average of 300 mg O₂ kg_{wet}⁻¹ h⁻¹ at normoxic conditions (95 % oxygen saturation) to 10 mg O₂ per kg_{wet}⁻¹ h⁻¹ at 5 % oxygen saturation. All eelpouts survived for 60 min in oxygen-free water. The results indicate that eelpouts are well adapted to environmental hypoxia and are able to survive under anoxic conditions for about an hour. The ecological benefit of this adaptation is discussed with respect to the increasing oxygen problems in the Western Baltic observed in recent years.

INTRODUCTION

Oxygen depletion in the coastal waters of the Western Baltic has recently become more frequent (Rumohr 1986, Babenerd & Meyerhöfer 1988, Weigelt 1988, Gerlach 1990). Mainly in the late summer months, when strong south-westerly winds cause upwelling of oxygen-free deep water, oxygen saturation in the shallows of the fjords drops from 100 to 0 % saturation in less than 1 h (Fig. 1). During such an event, on the night of 24 October 1987, more than 400 000 fish suffocated within a few hours in Eckernförder Bight (Western Baltic). Most of them were found washed ashore or floating in less than 1 m water with spread operculae, typical for death caused by asphyxiation. The most affected fish species were the benthic eelpout *Zoarces viviparus* L. and the seabull *Myoxocephalus scorpius* which accounted for more than 95 % of the dead fish biomass (Kils et al. 1989).

Species living under such unstable environmental conditions often show morphological, physiological or behavioural adaptations. They either try to escape from deteriorating areas (Whithmore et al. 1960, Kramer 1987) or they are able to survive under extreme environmental conditions (Magnuson & Karlen 1970,

Petrosky & Magnuson 1973, Davis 1975). The Blenniidae *Blennius pholis*, e.g. living in rockpools on stony coastlines, may tolerate changes in water oxygen saturation of up to 280 % within 24 h due to physiological adaptations of the haemoglobin (Bridges 1987). Brook sticklebacks *Culaea inconstans* can survive hypoxic conditions in ice-covered lakes ca 5 times longer when gas bubbles are present (Klinger et al. 1982). Because of their dorso-ventral flattened headshape and a hypoxic-induced upwards movement to the ice-covered surface they are able to use air-bubbles for additional oxygen supply.

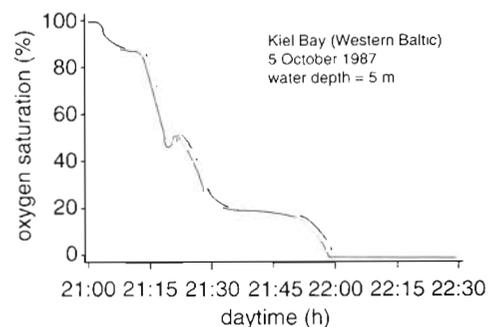


Fig. 1 Decrease of oxygen saturation in Kiel Bay (Western Baltic, water depth = 5 m) on 5 October 1987

In our paper, we focus on the behavioural and respiratory response of the benthic eelpout *Zoarces viviparus*, one of the most common species in the Western Baltic, to short-term hypoxia.

MATERIALS AND METHODS

The experiments were done *in situ* in May 1989 and July 1990 in the inner part of Kiel Fjord (Western Baltic). The swimming laboratory 'ATOLL', a circular experimental platform (diameter = 27 m, free-board = 2.1 m, draught = 0.38 m; Kils 1986) (Fig. 2), was anchored at a typical natural habitat of *Zoarces viviparus*, with big cobbles and dense macrophyte vegetation, in about 4 to 6 m water depth. The mean water temperature was $12.2 \pm 1.8^\circ\text{C}$, which is typical of late summer water temperatures, when hypoxia often becomes a problem in this area. The mean salinity was $13.8 \pm 0.8\text{‰}$. All experiments were conducted under natural daylight. The eelpouts were caught by scuba diving, dip-net (1 × 1 m) and trap close to the laboratory. The mean length and weight of the fish were 20.5 ± 4.9 cm and 40.26 ± 21.5 g respectively; the length-weight relationship was $W = 0.00486 \times L^{2.95}$.

For measurements, a cubic (length = 25 cm, height = 24 cm, depth = 38 cm, volume = 23.75 l) and a round (diameter = 44.5, height = 25 cm, volume = 20.56 l) respiration chamber were mounted 40 cm below the water surface in front of the underwater windows of the laboratory (Fig. 2). Oxygen saturation in the chambers was logged every 0.5 s with a polarographic electrode (WTW OXY-196). Oxygen saturation decreased due to respiration of the fish from 95 % (normoxic conditions) to 12 % (Expt 1), 2 % (Expt 2)

and 0 % (Expt 3) in 1.0, 2.5 and 3.2 h respectively. Respiration was calculated on a wet weight basis as $\text{mg O}_2 \text{ kg}_{\text{wet}}^{-1} \text{ h}^{-1}$, integrating the decrease of oxygen saturation in the chamber over 200 s. The general behaviour of the fish was observed directly from the underwater window of the laboratory. An underwater video camera, fixed 130 cm from the front glass of the cubic chamber allowed for quantification of the horizontal and vertical swimming activity. On a reference grid, dividing the transection of the chamber into 3 rows and 3 columns, swimming activity was evaluated as the number of horizontal or vertical field changes per fish per minute. For each saturation level, the horizontal and vertical swimming activity of 20 fish was measured over a period of 2 min each. In a control, respiration and activity were monitored under normoxic conditions (95 %) for a period of 70 min (Fig. 3).

RESULTS

The respiration rate of *Zoarces viviparus* declined nearly continuously with decreasing oxygen saturation (Fig. 4a): in all 3 experiments, oxygen consumption dropped from ca $300 \text{ mg O}_2 \text{ kg}_{\text{wet}}^{-1} \text{ h}^{-1}$ at 95 % saturation to ca $30 \text{ mg O}_2 \text{ kg}_{\text{wet}}^{-1} \text{ h}^{-1}$ at 12 % saturation. Corresponding to respiration, horizontal (Fig. 4b) and vertical swimming activity of *Z. viviparus* (Fig. 4c) decreased with reduced oxygen tensions. However, both activity measures showed a more rapid decrease at the higher saturation levels relative to respiration. A slight plateau or increase was observed in vertical swimming activity between 70 and 50 % oxygen saturation in Expt 3 and between 95 % and 80 % in Expt 2. Below 30 % oxygen saturation most of the eelpouts rested

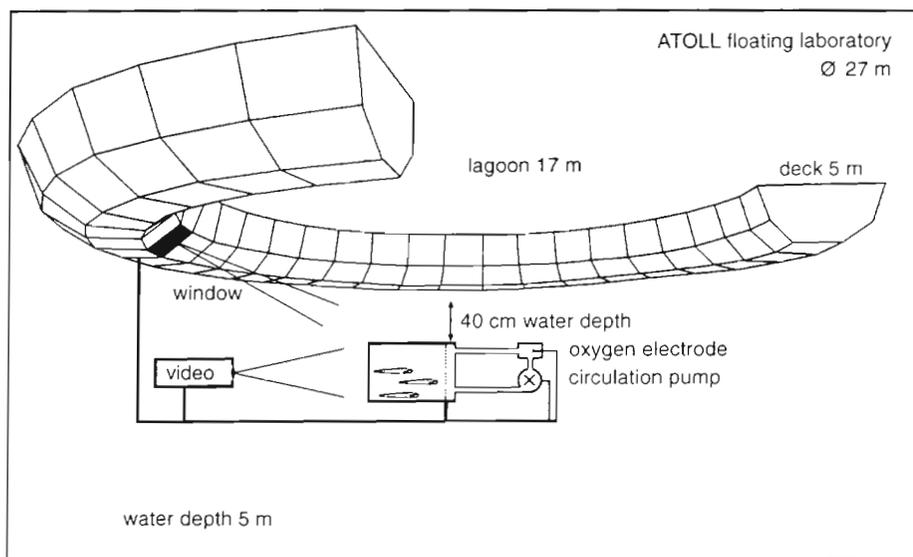


Fig. 2. *In situ* respiration and observation chamber, mounted in front of the underwater windows of the swimming laboratory 'ATOLL'

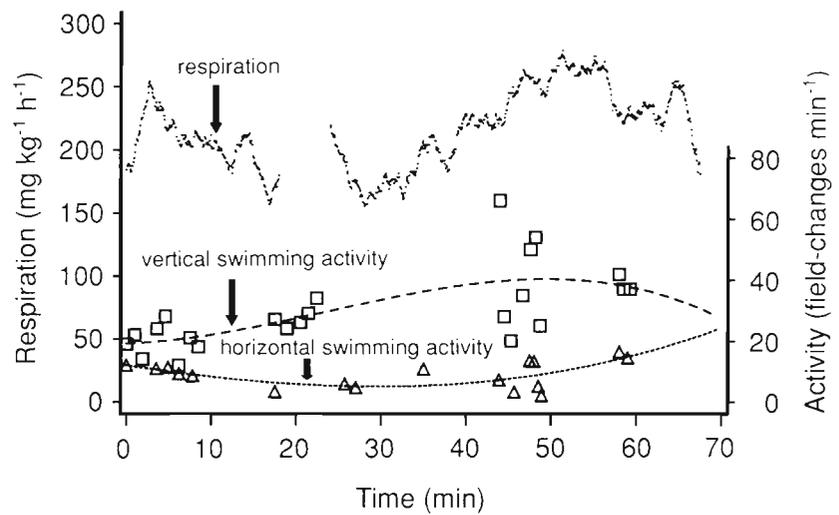


Fig. 3. *Zoarces viviparus*. Control experiment. Respiration rate ($\text{mg kg}^{-1} \text{h}^{-1}$), horizontal swimming activity (field-changes min^{-1}) and vertical swimming activity (field-changes min^{-1}) of eelpout at normoxic conditions (95%). Curves were eye-fitted

nearly motionless at the bottom of the chamber, showing only gill ventilation.

Expt 1 was terminated after 12% saturation was reached. In Expt 2, the eelpouts consumed oxygen until 2% saturation was reached. At this low level, respiration dropped to ca $10 \text{ mg O}_2 \text{ kg}_{\text{wet}}^{-1} \text{ h}^{-1}$ but all eelpouts still showed gill ventilation. In Expt 3, 0% saturation was reached in the chamber; swimming activity was no longer observed and the first eelpouts began to cease gill ventilation. Twenty minutes after 0% saturation was reached, all fish had stopped gill ventilation and appeared to be dead. After 60 min of anoxia, oxygen tension was raised back to 95% saturation. About 30 min later, the first eelpouts resumed gill ventilation as well as activity. After another 30 min, all eelpouts had recovered and showed normal activity. All individuals survived the subsequent 3 weeks without external sign of damage.

DISCUSSION

Eelpouts seem to be well adapted to short-term hypoxia. The rapid decreases in respiration and swimming activity with decreasing oxygen saturations indicate a completely different survival strategy to that observed in many other fish species during hypoxia. Rather than escaping from deteriorating areas (Randall 1970, Kramer 1987), *Zoarces viviparus* reduces activity and respiration at a very early phase of oxygen depletion and rests nearly motionless on the bottom. Furthermore, the eelpouts were able to take up oxygen from the water

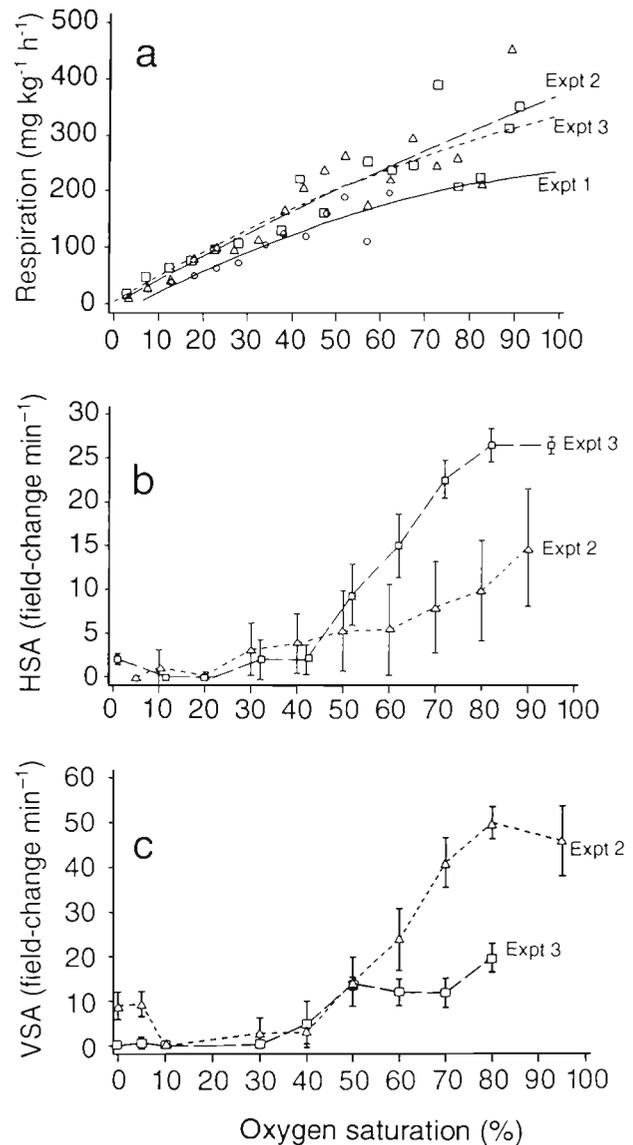


Fig. 4. *Zoarces viviparus*. (a) Respiration-rate, (b) horizontal swimming activity (HSA), and (c) vertical swimming activity (VSA) of eelpout at decreasing oxygen saturation. Curve (a) was eye-fitted. Vertical bars = SE

even at saturation levels below 5%. Many other fish species are only capable of taking up oxygen at saturations levels above 20 to 40% (Davis 1975).

Broberg & Kristoffersen (1983) found a similar trend in respiration rate in eelpout embryos and juveniles associated with a remarkably high lactate tolerance in their blood. They assumed that this might be an adaptation to viviparous reproduction in this species where the embryos may be exposed to hypoxic conditions in the abdominal cavity of the females. Furthermore, they supposed that embryonic eelpouts are able to excrete lactate directly into the surrounding medium to keep the lactate accumulation in the tissue low. These authors could not find such an excretion mechanism in adults. In our experiments, all eelpouts survived for 60 min in oxygen-free water. Although no gill ventilation could be observed after this time, all individuals resumed ventilation within 1 h after return to normal oxygen conditions. This high tolerance to short-term anoxia of adult eelpouts indicates an adaptation mechanism analogous to that observed in the embryos and juveniles. Therefore, the early reduction of respiration and activity during the onset of hypoxia might not only be forced by lack of oxygen causing respiratory dependence (Davis 1975) but can also be regarded as a behavioural response in order to minimize accumulation of anaerobic metabolic products in tissues, thus extending the survival time under hypoxic conditions. However, such a behaviour can only be advantageous when hypoxic conditions are of short duration.

In our experiments, we simulated hypoxic conditions for not longer than 3 to 4 h. However, field observation in the Western Baltic show that eelpouts are amongst the most affected species when oxygen depletion continues for longer periods (Kils et al. 1989). Therefore, further investigations are required to show whether the observed behaviour occurs only during short-term hypoxia or if eelpouts show a different behaviour under hypoxic conditions in general compared to other fish species. Nevertheless, eelpouts seem to be very sensitive to changes in water oxygen content. The early reduction of respiration and activity combined with the presumed high lactate tolerance of this species seems to be an appropriate adaptation for survival of short-term hypoxia. These physiological and behavioural responses will be important especially for a benthic fish species with low escape capacity and may be one of the reasons for the high reproductive success of eelpouts observed in the coastal waters of the Western Baltic, despite the wide-spread fish-kills in recent years. The mortality in a fish with such an extreme tolerance to quite low but short-term hypoxic conditions should alert countries bordering the Baltic Sea that deterioration of water quality in the Baltic may reach a point of increasing ecological instability.

Acknowledgements. We thank U. Piatkowski, H. Thetmeyer and U. Waller for helpful technical ideas in the design of our research and reviewing an early draft of the manuscript, R. Eckmann, I. Bussmann and C. Bofinger for providing valuable suggestions for the manuscript, ATARI and SONY for their friendly sponsoring and cooperation, the VOLKSWAGEN-foundation for funding, the Deutsche Forschungsgemeinschaft (DFG) for support, and the administration of the Kiel-Canal.

LITERATURE CITED

- Babenerd, B., Meyerhöfer, M. (1988). Studie zum Fischsterben in der Kieler Förde im Oktober 1986. Im Auftrag des Umweltbundesamtes/Forschungsvorhaben Wasser 102 04 234. Institut für Meereskunde, Kiel
- Bridges, C. (1987). Environmental extremes – the respiratory physiology of intertidal rockpool fish and sublittoral burrowing fish. *Zool. Beitr.* 30: 65–84
- Broberg, S., Kristoffersen, R. (1983). Oxygen consumption and lactate accumulation in intra-ovarian embryos and young of the viviparous fish *Zoarces viviparus* (L.) in relation to decreasing oxygen concentrations. *Ann. Zool. Fennici* 20: 301–306
- Davis, J. C. (1975). Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species. *J. Fish. Res. Bd Can.* 32: 2295–2332
- Gerlach, S. (1990). Nitrogen, phosphorus, plankton and oxygen deficiency in German Bight and Kiel Bay. Final report on the project 'Eutrophication of the North Sea and the Baltic Sea' *Kieler Meeresforsch. Sonderh.* 7: 1–379
- Kils, U. (1986). Verhaltensphysiologische Untersuchungen an pelagischen Schwärmen. Schwarmbildung als Strategie zur Orientierung in Umwelt-Gradienten. Bedeutung der Schwarmbildung in der Aquakultur. *Ber. Inst. Meeresk. Univ. Kiel* 163: 1–168
- Kils, U., Waller, U., Fischer, P. (1989). The fish-kill of autumn 1988 in Kiel Bay. *Comm. Meet. int. Coun. Explor. Sea C.M.-ICES/L.* 14: 1–6
- Klinger, A., Magnuson, J. J., Gallep, W. (1982). Survival mechanisms of central mudminnow (*Umbra limi*), fathead minnow (*Pimphales promelas*) and brook stickleback (*Culaea inconstans*) for low oxygen concentrations. *Environ. Biol. Fish.* 7: 113–120
- Kramer, D. L. (1987). Dissolved oxygen and fish behaviour. *Environ. Biol. Fish.* 18: 81–92
- Magnuson, J. J., Karlen, D. J. (1970). Visual observations of fish beneath the ice in a winterkill lake. *J. Fish. Res. Bd Can.* 27 (6): 1059–1068
- Petrosky, B. R., Magnuson, J. J. (1973). Behavioural response of northern pike, yellow perch and bluegill to oxygen concentrations under simulated winterkill conditions. *Copeia* 1: 124–133
- Randall, D. J. (1970). Gas exchange in fish. In: Hoar, W. S., Randall, D. J. (eds.) *Fish physiology*, Vol. IV. Academic Press, New York, p. 253–292
- Rumohr, H. (1986). Historische Indizien für Eutrophierungserscheinungen (1875–1939) in der Kieler Bucht (westl. Ostsee). *Meeresforsch.* 31: 115–123
- Weigelt, M. (1988). Auswirkungen von Sauerstoffmangel auf die Bodenfauna der Kieler Bucht. *Ber. Inst. Meeresk. Univ. Kiel* 176: 1–299
- Whithmore, C. M., Warren, C. E., Douderoff, P. (1960). Avoidance reactions of salmonid and centrarchid fish to low oxygen concentrations. *Trans. Am. Fish. Soc.* 89: 17–56