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Responses to hypoxia of plaice, *Pleuronectes platessa*, and dab, *Limanda limanda*, in the south-east Kattegat: distribution and growth

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Synopsis

Plaice, *Pleuronectes platessa*, and dab, *Limanda limanda*, were sampled with a Glommen lobster trawl at 25 to 40 m depth in the SE Kattegat during spring and autumn of 1984 to 1990. During autumn, hypoxia (O_2-concentration < 3 mg l^{-1}) occurred in the bottom water below the halocline for four to ten weeks every year, except in 1984 when moderate hypoxia (O_2-concentration 3–5 mg l^{-1}) occurred. Biomass of both species was shown to be negatively correlated with oxygen concentration during autumn. Further, a decrease in population mean total length was observed during the study period in both spring and autumn samples. Laboratory studies of growth of juvenile plaice and dab, at 15° C and 30–34‰, showed that growth is reduced at 50 and 30% O_2-saturation for both species during a 20 d period. There was some adaptation to hypoxia resulting in less reduction of growth during the second half of the experiment. The frequency of fish eating was reduced in plaice at 30% O_2-saturation. Reduced mean total length of the plaice and dab population of the SE Kattegat is discussed in view of sublethal effects of oxygen deficiency.

Introduction

The Kattegat is a shallow (mean depth 23 m) transition area between the brackish Baltic Sea and the more marine Skagerrak and North Sea. There was a high abundance of demersal fish in the SE Kattegat (Pihl 1989a) and the area is a traditional fishing ground for Danish and Swedish fishermen.

The Kattegat has received increasing amounts of nutrients, mainly nitrogen and phosphorous, over the last five decades and is now considered eutrophic (Rosenberg 1985). The supply of nitrogen has increased fourfold since 1930's with a doubling after 1970 (Rosenberg et al. 1990). It has been suggested that increased primary production has resulted in enhanced organic loading in the area, leading to higher oxygen consumption due to mineralization (Rydberg et al. 1990). In the period from 1981 to 1990, oxygen deficiency has occurred in the bottom water below the halocline in the southern Kattegat during the autumn in most years and has been reported to increase in both time and space (Baden et al. 1990a). Periods with O_2-concentrations < 3 mg l^{-1} of four to ten weeks duration have been recorded concurrently with a change in species composition of fishes and a reduction in the total biomass of demersal fishes (Pihl 1989a, Baden et al. 1990a). During the last decade the total catch of the dominant demersal species, cod, *Gadus morhua*, and plaice, *Pleuronectes platessa*, has decreased in the Kattegat by approximately 40 and 70%, respectively (Bagge

& Nielsen,[1] Pihl & Ulmestrand[2]). Furthermore, Swedish catch statistics revealed a 80 to 90% reduction in catch efficiency for cod during autumn in 1980s (Baden et al. 1990a). Concomitant with these occurrences adverse effects on benthic macrofauna (e.g. Rosenberg & Loo 1988) and the Norway lobster, *Nephrops norvegicus* (Baden et al. 1990b) has been reported from the area.

Similar reductions in demersal fish stocks during periods of low oxygen have been reported from the adjacent Baltic and the North Sea (Dyer et al. 1983, Rossignol-Strick 1985, Weigelt & Rumohr 1986). Few investigations have dealt with sublethal physiological effects of hypoxia on marine fish and most laboratory studies have been focused on respiratory and ventilatory responses (e.g. Steffensen 1982). Studies of respiration physiology may, however, be of limited value in predicting effects on fish stocks if not combined with studies of habitat shifts and effects on growth and reproduction.

In this investigation the aim was to combine field and laboratory studies in order to evaluate effects of sublethal hypoxia on plaice, *P. platessa*, and dab, *Limanda limanda*, by combining: (i) field observations on biomass and length distribution of the fish stocks subjected to moderate hypoxia, and (ii) laboratory study of growth at sublethal hypoxic oxygen saturations.

Materials and methods

Field study

Field sampling was carried out in the SE Kattegat (56°30′ N; 12°20′ E) at depth between 25 and 40 m in spring and autumn during the period 1984 to 1990 (Fig. 1). Trawl samples were taken during one week in spring from the first week in April to the first week in May each year (except in 1985) and during one week in autumn each year from late September to early November. The water body in the area is vertically stratified by salinity and a halocline is normally situated at 10–20 m depth. The vertical stratification is stable from April to November, partly due to the small tidal amplitude (0.1 m) in the area (Svansson 1975). Oxygen concentration in the bottom water was determined at all trawl stations and an average value for the area was estimated for each sampling occasion. Measurements were made within 0.5 m of the sediment surface using an air and Winkler calibrated YSI-dissolved oxygen meter. Differences between in situ measurements made with the two methods did not exceed 0.1 mg l^{-1}. Additional measurements of bottom water dissolved oxygen were made in connection with other research programs in the area investigated, where 8–12 stations were sampled each time. Altogether

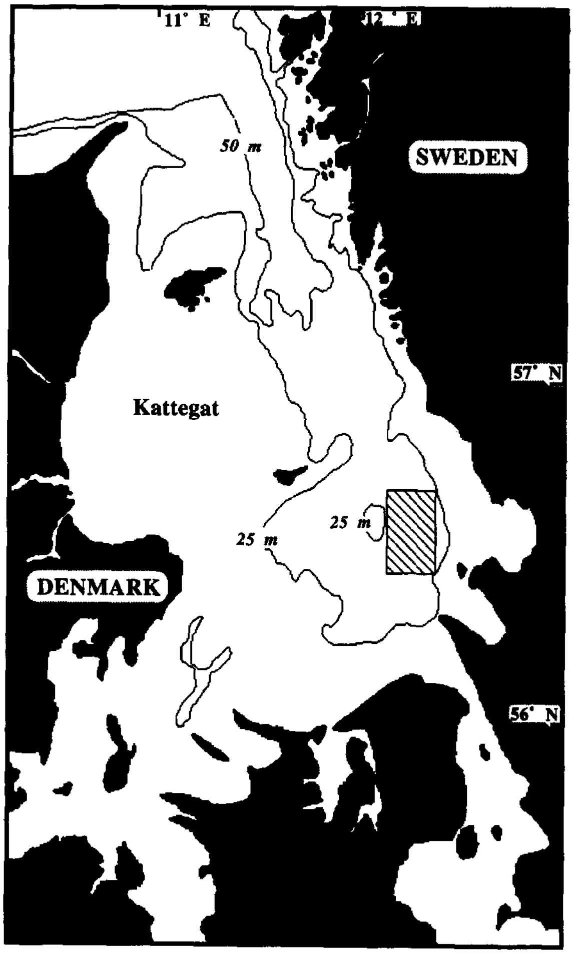

Fig. 1. Sampling area in SE Kattegat.

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[1] Bagge, O. & E. Nielsen. 1987. Growth and recruitment of plaice in the Kattegat. CM 1987/G:7 Demersal Fish Committee/Baltic Fish Committee, ICES. 23 pp.

[2] Pihl, L. & M. Ulmestrand. 1988. Kusttorskuntersökningar på svenska västkusten (Investigation of coastal cod on the Swedish west coast). Länsstyrelsen i Göteborg och Bohus Län. 61 pp.

sampling was conducted at least on one occasion in spring and in most years on four occasions during the autumn (once a month from September to December). Information on oxygen concentration was also provided from a local monitoring program in the area (unpublished data), that aided in estimating the duration of hypoxic conditions. Salinity and temperature measurements were conducted in the bottom water 1 m above the sediment surface with a CTD-probe. Sampling occurred at all stations and on all occasions salinity ranged between 32 and 34‰. Bottom water temperature ranged from 4° C in spring to 10° C in autumn. Sediment structure in the study area is silty-mud with an organic matter content of 5.4 to 15.3% ignition loss of dry weight (DW) (Rosenberg & Loo 1988)

The plaice and dab populations were sampled by means of a Glommen lobster trawl with a 60 mm cod end (Pihl 1989a). On each occasion 6 to 8 samples were taken by trawling for 30 min at a speed of 3 knots. All fish were enumerated, measured (standard length, cm) and weighed on board. Approximately the same stations were sampled on each occasion. Length measurements from all trawl stations were pooled for each species on each sampling occasion. Mean length was calculated from 200 plaice and 300 dab, randomly selected from the pooled samples on each occasion. Age was not determined for all individuals but from 10–20 random otolith analyses from each sampling date. Significance of decreasing mean length with time (sampling year) was tested with the Spearman Rank correlation test. Likewise, the relation between oxygen concentration and fish biomass was tested with Spearman Rank correlation test. A one-way ANOVA and a post-hoc Tukey-Kramer test were used to analyze the differences in biomass of plaice and dab at stations with low (< 30% O_2-saturation), moderate (30–50% O_2-saturation) and high (> 50% O_2-saturation) oxygen level.

Laboratory study

Juvenile dab (dab 1: 7–10 cm, dab 2: 16–22 cm) and plaice (10–15 cm) to be used in growth experiments were caught with a beam trawl (trawling for max. 30 min) at 5–20 m in Kungsbacka Fjord, E Kattegat in October 1988, and transferred to large holding tanks at the laboratory. The tanks were supplied with running seawater and the fish were acclimatized to laboratory conditions for 2–3 weeks and fed blue mussel, *Mytilus edulis*, soft parts.

The experimental setup for growth studies (Fig. 2) was placed in a temperature controlled room. Plaice and dab were placed individually in test aquaria containing about 6 l running seawater and a 3 cm sandy substrate. One fourth to one third of the total volume of water in reservoirs and aquaria was gradually changed every second day, in order to avoid contamination with waste products from the fish. The fish were gradually acclimatized to the experimental temperature and light during 3–4 weeks.

Growth experiments were carried out simultaneously at 50 and 30% O_2-saturation with 100% O_2-saturation as control. Six to eight fish were used for each experimental O_2-saturation. Hypoxia was induced by purging with N_2 at different rates in reservoir A and B (Fig. 2). The O_2-saturation was checked 3 times daily in the experimental chambers using an air and Winkler calibrated YSI-dissolved oxygen meter and purging was rate adjusted if the O_2-saturation had changed from the desired by more than 4% O_2-saturation. The fish were fed twice daily with blue mussel soft parts corresponding to 3–8% of fish wet weight and surplus food was removed after 1 h. Light (L:D = 14:10) was put on and off by means of a daylight simulator with a delay function, so that light was gradually turned on and off during 0.5 h. Experimental data are summarized in Table 1.

During the experiment the fish were weighed at day 0, 10 and 20. Before weighing the fish were anaesthetiziced with MS 222 (Sandoz) and water was gently removed from the fish surface. The substrate in the aquaria was changed in connection with weighing in order to avoid build up of waste products. Growth was calculated as specific growth rates according to Ricker (1979) and treatments were compared by means of a one-way ANOVA followed by a Scheffe multiple range test (Sokal & Rohlf 1981).

In order to examine whether food consumption was influenced by hypoxia, the appetite of plaice

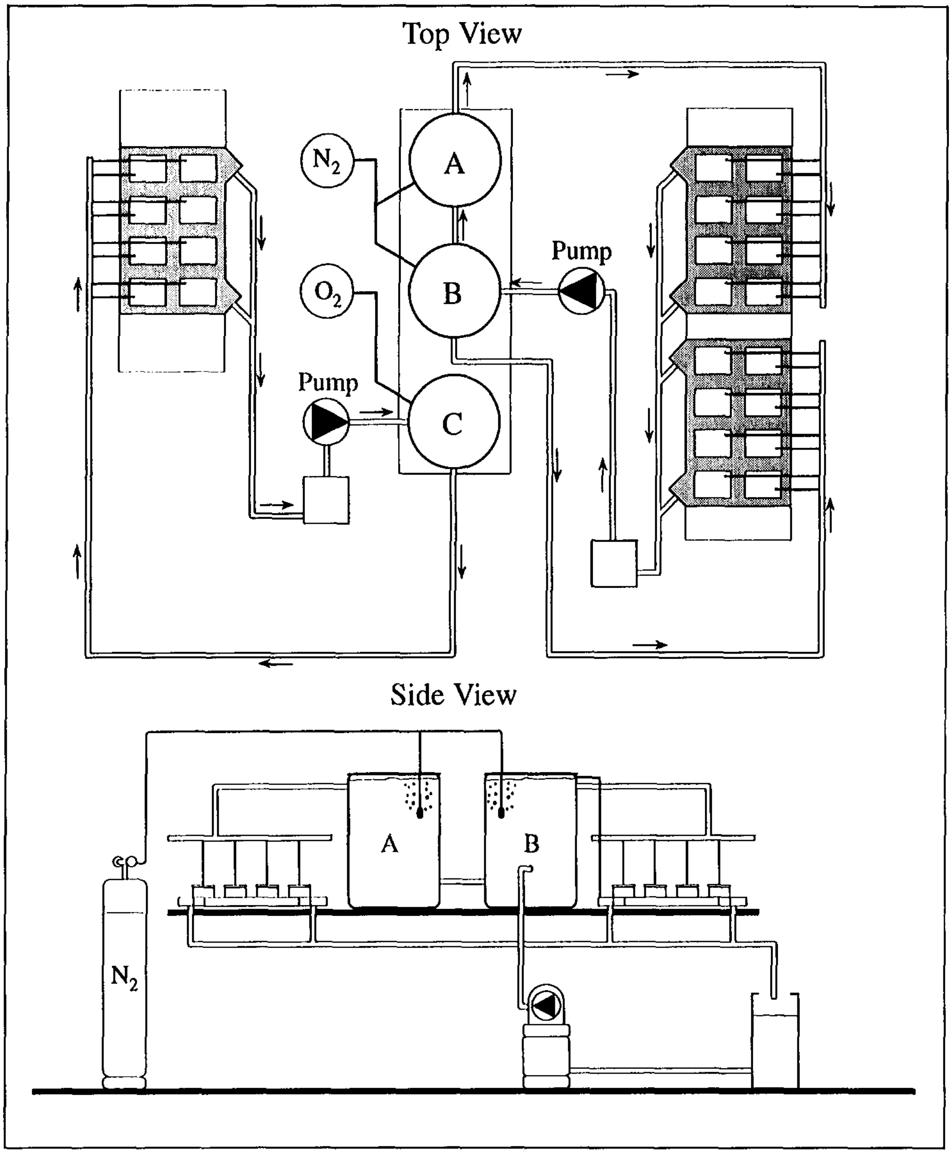

Fig. 2. Experimental setup for growth experiment. Schematical drawing of the experimental setup. From reservoirs (A, B, C) of approx. 250 l, water is led to test aquaria of 6 l. After leaving the test aquaria water is pumped back into the reservoirs. In normoxic reservoir C water is aerated and in B & C water is purged with nitrogen. The normoxic and hypoxic recirculating systems are kept separate. In bottom drawing only the hypoxic part is shown.

was assessed. When left overs of the offered food were collected, feeding was categorized in 2 ways: the fish had eaten all or some of the offered food, or nothing, based on visual judgement of mussel soft part pieces left over. Percent fish eating was compared between treatment using Student's t-test on arcsine $\sqrt{x}$ of daily percentage.

Results

Field study

Mean oxygen concentration in the bottom water in the SE Kattegat for 1984 to 1990 exhibited seasonal variability (Fig. 3). During spring mean oxygen concentration in the study area was measured at 5.8–

Table 1. Experimental data for growth experiment. Temperature, salinity and saturation is given as mean ± SD of daily measurements. At each saturation n = 8 for plaice and dab 1 and n = 6 for dab 2.

Species	Initial weight g	Temperature °C	Salinity ‰	100% saturation % sat. range	50% saturation % sat. range	30% saturation % sat. range
Plaice	22.8 ± 6.4	14.8 ± 0.4	32.0 ± 1.0	94.7 ± 1.9	51.7 ± 3.5	31.9 ± 2.5
				92–98	44–59	27–36
Dab 1	16.3 ± 4.4	14.6 ± 0.5	32.9 ± 0.5	95.3 ± 5.9	50.0 ± 7.2	33.0 ± 5.9
				82–101	38–63	23–40
Dab 2	30.7 ± 0.7	14.7 ± 0.3	30.7 ± 0.7	93.8 ± 1.0	51.4 ± 3.4	30.2 ± 2.8
				92–95	45–55	26–34

9.4 mg l^{-1} (60–95% O_2-saturation). Oxygen decreased from spring to autumn and lowest concentrations were always recorded in September and October, with levels gradually increasing to normal in winter during water column destratification. Hypoxia with O_2-concentration < 3 mg l^{-1} (approx. 30% saturation) occurred for approximately four, nine, five, ten, five and six weeks during 1985, 1986, 1987, 1988, 1989 and 1990, respectively, whereas in the autumn, 1984, oxygen deficiency was less severe. At some stations even lower oxygen levels (10–15% O_2-saturation) were recorded for shorter periods during some years.

During the autumn in 1986, 1987 and 1988 sampling was carried out each month and the development of oxygen concentration and fish biomass could be followed in detail. Each year a reduction in demersal fish biomass occurred during hypoxia (Table 2). During the most severe hypoxia (mean oxygen concentration 0.9 mg l^{-1}, 14% O_2-saturation) in September 1988, biomass of demersal fish were dramatically reduced. On this occasion no plaice were caught in the area and biomass of dab were reduced to about 10% compared to corresponding periods in other years.

In order to examine the relationship between O_2-saturation in the bottom water and the quantity of the two fish stocks, the biomass of each species and measured oxygen concentration was compared for each trawl sample taken in autumn 1984 to 1990. Fish biomass was found to be significantly correlated (plaice $p < 0.02$; dab $p < 0.01$) with oxygen concentration (Fig. 4). A reduction in fish biomass was observed at stations where oxygen concentration in the bottom water were less than 3 mg l^{-1} (approximately 30% O_2-saturation). At these low O_2-saturations plaice were absent in 11 out of 18 trawl samples, and mean biomass was estimated at 0.35 (SD =

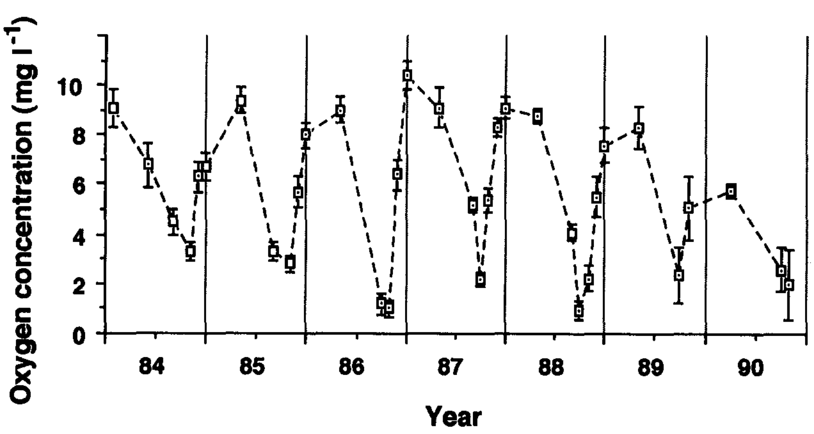

Fig. 3. Oxygen concentration in the bottom water of SE Kattegat 1984–1990. Oxygen concentrations, given as mean ± SD from 6–8 trawl stations on each occasion, were measured 0.5 m above sediment surface in connection with trawling at 4–9° C and 32–34‰.

Table 2. Mean oxygen concentration in the bottom water (measured 0.5 m above sediment surface) and mean biomass (WW, wet weight) of plaice, dab and total demersal fish in the study area in SE Kattegat during autumn 1986, 1987 and 1988.

Date	O_2-concentration	Fish biomass kg WW h^{-1} trawling		
		Plaice	Dab	Demersal fish
1986				
September	1.2	15	52	159
October	1.0	2	20	47
November	6.4	9	36	87
December	10.4	25	54	212
1987				
August	5.2	21	10	144
September	2.2	16	20	122
October	5.4	11	19	76
November	8.3	12	9	63
December	9.1	27	26	128
1988				
August	4.1	–	–	–
September	0.9	0	2	6
October	2.2	1	2	9
November	5.5	5	25	71
December	7.6	13	31	95

0.62) kg h^{-1}. Dab were present in 16 out of 18 trawl samples and mean biomass was found to be 2.3 (SD = 1.8) kg h^{-1}. At stations with moderate hypoxia (O_2-saturation between 30 and 50%) both species where present in all samples (n = 11) and biomass of plaice and dab was 3.6 (SD = 3.8) and 6.1 (SD = 6.8) kg h^{-1}, respectively. For plaice this difference in biomass between stations with low and moderate O_2-saturations was significant ($p < 0.05$). At stations with higher O_2-saturations (> 50%) (n = 25) fish biomass was significantly ($p < 0.05$) higher for both species compared with stations with low to moderate O_2-saturations, and mean biomass for plaice and dab was estimated to 15.1 (SD = 17) kg h^{-1} and 23.5 (SD = 24.6) kg h^{-1}, respectively.

Mean length of the sampled plaice and dab populations are shown for all sampling occasions in Fig. 5. Two to four years old fish (2- to 4-group) showed to be dominant for both species throughout the investigation. When mean fish length during spring was related to sampling year a significant decrease in mean length was found for plaice ($p < 0.05$) and dab ($p < 0.02$) during the study period. Also when autumn samples were related to time a length re-

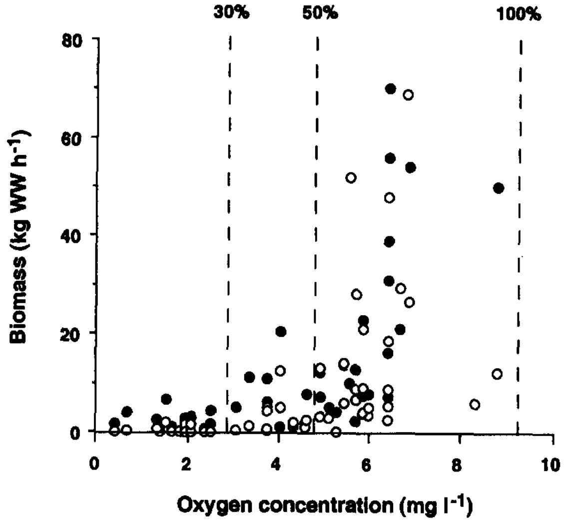

Fig. 4. Fish biomass and oxygen concentration in the bottom water of SE Kattegat. A significant relation was found between mean oxygen concentration and biomass in kg wet weight (WW) h^{-1} trawling of plaice (o, $p < 0.02$) and dab (•, $p < 0.01$) at all trawl stations (n = 54) sampled during autumn in the years 1984 to 1990. Levels of 30, 50 and 100% O_2-saturation (at 32‰ and 8° C) are indicated in the figure.

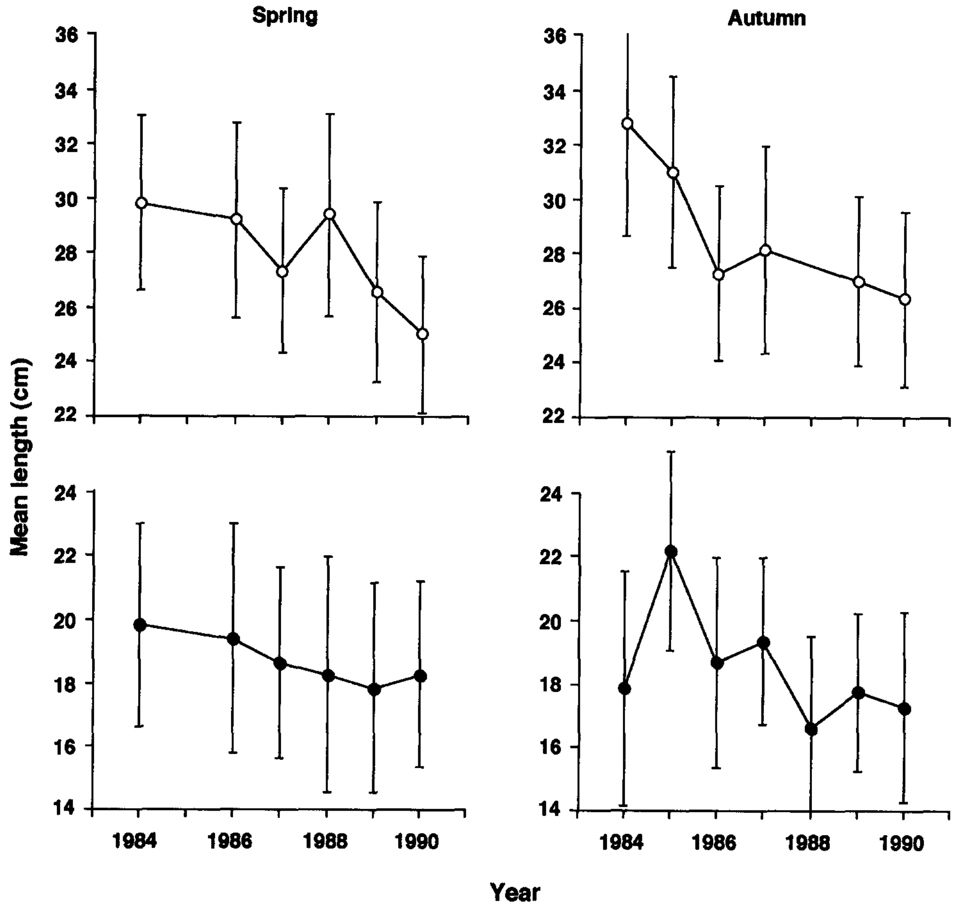

Fig. 5. Fish length in the SE Kattegat during spring and autumn 1984 to 1990. On each occasion 200 plaice (○) and 300 dab (●) were measured. Relation between fish length (mean ± SD) and time (sample year) was significant for plaice in spring ($p < 0.05$) and autumn ($p < 0.02$) and for dab in spring ($p < 0.02$).

duction was observed during the investigation period, but it was only significant for plaice ($p < 0.02$).

Laboratory study

There was a significant difference ($p < 0.01$) in growth between different O_2-saturations in both plaice and dab, except in the second period (d 11–20) in plaice (Fig. 6). The immediate response of the smallest dabs (dab 1) during the first 10 d of exposure to 50% O_2-saturation was a significant ($p < 0.05$) reduction of mean growth to about half of control. Mean growth of the largest dabs (dab 2) and plaice at 50% O_2-saturation were not significant different from control. In 30% O_2-saturation mean growth was negative and significantly ($p < 0.01$) different from control in all three test groups during the first 10 d of experiment. In the subsequent 10 d of exposure to 30% O_2-saturation, however, growth rates increased and the initial negative growth was succeeded by positive growth rates. In dab hypoxic growth rates were significantly ($p < 0.05$) different from control, but in plaice no significant difference in growth rate was observed, mainly due to a drop in normoxic growth rate. The overall result for 20 d showed that in dab there was a significant ($p < 0.05$) difference between control and hypoxic (50% and 30% O_2-saturation) growth rates in plaice between control and 30% O_2-saturation.

When plaice were exposed to 30% O_2-saturation

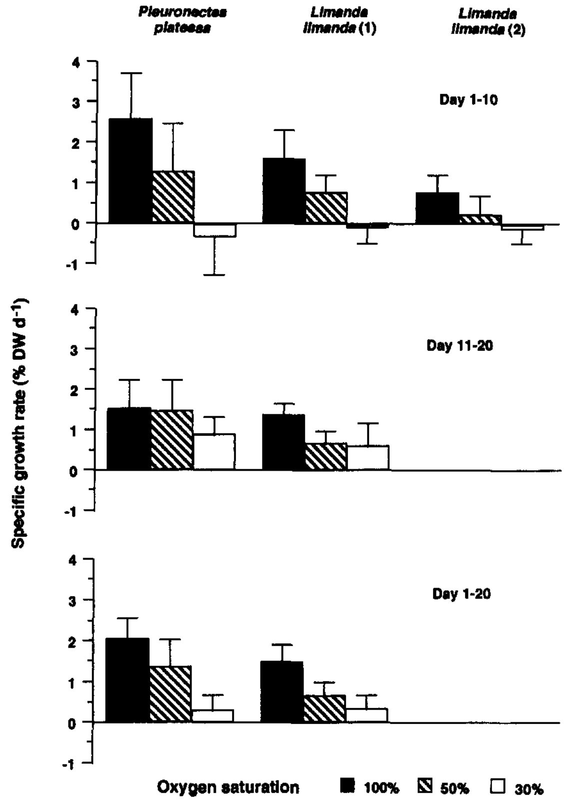

Fig. 6. Growth at different oxygen saturations. Mean ± SD specific growth rate in % dry weight (DW) d^{-1} at 15° C and 30–34‰ is shown for plaice and dab (1 & 2, see Table 1) at 3 different O_2-saturations in 1–10, 11–20 and 1–20 d. At each saturation n = 8 for plaice and dab 1 and n = 6 for dab 2.

34% of the fish were eating which was significantly ($p < 0.01$) lower compared to controls (71%) during the first 10 days of the experiment. During the second part of the experiment percentage of fish that ate increased to 47% in 30% O_2-saturation, but was still significantly ($p < 0.05$) different from control (71%). In 50% O_2-saturation percentage fish eating was 71 and 69% in the 2 ten day periods, which was not different from control.

Discussion

Results from the present investigation show that biomass of plaice and dab stocks in the SE Kattegat were significantly reduced when exposed to low O_2-saturations (< 50%) during autumn. Other species have also been negatively affected by hypoxia in SE Kattegat; total biomass of demersal fish has previously shown a reduction of 50 to 80% during several weeks in autumn during the years 1985 to 1987 (Pihl 1989a, Baden et al. 1990a). During the severe hypoxia in September 1988 total biomass of demersal fish was estimated to be 2% of biomass recorded during non-hypoxic conditions (Baden et al. 1990a). Of the dominant demersal species in the SE Kattegat, cod and whiting, *Merlangius merlangus*, were suggested to be the most sensitive to low oxygen and were considerably reduced when O_2-saturation was below 30% (Pihl et al.[3]). Plaice and dab are more tolerant to low O_2-saturations and are present in the area down to a level of 10 to 20% O_2-saturation.

During moderate hypoxia (30 to 50% O_2-saturation) the plaice and dab stocks were, in this study, found to be reduced to about 25% of the fish biomass recorded under normoxic (50 to 100% O_2-saturation) conditions. This reduction was probably caused by migration of stressed fish out of the area exposed to hypoxia, but may also be due to death. Such avoidance reactions to hypoxia are manifest by the fact that unusually large numbers of fish, mainly adult flatfish, have been caught in gillnets in a shallow water area close to the affected area and found to be dead despite the fact that the nets have been fishing for less than a day. In addition, a significant increase in fish biomass above, compared to below halocline, has been observed in the study area during hypoxia (Pihl et al.[3]). During the study period, the duration of conditions with moderate hypoxia (30–50% O_2-saturation) in the bottom water varied between different years from 2 to 3 months. At lower oxygen levels (< 30% O_2-saturation) approximately 10% of the dab population was still present in the affected area, whereas plaice were absent in most trawl samples and mean biomass was reduced to 2% compared to during normoxia. The different degree of absence between plaice and dab at severe hypoxia indicates a higher physiological tolerance in dab to low oxygen but

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[3] Pihl, L., I. Isaksson & H. Wennhage. 1992. Fish. Assessment of environmental effects on benthic macrofauna, *Nephrops norvegicus* and demersal fish in the Kattegat. Swedish Environmental Protection Agency no. 4055. 28 pp.

could also, as indicated by the growth experiments, be a result of difference in behavioural response to the same physiological stress.

Over the duration of the study period (1984–1990), mean lengths of plaice and dab stocks caught in the SE Kattegat during spring, exhibited significant decreases. For plaice also a significant reduction in length was observed during autumn catches over the same duration. This is in agreement with observations of reduced mean length from 31 to 25 cm of the plaice stock in the Kattegat from 1981 to 1991 (Ulmestrand 1992). In addition, Bagge et al.[4] found a significant reduction in length at age for plaice (age class 4–8) and dab (age class 2–3) during the period 1979 to 1985 in the Kattegat. Both severity and duration of hypoxia has generally increased in the Kattegat during the 1980's, resulting in an increased frequency of avoidance and a reduction in biomass of demersal fish in areas exposed to hypoxia (Pihl 1989b, Baden et al. 1990a). The reduction in the mean length in the stocks of plaice and dab, observed in these three investigations, might be a result of size-selective migration from hypoxic areas. Such migrations and changes in size structure have also been observed in fish stocks from other areas affected by hypoxia (Pihl et al. 1991). The observed reduction in length could also be due to reduced growth caused by physiological stress on individuals remaining in areas with moderate hypoxia.

Our laboratory experiments showed that growth was initially reduced at 50% O_2-saturation in dab and 30% O_2-saturation in plaice. Even if some adaptation to low oxygen (30% O_2-saturation) occurred during the second part of the experiment, a significant overall reduction in growth was found for both species during a 20 d period. Converting length into weight using the relationships described in Pihl (1989b) indicates that the normoxic growth rates for plaice and dab in our experiments are in general agreement with those (1.5–3.0% weight d^{-1}) measured in the SE Kattegat. Studies on other fish species, especially freshwater species, have shown similar reduction in growth at similar levels (20 to 60% O_2-saturation) of hypoxia (Herrmann et al. 1962, Stewart et al. 1967, Adelman & Smith 1970, Andrews et al. 1973, Brett & Blackburn 1981, Pedersen 1987).

Our field data suggests that parts of the plaice and dab stocks could be exposed to hypoxia during at least 20 days periods, and for up to 3 months each year to moderate hypoxia. Comparable exposures in the laboratory study resulted in reduced growth. It is likely that repeated and increasing physiological stress from hypoxia during autumn would result in a long-term decrease in population mean length. However other factors may also affect the length distribution of dab and plaice during the study period. The most possible factors are variation in recruitment and availability of food resources.

Recruitment of plaice and dab have been investigated in shallow water in the adjacent Laholm Bay during the period 1980 to 1986. During this period no significant trend in recruitment strength, settling time or mean size of 0- or 1 groups were found for the two species (Pihl 1989b). In addition, the number of small-size recruiting individuals was insignificant in our study due to size-selection of the gear, and age- and size-dependent depth distribution of both species. Juveniles of plaice and dab spend their first 2 years at water depths less than 10 m and join the parental stock during start of maturity the third year (Pihl 1989b). Thus, the observed reduction in mean length of the adult plaice and dab stocks may not be due to specific patterns in recruitment of juveniles.

Benthic infauna is the main food for plaice and dab in the SE Kattegat (Bagge et al.[4], Degel & Gislason,[5] Pihl 1994). The total biomass of benthic infauna has shown a significant increasing trend over the last decades in areas without severe hypoxic events (Pearson et al. 1985, Josefson 1990). Only a few stations with severe hypoxia have reduction in benthic fauna been registered (Rosenberg et al. 1992). Polychaetes and the brittle stars, mainly *Amphiura filiformis*, have increased in dominance and

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[4] Bagge, O., E. Nielsen, S. Mellergaard & I. Dalsgaard. 1990. Hypoxia and the demersal fish stock in the Kattegat (IIIa) and Subdivision 22. CM 1990/E:4 Marine Environmental Quality Committee, ICES.

[5] Degel, H. & H. Gislason. 1988. Some observations on the food selection of plaice and dab in Øresund, Denmark. C.M. 1988/G:50 Demersal Fish Committee, ICES. 19 pp.

these groups are also the dominant food items for plaice (polychaetes) and dab (*A. filiformis*). During hypoxic events benthic infauna emerge to the sediment surface (Rosenberg et al. 1992) resulting in an increased exposure to predation by fish (Pihl et al. 1992, Pihl 1994). As densities of demersal fish decrease and available food resources increase during hypoxia, observed reduction in growth is probably not a result of food limitation but rather due to the stress from low oxygen.

The stress exerted by low oxygen can result in various physiological responses. In this study it was shown that the frequency of eating decreased during hypoxic (< 30% O_2-saturation) conditions. Reduced feeding and reduced food conversion efficiency have been shown in other laboratory investigations (Herrmann et al. 1962, Stewart et al. 1967, Adelman & Smith 1970, Andrews et al. 1973, Brett & Blackburn 1981, Pedersen 1987). These studies are supported by an examination of the mean weight of the stomach content as percentage of the body weight of plaice and dab from Kattegat and the Sound. This index of consumption has decreased from 5% for plaice and 2–3% for dab in 1916 to 0.5% in 1987–1988 for both species (Bagge et al.[6]). Reduced growth at more moderate hypoxia (50% O_2-saturation) could have been a result of decreased food consumption even though the feeding incidence did not change. Alternatively would increased energetic costs to adaptations to low oxygen, like reduced O_2-uptake or increased gill ventilation (Steffensen et al. 1982) and increased O_2-capacity and O_2-affinity of the blood (Wood et al. 1975), leave less energy available for growth.

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