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Dwelling at the oxycline: does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea*?

JAN H. WANINK,* JEREMIAH J. KASHINDYE,† P.C. (KEES) GOUDSWAARD* and FRANS WITTE*
*Institute of Evolutionary and Ecological Sciences, University of Leiden, PO Box 9516, 2300 RA Leiden, The Netherlands
†Tanzania Fisheries Research Institute (TAFIRI), PO Box 475, Mwanza, Tanzania

SUMMARY

1. We tested the hypothesis that increased hypoxia in Lake Victoria provides a refugium for the cyprinid dagaa (*Rastrineobola argentea*) against hypoxia-sensitive Nile perch (*Lates niloticus*).
2. Hypoxia in the main habitat of dagaa was rare during 1979–80, but lasted 3–5 months in 1987 and 1988, during which time adult dagaa spent the day just above the oxycline instead of near the bottom.
3. Dissolved oxygen concentrations in the layer just above the oxycline were not critical for Nile perch, but a mass kill of this species following a sudden upwelling of hypoxic water suggested that oxycline-dwelling is risky.
4. Our data suggest no difference between dagaa and Nile perch in the level at which dissolved oxygen starts to limit their vertical distribution in the water column, but dagaa seems to be even more sensitive to extreme hypoxia ($< 1–2$ mg O_2 L^{-1}) than Nile perch.
5. We argue that oxycline-dwelling dagaa are not seeking a predation refugium but that they are limited by low oxygen levels in reaching their feeding areas near the bottom.

Keywords: hypoxia refugium, Lake Victoria, Nile perch, *Rastrineobola argentea*, vertical distribution

Introduction

During the 1980s several changes took place in the ecosystem of Lake Victoria. Many authors have reported the explosive population increase of the introduced Nile perch *Lates niloticus* (L.) and the concurrent disappearance of the dominating haplochromine cichlids from the sublittoral and offshore waters (e.g. Ogutu-Ohwayo, 1990; Witte *et al*., 1992a,b; Witte, Goldschmidt & Wanink, 1995). While the haplochromines disappeared from the sublittoral waters, the population of the sardine-like cyprinid *Rastrineobola argentea* (Pellegrin; local name: dagaa) strongly increased in this area (Wanink, 1991, 1999). At the same time, eutrophication of the lake became manifest and prolonged periods of hypoxia were observed in the deep waters (e.g. Ochumba & Kibaara, 1989; Witte *et al*., 1992a; Hecky, 1993; Mugidde, 1993; Hecky *et al*., 1994). Although thermal stratification, leading to hypoxia, is a long-known phenomenon in Lake Victoria (Worthington, 1930), it used to be restricted to the deepest waters (> 60 m) and to short periods during the rainy season (Talling, 1957, 1966). A recent study showed that the lake is now continuously hypoxic below 50 m depth, while the area between 25 and 50 m is subject to frequent severe hypoxia (Kaufman, 1992; Hecky 1993).

Various explanations have been suggested for the apparent persistence of dagaa with Nile perch (Wanink, 1996). Prey species of Nile perch may find

Correspondence: J.H. Wanink, EEW, University of Leiden, PO Box 9516, 2300 RA Leiden, The Netherlands.
E-mail: jwanink@hotmail.com

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refugia in hypoxic habitats, since this predator is thought to be extremely sensitive to low oxygen levels (Kaufman, 1992; Kolding, 1993). Support for this 'hypoxic predation refugium' hypothesis came from some exploratory dives by a remote operated vehicle, which filmed dagaa shoaling near the oxycline (Kaufman & Ochumba, 1993). The importance of the oxycline as a refugium for dagaa is questionable, however, because the species is most abundant in the sublittoral waters (Wanink, Goudswaard & Berger, 1999), which are supposed to be relatively well oxygenated (Kaufman, 1992). In addition, it is likely that the critical oxygen level that limits Nile perch distribution in the field is lower than 5 mg L^{-1}, the level used in the hypoxic predation refugium hypothesis. This level is based on experiments by Fish (1956), who found that, in the absence of carbon dioxide, the haemaglobin of Nile perch cannot be fully saturated unless the water in contact with the gills contains at least 5 mg O_2 L^{-1}. It has not been shown, however, that Nile perch are limited to water in which their haemoglobin is fully saturated. Conversely, bottom trawling in Mwanza Gulf of Lake Victoria yielded high Nile perch catches throughout the period 1986–87 (Ligtvoet & Mkumbo, 1990), whereas a previous limnological study in that area had shown that the level of dissolved oxygen near the bottom was below the level of 5 mg L^{-1} for several months per year (Akiyama, Kajumulo & Olsen, 1977). Hence, the hypoxic predation refugium hypothesis can only be tested after estimating critical field levels of dissolved oxygen for both predator and prey, with the critical level defined as the level at which dissolved oxygen concentration begins to negatively impact the abundance of the species.

In this paper we report seasonal patterns in dissolved oxygen at different locations in Mwanza Gulf, after the Nile perch boom. Pre-*Lates* data from one of the sampling stations allowed for an assessment of changes in sublittoral waters. We estimated the critical field level of dissolved oxygen for Nile perch by comparing bottom trawl catches with oxygen concentrations. We also related the depth distribution of dagaa to oxygen measurements over the whole water column. We discuss whether the vertical distribution of dagaa is likely to be set by the need for a refugium against Nile perch predation.

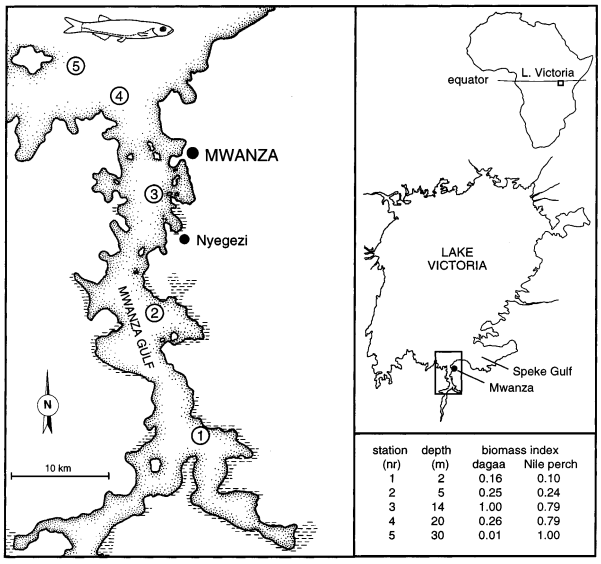
Methods

Study area

Data were collected at five sampling stations in or just outside Mwanza Gulf, Tanzania (Fig. 1). From stations 1–5, water depth increased from 2 to 30 m and the distance from shore from 100 to 3000 m (Wanink *et al*., 1999). Dagaa occurred throughout the Gulf, and were most abundant at the stations 2, 3, and 4 (Fig. 1). During 1983 and 1984, Nile perch massively invaded the study area (Witte *et al*. 1992a,b). Nile perch were caught at all stations, but catch rate in bottom trawls increased with water depth (Fig. 1).

Dissolved oxygen

Before the reported increase of hypoxia in Lake Victoria, the deeper waters (> 60 m) were seasonally stratified: deoxygenation of the lower part of the water column built up during the rainy season and was broken down at the beginning of the dry season



station (nr)	depth (m)	biomass index dagaa	biomass index Nile perch
1	2	0.16	0.10
2	5	0.25	0.24
3	14	1.00	0.79
4	20	0.26	0.79
5	30	0.01	1.00

Fig. 1 Location of the study area and details of the sampling stations. Biomass index represents catch per unit effort (CPUE) at each sampling station expressed as the fraction of CPUE at the station giving the highest yield (after Wanink *et al*., 1999). Data for dagaa (outlined at the top of the figure) are based on surface trawls made at night when the fish aggregate in this area. Nile perch data are based on daytime bottom trawls during the dry season when mixing of the water column prevented hypoxic conditions that might influence the spatial distribution of the fish.

(Talling, 1957, 1966). Since we expected hypoxia at Mwanza Gulf to be highest during the rainy season, we sampled the water at station 3 on 11 days between November 1979 and May 1980. We used a Yellow Spring Instrument (YSI) AQ model 57 to measure the amount of dissolved oxygen to the nearest 0.1 mg L^{-1} at every 0.5 m of the water column. During this period, sampling was usually done around 14.00 h.

Most of the measurements during 1987–88, after the Nile perch boom, were done in the morning between 10.00 and 11.00 h, as recommended by Wanink & Kashindye (1998) to avoid large variations in oxygen concentration caused by pelagic photosynthesis. To increase the number of samples for 1987–88, we also used measurements done at other times in the 24-h cycle, mainly at night. Day and night samples on the same date showed little variation below the value of 5 mg L^{-1}, in which we were most interested. The reported large fluctuations in oxygen level around noon were restricted to the surface layer (Wanink & Kashindye, 1998), while the process of deoxygenation occurs lower in the water column.

The term hypoxia, which is used for levels of dissolved oxygen below 100% saturation, is too broad to determine whether or not dagaa may use low oxygen levels as a refuge against Nile perch. Three studies on the haplochromine cichlids of Lake Victoria have indicated levels of dissolved oxygen which are critical for these fish. Chapman *et al*. (1995) have defined values of less than 1 mg L^{-1} as extremely hypoxic. In two other studies, oxygen concentrations of 1–2 mg L^{-1} (Galis & Smit, 1979) and 2–3 mg L^{-1} (Hoogerhoud, Witte & Barel, 1983) were mentioned as critical for haplochromines in habitats which are usually well oxygenated. Combining these three studies with the one of Kaufman (1992), who used 5 mg O_2 L^{-1} as a critical field value for Nile perch, we have used the isopleths of 1, 3 and 5 mg L^{-1} as the reference values in our analysis.

Rainfall

In the deeper waters of Lake Victoria, thermal stratification and hypoxia in the lower part of the water column develop during the relatively calm weather of the rainy season, and are broken down by the strong winds at the beginning of the dry season (Talling, 1957, 1966). To be able to relate the dissolved oxygen levels in Mwanza Gulf to seasonal changes, we measured daily rainfall during 1987 and 1988 in Nyegezi (Fig. 1). Rainfall during 1979 and 1980 was measured at the nearby Ministry of Agriculture Training Institute in Nyegezi (Witte, 1981).

Oxygen-related abundance of Nile perch

Between 1985 and 1990, monthly bottom trawl catches of Nile perch at the three deepest stations (3, 4 and 5) could be related to simultaneous dissolved oxygen measurements on 53 occasions. The plotted average values for catch rates were based on four successive trawlshots of 30 min each. Trawling was done with the 105 hp research vessel Kiboko (headrope: 18 m; cod end: 20 mm stretched mesh), which sampled the lower 1.5 m of the water column. Catch rates were plotted against the amount of dissolved oxygen measured at 1 m above the bottom.

To test for an ongoing trend in overall Nile perch abundance after the population boom during 1983–84 that might have obscured our results, we analysed catch data from June-November of the trawling program at stations 3, 4 and 5. Assuming absence of hypoxia between June and November, bottom trawl catches from this time of the year can be used as an estimate of Nile perch abundance. Catch rates were not significantly correlated with month number between 1985 and 1990 ($n = 85$, $r^2 = 0.010$, $P > 0.05$). The average ($\pm$ SD) catch rate for this period amounted to 158 ± 105 kg h^{-1}.

Vertical distribution of dagaa

Nylon monofilament gill nets (stretched mesh: 13 mm; net width: 5 m) covering the water column from the surface to the bottom, were used to catch dagaa. We attached markers every 50 cm, to estimate the depth at which fish were caught. The nets were selective for adult dagaa, which normally spend the night near the surface and the day just above the bottom (Wanink, 1992; Wanink *et al*.,1999). The nets were set around 10.00 h, when dagaa had settled at their daytime depth (Wanink, Berger & Witte, 1993), and emptied 4 h later. On 15 fishing days between 1987 and 1989, oxygen concentration was measured at every 0.5 m throughout the water column, close to the nets, between 10.00 and 11.00 h. Animals carrying tapeworms were excluded from the analysis, since

they are known to dwell continuously near the surface (Wanink, 1992).

Critical field levels of dissolved oxygen

In order to get comparable estimates of the critical oxygen levels for Nile perch and dagaa, we calculated cumulative percentages of catches over a range of oxygen concentrations. The critical field levels were defined as the oxygen concentrations at which the cumulative catches amounted to 50%. For Nile perch, the average catch rate from all days ($n = 10$) with more than 5 mg O_2 L^{-1} at 1 m from the bottom was calculated and set to 100%, under the assumption that such conditions are not limiting Nile perch abundance (Fish, 1956). After transforming the catch rates for individual sampling days ($n = 53$) to percentages of the 'non-limiting' average, catch rate means within classes of 1 mg O_2 L^{-1} (0–1, 1–2, until > 5) were plotted against oxygen means. For dagaa, we calculated for each of the 15 sampling days the cumulative percentage of the total catch of that day in each metre of the water column. After linking these individual data to the accessory oxygen concentrations, the mean cumulative dagaa catch was plotted as a function of dissolved oxygen.

Results

Hypoxia in Mwanza Gulf

Between November 1979 and May 1980, the oxygen level at the bottom at station 3 did not drop below 1 mg L^{-1}, although a concentration of 5 mg O_2 L^{-1} was found as shallow as 7–8 m between February and April (Fig. 2). Only on two sampling days were values below 3 mg L^{-1} found within about 4 m of the bottom. Infrequent sampling prevented a precise estimate of the duration of the first hypoxic period (in February), but the second one (in March) cannot have lasted more than 12 days.

Measurements between February 1987 and October 1988 showed that increased deoxygenation of the lake was not restricted to the deeper waters (Fig. 3). The 'deepwater pattern' of seasonal stratification (Talling, 1957, 1966) was found at all stations with the exception of station 1, a shallow-water station. Periods with relatively low oxygen levels

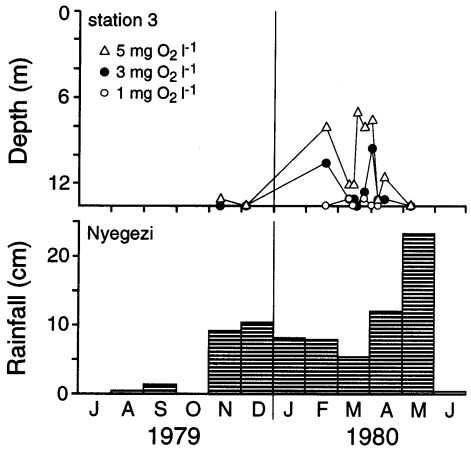


Fig. 2 Seasonal fluctuations in dissolved oxygen at station 3 in Mwanza Gulf and rainfall in Nyegezi during 1979 and 1980. The plotted isopleths represent the distance from the bottom at which the oxygen concentration reached values of 1, 3 or 5 mg O_2 L^{-1}, respectively.

were not extensive at station 2, but occurred in the lower half of the water column for several months per year at stations 3, 4, and 5. Comparison of the 1979–80 and the 1987–88 oxygen conditions at station 3 showed an increase in the duration of hypoxia. In addition, during the latter years, the isopleths of both 3 and 1 mg O_2 L^{-1} were situated further from the bottom. Extreme hypoxia (< 1 mg O_2 L^{-1}) did not occur during 1979–80 at station 3, while in 1987 and 1988 this was the almost year-round condition at the bottom, periodically extending to 4 m above the bottom.

Some severe storms in February 1988 were followed by an obvious drop in the depth of the oxycline at stations 4 and 5, and a subsequent sudden upwelling at the beginning of April at stations 3–5. This upwelling coincided with a massive kill of Nile perch in the area between stations 3 and 5. Although we have seen other such kills between 1985 and 1989, the number of fish floating at the surface was highest in the April 1988 incident. On 1 April, many Nile perch appeared at the surface and were collected alive by fishermen. The stomachs of the floating animals were extruded. This was probably caused by expansion of the swimbladder, which suggests that the fish had risen quickly to the surface, driven there by upwelling hypoxic water.

Oxygen-related abundance of Nile perch

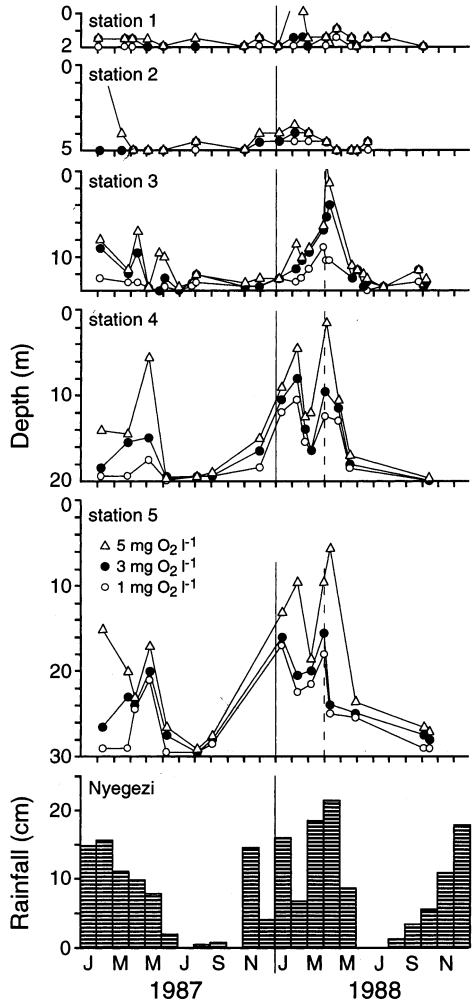


Fig. 3 Seasonal fluctuations in dissolved oxygen at stations 1–5 in Mwanza Gulf and rainfall in Nyegezi during 1987 and 1988. The plotted isopleths represent the distance from the bottom at which the oxygen concentration reached values of 1, 3 or 5 mg O_2 L^{-1}, respectively. At stations 1–3, markers on the isopleth of 5 mg L^{-1} were not plotted for sampling days on which this oxygen concentration was not even reached at the surface. Broken lines at stations 3–5 indicate the start of the mass Nile perch kill on 1 April 1988.

At the time of the kill in April 1988, dissolved oxygen concentrations over the whole water column at station 3 were below 5 mg L^{-1}, and higher levels were only found in the upper few metres at stations 4 and 5 (Fig. 3). The isopleths of 3 and 1 mg L^{-1} also suddenly shifted to shallow depths and, since the depth of Nile perch during the upwelling was not known, we could not establish critical oxygen levels for Nile perch during this event.

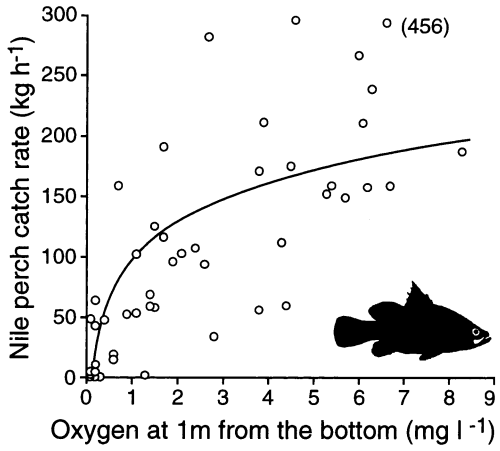


Fig. 4 Nile perch catch rate in bottom trawls as a function of dissolved oxygen. The plotted line represents the regression formula: $y = 95.99 + 47.13 \ln x$ ($r^2 = 0.55$, $P < 0.005$).

Plotting the catch rates of Nile perch in the bottom trawls as a function of dissolved oxygen near the bottom showed an asymptotic positive correlation (Fig. 4). As expected, almost no fish were caught when dissolved oxygen was less than 0.2 mg L^{-1}. However, catch rate increased rapidly with the concentration of dissolved oxygen, reaching a value of 100 kg h^{-1} (50% of the maximum predicted by the regression curve for the observed range of oxygen levels) at 1 mg L^{-1}. When the lowest oxygen values were successively removed from the regression, no significant correlation remained at levels above 2.5 mg O_2 L^{-1} ($P > 0.05$), suggesting that Nile perch abundance was not limited at such levels.

Dagaa dwelling at the oxycline

The depth distribution of adult dagaa during daytime was related to the level of dissolved oxygen in the water column (Fig. 5). When the lake was not stratified, dagaa spent the day near the bottom. Most fish were caught away from the bottom, just above the oxycline, during periods of stratification. It should be noted that the plotted depth distributions (Fig. 5) refer to adult dagaa during the day. Immature dagaa occupied the surface area by day, and most adults moved towards the surface around sunset (Wanink, 1992; Wanink *et al.*, 1999).

Critical field levels for Nile perch and dagaa

Plotting the cumulative catches of Nile perch and dagaa as functions of dissolved oxygen (Fig. 6) revealed that predator and prey did not differ in their sensitivity to moderate hypoxia (3–5 mg O_2 L^{-1}). Based on the 50% levels of the cumulative catches, our estimate of a common critical field level for the two species amounted to 2–2.5 mg L^{-1}. The data suggest a difference in relative abundances only under conditions of extreme hypoxia (< 1–2 mg O_2 L^{-1}). In contrast to the expectations, Nile perch seemed to be less sensitive to such low oxygen levels than dagaa.

Discussion

Hypoxia in Mwanza Gulf

The recent increase of hypoxia reported for deep waters in Lake Victoria (Kaufman, 1992; Hecky *et al.*, 1994) was also apparent in Mwanza Gulf (Figs 2 & 3). During the rainy seasons of 1987 and 1988, oxygen concentration in the lower part of the water column in the sublittoral waters (6–20 m; Greenwood, 1974) was below 3 mg L^{-1} for 3–5 months. Even in the littoral waters (0–6 m), low values were temporarily measured near the bottom. Thermal stratification, causing hypoxia in the lower part of the water column, occurred in Mwanza Gulf in former years,

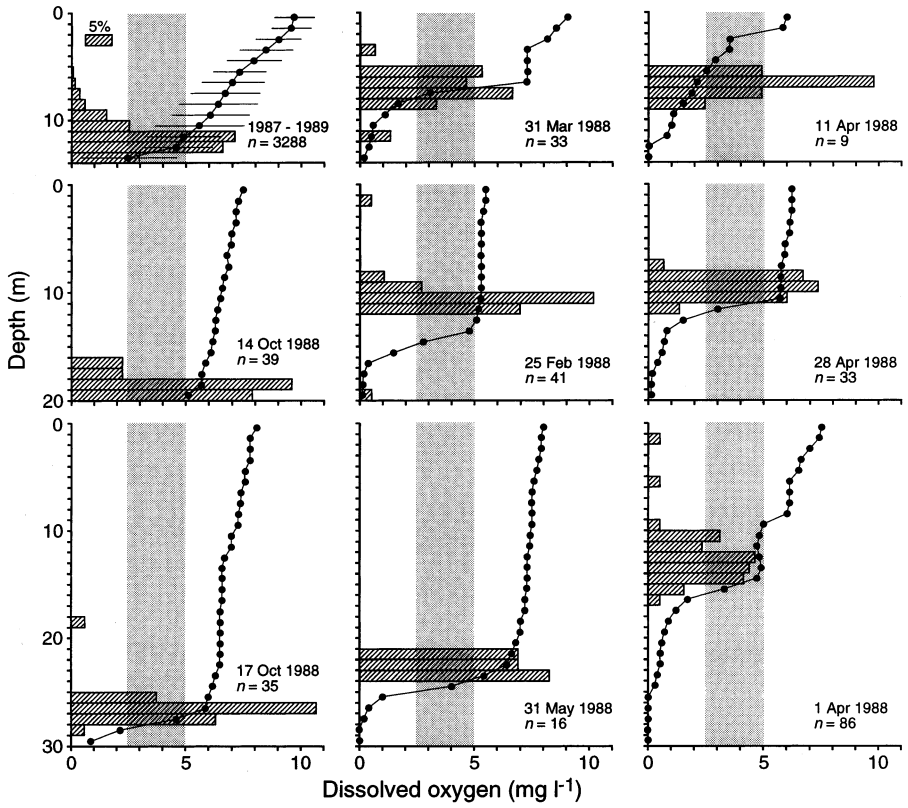


Fig. 5 Day-time depth distribution of dagaa in relation to the depth of the oxycline. From top to bottom the panels represent stations 3, 4 and 5. Mean oxygen concentrations ($\pm$SD) for seven sampling days without stratification are plotted (black dots) as a function of depth in the top left panel. All other profiles are based on single sampling days. Plotted sample sizes refer to the total number of dagaa on which the frequency distributions (hatched bars) were based. The vertical grey bars represent the oxygen concentrations below the level needed by Nile perch to fully saturate their haemoglobin (Fish, 1956), at which their abundance did not seem to be limited (this study). Note that the panels are arranged according to oxygen profile instead of time sequence.

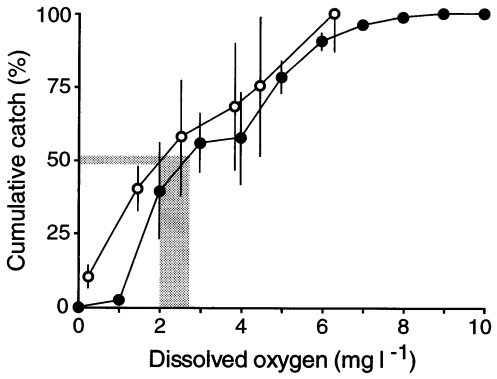


Fig. 6 Cumulative catches (mean ± SE) of Nile perch (open circles) and dagaa (black dots) as functions of dissolved oxygen. For Nile perch, cumulative means of bottom trawl catches (see Methods) per class of 1-mg L^{-1} dissolved oxygen (0–1, 1–2, until > 5) were plotted against oxygen means. For dagaa, cumulative means of gill net catches (see Methods) per 1-mg L^{-1} class of dissolved oxygen (< 0.5, 0.5–1.5, 1.5–2.5, etc.) were plotted against the midpoints of the dissolved oxygen classes. The vertical grey bar indicates the range for the common critical field level for Nile perch and dagaa: the oxygen level at which 50% of the fish were caught. Sample sizes of the plotted means, with ascending values for dissolved oxygen, were for Nile perch: 21, 10, 5, 3, 4 and 10, and for dagaa: 26, 21, 6, 14, 7, 33, 52, 60, 25, 21 and 8, respectively.

but was easily disturbed by wind and never lasted long (van Oijen, Witte & Witte-Maas, 1981). In a 2-year-long monthly sampling programme at an 8-m deep station between stations 2 and 3, pronounced hypoxia at the bottom (dissolved oxygen dropping from a mean level of 5–6 to 2–3 mg L^{-1}) was measured only in April 1974 and January 1975 (Akiyama *et al*., 1977).

Massive fish kills associated with sudden deoxygenation of the water are increasing in frequency in Lake Victoria and related to an increase in algal blooms (Ochumba & Kibaara, 1989; Ochumba, 1990). Apart from the toxic decomposition products of algal blooms, upwelling of hypoxic water can also cause fish mortalities (Kitaka, 1972). The mass mortality of Nile perch in April 1988 was probably caused by such an upwelling (Fig. 3), as we did not observe this during algal blooms.

In southern Lake Victoria, upwelling has been caused by a southward flow of deeper layers, compensating for a wind-induced northward flow of surface water (Newell, 1960). Kitaka (1972) recorded the strongest upwelling in the mouth of the Speke Gulf, close to our study area (Fig. 1). Our visual observations suggest northward flow of surface water in Mwanza Gulf preceding the upwelling in April 1988. On 4 February the water south of a point halfway between stations 1 and 2 (Fig. 1) appeared loaded with sediment and floating pieces of shore vegetation. A severe storm occurred in this area the previous day, accompanied by 35 mm rainfall in 30 min (M. Meijer, pers. comm.). Between 4 February and 5 April the front of the grey-coloured water moved northwards to halfway between stations 2 and 3.

The suspended matter reduced water transparency at station 1 to 20–30 cm Secchi depth. Shading probably minimized photosynthesis at this station, causing the low oxygen concentrations measured at the surface. A thunderstorm on 11 February may have caused mixing at stations 4 and 5, resulting in the observed sink of the oxycline (Fig. 3). Since no extreme weather conditions were recorded close to 1 April, the sudden rise of the oxycline was probably caused by upwelling of the hypoxic layer.

Hypoxia: a predation refugium?

Since the work of Fish (1956), Nile perch has been regarded as sensitive to low oxygen concentration, which led to the hypothesis that its prey might seek refuge in hypoxic waters (Kaufman, 1992; Kolding, 1993). This view was reinforced by the observations on fish kills in Lake Victoria (Ochumba, 1990; this study) and Lake Turkana (Kolding, 1993), where Nile perch formed the majority of the dead fish. In contrast to these authors, who used the value of 5 mg O_2 L^{-1} (derived from the experimental work of Fish (1956)) as a lower limit for the occurrence of Nile perch, we found that the abundance at the bottom of this species was not affected by oxygen levels above 2.5 mg L^{-1}. It should be realized, however, that the value of 5 mg O_2 L^{-1} published by Fish (1956) referred to the concentration of dissolved oxygen necessary to fully saturate the haemoglobin of Nile perch, while the fish can probably survive under lower oxygen conditions (G.E.E.J.M. van den Thillart, pers. comm.). Support for the latter view was found in recent experiments on hypoxia tolerance of Nile perch collected from the Lake Victoria basin (Schofield & Chapman, 2000). Being placed in well-oxygenated tanks in which the concentration of dissolved oxygen was gradually lowered, the first fish started to use aquatic surface respiration (ASR) at the

air–water interface when the oxygen tension fell below 40 mmHg (approximately 3.0 mg O_2 L^{-1}). Schofield & Chapman (2000) report a threshold value of 25.3 mmHg for the initiation of ASR (defined as the oxygen tension at which 10% of the fish used ASR). Since this was very close to their estimate of 24 mgHg (approximately 1.4 mg O_2 L^{-1}; L.J. Chapman, pers. comm.) for the critical oxygen tension (defined as the oxygen tension below which the metabolic rate of the fish is dependent on the level of dissolved oxygen), the authors suggest that Nile perch may initiate ASR at the point where they are no longer able to maintain their metabolic rate independent of oxygen concentration.

In the open waters off the Kenyan shores of Lake Victoria, Nile perch aggregated above the oxycline in water containing more than 3 mg O_2 L^{-1}, but occasionally large sonar targets, probably Nile perch, were observed in deeper layers with only 1–2 mg O_2 L^{-1} (Kaufman & Ochumba, 1993). Trawling on these occasions yielded Nile perch which had been feeding on the prawn *Caridina nilotica* (Roux). Since *Caridina* has been observed in high numbers below the oxycline (Kaufman, 1992), Nile perch might dive beneath the oxycline to forage (Kaufman & Ochumba, 1993). Our bottom trawl data showed that the presence of Nile perch at concentrations of oxygen of less than 3 mg O_2 L^{-1} is a common feature (Fig. 4) and supported the idea that Nile perch make at least short foraging trips into the hypoxic layer. A negative correlation between catch rate of Nile perch and distance between the oxycline and the bottom has also been observed (P.C. Goudswaard *et al*., unpublished data). Although there is a possibility that Nile perch may dive to the bottom in an escape response to the sound of the approaching trawler (Tumwebaze, 1997; J. Kolding, pers. comm.) our conclusions are supported by the results of D.J. Postma (pers. comm.), who regularly caught Nile perch at the bottom in a gill netting experiment at station 3 during the period of hypoxia in 1987.

Observations with a remote operated vehicle in the Kenyan waters of Lake Victoria revealed large numbers of dead or dying dagaa below the oxycline (Kaufman & Ochumba, 1993). The authors suggest that rapid shifts in the oxycline may have caused the mass mortality. Our data support their idea that dagaa is abundant near the oxycline during periods of stratification. In contrast to Nile perch, dagaa may sink to the bottom after dying from a sudden deoxygenation of the habitat, leaving no evidence of a kill at the surface. Nile perch may even cope better with extreme hypoxia than dagaa, since at levels below 1–2 mg O_2 L^{-1} the cumulative catch of Nile perch was higher than that of dagaa (Fig. 6).

We conclude that dagaa do not benefit from low oxygen refugia because our observations suggest no difference in the levels at which dissolved oxygen starts to limit the distributions of dagaa and Nile perch. Moreover, dagaa seems to be less tolerant of extreme hypoxia than Nile perch. The fact that we also recorded Nile perch below the oxycline also reduces the potential for hypoxic refugia for other prey species. The catfish *Bagrus docmak* (Forsskål) has declined to very low numbers, probably due to competition of adults with, and predation on juveniles by, Nile perch (Goudswaard & Witte, 1997). *Bagrus docmak* would have been a most likely species to use deep-water refugia because it is extremely tolerant of low oxygen concentrations (Fish, 1956). Experimental work on Lake Victoria cichlids, initially the principal prey of the introduced Nile perch, showed generally high levels of hypoxia tolerance (Chapman *et al*., 1995). The authors suggest that some cichlids may use the structural complexity of the rocky, littoral waters and fringing swamps as a defence against Nile perch where hypoxia is common. This suggestion is supported by relatively high haplochromine survival in rocky shore habitats of Lake Victoria (Witte *et al*., 1992b; Seehausen *et al*., 1997) and in the wetlands surrounding Lake Nabugabo, a small satellite lake of Lake Victoria, where Nile perch has also been introduced (Chapman *et al*., 1996). Although the cichlids from the open waters of Lake Victoria were not less tolerant to hypoxia than the inshore species (Chapman *et al*., 1995), the former disappeared almost completely (Witte *et al*., 1992a,b). We think that the ability of Nile perch to dive below the oxycline limited the use of this habitat as a refugium, although the increasing thickness of the hypoxic layer with distance from shore (Fig. 3) and its negative relationship with Nile perch abundance at the bottom (P.C. Goudswaard *et al*., unpublished data) may have allowed for refugia in the deeper waters. Chapman *et al*. (1995) suggested some species that are thought to have disappeared may be currently present in low-oxygen refugia in wetlands or near the oxycline in

deeper waters that have not been adequately sampled. The latter is not very likely, however, since we have shown that Nile perch regularly enters this habitat. Furthermore, most of the haplochromine cichlids depended on the bottom area for their feeding and they also disappeared from the catches of vertical gill nets, covering the water column from the surface to the bottom (Witte *et al*., 1992b; Goldschmidt, Witte & Wanink, 1993).

The oxycline as a barrier for dagaa

As predicted by life history theory, dagaa reacted to the increased predation pressure by Nile perch by increasing its growth rate, showing advanced maturation and reaching a smaller adult size (Wanink, 1998). A habitat shift after the disappearance of the demersal haplochromine cichlids probably allowed for the increased growth rate. Dagaa started to exploit the bottom area, switching from zooplankton to energetically richer macrobenthic prey (chironomid larvae and the prawn *Caridina nilotica*) whenever available (Wanink, 1998). Within a few years after invading the new habitat, dagaa showed morphological adaptations to reduced oxygen conditions (increased number of gill filaments) and to benthic feeding (decreased number of gill rakers) (Wanink & Witte, 2000). However, chironomids and *C. nilotica*, which both increased strongly in abundance after the Nile perch boom (Witte *et al*., 1995), might not be available to dagaa when the lake is stratified, as they have been observed in extremely hypoxic water.

In accordance with the predictions from the hypoxic predation refugium theory, we found that the daytime depth distribution of dagaa in Lake Victoria after the Nile perch boom was set by the occurrence and the position in the water column of the oxycline. Recent hydroacoustic research in the northern part of Lake Victoria has shown distribution patterns of dagaa in relation to the oxycline that are similar to those we have found (Tumwebaze, 1997). However, our data resulted in a rejection of the hypothesis that living at the oxycline provided a refugium against Nile perch. In contrast, the oxycline probably acted as a seasonal barrier, obstructing the exploitation of energetically rich food stocks, necessary for the life history changes which allow for coexistence with Nile perch.

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