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Distribution and exploitation of Nile perch *Lates niloticus* in relation to stratification in Lake Victoria, East Africa

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ABSTRACT

Stratification restricts habitable areas forcing fish to balance between favourable temperature and minimum dissolved oxygen requirements. Acoustic surveys conducted during the stratified and isothermal periods on tropical Lake Victoria indicated that stratification of temperature and dissolved oxygen (DO) affected vertical distribution of Nile perch. There was higher mean temperature (25.6 ± 0.5 °C) and lower DO (6.4 ± 1.8 mg/l) during stratified period compared to the isothermal period (mean temperature 24.9 ± 0.3 °C; mean DO 7.3 ± 0.6 mg/l). Higher mean densities of Nile perch were recorded in the coastal (0.44 ± 0.03) and deep (0.27 ± 0.02 g/m^3) strata during the stratified compared to the isothermal season (coastal: 0.24 ± 0.01; deep: 0.12 ± 0.02 g/m^3). In addition, Nile perch density in the upper 0–40 m depth layers in the coastal and deep strata increased by over 50% from the isothermal to the stratified season. Daily landings from 65 motorised fishing boats between October 2008 and September 2010 show higher mean catch (26.29 ± 0.17 kg/boat/day) during stratified compared to the isothermal (23.59 ± 0.15) season. Thermal stratification apparently compresses the habitat available to Nile perch and can potentially result in higher exploitation. Managers should evaluate the potential benefits of instituting closed seasons during the stratified period, and stock assessment models should take into account the seasonal niche compression.

Introduction

The spatial and temporal distribution and abundance of pelagic fishes is influenced by abiotic factors, such as temperature, salinity, depth, dissolved oxygen (DO), as well as biotic factors, such as the distribution of prey species (Brosse et al., 2007; Feyrer et al., 2007). Thus, seasonal changes of these factors, such as thermal stratification, can have dramatic effects on the vertical distribution of pelagic fishes (Ficke et al., 2007). In addition to influencing the productivity of limnetic systems, stratification delineates habitat for many pelagic fishes. Surface waters usually have sufficient DO, but may have temperatures that exceed the physiological tolerances of pelagic fishes while waters below the thermocline may have tolerable temperatures but could be hypoxic. The implication is that fish are squeezed between these two extremes and experience niche compression during the stratified season. Examples of niche compression have been observed in species such as the lake trout *Salvelinus namaycush* in north-western Canada (Plumb and Blanchfield, 2009) as well as Coho salmon *Oncorhynchus kisutch* and yellow perch *Perca lavescens* in Southern Lake Michigan (Magnuson et al., 1990). The ecological consequences of fish experiencing this compression of habitat ranges from concentrating individuals in the upper water layers and increasing their vulnerability to capture by near-surface fishing gears (Henderson and Crampton, 1997) to dispersal or migration to refugia (Ficke et al., 2007; Tate et al., 2007) to reductions in growth rates or survival (Eby and Crowder, 2002).

Whereas effects of stratification on habitat use and exploitation of temperate lake and reservoir fishes have been relatively well-studied (King et al., 1999), very little information is available on their tropical counterparts. Case studies of effects of stratification on vertical and horizontal distribution of fishes and other aquatic organisms in tropical systems such as Lake Victoria (East Africa) may be an important aid to managing productive and sustainable fisheries in these systems, particularly as anthropogenic impacts, such as changing land use practices and climate, continue to alter their ecology (Foster et al., 2003; Heller and Zavaleta, 2009). Lake Victoria, like other tropical lakes, experiences annual cycles of isothermal and thermal stratification periods, the latter being characterised by the formation of a hypoxic/anoxic hypolimnion allied to enhanced eutrophication, decreased water transparency, increased blue-green algal blooms and

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increased DO depletion (Hecky et al., 2010; Njiru et al., 2011). During the isothermal, mixed period of June–August, DO was almost uniform throughout the water column. However, steep gradients of DO are common during the November–March stratified period. Recent studies suggest stratification in the deeper waters of the lake may have become weaker than in the 1990s (Sitoki et al., 2010). In general, the DO profiles during the stratification period are closely related to temperature in Lake Victoria (Talling, 1957, 1966). While this seasonal stratification has the potential to compress pelagic fish habitat, the extent to which it actually alters fish distributions and influences exploitation patterns has not yet been documented, particularly those of commercially important species like Nile perch (*Lates niloticus L.*).

Nile perch was officially introduced into Lake Victoria amid controversy in 1962–63 with the goal of converting the abundant haplochromine cichlid stocks into fish of table size (Ogutu-Ohwayo, 1990) although there is evidence that some had been introduced earlier for diverse purposes (Pringle 2005, Hecky et al., 2010). While the thermal physiology of Nile perch has not been thoroughly investigated, the species is generally thought to be intolerant of low DO conditions (Schofield and Chapman, 2000), particularly at higher temperatures (Fish, 1956). This hypothesis is supported by the fact that significant catches have seldom been recorded at very low DO levels (<2 mg/l; Wanink et al., 2001), and even those few catches may be due to simply diving into anoxic zones in search of prey. Kolding et al. (2008) have identified eutrophication and the resulting hypoxia/anoxia as the primary threats to the Nile perch fishery in Lake Victoria. Adult fishes are usually less tolerant to environmental stresses as they have been demonstrated to exhibit ontogenetic shifts in habitat use (Schofield and Chapman, 2000). Adult Nile perch are thought to breed in shallow water and move into deeper water as they grow, resulting in low catches in deep water that are thought to be caused by the fact that deeper waters could have been too low in dissolved oxygen.

Causes of low DO in deep waters of Lake Victoria have been discussed frequently. Some authors believed that the introduction of Nile perch, an apex piscivorous fish led to the destruction of the detritivorous and phytoplanktivorous haplochromine cichlid guilds in the lake (Ogutu-Ohwayo, 1990; Witte et al., 1992). This set up a cascade causing an increase in algal communities and thus contributed to the eutrophication. However, this hypothesis has been discounted by empirical tests that suggested grazing abilities of fish and zooplankton combined had little impact on phytoplankton (Witte et al., 2012) and therefore attributed hypoxia to eutrophication (Kolding et al, 2008). According to this hypothesis, anthropogenically induced mobilisation of nutrients into the lake has been, and continues to be, the dominant process driving algal biomass whose death and decomposition results in hypoxia (Hecky et al., 2010; Witte et al., 2012).

In this paper we examine whether there are any relationships between seasonal thermal cycles (stratification and turnover) and Nile perch vertical and horizontal distributions, and analyse the relationship of seasonally induced Nile perch distribution patterns and fish catches (exploitation).

Study area, materials and methods

The study was conducted on Lake Victoria (Fig. 1), the largest tropical lake in the world (surface area: 68,800 km^2, average depth: 40 m, maximum depth: 84 m). The lake experiences a climate characterised by two rainy seasons, the long rains during April–June and the short rains during October/November, although the southern tip (<10% of the lake's area) south of latitude 2° S experiences one long rainy season from December to March (Lowe-McConnell, 1987). Wind speeds are generally low during the rainy season (0–3.5 m s^{-1}) due to the protection of the Rwenzori mountains in the west and the Rift valley escarpment to the east and south. Low wind speeds reduce mixing and enable the formation of a 0.5–1.7 °C difference in temperature between the surface and bottom layers of the lake (Talling, 1966). This thermocline degrades at the end of the rainy season as wind speeds increase and evaporative cooling increases, leading to overturn with associated upwelling of nutrients and return of normoxic conditions to deeper waters (Lowe-McConnell, 1987). Wind speeds increase during the dry season, between July and August when strong southerly winds exceeding 15 m/s blow over the region (Spigel and Coulter, 1996). These strong southerly winds cause high evaporation rates, water mixing, and a decrease of surface temperatures. Seasonal algal blooms affect seasonal transparency patterns in the lake and may also further increase stratification in the lake (Witte and Densen, 1995).

Six acoustic surveys were conducted twice each year (in August/September, when the lake was isothermal, and February/March, when it was stratified), beginning in August 2007 and ending in March 2010. A systematic survey design was adopted to ensure that sampling was carried out along specific pre-determined transects in all strata. The lake was divided into four quadrants: northeast (NE), northwest (NW), southeast (SE) and southwest (SW), for operational reasons and further stratified into three major depth strata within each quadrant, i.e. deep (>40 m), coastal (20–40 m), and inshore (<20 m).

The survey design consisted of 35 radial transects in the coastal stratum pointing towards the centre of the lake (total distance approximately 800 km) and 8 parallel cross-lake transects in the deep stratum (total 500 km) (Fig. 1). Activities were planned so that the collection of data used for the estimation of fish densities started after first light and ended before dusk since Nile perch are generally considered to be more abundant in the water column during the day (Goudswaard et al., 2004). Goudswaard et al. (2004) reported that catch rates of Nile perch in bottom trawls were greater during the night implying most fish were close to the bottom, which could lower water column densities when estimated using acoustics. Limiting survey periods to daylight hours therefore standardised the recording of these fish while they were distributed throughout the water column.

Acoustic data were obtained using a Simrad EK60 (Kongsberg Maritime AS, Horten, Norway) dual frequency echosounder of 70 and 120 kHz (operating at a ping rate of 0.5/s, pulse duration 0.256 m/s, and transmitted power 200 W) connected to two 7° beam transducers. Both transducers were hull mounted and directed vertically downwards and were calibrated at the beginning and towards the end of each survey. The results of the 70 kHz echosounders have not been used in the analyses in this paper. The draft of the ship was 2.2 m, and the transducers were mounted at a depth of about 2 m from the surface. To avoid near-field dynamics, only data 2 m and deeper below the transducer were analysed; thus information is lacking for the top 4 m of the water column. In addition, data 0.5 m from the bottom were excluded to avoid the near bottom acoustic dead zone (Ona and Mitson, 1996). Two analysis lines "Top line" 2 m from the transducer and "checked bottom" 0.5 m above the bottom were used to delimit useful acoustic records.

Catches from pelagic and bottom trawl nets during the August 2005 revealed that in the open, and deep areas of the entire lake nearly 99% of the fish >13.6 cm total length (TL) were Nile perch (Supplementary Tables 2 & 3). In addition, net hauls taken in the open coastal and pelagic areas (>20 m depth) conducted along acoustic surveys indicated similar proportions (Supplementary Table 3 and Kayanda et al., 2012). Length frequency distributions of the other two taxa present in the open pelagic zone of the lake, zooplanktivorous "Dagaa" (*Rastrineobola argentea*) and Haplochromines show mean lengths as 4.5 and 5.8 cm TL, and largest individuals caught as 9.7 and 13.8 for the two taxa respectively (Supplementary Fig. 1). Nile perch that is generally large bodied and sufficiently spaced in the water column was separated from the others through echo counting as opposed to echo-integration for the latter two species (not subject of the current paper). Consequently, for the purpose of this study, data extractions for single target detections were restricted to targets with higher Target Strength (TS) than −50 dB which corresponds to