Fisheries Research 186 (2017) 159–167

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

High stock density impairs growth, female condition and fecundity, but not quality of early reproductive stages in vendace (*Coregonus albula*)

Thomas Wanke[a,*], Uwe Brämick[a], Thomas Mehner[b]

[a] Institute of Inland Fisheries, Im Königswald 2, 14471 Potsdam, Germany
[b] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany

ARTICLE INFO

Article history:
Received 22 March 2016
Received in revised form 24 August 2016
Accepted 27 August 2016
Handled by George A. Rose

Keywords:
Maternal effects
Spawning stock biomass
Egg size
Egg quantity
Hatching success
Larval size

ABSTRACT

In fisheries science, stock density is one of the fundamental factors that affect growth and condition. However, reproductive traits like fecundity and also the size and quality of offspring (via maternal effects) can be modified by stock density. In the short-living freshwater fish species vendace (*Coregonus albula*), the impact of stock density via maternal condition on quantity and quality of eggs and larvae was often proposed as a driver of population fluctuations, but such mechanisms have only rarely been evaluated. We systematically analysed growth, female condition and reproductive traits (fecundity, egg size, hatching rate and size of hatchlings) of vendace in relation to stock density across three lakes over two years. Across populations of contrasting density, length at first maturity, female condition and relative fecundity strongly reflected the difference in stock density, while size of eggs and larvae and hatching success at artificial breeding were not correlated with stock density. Our results indicate that density-dependent female spawner traits do not alter reproductive success, but vendace maintain egg size and hatching rate at the expense of egg quantity even at low per-capita resource availability. Accordingly, the reproductive potential of vendace stocks is primarily driven by spawning stock biomass and relative fecundity. We conclude that besides spawning stock biomass and relative fecundity, the additional inclusion of spawner condition into stock assessment has little potential to improve vendace fisheries management.

1. Introduction

Stock density (respectively biomass) is the most surveyed and most managed parameter in marine and inland fisheries (Hilborn and Walters, 1992) and is known to directly or indirectly affect fundamental characteristics of a fish stock. Stock density is the key determinant for catch rate and fisheries yield but might also directly influence the reproductive potential of a stock (spawning stock recruitment theory; Ricker, 1954; Beverton and Holt, 1957). Moreover, stock density directly modulates intraspecific competition for resources, thus indirectly influencing individual somatic growth, condition and mortality, and also reproductive parameters like propagule and offspring quality (Green, 2008; Jakobsen, 2009). While the overall, species-unspecific influence of stock density on somatic growth, mortality and condition is well understood and forms the basis of fisheries theory (surplus production; Russell, 1931; Hjort et al., 1933; Graham, 1935), the influence of stock density on egg quality via maternal effects (here defined as the non-genetic contribution of the female to offspring condition, see Reznick, 1991) is substantially more complex and less generalizable among species (Green, 2008).

Maternal condition, and size and age of females, were shown to affect fecundity and offspring quality in many fish species (Solemdal, 1997; Marshall et al., 1998; Marteinsdottir and Begg, 2002) and incorporation of such female traits into recruitment models significantly improved their performance (Marteinsdottir and Thorarinsson, 1998; Marshall et al., 2003). Meta-analysis of time-series data of 25 marine species revealed that the importance of age- and size-related maternal effects increases with the reproductive life span of the populations (Venturelli et al., 2009), suggesting a low effect in short-living species due to their low variety in size and age of spawners. Furthermore, in species with short lifespan, offspring quality is de facto unrelated to the weakly

* Corresponding author.
E-mail addresses: thomas.wanke@ifb-potsdam.de (T. Wanke), uwe.braemick@ifb-potsdam.de (U. Brämick), mehner@igb-berlin.de (T. Mehner).

http://dx.doi.org/10.1016/j.fishres.2016.08.028
0165-7836/

varying size and age of females, but female condition may play a stronger role in affecting offspring quality. Female condition is primarily modified by stock density and the overall environmental conditions, and hence the reproductive potential of fish stocks with short lifespans is probably strongly density-dependent. Such a high impact of stock density on maternal condition and offspring quality was shown for short-living sardine (*Sardinops sagax*) (Kawasaki and Omori, 1995; Schwartzlose et al., 1999; Zwolinski and Demer, 2014).

Vendace (*Coregonus albula* L.) is a short-lived freshwater fish species inhabiting cold, well-oxygenated lakes in North and Central Europe. In most vendace populations, the quantitative relationship between the size of the spawning stock and recruitment is weak (Viljanen, 1988; Marjomäki, 2004; Wanke et al., 2016) and poor reproductive success was often observed despite high parental stock density (Valtonen and Marjomäki, 1988). These strong inter-annual recruitment fluctuations have often been explained by compensatory effects of stock density via maternal condition on quality and quantity of propagules and offspring (Hamrin and Persson, 1986; Helminen and Sarvala, 1994; Auvinen, 1995). Furthermore, high inter-annual and inter-population variations in growth and condition of spawners are associated with variation of stock density (Christianus, 1995; Marjomäki and Kirjasniemi, 1995; Karjalainen et al., 2016). With the exception of smelt (*Osmerus eperlanus* L.) in some cases, vendace rarely co-occur with other abundant cold-water species in the hypolimnetic areas of lakes in the northern lowlands (Diekmann et al., 2005; Mehner et al., 2005), and the pelagic dominance of vendace hence makes it likely that density-dependent intraspecific competition is the primary driver of growth and condition of vendace spawners. This pronounced variability of condition makes it likely that besides fecundity variation, there is a strong maternal effect on propagule and offspring quality, in particular because vendace reach maturity almost invariably at age 1+ (Hamrin and Persson, 1986; Huusko and Hyvärinen, 2005) in contrast to fish species with longer life span, which delay maturity in response to low per-capita food resources (Trippel, 1995; de Roos et al., 2006). However, only one study conducted in the northernmost part of the distribution range of vendace (Karjalainen et al., 2016) systematically analysed the relationship between stock density, maternal condition and the quantity and quality of their eggs. A better understanding of the female-offspring relationship in vendace could furthermore help to explain the strong population fluctuations and to improve the management of vendace stocks.

In this study we systematically analysed the effect of stock density on somatic and reproductive traits of female vendace across three lakes with a broad range of vendace stock densities over two successive years. We focused on females as they provide the majority of non-genetic material for embryonic development, even though paternal effects have also been demonstrated (Kamler, 2005; Green, 2008). We quantified size-at-age, length at maturity and water content of muscle tissue as a proxy for the energy status and condition of female vendace in relation to stock density (Lambert and Dutil, 1997; Green, 2008). Furthermore, we measured fecundity and the dry weight of ready-to-spawn eggs in all populations in both years. Finally, we ran incubation experiments to quantify the hatching success as a proxy for egg quality and measured the total length of hatchlings. We hypothesized that the strongly varying stock density of vendace across the three lakes has a corresponding impact on somatic and reproductive parameters. In accordance with other studies (Christianus, 1995; Marjomäki and Kirjasniemi, 1995), we predicted a strong negative correlation between stock density and growth and condition of female vendace. This inter-population difference in somatic traits was expected to be transmitted to quality and quantity of ovaries, propagules and offspring. Accordingly we expected that relative fecundity, egg size, hatching rate and larval size-at-hatch is higher in low-density than in high-density stocks.

2. Methods

2.1. Study sites

Lakes Breiter Luzin, Stechlin and Werbellin are located in northeast Germany in the ecoregion 'Central Plains' (Illies, 1978). This region forms the southern boundary of the European distribution area of vendace and hence vendace occur in this area only in deep, stratified lakes with a cold hypolimnion. All three lakes are characterized by an extended pelagic habitat, but differ in their productivity (Table 1). Commercial fisheries, as indicated by the annual fisheries yield in relation to standing stock biomass, are strongest in Lake Werbellin, low in Lake Stechlin, and absent in Lake Breiter Luzin (Table 2). Lake Stechlin is inhabited by a total of 13 fish species. The hypolimnetic fish community is dominated by vendace, but the numerically less abundant endemic Fontane cisco (*Coregonus fontanae* Schulz & Freyhof) co-occur with vendace (Mehner and Schulz, 2002; Helland et al., 2009). Lake Breiter Luzin is also inhabited by a species pair of coregonids, with vendace dominating the hypopelagic area, and the endemic cisco *Coregonus lucinensis* Thienemann being less abundant (Waterstraat, 1990). Lake Werbellin is inhabited by 13 fish species (Eckmann, 1995). Vendace and smelt are the dominating species found in the hypopelagic zone (Jůza et al., 2012).

2.2. Hydroacoustics

To estimate vendace areal density and biomass, hydroacoustic night-time surveys (beginning at least 1.5 h after sunset) using a SIMRAD EY-60 split beam echo sounder were conducted in all lakes during autumn 2012 and 2013. Surveys were designed as a set of systematic parallel transects with the total transect length adjusted to meet an acoustic degree of coverage of six (Breiter Luzin 11.3 km, 15 transects; Stechlin 13.9 km, 19 transects; Werbellin 18.5 km, 22 transects). Operating frequency was set to 120 kHz ($7^\circ \times 7^\circ$ circular transducer, pulse length 0.256 ms, 3.34 pings s^{-1}). Before each field season, the echo sounder was calibrated with a standard copper sphere. Raw data were stored on a computer and analysed after conversion (−100 dB base Sv threshold) using the post-processing software Sonar5-Pro version 6.0.2 (Balk and Lindem, 2011). Areal density was calculated based on the single echo detection algorithm (max. angel std. dev. = 0.80, max. gain comp. = 3 dB (one way), echo length (relative to pulse length) = 0.6–1.6). Mean target strength (TS) of single echoes was converted into total length (TL) of fish following the vendace-specific formula TS (dB) = 25.5× $\log_{10}$ TL (cm) – 70.9 (Mehner, 2006). For biomass estimation, TL of single echoes was converted into fish weight by applying the vendace-specific formula weight (g) = 0.0012× TL $(cm)^{3.58}$ which was derived as average from multi-mesh gillnet catches in the study lakes. For the analysis, −55 dB was used as the lower threshold for target strength and volume backscattering, excluding echoes from fish with a total length of less than about 4 cm.

Catches by pelagic multi mesh gillnet surveys (see below) confirmed that vendace occurred only in the hypo- and metapelagic layers. Therefore, analysis was restricted to the layers between a depth of 12 m (thermocline) and the lake bottom. For improved comparability between the lakes, which differ in bank slope and share of shallow area, only those parts of acoustic transects with more than 20 m depth were analysed. Each transect was split into elementary sampling units (ESU) with a length of 50 m each in Lakes Breiter Luzin and Stechlin and with a length of 200 m in the bigger but sparsely populated Lake Werbellin. In Lake Werbellin,