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Year-class strength, physical fitness and recruitment cycles in vendace (Coregonus albula)

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ABSTRACT

Vendace, an obligate zoo-planktivore through all life stages, is a key-stone species in many large lakes in northern Eurasia. Vendace often produces strong year-classes in cycles of various length. To better understand the factors that determine the emergence of strong year-classes we analyzed long timeseries hydroacoustic data on abundance of young-of-the-year and older vendace, and representative samples of vendace from trawl catches measured for length, weight and age. Data were collected in the three largest lakes in Sweden - Lakes Vänern, Vättern and Mälaren - for 1995-2012, 1992-2012 and 2008-2012, respectively. The lakes range from ultra-oligotrophic to mesotrophic. In L. Vänern there is an extensive commercial fishery on vendace, whereas the fishery, at present, is small in L. Mälaren and negligible in L. Vättern. Size of mature vendace, expressed as 90% of L_{max} , differed between the lakes and was positively correlated with lake nutrient levels. Strong year-classes did not occur in synchrony between lakes, not even between the two main basins within oligotrophic L. Vänern, and were less frequent in the ultra-oligotrophic and commercially unfished L. Vättern. Strong year-classes negatively affected physical fitness (Fulton's condition factor) of older fish. During years of low physical fitness in sexually mature fish no strong year-classes would appear. Recovery of physical fitness might take several years and depended on food availability, expressed as nutrient levels or population density. Not until fish had regained individual physical fitness and could allocate energy to gonads, other factors - as physical environmental conditions - might become important for the emergence of a strong year-class.

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1. Introduction

Vendace (Coregonus albula) inhabits lakes in northern Eurasia and is also found in weak brackish water in the Baltic Sea, e.g. in the Gulfs of Finland and Bothnia (Järvi, 1950; Enderlein, 1981a). Unlike most other fish, vendace is an obligate zoo-planktivore through all life stages, which means that all age-groups of vendace compete for the same food resource (Enderlein, 1981b; Viljanen, 1986; Northcote and Hammar, 2006). Vendace is a key-stone species in many large lakes. It has been commercially fished - principally for the roe from the late 1960s - in the three largest lakes in Sweden, but nowadays mainly in Lake Vänern (310 tonnes of vendace landed in 2012). Vendace is also an important prey fish











for, e.g. pikeperch (L. Vänern and Mälaren), salmon (L. Vänern and Vättern) and Arctic char (L. Vättern; e.g. Nilsson, 1979), all important species in the inland commercial and recreational fisheries.

Vendace recruitment has been described as occurring in cycles with strong year-classes followed by often several years of weak recruitment. This pattern has been described as caused by intraspecific, density-dependent competition (Aas, 1972; Hamrin and Persson, 1986; Marjomäki and Huolila, 2001), physical factors (Nyberg et al., 2001; Marjomäki et al., 2004; Sandström et al., 2014) or both (Helminen and Sarvala, 1994). Marjomäki et al. (2004) reported a spatial synchrony between Finnish lakes in inter-annual population variation. It has also been suggested that the pattern might be less obvious or changed as a result of predation pressure, inter-specific competition and fishing mortality (Karjalainen et al., 2000; Auvinen et al., 2004). Salojärvi (1987) proposed that vendace populations are regulated by fecundity, starvation of larvae and predation, while Haakana and Huuskonen (2009) found

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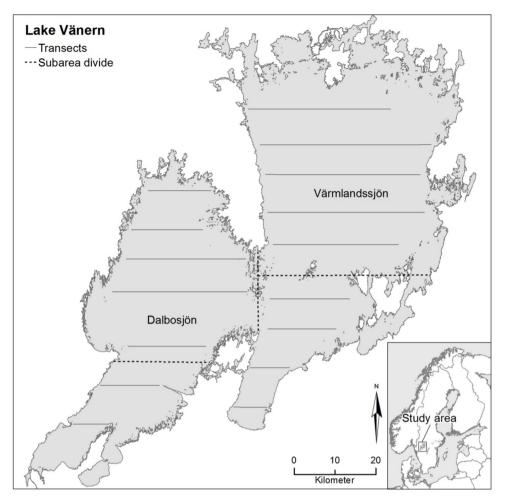


Fig. 1. Lake Vänern (Sweden). Hydroacoustic transects in the two basins Dalbosjön and Värmlandssjön. Subareas are separated by a dotted line. Representative and depth stratified trawling was performed in all subareas.

that larval starvation and mortality was not much affected by food availability.

This study used individual physical fitness (Fulton's condition factor) and year-class strength in vendace together with abundance estimations from hydroacoustic surveys from three nutrient contrasting lakes to explore how these data fitted the pre-existing theories on recruitment cycles in vendace. In two of the lakes practically no fishing for vendace is carried out. Our hypothesis was that the recruitment cycles were primarily determined by intra-specific competition affecting the physical fitness of potential spawners, and secondarily mediated by physical environmental factors.

2. Material and methods

2.1. Lake Vänern

Lake Vänern is the largest lake in Sweden and in the European Union, and the third largest lake in Europe (Fig. 1, Table 1). The level

 Table 1

 General information on lakes Vänern, Vättern and Mälaren, the largest lakes in Sweden.

Lake	Latitude	Longitude	Area	Depth	Altitude
	(outlet)	(outlet)	(km ²)	(average, m)	(m, a.s.l.)
Vänern	N 58.80	E 13.40	5648	27	44
Vättern	N 58.30	E 14.50	1893	40	88
Mälaren	N 59.50	E 16.90	1096	13	1

of total phosphorus in the offshore regions has stabilized since the mid-90s around historical reference levels $(4.5-5.5 \ \mu g l^{-1})$ indicating oligotrophic conditions. Total nitrogen level is still heightened because of emissions from farming, mainly originating from rivers in the southern parts (Sonesten, 2013). L. Vänern is species-rich with 36 different species of fish (Degerman et al., 2001). The most important species in the commercial fishery are vendace and pikeperch (*Sander lucioperca*) although another 5–6 species are also targeted in the fishery. Salmon (*Salmo salar*) and trout (*Salmo trutta*) are the most important species in the recreational fishery. The most common pelagic species in numbers is smelt (*Osmerus eperlanus*). Results from L. Vänern are given for the two main basins (Dalbosjön and Värmlandssjön; Fig. 1) separately.

2.2. Lake Vättern

Lake Vättern, 1893 km², is the second largest lake in Sweden (Fig. 2, Table 1). Recovering from eutrophication in the 1960s and 1970s, the total phosphorus level is now close to historical reference levels $(3-5 \mu g l^{-1}; Renberg et al., 2003)$ and the lake is at present regarded as ultra-oligotrophic. L. Vättern holds over thirty different species of fish (Degerman et al., 2001). The most important species for the commercial and recreational fishery are white-fish (*Coregonus maraena*), Arctic char (*Salvelinus alpinus*) and two introduced species – salmon and signal crayfish (*Pasifastacus lenius-culus*). The fishery on vendace has been negligible since the 1980s because of low abundance. The most dominant pelagic species

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