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Fast somatic growth may cause recruitment overfishing in vendace (*Coregonus albula*) gillnet fisheries

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Vendace is commonly assumed at low risk to recruitment overfishing. This assumption has been confirmed for boreal stocks but might not apply at lower latitudes. We evaluated the risk of recruitment overfishing at the southernmost extent of vendace populations by comparing fecundity, natural mortality, and fishing mortality of two stocks differing in growth with those of a population not subject to fishing. Although in one study lake vendace grew faster owing to high lake productivity and low stock density, and had substantially higher age-specific fecundity, intense harvest before first spawning negatively affected the stock's recruitment potential by reducing spawner abundance. In contrast, in the slow-growing stock, vendace entered the fishery after first spawning, and egg production per recruit was similar to that of the population not subject to fishing. We conclude that vendace stocks characterized by fast somatic growth may be at higher risk of recruitment overfishing, which can be reduced by protecting first-time spawners.

Introduction

Recruitment overfishing is the most prominent form of overfishing which occurs when the spawning stock and its resulting recruitment into the exploited age groups are seriously reduced by fishing (Cushing 1975, Hilborn & Walters 1992). Persistent recruitment overfishing of fish stocks around the globe frequently led to stock decline or collapse, and poor environmental conditions can further exacerbate this decline (Hilborn & Walters 1992, Allan *et al*. 2005). Today, recruitment overfishing ranks among the highest threats to fish populations worldwide (FAO 2016).

In general it is assumed that, up to stock-specific thresholds, fishery exploitation is outweighed by density-dependent compensatory processes, which result in increased individual reproductive output despite enhanced fishing mortality (Schaefer 1954, Beverton & Holt 1957, Ricker 1975). Among multiple density-dependent compensatory processes (reviewed by Rose *et al.* 2001), somatic growth is of central importance for the reproductive compensation of fishery losses: in most teleost fishes, size is positively linked to fecundity (Wootton 1990, Jobling 1995, Kamler 2005). Somatic growth is further affected by the (density-independent) productivity of the envi-

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ronment which largely determines the carrying capacity of a lake (Rieman & Myers 1992, Downing & Plante 1993). Increase in somatic growth does, however, reduce the age at which individuals reach a marketable size and become vulnerable to size-selective fishing gear such as gillnets, thereby possibly removing fecund individuals and reducing the stock's recruitment potential if fish are not given enough time to reproduce before harvest. The ease by which somatic growth can be measured makes it a particularly effective indicator of a population's fishery potential or its stage of exploitation, thereby providing important information for stock managers to avoid recruitment overfishing (Healey 1975).

Vendace (*Coregonus albula*) is a short-lived freshwater coregonid species that is commonly assumed to be at a low risk of recruitment overfishing due to its high compensatory growth and fecundity plasticity (Karjalainen *et al.* 2016, Marjomäki *et al.* 2016). Considering the large number of studies that analysed potential causes for the frequently observed fluctuations and declines of vendace stocks (i.e., Hamrin & Persson 1986, Auvinen 1988, Helminen *et al.* 1993 and reference therein), relatively few studies analysed the effects of fishing on the recruitment of vendace (Salojärvi 1987, Helminen *et al.* 1992, Marjomäki & Huolila 2001, Huusko & Hyvärinen 2005). To date, a substantial fishery contribution could be demonstrated for the decline of only one vendace stock: that of Pyhäjärvi in SW Finland (Sarvala & Helminen 2002, Sarvala *et al.* 2020). In contrast, recruitment overfishing through shifts of exploitation towards younger age groups was frequently observed as consequence of eutrophication or stock depletion of several whitefish (*Coregonus*) species in the past (*C. lavaretus*, *C. wartmanni*, *C. macrophthalmus*, *C. areniculus* and *C. clupeaformis*; Mills *et al.* 1995, Eckmann *et al.* 2007). Consequently, proper adaptation of gillnet mesh size to avoid harvesting of fish before first spawning became a key component in the management of many whitefish stocks (Eckmann *et al.* 2007 and reference therein). Today, in Germany most whitefish fisheries have strict mesh size regulations and the legal mesh size is frequently adjusted based on scientific analyses of growth and maturation (Schubert 2015, Kugler *et al.* 2016). In contrast, the size selectivity of vendance fisheries has received little attention, and mesh size in German gillnet fisheries for vendace is currently not regulated on the basis of stock assessment.

This regulatory discrepancy is especially surprising when considering the different plasticity in age at maturation between whitefishes and vendace. In the larger-sized and longer-lived whitefishes, age at maturation is plastic and mainly determined by size (Beauchamp *et al.* 2004, Ficker *et al.* 2014), indicating that in fast-growing stocks, fish mature earlier and hence always can contribute to population recruitment before being harvested. In contrast, vendace show no plasticity in maturation and reach maturity independently of size at age 1+ (2nd summer) (Huusko & Hyvärinen 2005, Czerniejewski & Wawrzyniak 2008, Karjalainen *et al.* 2016). Accordingly, differences in the age pattern of exploitation caused by variable somatic growth may have greater effect on the recruitment potential of vendace as compared to whitefish.

Especially for the southern part of the distribution area of vendace (Germany, Poland; https://www.cabi.org/isc/search/index?q=Coregonus%20albula), comprehensive analyses of potential effects of variable somatic growth on recruitment overfishing are not available. At lower latitudes, longer growing seasons and a higher average trophic status of lakes significantly increase the maximum growth potential of vendace (Viljanen 1988) and hence may magnify the inter-stock variability of somatic growth (Viljanen 1988). In contrast, the few studies that systematically analysed the effects of fishing on the recruitment potential of vendace stocks were all conducted in the northernmost part of the distribution area of vendace (primarily in Finland), where climatic and environmental conditions are more favourable for reproduction and survival of vendace, but limit the somatic growth (Bauch 1949, Järvi 1950, Żuromska 1982). Therefore, results from Finnish lakes cannot simply be applied to southern vendace stocks, such as those in Germany.

To fill this knowledge gap, we present a comprehensive data set from three German vendace lakes, thereby allowing us to systematically analyse the effects of current fishing practices on recruitment potential. Over the course of three years, we estimated age-specific fecundity, rates of stock exploitation, age-specific fishing, and natural mortality rates, as well as their overall effect on spawner abundance and cumulative egg production. In this study, we observed two stocks with low and high rates of somatic growth, respectively, and compared our results with those from a population not subject to fishing. We hypothesized that the previously-known differences in somatic growth of vendace among the lakes (Wanke *et al.* 2017) induced differences in age-specific fecundity. Furthermore, we assumed that growth-related differences in the exploited age classes would affect each stock's recruitment potential through highly variable life-time cumulative egg production of females in these lakes. Therefore, the study aimed to evaluate whether the risk of recruitment overfishing of vendace stocks in its southern population extent may be much higher than commonly assumed, and furthermore may increase with somatic growth. If this is the case, then somatic growth would be a potential indicator to easily assess the risk of recruitment overfishing of vendace.

Methods

Study sites

Lakes Breiter Luzin, Stechlin and Werbellin are located in northeastern Germany, and lie within the 'Central Plains' ecoregion (Illies 1978). This region forms the southern boundary of the European distribution area of vendace and hence vendace here occur only in deep, stratified lakes with a cold hypolimnion (more information on seasonal temperature and oxygen distributions of study lakes in Wanke 2018). All three lakes are characterized by an extended pelagic habitat, but differ in their productivity (total phosphorus and chlorophyll-*a* concentrations; Table 1). The hypopelagic fish community in Lake Breiter Luzin is dominated by vendace co-occurring with less abundant endemic cisco (*Coregonus lucinensis*) (Waterstraat 1990). Lake Stechlin is also inhabited by a species pair of coregonids, with vendace dominating the hypopelagic area, and the endemic Fontane cisco (*Coregonus fontanae*) being less abundant (Mehner & Schulz 2002, Helland *et al.* 2009). In Lake Werbellin, vendace and smelt (*Osmerus eperlanus*) are the dominant species in the hypopelagic zone, howwever density of smelt was often observed to increase in response to decline of the vendace population indicating interspecific competition but no significant predatory effect of smelt on the vendace population (Jůza *et al.* 2012).

In the study area, vendace fishing is usually conducted with monofilament pelagic gillnets that are set below the thermocline and left overnight. This contrasts with practices in commercial vendace fisheries at higher latitudes (i.e., those in Finland and Sweden), which commonly employ trawls and seines (Borges *et al.* 2015, Marjomäki *et al.* 2016). In Germany and Poland, the mesh size of commercial vendace gillnets ranges from 18 to 28 mm (knot to knot) with 24 mm being the standard mesh size in most vendace fisheries (Dauster 1995, Czerniejewski

Table 1. Morphological and limnological parameters of the study lakes. Areas within lakes with a minimum depth of 20 m were considered to be vendace habitat (proportion (%) of total lake area in parentheses). Epilimnetic chlorophyll *a* (Chl *a*), epilimnetic total phosphorus (P_{tot}), and secchi depth are mean values for May–October. The trophic state was assessed according to LAWA (1998) guidelines; data (collected in 2008–2013) were provided by the Ministry of Agriculture, Environment and Consumer Protection of the Federal State of Mecklenburg-Vorpommern (Breiter Luzin), the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin (Stechlin) and the Ministry of Rural Development, Environment and Agriculture of the Federal State of Brandenburg (Werbellin).

Lake	Depth (m)		Total area (ha)	Vendace habitat area (ha)	Trophic state	Chl *a* (μg l^{-1})	P_{tot} (μg l^{-1})	Secchi depth (m)
	max	mean						
Breiter Luzin	58	22	345	157 (46%)	mesotrophic	3.1	15.0	2.9
Stechlin	70	24	452	225 (50%)	oligotrophic	2.7	12.0	6.3
Werbellin	55	22	782	370 (47%)	mesotrophic	4.4	30.0	3.8

& Wawrzyniak 2006). In lakes Stechlin and Werbellin, vendace were exclusively harvested with gillnets during the six-month fishing season from May to October. In Lake Breiter Luzin, vendace fishing ceased in 2009, allowing it to be a control (population not subject to fishing) in our study.

Sampling of vendace and fish vertical distribution

To sample vendace for laboratory analyses of growth, maturation and fecundity, and to provide information on the vertical distribution of pelagic fish species during hydroacoustic surveys, in 2011–2014 we conducted stratified multi-mesh gillnet surveys in all three study lakes at the end of the fishing season shortly before the hydroacoustic surveys. Pelagic multi-mesh gillnets were modified from the NORDIC type (Appelberg 2000). Specifically, each net was 30 m long and 6 m deep and was composed of 12 mesh panels (each 2.5 m long) of different mesh sizes (6.25/8/10/12.5/15.5/19.5/24/29/35/43/55/70 mm knot to knot). Every year, sampling in each lake was conducted simultaneously at two locations close to the maximum depth. At each location, we sampled the pelagic zone by setting the nets in a cascade design, in which we tied the multiple nets together to increase their vertical extent and cover the entire depth range from the surface to the bottom of the lake. Nets were set before dusk and hauled after dawn. After removing individuals from the nets, we counted them and sorted by species, as well as measured their body mass to the nearest 1 g and total length (TL) to the nearest 1 mm. We froze a sub-sample of at least 100 vendace at –20 °C for later processing in the laboratory.

Laboratory analyses

In the laboratory, we thawed the vendace, weighed them to the nearest 0.1 g, and extracted scales for age analysis from the region above the lateral line between the dorsal and adipose fins. Subsequently, we identified gender and sexual maturity by visual inspection of the gonads. If the fish had ovaries, we dissected these and weighed them to the nearest 0.1 g. We then extracted a subsample of the ovarian tissue (comprising pieces from the anterior, posterior and middle sections of the ovary), and then weighed it to the nearest 0.1 g and stored in Gilson fluid (Lagler 1978). Gilson fluid has a hardening effect on eggs and facilitates their separation by breaking down the surrounding ovary tissue. After around two weeks of incubation (with occasional shaking), we counted the eggs under a dissecting microscope and calculated the total fecundity of each fish by multiplying the number of eggs in the subsample by the ratio between the total weight of both ovaries and the weight of the subsample.

Hydroacoustics

To obtain size-resolved estimates of vendace areal density and biomass, which formed the basis for calculations of age-specific mortality and fishery exploitation explained below, at the end of each fishing season in 2011–2014 we conducted hydroacoustic nighttime surveys (beginning at least 1.5 h after sunset) using a SIMRAD EK60 split beam echo sounder. We carried out the surveys along a set of parallel transects with the total transect length adjusted to meet an acoustic degree of coverage $\Lambda = 6$ (Breiter Luzin 11.3 km, 15 transects; Stechlin 13.9 km, 19 transects and Werbellin 18.5 km, 22 transects). The circular transducer (depth 0.6 m, 7° × 7°, 3.3 ping s^{-1}) operated at 120 kHz with a pulse length of 0.256 ms in 2011–2013 and 0.128 ms in 2014. During the study period, we regularly calibrated the echo sounder using a standard copper sphere. The raw data were collected using the acquisition software SIMRAD ER60, stored on a computer, and analysed after conversion (–100 dB base Sv threshold) using the post-processing software Sonar5-Pro ver. 6.0.2 (Balk & Lindem 2011). We calculated areal density of fish individuals based on the default single-echo detection algorithm (max. angle SD = 0.20, max. gain comp. = 3 dB (one way), echo length (relative to pulse length) = 0.7–1.3). We converted the mean target strength (TS) of single echoes into TL of fish using a newly developed, vendace-specific formula — $\mathrm{TS}\ (\mathrm{dB}) = 29.7 \times \log_{10}\mathrm{TL}\ (\mathrm{cm}) - 74.7$ — based on a comparison of catches by multi-mesh gillnets and hydroacoustic surveys (for details of the formula development, *see* Appendix). For biomass estimation, we converted TL of single echoes into fish weight by using the following vendace-specific formula: weight (g) = 0.0012 × $TL^{3.58}$ (cm), which we derived as average from multi-mesh gillnet catches in the study lakes. In accordance with the earlier study by Mehner and Schulz (2002), we used –55 dB as the lower threshold for target strength and volume backscattering, which returns echoes from fish with TL of approximately 5 cm or greater.

Our catches by pelagic multi-mesh gillnet surveys (*see* above) confirmed that vendace occurred only in the hypo- and metapelagic layers of all three lakes. Accordingly, we restricted the analysis to the layers between a depth of 12 m (the thermocline) and the lake bottom. Further, visual inspection of echograms revealed that hypopelagic echoes increased sharply when the lake bottom was below 20 m depth. The study lakes' bank slope and fraction of shallow area differ, so in order to build an intercomparable data set, we analysed only those parts of acoustic transects for which the lake depth exceeded 20 m. In order to obtain relatively homogenous fish densities and a sufficient number of echoes in analysis cells, we split each transect into 50-m long by 6-m high "elementary distance sampling units" (EDSUs). For each EDSU, we calculated density (fish ha^{-1}) and biomass (kg ha^{-1}). We then converted this into sums across the water column by summing over the respective layers (12 m to bottom). For each lake and year, we then calculated population biomass density as the arithmetic mean of these values.

In lakes Breiter Luzin and Stechlin, density and biomass estimates refer to the sum of both vendace and the lake-specific endemic coregonid species (*see* above), as the echoes of these distinct species cannot be separated by hydroacoustics. Due to their smaller maximum size (Kottelat & Freyhof 2007), endemic ciscoes mainly overlapped with 0+ and 1+ vendace. Nonetheless, we assumed any bias (i.e., overestimation of density) to be low due to the low relative abundance of cisco as shown for Lake Stechlin (Mehner 2015). In Lake Werbellin, TS of the youngest vendace (age 0+) overlapped with TS of co-occurring smelt (TL 9–16 cm). Accordingly, hydroacoustic estimates of area density and biomass in the TS range between –55 dB (4.6 cm TL) and –37 dB (18.5 cm TL) could not be distributed among the two species without the simultaneous estimation of their relative abundance by appropriate fishing methods. Unfortunately, trawl fishing (Emmrich *et al.* 2010) did not sufficiently catch fish in Lake Werbellin due to the low overall fish density in this lake. Furthermore, species proportions in multi-mesh gillnet catches were biased due to the fact that smelt may entangle in these nets not only with their opercula, but also with their jaws and teeth (Kurkilahti *et al.* 1998). Accordingly, areal density and biomass of 0+ vendace could not be estimated reliably for Lake Werbellin, and thus they were back-calculated from the density estimates of 1+ vendace in the subsequent year following the assumption of equal total mortality during the second and third years of life.

Fishery assessment

To estimate overall fishing intensity and fishing mortality, the two single-enterprise fisheries recorded fishing effort (mesh size, gillnet dimensions and number of nets applied) and vendace catch (nearest 1.0 kg) for every fishing day. To later analyse the distribution of fishing mortality among the different age groups, in the 2011–2014 fishing seasons we occasionally took and immediately froze random subsamples (approx. 10 fish each) from commercial gillnet catches. We sampled a total of 91 vendace in Lake Stechlin and 254 vendace in Lake Werbellin. In the laboratory, we thawed the vendace, measured TL and weight, and then determined fish age by analysing their scales.

Calculations

To illustrate lake-specific fish growth, we fitted von Bertalanffy growth curves (Beverton & Holt 1957) to pooled size-at-age data of vendace sampled with multi-mesh gillnets and commercial gillnets from 2011–2014 (Breiter Luzin $n = 498$, Stechlin $n = 461$, Werbellin $n = 713$). Lower and upper 95% confidence limits for the mean total length-at-age from the von Bertalanffy growth models were constructed by bootstrapping. We conducted model fitting and calculation of confidence limits according to Ogle (https://derekogle.com/fishR/examples/oldFishRVignettes/VonBertalanffy.pdf) using the R packages *FSA* (http://CRAN.R-Project.Org/Packages=FSA) and *nlstools* (Baty *et al.* 2015).

To compare fishing effort among the lakes, we calculated fishing intensity (m^2 net ha^{-1} yr^{-1}) as cumulative sum of area of gillnets exposed in different nights during the fishing period, divided by the area of vendace habitat. According to our hydroacoustic observations of vendace distribution and the fact that deployment of commercial vendace gillnets requires sufficient depth (depth of upper line at 10–15 m), we considered vendace habitat only those parts of the lake whose depth was more than 20 m.

Although all the following calculations used instantaneous mortality rates (F, Z), we alternatively expressed total annual mortality as a finite rate in percent, because we find percentages more intuitive to understand than instantaneous rates.

We calculated total mortalities for the different age groups of vendace from the age-group specific density estimates derived from hydroacoustics. To this end, we distributed the mean total fish density from each depth layer into density estimates for 0.5-cm TL intervals according to the interval's proportion of the number of single echo detections in the respective depth layer. For each lake, we calculated the total density per TL interval as sum over all depth layers. The resulting length-resolved areal density estimates were transferred into approximately age-resolved areal density estimates by applying lake-specific age–length keys (based on our TL-at-age data explained above) following Ogle (https://derekogle.com/fishR/examples/oldFishRVignettes/AgeLengthKey.pdf). Finally, we calculated annual total mortality A (%) for the different years of life of vendace as follwos:

$$\text{for } i \rightarrow i+1: A_{i,j} = \frac{\left(n_{i,j} - n_{i+1,j+1}\right)}{n_{i,j}} \times 100, \qquad (1)$$

where n is the areal density (ha^{-1}), i is the age of the fish (year) and j is the year of hydroacoustic survey.

Because the majority of each one-year period between two autumn sampling campaigns, including the mortality-inducing fishing season, was spent at age $i + 1$, we simplified our notation of mortality suffered from autumn at age i to autumn at age $i + 1$ as mortality $i + 1$. As an example, the mortality rate of 2+ vendace refers to the abundance decline of the 1+ vendace estimated in the previous autumn to 2+ vendace estimated in the current autumn.

To analyse the contribution of fishing to mortality, we used the rate of exploitation (F/Z), which is commonly defined as the instantaneous rate of fishing mortality (F, yr^{-1}) divided by the instantaneous rate of total mortality (Z, yr^{-1}). According to the catch equation (Baranov 1918), the rate of exploitation is further defined by the ratio between deaths induced by fishing (Catch, ha^{-1}) and total deaths. Accordingly, we calculated the rate of exploitation for the different age groups of vendace from commercial catch data, to which we assigned age groups based on our fishery subsamples, and age-specific hydroacoustic density estimates as follows:

$$\text{for } i \rightarrow i+1: \frac{F_{i,j}}{Z_{i,j}} = \frac{\text{Catch}_{i \rightarrow i+1, j \rightarrow j+1}}{\left(n_{i,j} - n_{i+1,j+1}\right)}, \qquad (2)$$

where Catch is the commercial catch (ha^{-1}) drawn from the respective cohort during the one-year period between hydroacoustic surveys, n is the area density (indiv. ha^{-1}), i is the age (year) and j is the year of hydroacoustic survey.

In addition, we calculated the average rate of exploitation of the combined age groups 0+ to 4+.

To analyse the effect of size-selective fishery management on the reproductive potential of the stocks, we calculated age-specific and cumulative (sum over ages 1+ to 4+) potential egg production of female vendace. For each age group, we multiplied age-specific absolute fecundity by annual survival rate (100% – annual mortality rate). Additionally, we calculated fishery-induced reduction of survival according to the rate of exploitation (F/Z) per age group in lakes Stechlin and Werbellin, thus obtaining the potential life-time egg production per female 0+ recruit corrected by natural and fishing mortality for each lake. To take into account the differing stock densities in the lakes, age-specific individual fecundity was multiplied by the average

age-specific abundance of females and the average age specific yield of female vendace, obtaining the number of eggs per hectare available for reproduction, corrected by losses through natural and fishing mortality. We calculated female abundance and fishery losses of female vendace by multiplying total values with 0.5 because Wanke *et al*. (2017) found fairly balanced sex ratios in all three stocks.

Finally, for every lake and year we calculated an estimate of early survival (‰) by dividing the density of 0+ vendace (indiv. ha^{-1}) by the estimate of the stock's egg production (eggs ha^{-1}) in the previous year.

Results

Stock characteristics

Vendace stock density and biomass differed substantially among the lakes during the study period 2011–2014. Whereas in the vendace habitat of lakes Breiter Luzin and Stechlin, hydroacoustic surveys in autumn revealed coregonid stock densities between 7096 and 14 746 fish ha^{-1} and stock biomasses between 114 and 243 kg ha^{-1} each year, vendace stock density and biomass in Lake Werbellin steadily decreased from 488 fish ha^{-1} (26.9 kg ha^{-1}) in autumn 2011 to 37 fish ha^{-1} (1.7 kg ha^{-1}) in autumn 2014 (Tables 2 and 3). Lake-specific growth patterns of vendace reflected the differences in stock densities. In Lake Werbellin, vendace grew faster and reached substantially greater size-at-age than their conspecifics in lakes Breiter Luzin and Stechlin (body mass Table 2, TL Fig. 1). In all three lakes, vendace invariably reached maturity at age 1+ and spawned for the first time at the end of their second year of life. However, average TL at first maturity (solid horizontal lines in Fig. 1) in Lake Werbellin (22.9 cm) was 50% greater than in lakes Breiter Luzin (14.8 cm) and Stechlin (15.6 cm). Accordingly, in Lake Werbellin vendace body mass at first maturity was five- to six-fold and absolute fecundity at first maturity six- to eight-fold as compared with those of vendace in lakes Breiter Luzin and Stechlin. The lake-specific differences in size and size-dependent reproductive parameters persisted as vendace grew older (Table 2).

Fisheries

Intensity of commercial gillnet fishing differed consistently between the lakes. In adaptation to the different stock densities, dimensions of commercial gillnets differed between the two lakes. In Lake Stechlin each gillnet measured 250 m^2

Table 2. Biological characteristics of vendace stocks in the study lakes in 2011–2014. Each autumn, coregonid density was estimated by hydroacoustics. Body mass (g) and absolute fecundity (eggs fish^{-1}) were measured for vendace of age 0+ (one summer old), 1+ (two summers old), 2+ (three summers old), 3+ (four summers old) and 4+ (five summers old).

	Breiter Luzin		Stechlin		Werbellin	
	n	mean ± SD	*n*	mean ± SD	*n*	mean ± SD
Coregonid density (fish ha^{-1})	4	8740 ± 1188	4	10832 ± 3175	4	193 ± 178
Body mass, wet (g)						
0+	36	7.6 ± 1.6	61	9.4 ± 3.2	23	20.7 ± 5.0
1+	76	16.1 ± 3.8	89	21.1 ± 7.5	52	97.9 ± 20.1
2+	62	33.8 ± 11.4	34	39.1 ± 9.8	98	115.9 ± 23.1
3+	21	50.1 ± 11.2	12	50.2 ± 6.5	46	142.2 ± 22.6
4+	3	60.3 ± 14.8	2	55.0 ± 12.7	21	193.0 ± 20.8
Fecundity (eggs per female)						
1+	63	1572 ± 520	47	2142 ± 886	63	12287 ± 2932
2+	55	2541 ± 941	35	3402 ± 1378	45	15684 ± 3999
3+	12	4257 ± 1793	19	4597 ± 1214	29	18485 ± 4240
4+	2	4605 ± 1951	4	5516 ± 1190	20	22078 ± 4264

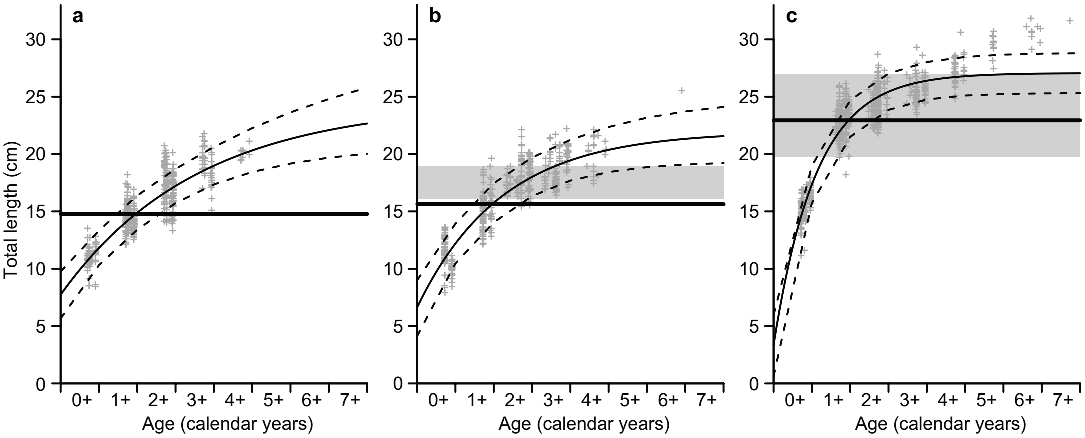

Fig. 1 Von Bertalanffy growth curves (solid black) with 95% confidence limits (dashed lines) fitted to size-at-age data (grey crosses) of vendace in lakes (**a**) Breiter Luzin, (**b**) Stechlin and (**c**) Werbellin. Mean total length at first maturity (solid horizontal line) and size selectivity of commercial gillnets (mean ± 2 SD; grey area) indicate the onset of sexual maturity and commercial fishery in each lake, respectively. No commercial fishing was conducted in Lake Breiter Luzin.

and a variable number of nets (2–9) was used on each fishing day (500–2250 m^2 total net area). In contrast, in Lake Werbellin, single nets were combined into a standard fishing set with a total area of 3600 m^2 used on each fishing day. During the study, the number of fishing days per year (111–141 days) in Lake Stechlin, was constant. In contrast, the fishery in Lake Werbellin aimed to preserve a sufficient number of spawners and therefore the number of fishing days was successively reduced (from 130 days in 2012 to 74 days in 2014) in response to the stock decline during the study period, but the average fishing intensity (area of gillnets per ha and year) across all years was still 1.6-fold compared with that in Lake Stechlin (Table 3).

In addition, size selectivity differed substantially between the lakes. To facilitate efficient harvesting of market-sized vendace, the mesh size of commercial gillnets was 18 mm (knot to knot) in Lake Stechlin, catching vendace 16.1–18.9 cm TL (grey area in Fig. 1b). In Lake Wer-

Table 3. Characteristics of vendace fisheries in the study lakes. Each year, fishing season lasted from May to October, and the initial vendace stock biomass was estimated hydroacoustically in the previous autumn. Intensity of fishing in the vendace habitat and annual vendace yield were calculated from catch-effort statistics. Mean ± SD values for the period 2012–2014 are set in boldface. No fishing was conducted in Lake Breiter Luzin.

Lake	Fishing season	Initial vendace stock (kg ha^{-1})	Fishing intensity (m^2 net ha^{-1} yr^{-1})	Yield (kg ha^{-1})
Breiter Luzin	2012	156.4	0	0
	2013	125.1	0	0
	2014	114.0	0	0
	2012–2014	**131.8 ± 18.0**	**0**	**0**
Stechlin	2012	225.8	495	16.6
	2013	242.8	639	15.7
	2014	181.0	697	12.8
	2012–2014	**216.5 ± 26.1**	**610 ± 85**	**15.0 ± 1.6**
Werbellin	2012	26.9	1265	25.2
	2013	8.3	915	9.9
	2014	2.9	720	3.1
	2012–2014	**12.7 ± 10.3**	**967 ± 225**	**12.7 ± 9.2**

bellin, the mesh size of gillnets was 24–26 mm (knot to knot), catching vendace with 19.8 to 27.0 cm TL (grey area in Fig. 1c). Despite the greater mesh size used in Lake Werbellin, age at first capture was substantially lower in Lake Werbellin than in Lake Stechlin. In Lake Werbellin, vendace entered the fishery about half a year before their first spawning at age 1+ (TL of fish at first capture lower than TL at first maturity; Fig. 1c), and were fished by gillnets until reaching ages 3+ to 4+. In Lake Stechlin, vendace first entered the fishery after the first spawning (age 2+), and fishing continued until age 3+ (Fig. 1b). The results obtained from the comparison between size selectivity of commercial gillnets and lake-specific growth patterns (Fig. 1) were confirmed by age analysis of random samples from commercial catches, which were strongly dominated by vendace of ages 1+ (66%), 2+ (30%) and 3+ (4%) in Lake Werbellin, whereas catches from Lake Stechlin comprised vendace of ages 2+ (34%), 3+ (59%), and 4+ (7%), but lacked vendace of age 1+ (0%).

Annual natural mortality rates and fishing mortality confirmed the differences between the lakes. In the unexploited Lake Breiter Luzin, the oldest vendace experienced the highest total annual mortality (A_{4+} = 88%: Table 4), whereas annual mortality was lowest for age group 2+. In Lake Stechlin, total annual mortality was lowest for the youngest age group analysed (A_{1+} = 45%) and increased with age up to 76% during the fifth year of life (A_{4+}; Table 4). In contrast, in Lake Werbellin, the younger age groups (1+ and 2+) experienced high total annual mortality (87%), and hence mortality did not further increase with age (mean across all age groups = 84%; Table 4). Considering the mature stock as a whole (mean ± SD of age groups 1+ to 4+), the fishery caused 8.3% ± 3.8% of total annual mortality ($F/Z = 0.08$) in Lake Stechlin, but 52.2% ± 7.5% of total annual mortality ($F/Z = 0.52$) in Lake Werbellin. The mean rate of exploitation per age group (F/Z) never exceeded 0.26 for any age group in Lake Stechlin, but was 0.51 for 1+ vendace and 0.74 for 2+ vendace in Lake Werbellin (Table 4).

Recruitment overfishing

The potential lifetime egg production per female recruit corrected by age-specific natural annual mortality rates in Lake Werbellin (9338 eggs female^{-1}) was three- to four-fold compared with the less-fecund recruits in lakes Breiter Luzin (2348 eggs female^{-1}) and Stechlin (3003 eggs female^{-1}) (Σ; Fig. 2a–c). However, fishing prior

Table 4. Total annual mortality (A, %) and exploitation rate (F/Z) for different vendace year classes in lakes Breiter Luzin, Stechlin and Werbellin. A and F/Z were calculated from age-specific areal density estimates from hydroacoustic surveys in autumn of 2011–2014 and age-specific commercial yields between subsequent hydroacoustic surveys. 1+ is the one-year period (autumn to subsequent autumn) of vendace life, which comprises their second summer (age 0+ at beginning and age 1+ at end of period); and 2+, 3+ and 4+ are defined accordingly. Additionally, average total annual mortality and exploitation rate (mean ± SD) were calculated for the whole study period.

Lake	Year	1+		2+		3+		4+	
		A (%)	F/Z	A (%)	F/Z	A (%)	F/Z	A (%)	F/Z
Breiter Luzin	2011/12	31	0	22	0	72	0	92	0
	2012/13	62	0	34	0	74	0	91	0
	2013/14	50	0	24	0	61	0	81	0
	2011/12–2013/14	**48 ± 13**	**0**	**27 ± 5**	**0**	**69 ± 6**	**0**	**88 ± 5**	**0**
Stechlin	2011/12	26	0	23	0.33	61	0.42	76	0.07
	2012/13	51	0	67	0.04	79	0.21	82	0.08
	2013/14	57	0	57	0.06	76	0.16	70	0.10
	2011/12–2013/14	**45 ± 13**	**0**	**49 ± 19**	**0.14 ± 0.13**	**72 ± 8**	**0.26 ± 0.11**	**76 ± 5**	**0.08 ± 0.01**
Werbellin	2011/12	88	0.66	88	0.80	88	0.26	90	0
	2012/13	90	0.49	90	0.78	83	0.33	74	0
	2013/14	84	0.39	84	0.63	72	0.40	79	0
	2011/12–2013/14	**87 ± 2**	**0.51 ± 0.11**	**87 ± 2**	**0.74 ± 0.08**	**81 ± 7**	**0.33 ± 0.06**	**81 ± 7**	**0**

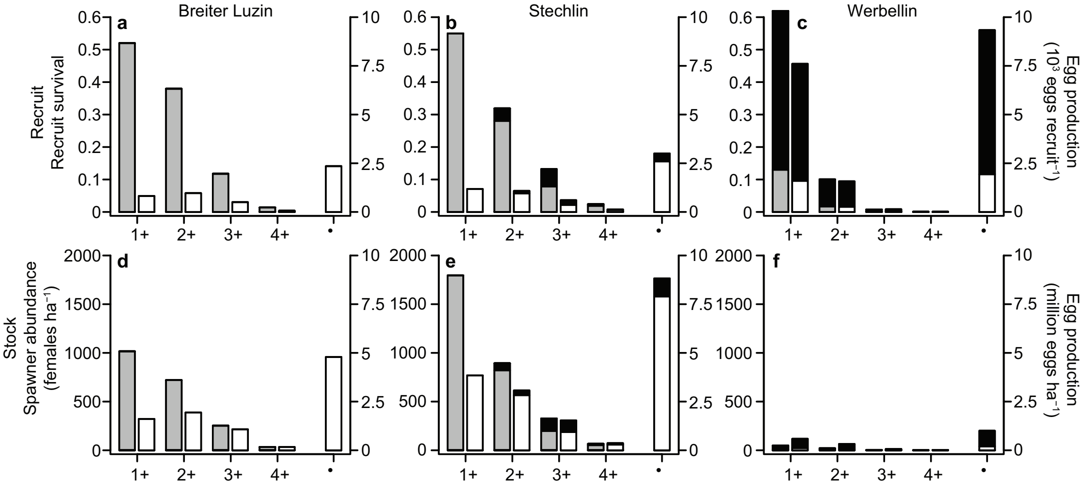

Fig. 2. (**a**–**c**) Average survival (grey) and corresponding egg production (white) per female recruit, and (**d**–**f**) average abundance of female spawners (grey) and corresponding egg production (white) for vendace of ages 1+ to 4+ in the study lakes in the years 2012–2014. Black bars display the proportion of females and corresponding eggs that were taken by the fisheries. Σ (rightmost bars) shows the cumulative egg production between ages 1+ and 4+. No fishing was conducted in Lake Breiter Luzin.

to the first spawning in Lake Werbellin depleted the potential life-time egg production per female recruit to 1935 eggs (–79.3% compared with expectations for natural morality). In contrast, in Lake Stechlin, only 13.5% of potential lifetime egg production per female recruit was depleted by fisheries, and thus the realized lifetime egg production per female recruit (2597 eggs) was similar to that in the unexploited Lake Breiter Luzin (2348 eggs). Extrapolated to the differing stock densities, areal egg production in Lake Stechlin was the highest (8.8×10^6 eggs ha^{-1}), followed by that in Lake Breiter Luzin (4.8×10^6 eggs ha^{-1}), while it was the lowest in Lake Werbellin (1.0×10^6 eggs ha^{-1}) (Σ; Fig. 2d–f). Losses of egg production due to fisheries accounted for a total of 0.9×10^6 eggs ha^{-1} in Lake Stechlin and 0.8×10^6 eggs ha^{-1} in Lake Werbellin, meaning that only 0.2×10^6 eggs ha^{-1} remained available for reproduction in Lake Werbellin in contrast to 7.9×10^6 eggs ha^{-1} in Lake Stechlin. This pronounced difference in recruitment potential was further magnified by the difference in survival from the egg to the juvenile stage (age 0+), which was 0.10‰ ± 0.01‰ (mean ± SD) in the more eutrophic Lake Werbellin and therewith amounted only 9%–14% of those in lakes Breiter Luzin (1.13‰ ± 0.11‰) and Stechlin (0.68‰ ± 0.36‰).

Discussion

By comparing vendace stocks in three lakes in Germany, we demonstrated that gillnet fishing practices which target the most abundant cohort of market-sized fish endanger vendace stocks characterized by fast somatic growth through recruitment overfishing. In all stocks and irrespective of massive differences in density and exploitation pressure, vendace matured at the same age. Fast-growing vendace had substantially higher age-specific fecundity which resulted in a higher individual reproductive potential to compensate for fishery losses as compared with the two stocks in which individuals grew slowly. However, despite the application of greater-meshed gillnets, vendace harvest of the fast-growing stock began at a younger age, prior to their first spawning. In case of the stock with slow somatic growth however, commercial harvest targeted fish only after their first spawning.

Massive harvesting of vendace before their first spawning significantly eroded the stock's reproductive potential and resulted in severe recruitment overfishing of the fast-growing stock. The low stock density and higher lake trophic status — the main drivers of fast somatic growth — further resulted in higher harvest rates and reduced survival from egg to the juvenile stage, which both significantly decreased recruitment of the fast-growing stock. To ensure sufficient recruitment into the spawning stock and to take the full advantage of the increased reproductive potential of fast-growing fish, it is important to apply strict technical measures that prevent fish from being caught before first spawning, an aspect that is often overlooked in the current practice of gillnet fishing for vendace in northern Germany.

Growth and size-dependent compensatory potential

Somatic growth of vendace differed substantially between the study lakes. Among various factors that were shown to regulate growth in teleost fishes (reviewed in Dutta 1994), food availability is considered the main driver of somatic growth (Kamler *et al.* 1982, Hilborn & Walters 1992). Accordingly, in zooplanktivorous fishes such as vendace (Viljanen 1983, Hamrin 1986, Helminen & Sarvala, 1994), zooplankton production largely determines somatic growth potential. A positive relationship between somatic growth and lake productivity was shown for several coregonids (Nümann 1972, Kirchhofer 1995, Müller & Mbwenembo 1998). However, per capita food availability is not only a function of food production, but also depends further on competition. In vendace, intraspecific competition is of major importance, because vendace rarely share their hypolimnetic habitat with other cold-water species with the exception of smelt (*Osmerus eperlanus*) (Diekmann *et al.* 2005, Mehner *et al.* 2005). A high plasticity in somatic growth in response to density is typical for vendace (Auvinen 1995, Marjomäki & Kirjasniemi 1995, Karjalainen *et al.* 2016). However, vendace stock density and lake productivity are not independent parameters, because increasing trophic state was shown to impair successful development of coregonid eggs through increasing sedimentation of organic matter and oxygen consumption on spawning grounds (Żuromska 1982, Müller 1992).

Accordingly, the observed differences in somatic growth most likely resulted from the interplay between stock density and the trophic status of a lake. In lakes Breiter Luzin and Stechlin, somatic growth of vendace was slow. While the oligotrophic Lake Stechlin has long been known for its exceptionally dense stock of slow-growing vendace (Mehner & Schulz 2002), growth of vendace in Lake Breiter Luzin successively decreased during the last decade due to reduced nutrient run-off from a connected lake (Kasprzak *et al.* 2003), which decreased the production of zooplankton prey. However, this same reduction of nutrients may have contributed to the development of a high stock biomass in Lake Breiter Luzin by improving the conditions for natural reproduction. In contrast, fast somatic growth of vendace in Lake Werbellin was probably fuelled by higher per-capita zooplankton availability as indicated indirectly by higher P_{tot} and Chl-*a* concentrations. In turn, the high trophic state of Lake Werbellin resulted in low oxygen concentrations in profundal areas (database of the Institute of Inland Fisheries Potsdam, Germany). Although this reduction in dissolved oxygen did not reduce the habitat of juvenile and adult vendace, it may have impaired survival of vendace eggs on spawning grounds (Müller 1992). This, in turn, may have contributed to the low stock density during the years of our study.

The pronounced difference in somatic growth of vendace among the study lakes is not unusual for this region and fits within the range of growth rates thus far reported from exploited vendace stocks in northern Germany (Dauster 1995, Steffens 1995) and Poland (Christianus 1995, Czerniejewski *et al.* 2007). Indeed, the regional variability in vendace somatic growth rates markedly exceeded the maximum range of somatic growth observed in boreal vendace stocks (Viljanen 1986, Karjalainen *et al.* 2016). The substantial differences in somatic growth rates among these three study lakes approach the regional maximum and minimum rates. This, combined with the fact that lakes Stechlin (slow growth, high stock density, low trophic status) and Werbellin (fast growth, low stock density, high trophic status) displayed opposing patterns of interrelated growth-determining parameters, makes the study lakes ideal candidates for a systematic analysis of the mechanisms that drive growth-rate dependent recruitment overfishing of vendace stocks.

The pronounced differences in somatic growth of vendace were reflected in strong differences in age-specific fecundity. Such notable correspondence between body size and absolute fecundity is typical for most teleost fishes and was often shown for vendace (Sarvala *et al.* 1992, Kamler 2005, Karjalainen *et al.* 2016). Increased age-specific fecundity at an invariable age of maturation substantially increased individual reproductive output. This increase was further intensified by greater relative fecundity (eggs per body mass) of the fast-growing individuals in Lake Werbellin when compared with the slow-growing vendace in lakes Breiter Luzin and Stechlin (Wanke *et al.* 2017). As a consequence of their higher individual reproductive output, stocks of fast-growing vendace should be able to withstand higher absolute harvest rates than vendace stocks characterized by slow somatic growth and lower individual fecundity, as was shown by Adams (1980) who compared fisheries effects on species differing in growth and growth-related life history traits.

Effects of fisheries

Our analyses revealed substantial differences in fishing intensity between the lakes, which was highest for the sparse stock of fast-growing vendace. Such increased fishing effort at low stock density is a typical but problematic response of commercial fisheries aiming to compensate for the reduction of catches at low fish density (Marjomäki *et al.* 1995, Marjomäki 2003). Higher fishing effort resulted in high fishery mortality and exploitation rate in the comparably small stock of fast-growing vendace. In contrast, in the stock characterized by slow somatic growth, the rate of exploitation was low and therefore total mortality was only marginally increased by fisheries in comparison with the stock not subject to fishing. Since vendace-specific reference points were not available, results were compared with findings for similarly short-lived marine species. For the latter, Patterson (1992) empirically estimated that ratios of fishing mortality to total mortality (exploitation rate, F/Z) above 0.4 were associated with stock declines, and that when $F/Z > 0.5$, very few stocks persisted sustainably. If $F/Z < 0.4$, however, most stocks recovered after overfishing. Following the more conservative approach of Froese *et al.* (2016), an exploitation rate of 0.3 may be a precautionary target for sustainable fisheries and should not be exceeded for any age class. In the lakes studied here, exploitation rates differed substantially and constituted the risk of overfishing of the fast-growing vendace stock: the average rate of stock exploitation was 0.52 and the maximum F/Z value for the most exploited age class was 0.74. In contrast, in the lake with slow-growing vendace, the average rate of stock exploitation was only 0.08 and the highest average age-specific rate of exploitation was 0.26 in age class 3+, suggesting that the vendace fishery in this lake was sustainable.

In addition, the age structure of vendace caught by commercial fisheries differed between lakes. In Lake Stechlin, relatively small-meshed gillnets were used to catch vendace, because individuals > 20 cm TL were almost absent. Nevertheless, immature vendace do not contribute to the commercial catch. However, due to the greater average size of vendace in Lake Werbellin, fishers apply greater mesh sizes of 24–26 mm (knot to knot); this is the standard mesh size used in German and Polish vendace fisheries (Dauster 1995, Czerniejewski & Wawrzyniak 2006). Despite this greater mesh size, numerous vendace were harvested before their first spawning, and thus the basic rule of precautionary fisheries management to prevent recruitment overfishing was violated (Myers & Mertz 1998). Indeed, this rule was recently confirmed to guarantee sufficient reproduction at high fishing intensity (Vasilakopoulos *et al.* 2011), and is often applied in the management of larger-sized and longer-lived coregonids (i.e., Ebener & Copes 1985, Eckmann *et al.* 2007). Only at low to moderate rates of stock exploitation has a dominance of juveniles in the catch been recommended; in these cases, the aim is to reduce fishing mortality among reproducing adults (Wolff *et al.* 2015). Accordingly, the effect of mesh size on the recruitment potential increases with fishing intensity, suggesting that in the lake with fast somatic growth, the growth-induced enhanced fishing mortality of vendace before first spawning strongly accelerated recruitment overfishing, which was already indicated by the high exploitation rate alone.

However, in our study lakes in which reproductive capacities of individuals strongly differ, recruitment overfishing cannot be concluded merely from comparisons of fishing mortality, but rather requires age-specific analysis of abundance, fecundity and natural and fishing mortality. According to the estimates of the reproduction potential and the losses caused by the fisheries, the compensatory advantage of fast-growing fish for stock fecundity was counteracted by the fishing mortality of rapidly grown pre-spawning fish. A hypothetical protection of 1+ vendace from exploitation in Lake Werbellin (by virtually taking the contribution of harvested 1+ vendace during their first spawning into account) would more than triple the life-time cumulative egg production per recruit. However, albeit such calculation might be oversimplified because it does not take the effect of increased abundance of 1+ vendace on natural mortality or on the abundance of subsequent age groups into account, it demonstrates the high potential of protecting first-time spawners to increase the stock's reproductive potential. On other hand, the moderate exploitation rate in Lake Stechlin and the complete protection of immature vendace resulted in a low overall impact of the fishery on spawner survival and average life-time cumulative egg production, and hence the stock fecundity was similar to that in the unexploited Lake Breiter Luzin.

Our conclusion that stocks of fast-growing vendace are at higher risk of recruitment overfishing are further supported by Healey (1975), who found that stocks with somatic growth rate already close to the maximum growth rate, have little potential for compensation for additional fishing mortality. Such situation was indicated by our limited data on growth of 0+ vendace in Lake Werbellin, where the few 0+ vendace that were caught in autumns of the years 2011–2014 were all of similar size, even though vendace stock density successively decreased to less than a tenth during this period. In turn, the slow growth rate and high stock density of vendace in Lake Stechlin implies a high, yet unexploited fishery potential. Furthermore, in Lake Stechlin yields could probably be maximised by focusing exploitation mainly on juvenile fish, a way of optimising yields in stocks in which high stock density impairs growth and survival of adult fish (Andersen *et al.* 2017).

Our results on the effects of fishing intensity and fishing selectivity on the reproductive potential of vendace stocks in northern Germany are in strong contrast to the results from the few available studies on recruitment overfishing of vendace stocks, all of which were conducted in Finnish lakes. In Finland, about 90% of the commercial vendace yield is caught by trawling and seining, in which mesh size of the gear is typically so small that vendace reach catchable size already during or soon after the first growing season (Marjomäki *et al.* 2016). Accordingly, substantial fishing mortality of up to 90% of pre-spawning vendace (Helminen *et al.* 1992, Sarvala *et al.* 2020) is frequently observed in Finnish vendace fisheries. Nevertheless, the Finnish practice of vendace harvesting is considered sustainable (Marjomäki *et al.* 2016) because exploited stocks were shown to tolerate the immense fishery losses and remain viable and very productive (Helminen *et al.* 1992, Marjomäki *et al.* 2016). The pronounced difference in fishery resilience to exploitation between northern and southern stocks is most likely a consequence of the more favourable environmental conditions for reproduction and survival of vendace at higher latitudes (Bauch 1949, Järvi 1950, Helminen *et al.* 1992), and calls for regional adaptation of vendace fisheries management. Differences in fishery stock management in response to climatic and environmental variation within a species' distribution area have long been acknowledged for many of the most commercially valuable species (e.g., Parmanne 1998, Stergiou 1999, Rätz & Lloret 2003).

Based on our observations of harvest prior to first spawning, we conclude that a real and underestimated risk of recruitment overfishing exists in German vendace fisheries. Compensatory rapid growth, combined with unregulated gillnet mesh sizes, acts as a feedback that moves fisheries towards collapse. Protection of vendace before first spawning would be effective to reduce the negative effects of fishing on spawner recruitment. Therefore, to reduce the risk of recruitment overfishing, we recommend regular monitoring of somatic growth and appropriate adjustment of mesh size, as it is often implemented when managing larger-sized and longer-lived coregonid fisheries.

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Appendix. Calculation of regression between hydroacoustic target strength (TS) and fish total length (TL) for vendace from the studied lakes.

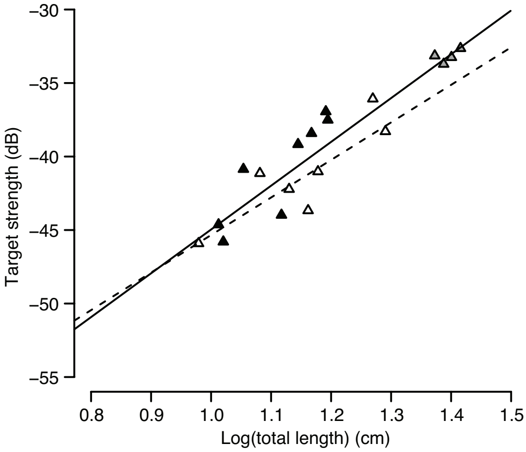

Fig. A1. Scatter plot (triangle) and linear regression (solid line) between modal values of $\log_{10}$(total length) (cm) and target strength (dB) of vendace in lakes Breiter Luzin (black), Stechlin (white) and Werbellin (grey) in the years 2011–2014. For comparison, the equation of Mehner (2006) (dashed line) is also given.

The existing vendace-specific formula for conversion of hydroacoustic target strength (TS) into fish total length (TL), developed by comparing trawl catches and concurrent hydroacoustic surveys of the stunted vendace stock (small average size, narrow size distribution) in Lake Stechlin (Mehner 2006), produced unrealistic results (vendace TL > 35 cm) when applied to bigger vendace found in Lake Werbellin. Accordingly, we derived a new vendace-specific TS–TL regression based on data from hydroacoustic surveys and multi-mesh gillnet surveys in three vendace-dominated lakes, covering the entire range of vendace growth. Hydroacoustic surveys and multi-mesh gillnet surveys were repeatedly conducted in lakes Breiter Luzin, Stechlin and Werbellin during the years 2011–2014 as described in Methods. TS frequency distributions were based on maximum TS values of tracks detected by the automatic tracking algorithm (minimum track length: 4, maximum ping gap: 0, gating range: 0.3 m) implemented in the post-processing software Sonar 5-Pro ver. 6.0.2 (Balk & Lindem 2011). Tracking was based on single-echo detections as described in Methods. For each occasion, TS frequency distribution was calculated in 0.25 dB classes between –55 and –30 dB to match the fish-length distribution in the multi-mesh gillnet catches (7–31 cm TL). The respective TL frequency distributions were obtained from the total catch of hypopelagic multi-mesh gillnets by grouping the fish into 0.25 cm TL classes. Modal lengths in both TS and TL frequency distributions were calculated using the R package *mixdist* (http://CRAN.R-Project.Org/Package=mixdist), which decomposes the cumulative frequency distributions into cohort-specific normal distributions using the method of maximum likelihood. Resulting numbers of distinctive modes differed between the years and populations, ranging from three distinctive modes that referred to vendace of ages 0+, 1+ and 2+ in Lake Stechlin 2011, to only one mode that referred to adult vendace and was distinct from the modes of 0+ and 1+ smelt in Lake Werbellin in 2011–2014. Finally, a highly significant linear regression — $\text{TS (dB)} = 29.7 \times \log_{10}\text{TL (cm)} - 74.7$, $R^2 = 0.85$, $F_{1,17} = 99.06$, $p < 0.0001$ (Fig. A1) — could be calculated from the resulting 19 data pairs between modal TS (dB) and $\log_{10}$ modal TL (cm). The newly derived formula predicted lower TS values for vendace up to about 8 cm TL, but about 2.0 dB higher target strengths for about 24 cm long vendace in comparison with the parameters of the equation of Mehner (2006) (Fig. A1).