



## Full length article

# Synchronous decline of three morphologically distinct whitefish (*Coregonus lavaretus*) stocks in Lake Oulujärvi with concurrent changes in the fish community



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## ABSTRACT

Identification of ecologically mediated mechanisms that drive population dynamical changes in fish communities and polymorphic fish stocks such as those of whitefish, *Coregonus lavaretus*, requires data that are seldom available in freshwater systems. We assessed the stock of each morphologically distinguishable whitefish form (native lesser sparsely-rakered whitefish, native blue whitefish and stocked northern densely-rakered whitefish) in the Lake Oulujärvi during 1973–2014, and related temporal variations in population dynamics to environmental data and catch per unit of effort (CPUE) data on other species having fisheries significance. The results demonstrated a synchronous major decline in the abundance of the native whitefish forms and a decline in the length-at-age of all forms. During the study period, summer time water temperature increased and surface water phosphorous concentration decreased. Recruitment in all whitefish forms showed Ricker-type dependence on spawning stock biomass but little residual correlation with the environmental parameters. Cross-correlation analyses suggested that the re-establishment of pikeperch *Sander lucioperca* population affected negatively both the recruitment and biomass of whitefish but the exact effect mechanisms require further assessment. Our results exemplify that ecosystem-based fisheries management in inland waters must take into account both natural and human-induced environmental changes as well as stockings, and that knowledge-based inland fisheries management is inherently data-intensive.

## 1. Introduction

Effective ecosystem based fisheries management requires science-based knowledge on the functioning of aquatic ecosystems and their responses to fishing, environmental changes and other human-induced pressures (Pikitch et al., 2004; Zhou et al., 2010; Frid et al., 2006; Cooke et al., 2016). Fish assemblages are non-random (Evans et al., 1987; Jackson et al., 1992); they are determined by biotic (predation, competition), abiotic (climatic, physical, chemical) (Jackson et al., 2001), and anthropogenic factors (stockings, harvesting). Exploited fish communities face structural changes in the abundance of different species (Greenstreet and Hall, 1996; Jennings et al., 1999), and even changes in the life-history traits of individual species (Jørgensen et al., 2007; Sharpe and Hendry, 2009; Laugen et al., 2014). Fisheries can also differentially impact different forms of genetically and morphologically polymorphic species, such as whitefish, *Coregonus lavaretus*, and as such create conservation challenges (Sandlund and Næsje, 1989).

However, identifying mechanisms that drive changes in the abundance of different species and ecotypes within fish communities requires data that are seldom available in freshwater systems.

As a result of adaptive specialization on distinct resources (Lu and Bernatchez, 1999; Lundsgaard-Hansen et al., 2013), phylogenetically related (Jacobson et al., 2012) whitefishes *C. lavaretus* and *C. clupeaformis* are polymorphic species with several different sympatric ecotypes present in their native range, varying from large-bodied river-spawning migratory forms to small-bodied lake-spawning plankton or benthic feeders (Siwertsson et al., 2013). Non-migratory whitefishes spawn in autumn in shallow lake areas on sand and gravel bottoms (Etheridge et al., 2011), and their recruitment can therefore suffer from eutrophication (Fudge and Bodaly, 1984; Bninska, 2000) and water level regulation through the destruction of eggs when the water level decreases before the larvae hatch (Sutela et al., 2002). Migratory whitefish, on the other hand, migrate to rivers for spawning and therefore suffer greatly from damming and other alterations of natural

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river systems (Aronsoo and Huhmarniemi, 2004; Haakana and Huuskonen, 2012; Huuskonen et al., 2012). Both microsatellite based population genetic studies (Douglas et al., 1999; Bittner et al., 2010; Winkler et al., 2011; McCairns et al., 2012; Huuskonen et al., 2017; but see Säisä et al., 2008) and studies utilizing modern genomic methods (Gagnaire et al., 2013; Hebert et al., 2013) have revealed significant and temporally stable divergence among whitefish forms and populations. In addition to differences in spawning behaviour, whitefish forms differ in feeding behaviour (Lundsgaard-Hansen et al., 2013), parasite loads (Karvonen et al., 2013), growth rate, size and age at maturation (Heikinheimo et al., 2000) and especially in the number of gill-rakers: the denser the rakers are the smaller food items the fish has adapted to forage on (Kahilainen et al., 2011; Roesch et al., 2013). The ecotypes are able to interbreed (Bittner et al., 2010; Huuskonen et al., 2012; Stott et al., 2013). For example, eutrophication, water level regulation and introduction of new species can induce mixing of the ecotypes through introgression (Bittner et al., 2010; Vonlanthen et al., 2012; Bhat et al., 2014; Huuskonen et al., 2017). Resource competition with other species is known to affect the frequency distributions of gill-raker counts in lake whitefish (Lindsey, 1981). In addition, stockings of novel forms have often altered the abundance and typical morphology of the native forms through interbreeding (Haakana and Huuskonen, 2012; Pamminger-Lahnsteiner et al., 2012; Huuskonen et al., 2017). Stocking of novel forms or related species may also create pressures on the native forms through ecological interactions such as competition for food and habitats (Heikinheimo et al., 2000; Sandlund et al., 2013). To compensate for the losses caused by water level regulation and hydropower production, large numbers of whitefish, usually plankton feeding densely gill-rakered whitefish forms are stocked nationwide in Finnish freshwaters (Heikinheimo et al., 2000; McCairns et al., 2012).

Whitefish are preyed by piscivorous fishes such as brown trout (*Salmo trutta*) (Kahilainen and Lehtonen, 2002), pike (*Esox lucius*), perch (*Perca fluviatilis*), burbot (*Lota lota*) (Amundsen et al., 2003), and pikeperch (Vehanen et al., 1998a; Keskinen and Marjomäki, 2004). Whitefish growth rate is affected by resource competition with roach (*Rutilus rutilus*) and vendace (*Coregonus albula*) (Raitaniemi et al., 1999). Introduced vendace has strong negative impacts on native whitefish populations (Sandlund et al., 2013; Bhat et al., 2014), which highlights the potential importance of competition between these two *Coregonus*-species also in naturally sympatric populations (Bøhn et al., 2008).

Lake Oulujärvi is the fifth largest lake in Finland, and together with its surrounding lakes one of the nationally most important areas for both commercial and recreational freshwater fisheries (Vehanen et al., 2002). The lake is regulated for the purposes of hydroelectric power generation by eight hydroelectric power plants in the outflowing River Oulujoki. It supports three whitefish forms: 1) native blue whitefish (number of gill rakers [mean  $\pm$  S.D.]  $33.5 \pm 3.2$ ), 2) native but relatively rare and commercially unimportant benthic lesser sparsely-rakered whitefish (number of gill rakers  $22.7 \pm 2.3$ ) and 3) stocked plankton feeding northern densely-rakered whitefish (number of gill rakers  $52.5 \pm 4.2$ ) (Salojärvi, 1992). Due to water level regulation whitefish populations have been supported by a compensatory stocking program (Salojärvi, 1992). No other management measures have been taken to regulate the catches of whitefish in Lake Oulujärvi (Vehanen et al., 2002).

In this study, our aim was to first estimate the development of abundance and recruitment of different whitefish forms through stock assessment for the years 1973–2014 and second, relate the observed abundance changes and recruitment variations to abundance data of potential predators pike, perch, pikeperch, brown trout and burbot, to abundance data of potential resource competitors (vendace, smelt (*Osmerus eperlanus*), roach and bream (*Abramis brama*)), and to water temperature, amplitude of water level regulation, water transparency and phosphorus concentration. We also examined if the growth of different whitefish forms has changed over time, and whether any

growth changes would have been density-dependent. We assumed that the three whitefish forms remained genetically original through the study period, and we did not address any effects of potential interbreeding among the forms. We hypothesized that given the whitefish forms are ecologically specialized to certain niches, environmental changes should induce differential development among the forms. In particular, the lesser-sparsely rakered whitefish should have been affected by interactions with other benthic feeders, while the plankton-feeding northern densely-rakered whitefish should have shown the tightest interactions with other plankton-feeders such as vendace and smelt (Sandlund et al., 2013). Predation and fishing were predicted to have caused synchronous changes in all forms because there was little targeted fishing on certain whitefish forms and predation is present generally in the whole lake due to its shallowness.

## 2. Materials and methods

### 2.1. Lake Oulujärvi and its fishery

The mean water surface area of Lake Oulujärvi is 928 km<sup>2</sup>. Its mean depth is 7.6 m and the mean elevation above sea level is 121 m. The average amplitude of water level regulation for hydroelectric power generation has been 1.7 m. After the damming of outflowing River Oulujoki and the major upstream tributaries in 1960's, the migratory northern densely-rakered whitefish lost its main breeding areas. As a compensation, more than 25.5 million fingerlings of this whitefish form (but originating from various non-native sources) has been stocked into the lake over the period of 1977–2014 (Salojärvi, 1992, see also [www.kfrs.fi](http://www.kfrs.fi)). The other two whitefish forms reproduce naturally in the lake and are not supported by stocking. No management measures are taken to regulate the total catches in Lake Oulujärvi and fishing effort is practically unlimited (Vehanen et al., 2002). Size limits are not applied in whitefish fisheries, but minimum size limit for pikeperch was 370 mm during 1973–2009 and 450 mm during 2010–2014. Minimum size limit of brown trout was 300 mm during 1973–1982, 350 mm during 1983–1992, 400 mm during 1993–2009 and 500 mm during 2010–2014. The minimum size limit for pike was 400 mm until 01.03.1993. Trawl fishery started in 1987 with a maximum of 8 trawls, fyke net fishing started in 1984 without realized restrictions and gillnet fishing had no effort regulations during the study period. During 2011–2014 gillnet mesh sizes between 20 and 49 mm were prohibited in winter (1.11.–30.4.), and mesh sizes between 20 and 40 mm were prohibited during 1.5.–30.6. Surface gillnets with mesh size 20–64 mm were prohibited during the open water season. Other gears are not regulated.

The total annual catch of all species in Lake Oulujärvi has varied between 354 and 818 tons during the study period of 1973–2014 ( $3.8\text{--}8.8\text{ kg ha}^{-1}$ ). The most important species for fisheries were (in alphabetical order) brown trout, burbot, perch, pike, pikeperch, smelt, vendace and whitefish. All species were harvested both commercially and recreationally. The proportion of commercial catch of the annual total catch varied between 46 and 63%.

Whitefish in Lake Oulujärvi was targeted using seines, fykenets, gillnets, trapnets, and trawls, and caught as a bycatch in ice fishing. The total whitefish catch varied between 4 and 120 tons during 1973–2014 (Fig. 1a). In 1973–1983 over 95% of the whitefish catch was caught with gillnets (Fig. 1b). After fishing with fykenets was allowed in 1984, the fykenet catch rapidly increased to 10–42% of the total catch (Fig. 1b). Commercial trawling constituted 1–29% of the total whitefish catch during years 1987–2014 (Fig. 1b). Correspondingly, the share of gillnet catch decreased to the level of 51–86% in 1984–2014 (Fig. 1b).

### 2.2. Environmental data

Average water temperature during the growth season (from June 1st to November 1st) was available from the daily temperature

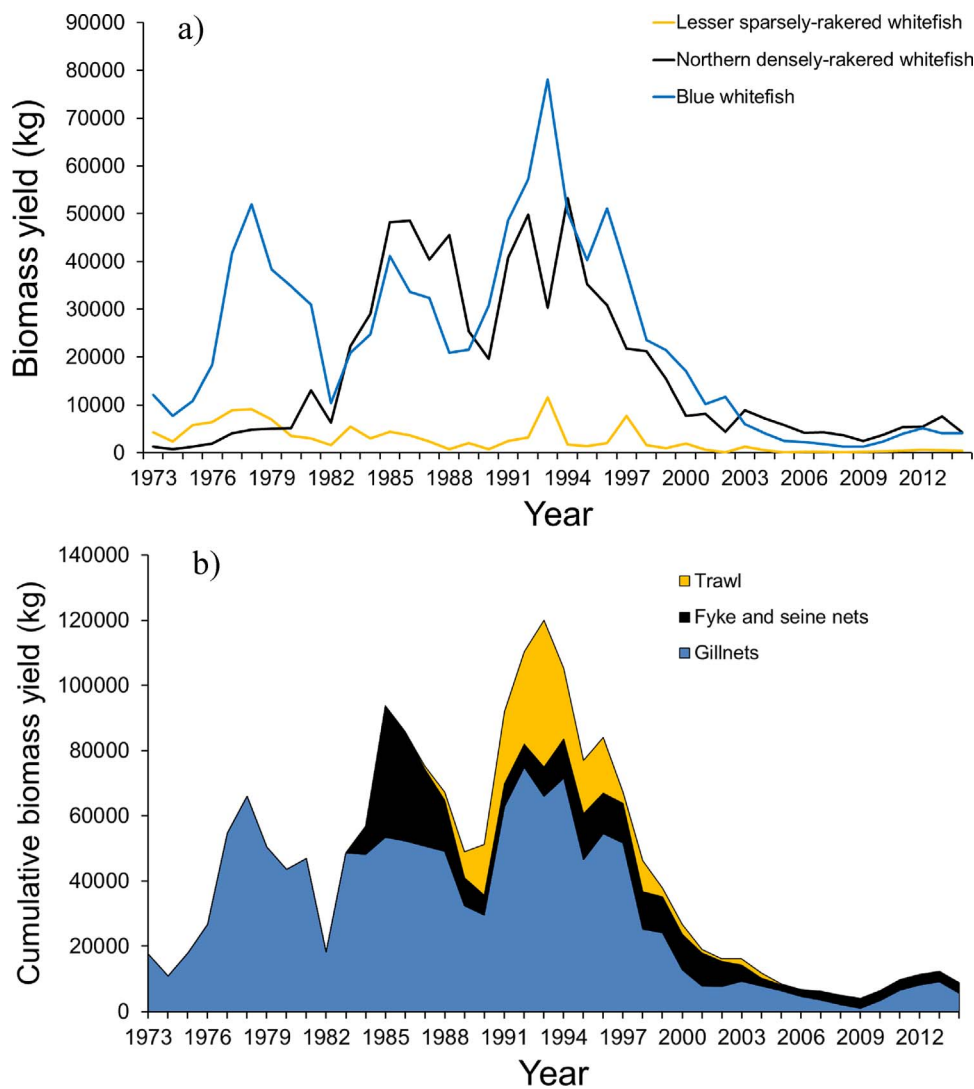


Fig. 1. (a) Whitefish yields (kg) by form in Lake Oulujärvi during 1973–2014 as estimated from the total catches based on individual samples from the catches. (b) Whitefish yields (kg) by fishing gear in Lake Oulujärvi during 1973–2014.

measurements by Kainuu Fisheries Research Station ([www.kfrs.fi](http://www.kfrs.fi)) for 1992–2014, and from the River Oulujoki for 1973–2000. The time series were combined based on linear regression during the overlapping data period ( $T_{KFRS} = 0.879 T_{Oulujoki} + 1.703$  °C,  $R^2 = 0.775$ ). Water level amplitude was calculated as a difference between water level in spawning time (last week of October) and late winter/minimum water level of the year in April–May. Summer time surface water (0–3 m) phosphate phosphorous concentration and colour data were obtained from public Hertta database of Finnish Environmental Institute by first calculating the averages per main basin (Paltaselkä, Ärjänselkä and Niskanselkä) and using the average of the basin averages as representative for the whole Lake Oulujärvi.

### 2.3. Catch data

The total catch data for 1973–1990 were taken from Salojärvi (1992), who estimated the catches using annual postal surveys. During 1991–2014 the postal surveys were conducted every 5 years, and the total catches for the intermittent years were estimated based on the catches of bookkeeping fishermen (on average 29 fishers (S.D. 4.5), of which 7 fished with trawls and 22 fished with other gears, Table 1). In detail, the unknown total catches were predicted using sliding average (span 3) on logbook data of bookkeeping fishermen recording all of their catches and fishing effort (catch per unit effort, CPUE) as described below assuming a constant total fishing effort (Total catch =  $382.74 \times 3$  year's average CPUE (g gillnet<sup>-1</sup>),

$R^2 = 0.606$ ). The bookkeeping fishers were selected among the most active subsidizing and commercial fishers based on volunteering (for further info see [www.kfrs.fi](http://www.kfrs.fi)). The annual catches of bookkeeping fishers comprised on average 19.92% (S.D. = 8.70%) of the total whitefish catches in the Lake Oulujärvi during 1991–2004. The postal questionnaire was sent to 25–40% of the recreational fishers and almost all of the commercial fishers were interviewed and enquired for their catch.

The catch per unit of effort (CPUE, g lifted gillnet<sup>-1</sup>) data on whitefish, burbot, pike, pikeperch, brown trout, perch, bream and roach were calculated from bookkeeping fishermen's (during the whole period,  $N = 23.33$ , S.D. = 9.40) gillnet catches with mesh sizes between 27 and 70 mm (Table 1). Minor catchability changes due to the development of fishing gears and methods were considered meaningless as a whole, but in particular, any increasing trends in CPUE should be interpreted with this in mind. Gillnet (30 m) lift was used as a unit of effort, because it corresponds better the efficient fishing time than strict time that varies between seasons (P. Hyvärinen, unpublished data). In total, over the study period 615,967 gillnets of 30 m length and 1.5–5 m in height (with 27–70 mm mesh size) were lifted. CPUE of vendace was calculated from gillnet catch with mesh sizes of 10–20 mm. In total, over the period of the study 94,739 gillnets of 30 m length and 1.5–5 m height with mesh sizes of 10–20 mm were lifted. There were no solid data series available to calculate CPUE of smelt from one gear only for the entire study period. Therefore, the data from seine nets and trawls were combined by predicting the missing seine net CPUE values

**Table 1**

Number of catch samples, number of individual fish analysed for age, size and gill-raker count, number of bookkeeping fishers and number of gill-nets lifted per year by the bookkeeping fishers.

Year	# fish	# samples	#bookkeeping fishers	#Gill-nets lifted
1973	218	44	1	86
1974	118	13	34	10830
1975	309	25	3	2197
1976	92	20	4	866
1977	99	20	14	3114
1978	228	45	13	6576
1979	323	33	20	7826
1980	870	34	15	5596
1981	2204	99	16	7114
1982	3435	109	13	5997
1983	5289	197	15	8304
1984	6510	215	13	4995
1985	6369	194	14	5145
1986	7599	213	12	4651
1987	6165	187	17	8973
1988	1548	94	20	12613
1989	942	116	26	7814
1990	529	43	25	7738
1991	568	59	23	4161
1992	451	28	23	10934
1993	156	4	30	18229
1994	422	15	33	15304
1995	992	53	32	10274
1996	359	48	32	9223
1997	581	9	33	8654
1998	305	3	31	7235
1999	359	5	34	9641
2000	623	16	29	8074
2001	350	5	25	10050
2002	100	1	31	13331
2003	354	4	31	18296
2004	309	7	31	18957
2005	355	7	29	19924
2006	300	3	30	31238
2007	219	4	27	22543
2008	410	4	28	26785
2009	300	4	26	24178
2010	300	22	27	31185
2011	298	26	25	42470
2012	300	26	25	50478
2013	300	33	26	43793
2014	300	29	28	50575

(kg haul<sup>-1</sup>) using equation  $CPUE_{\text{seine-net}} = 2.81 \times CPUE_{\text{trawl}} + 3.57$  ( $R^2 = 0.345$ ,  $P = 0.006$ ). However, all data were missing for 1973, 1975–1977, 1981 and 1986–1988 which limited the usability of smelt data. Exceptionally high trawl CPUE of smelt in year 1994 (29.9) was omitted from the data, because in this particular year smelt were specifically targeted in a special project while in other years smelt was only caught as bycatch. In total, these data consisted of 3 303 seine net hauls and 57 395 trawling hours. On average seine nets were used 84.7 (S.D. 66.9) times per year (1973–2014) and on average trawls were used 2 207.5 (S.D. 1656.0) hours per year (1987–2014).

## 2.4. Whitefish forms

Individual samples ( $N = 51,858$ , 48,112 after removing missing age and gill raker count values) were collected as representatively as possible from gillnet, fyke net, seine net and trawl catches ( $N = 50.4 \pm 63.2$ , mean  $\pm$  S.D. samples per year; on average  $1235 \pm 2025$  individual fish per year; Table 1) assuming that different fishing gears were not selective on gillraker count. Individual fish were selected haphazardly from the sampled catches. Gillraker numbers were counted to identify the morphs: whitefish with less than or equal to 25 gill rakers were classified lesser sparsely rakered, fish with 26–43 gill rakers blue whitefish, and fish  $\geq 44$  northern densely rakered whitefish (Salojärvi, 1992) (Fig. 2). Gillraker counts have been shown to reliably

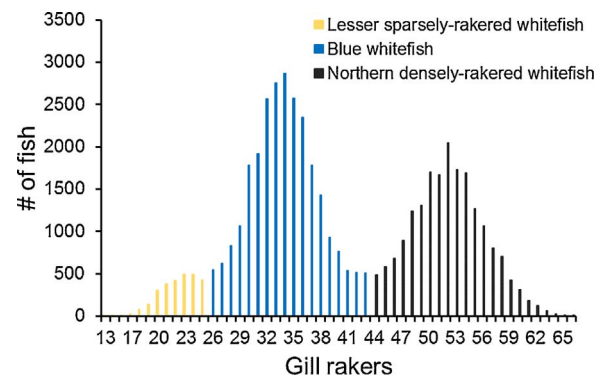


Fig. 2. Distribution of gill-raker count among all studied individual whitefish ( $N = 48,111$ ).

identify genetically distinct whitefish morphs (Huuskonen et al., 2017). Fish length and body mass were measured, and age was determined from scales. Sex and maturity was examined and classified according to Bagenal and Braum (1978). The annual whitefish catch in kilograms (yield) was first divided into different whitefish forms according to the weight proportion of different forms in the catch samples each year (Fig. 1). The total yield peaked in 1993 at 120 t but has decreased since then to current (2004–2014) level of 4–12 t per year (Fig. 1). Second, the catch in numbers for cohort analysis was calculated per age group in each year using the individually specific data from the catch samples.

## 2.5. Cohort analysis

Cohort analysis (Hilborn and Walters, 1992) was carried out separately on each form to estimate the whitefish population size and annual instantaneous fishing mortality rate ( $F$ ) per age group in 1973–2014. The fish recruited fully to catches in their fourth year (3+) and only a few fish older than twelve years were found in the catch samples. Thus, the oldest age group used in cohort analysis was twelve years, which also included all fish older than twelve years. As no precise size or age dependent natural mortality estimates were available, a constant annual natural mortality rate of 0.25 was applied, and the error arising from variation in natural mortality was assessed by conducting the cohort analysis additionally with  $M$  values 0.10 and 0.4 (c.f. Salojärvi, 1992). Annual natural mortality rate 0.25 was assumed when extrapolating the cohort analysis to yield the number of 0-year old recruits.

The terminal fishing mortality rate assumption was tuned by averaging the current values over the last three years and repeating the Pope's VPA-approximation procedure with revised values until the difference of the terminal  $F$ 's and calculated averages converged to zero (Hilborn and Walters, 1992). Finally, the spawning stock biomass of all whitefish forms was calculated using maturity ogives and weight-at-age keys based on individual data. Maturity ogives were estimated using individual data from September until mid-November, with the assumption that all fish under age 2 were immature. Spawning stock biomass (SSB) was calculated by summing the age-specific products of biomass and the proportion of mature fish.

## 2.6. Statistical analyses

Principal component analysis (PCA) with Varimax rotation and replacement of missing values (1 year for vendace and abovementioned years for smelt) with mean was used to capture the main axes of covariation in the fish community. Natural logarithm transformed and standardized catch per unit of effort (CPUE) values for whitefish (all forms pooled), burbot, pike, pikeperch, brown trout, perch, bream, roach, vendace and smelt were entered into the PCA. Whitefish CPUE was partially redundant in this analysis (because CPUE data were used



to predict the missing total catch values), but it was included to examine how it would relate to the CPUE of other species, and how well it would eventually correlate with the estimated biomass of different whitefish forms. The resulting rotated principal component values were saved using the regression method.

Linear regression was used to analyse temporal trends. Cross-correlation analysis (i.e. Pearson's correlation on de-trended data) was used to study if the variation in the biomass of different whitefish forms of 3-years old and older correlated with CPUE of individual fish species (with lags of  $\pm 2$  years). Cross-correlation analysis with lags up and down to one year was used to analyse the relationship between environmental variables and variation in the biomass of different whitefish forms of 3-years old and older. Cross-correlation was also used to analyse the relationship between the estimated fishing mortality rates and catches. The “explanatory” variable was always entered first so that negative lags refer to the effect arising from conditions before the year of assessment and vice versa. It should be noted that because all linear trends are removed in cross-correlation analysis, any potential trends in catchability are thus controlled for in these analyses.

Growth of whitefish was analysed by first fitting von Bertalanffy's growth curve on each form, and each cohort separately using FSA-package (Ogle, 2016) in R 3.3.1. Because cohort and form specific fitting of von Bertalanffy's growth curve was successful only for a small subset of cohorts, temporal trends in growth were analysed by focusing on 5–6 years old whitefish ( $N = 10,745$ ). Individual length-at-ages at ages 5–6 years were projected to the first of January at age 5 by first fitting a general linear model with age class (5 or 6), morph and their interactions as factors, and cohort and precise decimal age as variables. The individual relation of observed length to predicted length was used to multiply the model-predicted length at the first of January at age 5. Finally, the cohort-specific individual lengths projected to the first of January at age 5 were studied for correlation with the total abundance of whitefish (3-years and older) two years before (at age 3) using Spearman rank order correlation and cross-correlation in order to study if the whitefish growth was density-dependent. For the analysis, 1973–2012 data were available for blue whitefish, 1977–2012 data for northern densely rakered whitefish. For lesser sparsely-rakered whitefish only period 1975–2011 could be used with replacement of five missing length-at-age 5 values with the period average (224.9 mm).

Two major recruitment functions Ricker (1954) and Beverton and Holt (1957) were fitted to the SSB at previous year (whitefish spawns in autumn) vs. number of 0-year old recruits data of each whitefish form using FSA and FSAsim (available from GitHub <https://github.com/droglenc/FSAsim>) packages in R 3.3.1 (Ogle, 2016) with lognormal errors. Residual recruit counts, i.e. recruitment not explained by spawning stock biomass, were studied for cross-correlations (with lags up and down to  $\pm 1$  years) with CPUE data of different fish species and the environmental parameters.

Cross-correlation and Spearman's correlation analyses were performed in AV Bio-Statistics 5.2 and other standard analyses in IBM SPSS Statistics 21.

### 3. Results

#### 3.1. Stock assessment

Blue whitefish was the most abundant whitefish form with the estimated average population size of 659,000 3-years-old and older individuals (454,000–1,167,000 with  $M = 0.1$ –0.4), and the lesser sparsely-rakered whitefish the least abundant with the average of 79,000 (57,000–125,000) 3-years-old and older individuals (Fig. 3). The average population size of northern densely-rakered whitefish during the period 1973–2014 was 262,000 (190,000–415,000) 3-years-old and older individuals (Fig. 3). The respective average spawning stock population sizes were 79.5 t (53.6 t–146.3 t), 12.0 t (8.4 t–19.8 t) and 16.4 t (11.8 t–26.3 t). The estimated annual instantaneous fishing mortality rates were highly variable among

years, but on average at relatively high level (Fig. 3). The average annual instantaneous fishing mortality rate was  $0.69 \text{ y}^{-1}$  ( $0.57 \text{ y}^{-1}$ – $0.83 \text{ y}^{-1}$  with  $M = 0.1 \text{ y}^{-1}$ – $0.4 \text{ y}^{-1}$ ) for blue whitefish,  $0.62 \text{ y}^{-1}$  ( $0.47 \text{ y}^{-1}$ – $0.77 \text{ y}^{-1}$ ) for lesser sparsely-rakered whitefish and  $0.73 \text{ y}^{-1}$  ( $0.62 \text{ y}^{-1}$ – $0.86 \text{ y}^{-1}$ ) for northern densely-rakered whitefish. The fishing mortality showed an increased trend in blue whitefish (linear regression,  $R^2 = 0.175$ ,  $F_{1,40} = 8.497$ ,  $P = 0.006$ ) but no trends in the other forms. The estimated average annual fishing mortality rates for age 3–10 y (2–10 y for northern densely-rakered whitefish) cross-correlated significantly but not particularly strongly with the annual total catches ( $R = 0.328$ ,  $P = 0.036$  for blue whitefish;  $R = 0.427$ ,  $P = 0.005$  for lesser sparsely-rakered whitefish;  $R = 0.362$ ,  $P = 0.018$  for northern densely-rakered whitefish).

Northern densely-rakered whitefish stock mainly relied on stockings (Fig. 3), but the strong abundance and yield peak in mid-1980's coincided with the estimated recruitment exceeding the stockings suggesting a significant role for natural reproduction at this time. There was no overall linear trend in the stock biomass development (linear regression,  $F_{1,40} = 1.893$ ,  $P = 0.177$ ). The native whitefish forms, the lesser sparsely-rakered whitefish and the blue whitefish both showed a declining trend (linear regression,  $F_{1,40} = 123.98$ ,  $P < 0.001$ , stock biomass = 1,218,000 kg–606 kg  $\times$  year;  $F_{1,40} = 141.69$ ,  $P < 0.001$ , stock biomass = 9,599,000 kg–4772 kg  $\times$  year, respectively). The decline was visible also in the declining CPUE of all whitefish (Table 3). Also recruitment decreased in all forms (Fig. 3., linear regression, blue whitefish,  $-19036$  0-year-old fish year $^{-1}$ ,  $F_{1,40} = 15.25$ ,  $P < 0.001$ ; lesser sparsely-rakered whitefish,  $-2956$  0-year-old fish year $^{-1}$ ,  $F_{1,40} = 16.93$ ,  $P < 0.001$ ; northern densely-rakered whitefish,  $-9169$  0-year-old fish year $^{-1}$ ,  $F_{1,40} = 6.13$ ,  $P = 0.018$ ).

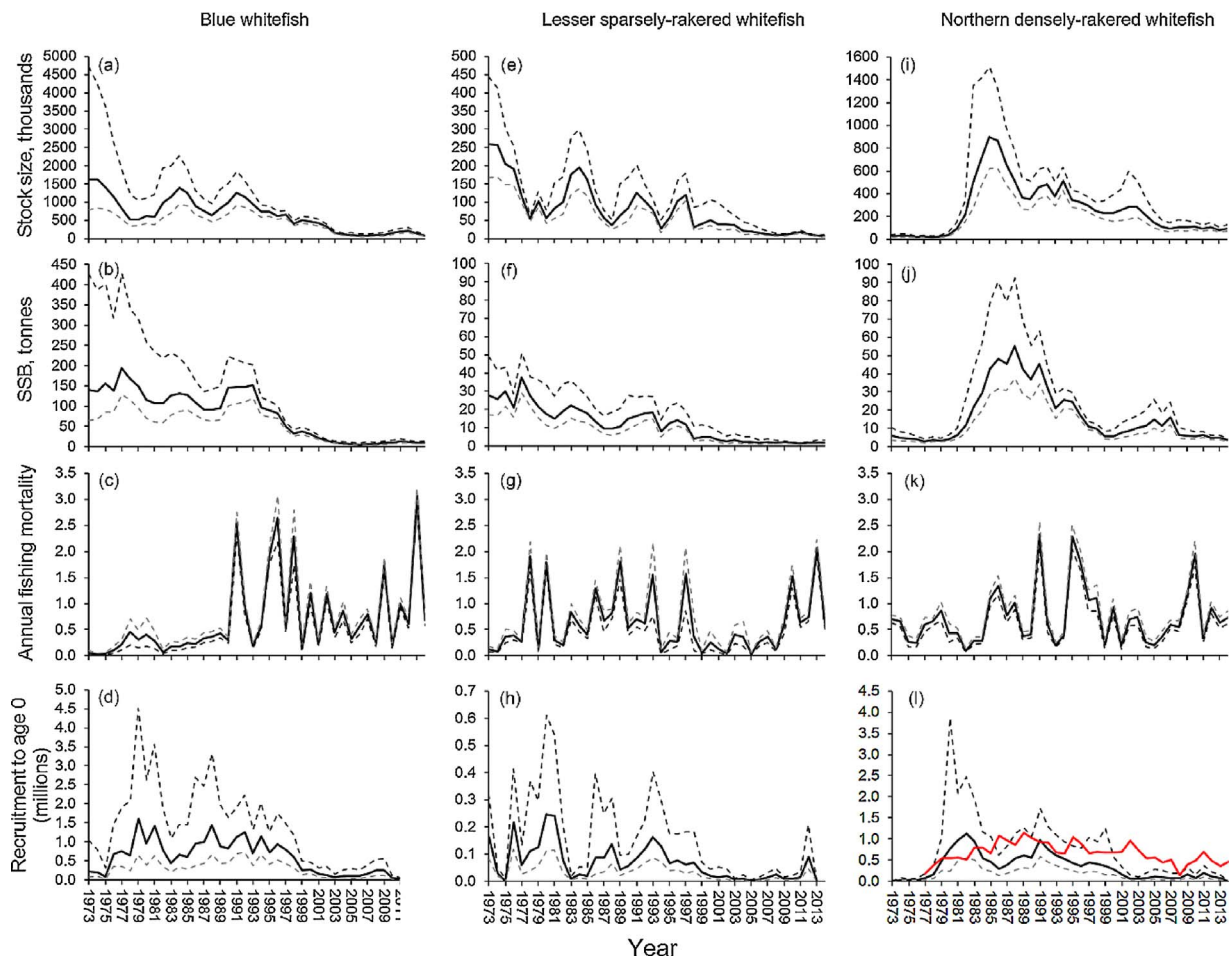
#### 3.2. Principal component analysis of CPUE data and trends in fish community scores

The Varimax-rotated solution of principal component analysis explained 76.5% of the total variation in the standardized fish CPUE data by yielding four principal components having eigenvalue  $> 1.0$  (Table 2). The first component, explaining 32.4% of the total variance, reflected mostly CPUE of whitefish, perch and roach, and was strongly negatively related to pikeperch CPUE (Table 2). The second component explained 20.3% of the variance, and reflected mostly the CPUE of coldwater predators, i.e. CPUE of burbot and brown trout (Table 2). The third component was dominated by vendace and bream CPUE, and explained 12.3% of the total variance (Table 2). The fourth component explained 11.6% of the variance, and was most clearly related to the abundance of pike and smelt (Table 2).

Principal components 1 and 3 showed a statistically significant negative linear trend (Fig. 4, linear regression,  $F_{1,40} = 51.33$ ,  $P < 0.001$ ,  $R^2 = 0.562$ ;  $F_{1,40} = 7.51$ ,  $P = 0.009$ ,  $R^2 = 0.158$ , respectively) while principal components 2 and 4 showed increase until early 2000's and subsequent decrease but no overall linear trend (linear regression,  $F_{1,40} = 1.37$ ,  $P = 0.249$ ,  $R^2 = 0.033$ ;  $F_{1,40} < 0.001$ ,  $P = 0.994$ ,  $R^2 < 0.001$ , respectively) (Fig. 4).

#### 3.3. Trends in CPUE data and cross-correlations with whitefish biomass

Catch per lifted gillnet increased for pikeperch but decreased for perch, roach, bream and vendace (Table 3). Blue whitefish and northern densely-rakered whitefish biomasses had the strongest cross-correlation with whitefish CPUE (Table 3). Among potential predators of whitefish, pike CPUE did not cross-correlate with whitefish biomass and brown trout CPUE showed only one positive cross-correlation with whitefish biomass (Table 3). Pikeperch CPUE cross-correlated negatively with the biomass of northern densely-rakered whitefish as well as the burbot CPUE with lesser sparsely-rakered whitefish biomass (Table 3). Perch CPUE cross-correlated positively with lesser sparsely-rakered whitefish but negatively with northern densely-rakered whitefish (Table 3). Smelt CPUE cross-correlated positively with the



**Fig. 3.** Results of cohort analysis on Lake Oulujärvi whitefish forms. The dotted lines represent lower and upper natural mortality estimates (0.15 vs. 0.40), while the solid lines are based on the assumption of 0.25 annual natural mortality rate. Stock size in numbers includes all 3-years-old and older individuals. The red (gray) line in the panel (l) indicates the number of stocked northern densely rakered whitefish.

**Table 2**

Rotated component matrix of PCA on standardized fish catch-per-unit-of-effort data. Loadings with absolute value greater than 0.5 are indicated in bold. Whitefish CPUE pools all whitefish forms.

Parameter	PC-1	PC-2	PC-3	PC-4
Whitefish CPUE	0.734	0.507	0.062	0.074
Burbot CPUE	−0.130	<b>0.904</b>	0.033	0.038
Pike CPUE	−0.206	0.220	0.322	<b>0.801</b>
Pikeperch CPUE	<b>−0.855</b>	0.111	−0.026	−0.021
Brown trout CPUE	0.105	<b>0.883</b>	−0.030	0.107
Perch CPUE	<b>0.565</b>	−0.175	0.247	−0.164
Bream CPUE	0.090	−0.090	<b>0.879</b>	−0.036
Roach CPUE	<b>0.655</b>	<b>0.506</b>	0.390	0.116
Vendace CPUE	0.464	0.225	<b>0.661</b>	0.007
Smelt CPUE	0.145	−0.021	−0.294	<b>0.858</b>

biomass of lesser sparsely-rakered whitefish, but vendace CPUE cross-correlated negatively with the biomass of blue whitefish and lesser sparsely-rakered whitefish (Table 3).

### 3.4. Trends in environmental parameters and cross-correlations with whitefish biomass

Growth season average water temperature (average 11.52 °C) increased 0.053 °C y<sup>−1</sup> (Fig. 4, linear regression,  $F_{1,40} = 37.63$ ,  $P < 0.001$ ,  $R^2 = 0.485$ ). The average water level fluctuation amplitude was 166.5 cm, which showed a declining trend by 1.3 cm y<sup>−1</sup>

(linear regression,  $F_{1,40} = 10.13$ ,  $P = 0.028$ ,  $R^2 = 0.202$ ). Water colour (average 66.9 mg Pt l<sup>−1</sup>) did not show any linear trend (linear regression,  $F_{1,40} = 0.662$ ,  $P = 0.421$ ,  $R^2 = 0.016$ ), but phosphate phosphorous (average 4.3 mg l<sup>−1</sup>) showed a negative trend (linear regression,  $F_{1,40} = 7.942$ ,  $P = 0.008$ ,  $R^2 = 0.166$ ).

Growth season average water temperature cross-correlated negatively with blue whitefish biomass but not with the biomass of other whitefish forms (Table 4). Other environmental parameters did not cross-correlate with whitefish biomass except for the one significant negative correlation between water level amplitude on previous year and the biomass of lesser sparsely-rakered whitefish (Table 4).

### 3.5. Length-at-ages

The average growth of blue whitefish during the study period was described by von Bertalanffy's growth function as  $L(t) = 365.4 \text{ mm} (1 - e^{-0.152(t + 2.686)})$  (non-linear regression,  $P < 0.001$  for all parameters). The growth of lesser sparsely-rakered whitefish was described by  $L(t) = 381.2 \text{ mm} (1 - e^{-0.133(t + 2.682)})$  (non-linear regression,  $P < 0.001$  for all parameters), and that of northern densely-rakered whitefish by  $L(t) = 419.0 \text{ mm} (1 - e^{-0.194(t + 1.057)})$  (non-linear regression,  $P < 0.001$  for all parameters).

Temporal variation in the length at age 5 (predicted to the 1st of January) was highly synchronous among the three whitefish forms (Fig. 5). All whitefish morphs showed a negative linear temporal trend in the length-at-ages at ages 5–6 over the cohorts 1971–2011 (GLM,  $F_{1,10737} = 867.67$ ,  $P < 0.001$ ), and the morphs also differed in

**Table 3**

Linear trends in CPUE (g gillnet<sup>-1</sup>) of the most important fishes in Lake Oulujärvi and their cross-correlations (CC, with no lag) with the biomass of the 3-years-old and older whitefish forms. Statistically significant correlations and regression slopes are indicated in bold.

	Whitefish	Pike	Burbot	Brown trout	Pikeperch	Perch	Roach	Bream	Vendace	Smelt
Linear trend, constant (g gillnet <sup>-1</sup> ) <sup>a</sup>	5395.19	−3265.99	287.09	59.56	−38161.2	722.32	4096.45	834.93	705730	333.32
Linear trend, slope (g gillnet <sup>-1</sup> year <sup>-1</sup> ) <sup>a</sup>	<b>−2.65</b>	1.79	−0.05	−0.02	<b>19.25</b>	<b>−0.35</b>	<b>−2.04</b>	<b>−0.41</b>	<b>−34.69</b>	−0.16
F	5.05	0.92	0.00	0.03	92.74	16.87	7.97	13.04	12.56	0.35
d.f.	1,40	1,40	1,40	1,40	1,40	1,39	1,40	1,40	1,39	1,32
P	0.030	0.343	0.970	0.863	0.000	0.000	0.007	0.001	0.001	0.559
R <sup>2</sup>	0.112	0.023	0.000	0.001	0.699	0.302	0.166	0.246	0.244	0.011
CC with blue whitefish	<b>0.555</b>	−0.262	−0.302	−0.026	−0.247	0.114	0.046	−0.158	<b>−0.495</b>	0.359
P	N.A. <sup>**</sup>	0.093	0.052	0.871	0.116	0.476	0.770	0.318	0.001	0.072
CC with lesser sparsely-rakered whitefish	0.045	−0.224	<b>−0.487</b>	−0.089	0.172	<b>0.367</b>	−0.153	−0.054	<b>−0.431</b>	<b>0.436</b>
P	N.A. <sup>**</sup>	0.153	0.001	0.577	0.277	0.018	0.335	0.735	0.005	0.026
CC with northern densely-rakered whitefish	<b>0.559</b>	0.034	0.238	<b>0.321</b>	<b>−0.500</b>	<b>−0.338</b>	−0.093	<b>−0.447</b>	−0.148	0.099
P	N.A. <sup>**</sup>	0.832	0.128	0.038	0.001	0.031	0.560	0.003	0.355	0.631

<sup>a</sup> Unit of CPUE for smelt kg seine net pull<sup>-1</sup>.

<sup>\*\*</sup> Significance testing not meaningful because CPUE data were used in biomass estimation.

average total length (GLM,  $F_{2,10737} = 3780.35$ ,  $P < 0.001$ ) the northern densely-rakered whitefish being the fastest-growing and the lesser sparsely-rakered whitefish the slowest-growing (Fig. 5). The declining trend in the length at age 5 seemed to reverse between 1994 and 2009 (Fig. 5) but the linear trend during this time period was statistically significantly increasing only in the northern densely-rakered whitefish (blue whitefish,  $P = 0.077$ ; lesser sparsely-rakered whitefish,  $P = 0.658$ ; northern densely-rakered whitefish, slope =  $2.5 \text{ mm y}^{-1}$ ,  $P < 0.001$ ).

Spearman's rank order correlations indicated positive relationship between stock abundance and length-at-age 5 for both native whitefish forms (Spearman's  $\zeta = 0.558$ ,  $P < 0.001$  for blue whitefish;  $\zeta = 0.506$ ,  $P = 0.001$  for lesser sparsely-rakered whitefish and  $\zeta = 0.112$ ,  $P = 0.516$  for northern densely-rakered whitefish). The respective non-lagged cross-correlations were not statistically significant ( $R = -0.229$ ,  $P = 0.156$ ;  $R = -0.081$ ,  $P = 0.635$  and  $R = -0.203$ ,  $P = 0.236$ ).

### 3.6. Recruitment

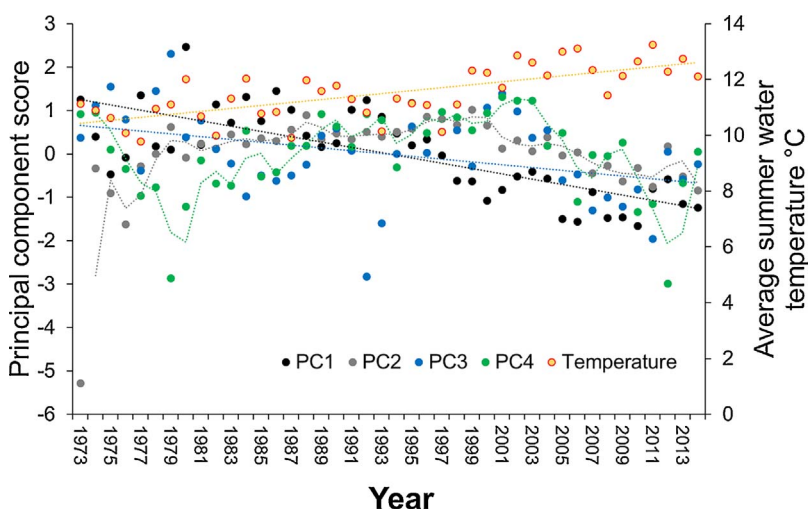
Ricker model had a marginally (but not statistically significantly) better coefficient of determination than Beverton-Holt model for all the three whitefish morphs (Fig. 6). Blue whitefish recruitment was predicted by  $R = 9.28 \times \text{SSB} e^{-0.0000370 \times \text{SSB}}$  with  $r^2$  of 0.559 ( $P$ -values for parameters were 0.002 and 0.214, respectively) while the Beverton-Holt model,  $R = 9.32 \times \text{SSB}/(1 + 0.00000474 \times \text{SSB})$  had  $r^2$  of 0.550 ( $P$ -values for parameters were 0.004 and 0.370, respectively) (Fig. 6). Recruitment of lesser sparsely-rakered whitefish was best predicted by

$R = 4.41 \times \text{SSB} e^{-0.0000152 \times \text{SSB}}$  with  $r^2$  of 0.316 ( $P$ -values for parameters were 0.008 and 0.515, respectively) while the Beverton-Holt model,  $R = 4.31 \times \text{SSB}/(1 + 0.0000152 \times \text{SSB})$  had  $r^2$  of 0.309 ( $P$ -values for parameters were 0.014 and 0.656, respectively) (Fig. 6). For the stocked northern densely-rakered whitefish the recruitment functions fitted poorly but indicated that natural recruitment might occur as recruitment statistically related to the SSB. Ricker-model for northern densely-rakered whitefish was described by  $R = 23.77 \times \text{SSB} e^{-0.0000151 \times \text{SSB}}$  with  $r^2$  of 0.153 ( $P$ -values for parameters were 0.001 and 0.193, respectively) while the Beverton-Holt model,  $R = 25.90 \times \text{SSB}/(1 + 0.0000281 \times \text{SSB})$  had  $r^2$  of 0.151 ( $P$ -values for parameters were 0.006 and 0.355, respectively) (Fig. 6). In all morphs, the recruitment was on the increasing side of the Ricker curve, and the overcompensation built-in Ricker type recruitment was not supported by data within the observed range of SSB:s.

### 3.7. Cross-correlations between recruitment and environmental factors

Principal components 1 and 2 correlated positively with the recruitment of almost all whitefish forms, while the components 3–4 had only two statistically significant lagged negative correlations with recruitment (Table 5).

Residual variation in the recruitment of different whitefish forms, i.e. variation not explained by the spawning stock biomass of the respective form, showed statistically significant cross-correlations especially with the CPUE of pikeperch, perch, brown trout, roach and bream (Table 6). Vendace CPUE showed only one marginally significant correlation with northern densely-rakered whitefish with lag + 1 ( $C = 0.326$ ,  $P = 0.040$ ) and CPUE of potential predators, pike and



**Fig. 4.** Temporal development of summer average water temperature (yellow (light gray, open circles) line), and the development of fish community as indicated by the four principal components capturing most variation in the CPUE and abundance data. The dotted straight lines represent statistically significant linear trends and dotted curved lines represent moving averages with radius 2.

**Table 4**

Cross-correlations (CC, with minus and plus one year lags) between the biomass of the 3-years-old and older whitefish forms and the addressed environmental parameters. Statistically significant correlations are highlighted in bold.

	Water T	Sig.	PO <sub>4</sub> -P	Sig.	Water level amplitude	Sig.	Water colour	Sig.
<b>Blue whitefish</b>								
CC, lag -1	<b>-0.350</b>	<b>0.025</b>	-0.035	0.830	-0.111	0.489	0.039	0.808
CC, no lag	<b>-0.304</b>	<b>0.050</b>	0.138	0.384	0.011	0.944	0.088	0.580
CC, lag +1	-0.079	0.622	0.199	0.213	0.053	0.744	0.169	0.290
<b>Lesser sparsely-rakered whitefish</b>								
CC, lag -1	-0.243	0.126	0.126	0.433	<b>-0.319</b>	<b>0.042</b>	-0.096	0.550
CC, no lag	-0.221	0.160	0.279	0.073	-0.118	0.457	-0.018	0.911
CC, lag +1	0.123	0.443	0.229	0.149	-0.225	0.158	0.044	0.781
<b>Northern densely-rakered whitefish</b>								
CC, lag -1	-0.211	0.184	-0.074	0.644	0.275	0.082	0.145	0.367
CC, no lag	-0.136	0.391	-0.077	0.629	0.264	0.091	0.182	0.250
CC, lag +1	-0.140	0.384	-0.092	0.566	0.296	0.061	0.251	0.114

burbot, did not correlate with the residual recruitment variation of any of the morphs.

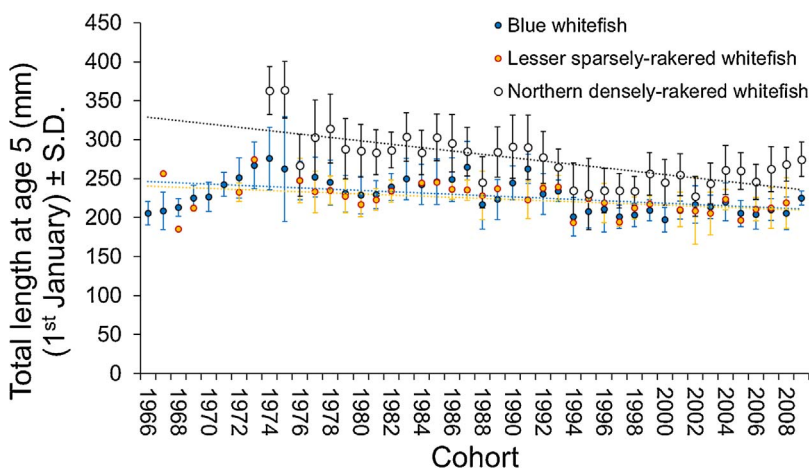
Cross-correlation estimates between surface water phosphate-phosphorous and residual recruitment variations were generally negative but only the northern densely-rakered whitefish showed a statistically significant correlation with phosphate ( $CC = -0.344$ , lag = 0,  $P = 0.028$ ). Water colour showed only a marginally significant cross-correlation with the residual recruitment of lesser sparsely-rakered whitefish with -1 lag ( $CC = 0.321$ ,  $P = 0.043$ ). Water level amplitude showed positive cross-correlation with the residual recruitment of blue whitefish ( $CC = 0.346$ , lag = 0,  $P = 0.027$ ) and lesser sparsely-rakered whitefish ( $CC = 0.392$ , lag = -1,  $P = 0.012$ ). Summer time surface water temperature did not correlate with the residual recruitment in any of the forms ( $P \geq 0.105$ ).

Total recruitment of northern densely-rakered whitefish correlated positively with the total number of stocked northern densely-rakered whitefish (Pearson's  $R = 0.383$ ,  $N = 38$ ,  $P = 0.018$ ) but the residual recruitment of northern densely-rakered whitefish showed no statistically significant cross-correlation with stockings ( $CC = 0.299$  with lag 0,  $P = 0.068$ , Fig. 3). Neither did the residual recruitment of other whitefish forms cross-correlate with the number of stocked northern densely-rakered whitefish ( $P \geq 0.288$ ).

#### 4. Discussion

Whitefish was a commercially important species in Lake Oulujärvi with the peak annual yield of 120 tons in 1993 until the recovery of the pikeperch stock in late 1990's (Vehanen et al., 2002). In 2000s, the stocked northern densely-rakered whitefish has constituted about half of the catch that has remained at the level of only 4–12 tons annually.

At the same time, pikeperch yield has increased from zero to more than 100 tons per year (Vainikka and Hyvärinen, 2012). Cohort analyses revealed that the recent decrease has not only occurred in catches, but also the estimated population sizes and recruitment of different whitefish forms have decreased while the fishing mortality rates have remained at relatively high level. Because the stocked northern densely-rakered whitefish showed very similar dynamics as the native forms also in growth, some common mechanisms likely affected the dynamics of all different whitefish forms. The most obvious environmental change was the steadily increasing summer water temperature, which also showed negative cross-correlation with the biomass of blue whitefish. Although the pikeperch recovery co-occurred with the decline of whitefish stocks, the only direct indication of a negative effect of pikeperch on whitefish was the strong negative cross-correlation between the pikeperch CPUE and the biomass of the northern densely-rakered whitefish. However, also principal component analysis on the CPUE data suggested a strong negative dependence between the whitefish CPUE and the pikeperch CPUE. The first principal component negatively dominated by the pikeperch CPUE also showed a positive cross-correlation with the total recruitment of all whitefish forms to age 0. However, while the estimated cross-correlation between the pikeperch CPUE and the residual recruitment success was negative in all whitefish forms, none of the correlations proved statistically significant. Gobin et al. (2016) proposed that the declined lake whitefish populations in Lake Huron should not be exposed to instantaneous fishing mortality rates exceeding 0.5. Compared to this, instantaneous fishing mortality rates in Lake Oulujärvi (on average  $0.62\text{--}0.73\text{ y}^{-1}$ ) may be unsustainably high in the current environment with strong pikeperch and vendace stocks, and the whitefish stock recoveries are pending on a decrease in fishing mortality rate.



**Fig. 5.** Temporal changes in the length of 5–6 years old whitefish (predicted to 1st of January at age 5) during the study period in the three whitefish forms in Lake Oulujärvi. The lines represent statistically significant linear trends over time (blue line for blue whitefish, gray line for lesser sparsely-rakered whitefish and green line for northern densely-rakered whitefish).



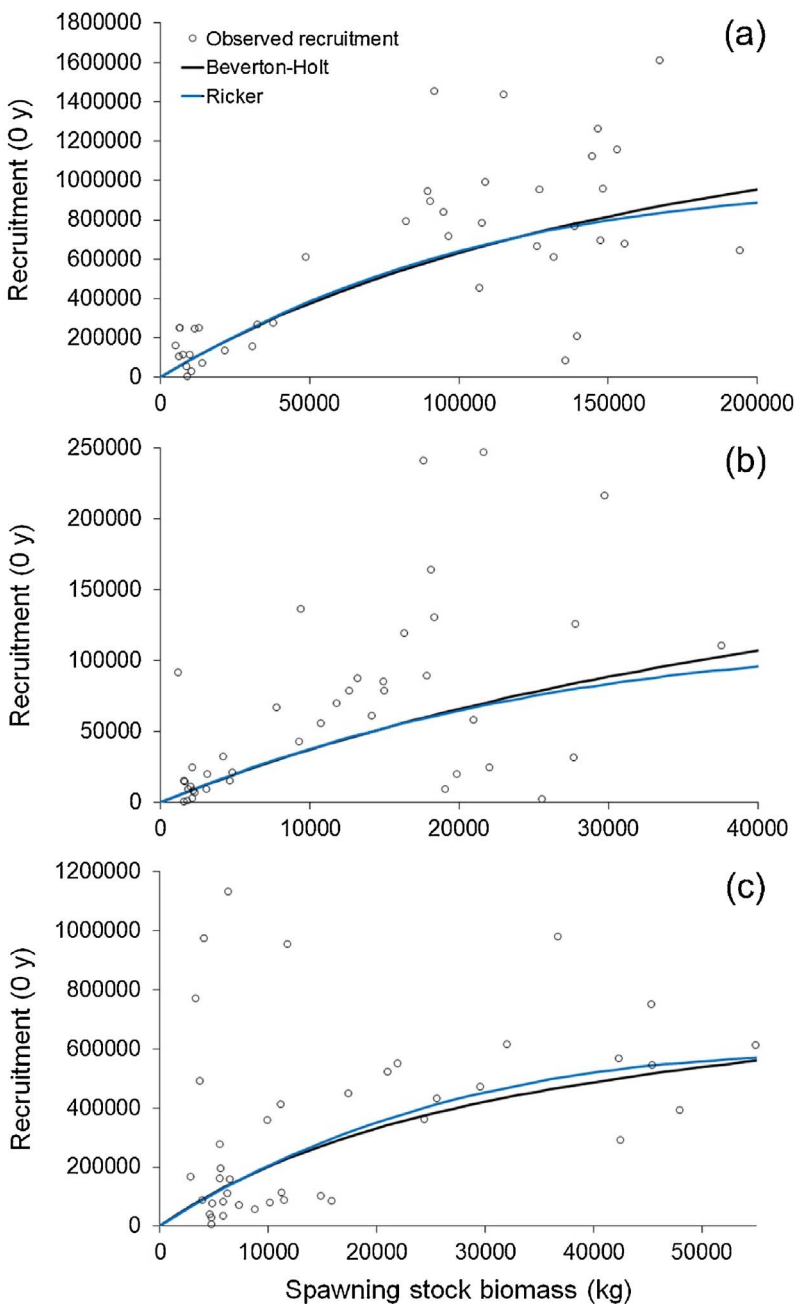


Fig. 6. Estimated stock-recruitment relationships for (a) blue whitefish, (b) lesser sparsely-rakered whitefish and 3) northern densely-rakered whitefish. The level of natural reproduction in northern densely-rakered whitefish is unknown.

**Table 5**  
Cross-correlations (CC, with minus and plus one year lags) between the fish community components (principal components 1–4) and the estimated total recruitment of whitefish forms to age 0. Statistically significant correlations are highlighted in bold.

	PC-1	Sig.	PC-2	Sig.	PC-3	Sig.	PC-4	Sig.
Blue whitefish								
CC, lag -1	<b>0.601</b>	< 0.001	<b>0.532</b>	< 0.001	-0.248	0.119	0.152	0.343
CC, no lag	<b>0.440</b>	0.004	<b>0.547</b>	< 0.001	-0.155	0.327	-0.151	0.340
CC, lag +1	<b>0.466</b>	0.002	<b>0.475</b>	0.002	-0.158	0.324	-0.159	0.322
Lesser sparsely-rakered whitefish								
CC, lag -1	0.241	0.130	0.240	0.130	-0.067	0.677	-0.023	0.886
CC, no lag	<b>0.332</b>	0.032	-0.050	0.755	-0.100	0.527	-0.203	0.197
CC, lag +1	0.240	0.130	0.234	0.140	-0.088	0.585	- <b>0.317</b>	0.044
Northern densely-rakered whitefish								
CC, lag -1	<b>0.558</b>	< 0.001	<b>0.526</b>	< 0.001	- <b>0.411</b>	0.008	0.172	0.284
CC, no lag	<b>0.511</b>	< 0.001	<b>0.524</b>	< 0.001	-0.254	0.104	-0.024	0.881
CC, lag +1	<b>0.447</b>	0.003	<b>0.537</b>	< 0.001	-0.112	0.486	-0.132	0.412

**Table 6**

Cross-correlations (CC, with minus and plus one year lags) between the residual recruitment not explained by the SSB of the respective whitefish form and CPUE of potentially interacting fishes. Statistically significant correlations are highlighted in bold.

	Pikeperch CPUE	Sig.	Perch CPUE	Sig.	Brown trout CPUE	Sig.	Roach CPUE	Sig.	Bream CPUE	Sig.
Blue whitefish										
CC, lag -1	<b>-0.330</b>	0.038	0.291	0.068	<b>0.341</b>	0.031	<b>0.400</b>	0.011	<b>-0.342</b>	0.031
CC, no lag	-0.265	0.094	-0.024	0.881	<b>0.399</b>	0.010	0.018	0.912	-0.279	0.077
CC, lag +1	-0.197	0.223	0.252	0.117	0.257	0.109	0.282	0.078	-0.057	0.725
Lesser sparsely-rakered whitefish										
CC, lag -1	-0.159	0.328	0.064	0.694	0.097	0.550	0.131	0.422	-0.221	0.170
CC, no lag	-0.112	0.486	<b>0.335</b>	0.032	0.140	0.381	<b>0.370</b>	0.017	-0.175	0.274
CC, lag +1	-0.059	0.720	<b>0.510</b>	0.001	0.050	0.760	<b>0.382</b>	0.015	0.227	0.159
Northern densely-rakered whitefish										
CC, lag -1	-0.187	0.249	0.112	0.492	-0.043	0.791	0.203	0.208	-0.301	0.059
CC, no lag	-0.155	0.333	0.278	0.078	0.062	0.700	<b>0.331</b>	0.034	-0.108	0.502
CC, lag +1	-0.061	0.710	<b>0.366</b>	0.020	0.155	0.340	<b>0.366</b>	0.020	0.033	0.838

Whitefish stocks have recently declined in many parts of the Northern Hemisphere due to multiple reasons (e.g. De Groot, 1990; Degerman et al., 2001; Gobin et al., 2016). Eutrophication has been linked with coregonid declines (Wolos et al., 1998; Kangur et al., 2007), but also re-oligotrophication of lakes can lead to declining whitefish catches and slower growth rate especially in pelagic whitefish forms (Eckmann et al., 2007). Surface water phosphate phosphorous concentration showed a declining trend in Lake Oulujärvi. However, even after the decline, Lake Oulujärvi cannot be considered oligotrophic or too low in productivity for coregonids. In addition, there are no indications of species distribution shifts (according to total catch data, see [www.kfrs.fi](http://www.kfrs.fi)) among the three main basins (Paltaselkä, Ärjänselkä and Niskanselkä) that differ in the water colour and nutrient concentrations. If nutrient-dependent food resources were limiting whitefish abundance, especially the northern densely-rakered whitefish should increase in abundance in the eutrophic Paltaselkä area and decrease in abundance in the most oligotrophic Niskanselkä area. Typically, proportions of coregonids and percids increase when the proportion of cyprinids decreases (Peltonen et al., 1999). In Lake Oulujärvi, PCA indicated a positive link between whitefish CPUE and both Eurasian perch and roach CPUE suggesting a bottom-up regulation on all of these species instead of eutrophication-induced cyprinid dominance over coregonids. Cross-correlation analyses showed very little support for negative effects arising from competition with cyprinids, as only the CPUE of bream – that is a benthic feeder – correlated negatively with the biomass of northern densely-rakered whitefish.

Invasive and introduced species can significantly shape aquatic ecosystems as has happened in The Laurentian Great Lakes due to invasion of dreissenid mussels and consequent decline in the abundance of benthic amphipod *Diporeia* spp. (Bunnell et al., 2014; Gobin et al., 2016). Lake Oulujärvi has not experienced major invasions but instead a recovery of the pikeperch stock, although a genetically alien population was used in the introductions that started on 1985 (Salminen et al., 2012). The native stock had disappeared practically completely by 1980s. Pikeperch recovery was supported by warming summer temperatures, as pikeperch recruitment is highly temperature-dependent (Heikinheimo et al., 2014). In general, pikeperch stocks have increased during past decades at the cost of Eurasian perch stocks, and pikeperch has become the predominating predatory fish in several northern European lakes (Rundberg, 1977; Kangur et al., 2007). While the whitefish constituted a significant share of pikeperch diet in 1994–1996 (Vehanen et al., 1998a), whitefish share has been marginal (0.6%) in more recent and more extensive unpublished pikeperch stomach content data ( $N = 4002$ ). However, the current sustainable pikeperch yield is estimated to be ca. 100 tons per year and the pikeperch population has been estimated to consume up to 700,000 kg of prey fish (Vainikka and Hyvärinen, 2012), more recently even up to 1.9 million kg of prey fish (Vainikka et al., 2017). Already a 0.6% share of

whitefish in pikeperch diet with the 1.9 million kg consumption estimate would mean predated whitefish biomass of 11,400 kg which is well with the level of current fisheries catches and could thus significantly impact the whitefish stocks. While we did not find statistically solid evidence for a direct predation effect on whitefish, we cannot either exclude the possibility that the estimated fishing mortality rates partially reflected increased natural mortality rates due to pikeperch predation. In order to conclusively answer if pikeperch predation directly drives whitefish population dynamics, multispecies virtual population analysis (Magnússon, 1995) with representative stomach content data would be needed. However, reaching such complete data remains a challenge for any inland fisheries system. Pikeperch stockings contributed only marginally to the pikeperch recruitment after the start of natural reproduction and were thus not analysed separately here (see Vainikka and Hyvärinen, 2012; Vainikka et al., 2017).

Compared to the magnitude of pikeperch predation, predation of whitefish by Eurasian perch, burbot and brown trout are likely mostly negligible despite burbot CPUE showed a negative cross-correlation with the biomass of lesser sparsely-rakered whitefish, and perch CPUE negatively correlated with the biomass of northern densely-rakered whitefish. Both burbot and perch predation can be mostly significant for the survival of young whitefish and especially stocked 0+ whitefish during their first year in the lake. Northern pike CPUE showed a non-significant negative cross-correlation with the biomass of native whitefish forms suggesting that there is pike predation for whitefish but this is not any major driver of the whitefish stocks (Amundsen et al., 2003). Brown trout, that relies practically entirely on stockings in Lake Oulujärvi, showed mostly positive relationships with whitefish forms suggesting dependence on similar environmental factors, and on the other hand, the abundant problem of brown trout bycatch in whitefish fisheries (Syrjänen and Valkeajärvi, 2010).

Fish population dynamics are often related to exploitation rate in heavily fished systems. Intensive fishery was blamed to be responsible for whitefish stock decline in Lake Winnipeg in 1960s through recruitment overfishing (Davidoff et al., 1973). While the fishing mortality rates estimated for 1990s were very high especially in some years they did not seem to correlate very well with the stock development. Annual catches explained only 10.6–18.2% of the variation in the estimated annual fishing mortality rates. This might be related to the inherent uncertainties in the fisheries-dependent data but also arise from unaccounted bycatch. In Fig. 3, the start of the highly varying  $F$  estimates in the beginning of 1990s for blue whitefish precedes the stock decline starting clearly a few years later. This suggests that trawl and fyke net fisheries that started on 1987 and 1984, correspondingly, may have had contributed both to the high fishing mortality rate and decline of the blue whitefish, the most abundant native whitefish form in Lake Oulujärvi. Because whitefish and vendace share similar habitats in the Lake Oulujärvi (Salojärvi, 1991b), by-catch mortality in the trawl

fishery for vendace (on which there is no direct data) might partially explain the decline of native whitefish forms in particular. However, especially in early 2000s the estimated fishing mortality rates were small, but the stock sizes low suggesting stronger driving effect for environmental reasons than for fishery-dependent reasons. Even emigration downstream to River Oulujoki might represent a potential but unlikely population sink (Vehanen et al., 1998b).

Highly size-selective gillnet fishing has been suggested and shown to induce selection and evolution towards slower growth rate in whitefish populations (Handford et al., 1977; Heikinheimo and Mikkola, 2004; et al., 2008, 2011; et al., 2008, 2011). While the fishing-mortality estimates obtained by cohort-analysis were generally relatively high, the targeted fishing pressure on whitefish has decreased in recent years due to generally larger pikeperch becoming the most important target species. Thus, the disappearance of the trend in the length-at-ages during the past 16 years (1994–2009) in the native whitefish forms and an increasing trend in the northern densely-rakered whitefish length at age 5 years may suggest two things: 1) either the ecological growth conditions have improved or 2) the total selection pattern on the growth rate has reversed due to declined fishing pressure (c.f. Edeline et al., 2007). Despite the estimated fishing mortality rates were high also in recent years, they bore large uncertainties due to the inherent inability of cohort analysis to capture very recent changes. Fishing-induced life-history changes should be more evident in maturation schedules (Jørgensen et al., 2007; Laugen et al., 2014), but unfortunately, the maturity data were too scarce for the estimation of any linear trends in maturation patterns among the whitefish forms in Lake Oulujärvi.

It is possible that pikeperch predation increases the strength of apparent competition between vendace and whitefish. Potential compensatory increase in vendace recruitment due to pikeperch predation would increase the intensity of resource competition between small vendace and small whitefish, and as such mediate the negative effect observed here as negative cross-correlation between vendace CPUE and the biomass of native whitefish forms. Despite the temporal trend of vendace CPUE was negative, the vendace population in Lake Oulujärvi shows indications of increased and more stable recruitment and generally smaller individual size than during earlier decades (Salojärvi, 1991a,b; Huusko and Hyvärinen, 2005). Vendace is more effective plankton feeder than whitefish and is supposed to outcompete it (Svardson, 1976). For example, Salojärvi (1992) concluded that high abundance of vendace was the main reason for unsuccessful whitefish stocking in the late 1970s. On the other hand, whitefish can affect vendace recruitment (Salojärvi, 1991b) through predation on vendace eggs, larvae and juveniles (Heikinheimo-Schmid, 1982; Huusko and Sutela, 1991; Korhonen and Turunen, 1991). Whether pikeperch was ultimately inducing this effect remains unclear and would require a better coverage of data also on the other major pelagic plankton feeder, smelt. However, inherently large uncertainties in fisheries-dependent data like collected in this study may have also reduced our capacity to detect statistically significant relationships suggesting that even cross-correlations that are statistically nearly significant can be ecologically relevant. Anyhow, the rapid re-establishment of pikeperch population has likely contributed to the major changes in the fish community of Lake Oulujärvi both in interaction with fisheries and directly through altered ecological interactions.

Variations in individual growth rate can reveal ecological factors that drive also population dynamics. Length at age 5 years showed highly synchronous fluctuations among all whitefish forms and a negative linear trend over the study period in all whitefish forms despite some indications of recovery during the past 10 years. Surprisingly, the correlation between total population size and the length at age 5 years was strongly positive while the negative cross-correlation estimates, suggestive of density-dependence in growth, were statistically non-significant. This suggests that rather than being strongly density-dependent (Salojärvi and Huusko, 1990), whitefish growth rate was

largely regulated by the same factors that affected the recruitment and population size. As observed by Heikinheimo et al. (2000), the plankton-feeding northern densely-rakered whitefish showed faster growth rate than the lesser sparsely-rakered whitefish or blue whitefish. Heikinheimo et al. (2000) also showed that the diet of different whitefish forms differed clearly only at old ages, which may partially explain why the lengths at relatively young age 5 showed such strong synchrony among different forms (due to niche overlap). The overall difference in the length-at-age 5 between blue whitefish and lesser sparsely-rakered whitefish was marginal (8 mm). This suggests that intensive fishing targeting already 3-years old fish is able to reduce the potential for niche differentiation among the native forms, and as such synchronize the stock development between these two forms. Therefore, fisheries impact on the whitefish forms could be relatively more divergent if fish recruited to fishing at later age (larger size) creating stronger differences in the form-specific fishing mortality.

Global climate change is predicted to eventually influence cold-water species negatively, but at first, the individual growth rates might increase at least in environments with low resource-limitation (Ficke et al., 2007). Climate-change induced increased run-off from land might also increase eutrophication (Ficke et al., 2007), and as such have indirect effects on fish communities. According to some authors (Eckmann et al., 1988) recruitment of coregonids mostly depends on density-independent factors, like wind conditions and water temperatures. More or less regular population oscillations are also common in coregonids (Holling, 1973). We detected strong density-dependence in the whitefish recruitment, indicated not only by statistically significant fit of both Beverton-Holt and Ricker recruitment curves to SSB vs. recruitment data, but also by a strong correlation between total recruitment and the first principal component that strongly reflected whitefish abundance. Both perch and roach CPUE showed a positive cross-correlation with the residual recruitment of lesser sparsely rakered whitefish suggesting that common environmental factors determine the recruitment success of these species. Henderson et al. (1983) found that lake whitefish growth during the 1st year depended on the surface water temperature. The simple mean growth-season water temperature did not directly correlate with recruitment success in Lake Oulujärvi. However, an indirect temperature effect on the recruitment of many species might explain the positive correlation of whitefish recruitment not only with perch and roach CPUE but even the lack of negative impact of pikeperch, if the environmental control was stronger than the direct predation effect. Against expectations, the annual water level amplitude did not correlate with the residual recruitment success in any of the whitefish forms. The link between the number of stocked northern densely-rakered whitefish and the recruitment of this form was surprisingly weak suggesting two things: First, northern densely-rakered whitefish might reproduce also naturally in significant numbers as must have been the case in early 1980s (Fig. 3). Second, stocking success appears to be determined more strongly by other factors than the number of fish released. Notably, the estimated recruitment decreased more than the number of stocked northern-densely rakered whitefish indicating a declined stocking success since the beginning of the 2000s (Fig. 3).

## 5. Conclusions

In conclusion, all three whitefish forms showed synchronous dynamics both in the population size and individual growth suggesting a strong environmental control that exceeded the intensity of stockings. The whitefish stocks produced a significant catch of 20–120 tons until early 2000s, when pikeperch became the most important commercial fish in Lake Oulujärvi and the whitefish catches decreased to 4–12 tons per year. Pikeperch CPUE data showed a negative cross-correlation with northern densely-rakered whitefish biomass, but no effect on whitefish recruitment was found. Individual growth rate of all whitefish forms decreased until 1994 after which the trend has disappeared or

reversed. The recovery of whitefish stocks is likely pending on a decrease in fishing (c.f. Gobin et al., 2016) and predation mortality of whitefish. Our results based on an extensive time-series of 41 years with data on multiple species exemplified that ecosystem-based management of inland fisheries must take into account both direct fishing-induced effects and indirect ecologically mediated effects. Complete understanding of indirect effects of introduced predators often requires data that are only seldom available.

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