ABSTRACT

Marjomäki, Timo J.
Recruitment variability in vendace, *Coregonus albula* (L.), and its consequences for vendace harvesting
Jyväskylä: University of Jyväskylä, 2003, 66 p.
(Jyväskylä Studies in Biological and Environmental Science,
ISSN 1456-9701; 127)
ISBN 951-39-1652-9
Yhteenveto: Muikun, *Coregonus albula* (L.), vuosiluokkien runsaudenvaihtelu ja sen vaikutukset kalastukseen
Diss.

This thesis analyses the characteristics and causes of interannual variability in vendace recruitment and its consequences for, and interactions with, vendace harvesting. The interannual variability of prerecruit mortality was high. The daily mortality during the stage 1-3 weeks after hatching was about 10% and in stage 3 weeks - recruitment about an order of magnitude lower. Yet, the stagespecific total mortalities and their variability were of the same order of magnitude. Thus, both stages had potential for determination of the year-class strength. The variability was largely caused by factors external to the population. The synchrony found in the population dynamics of proximal lakes supported this conclusion. Sparse evidence of compensatory density dependence in mortality was found between hatching and recruitment, but good evidence for compensation was found when the whole period from spawning to recruitment was studied. Considerable model and parameter uncertainty concerning the spawning stock-recruitment relationship existed and methodological biases handicapped the analysis. High larval abundance was required to produce an abundant year-class indicating a positive association between the spawning stock and recruitment in low stock level. Symptoms were found of delayed density dependent mortality induced by a previous year-class causing two year cyclicity. However, tendency for two year cyclicity was also detected for a simulated vendace population under high mortality without delayed density dependence. Observations and conceptual modelling revealed that fulltime commercial fishers diminish interannual yield and income variability by increasing fishing effort during stock decline. Fishing was stopped when the revenue per unit effort went below a certain minimum level. Simulation showed that the strategy of moderately adjusting fishing effort gained compromises of almost as high annual revenue as a constant effort strategy but with lower annual variation and lower risk to spawning stock than the strategy aiming at constant revenue. Successful reduction of variability requires lower mean fishing effort than that producing maximal sustainable revenue. No detrimental effects on pelagic fish stocks associable with fishing were found in a case study comparing zones of a lake with different intensities of trawl fishing. The results thus support high compensation capacity in vendace population dynamics. Means for regulating the number of fishing enterprises based on stock productivity was considered to be a precondition for successful attenuation of yield and revenue variability. Threshold control to secure a spawning stock sufficient to ensure sustainable fisheries was also considered necessary.

Key words: Fisheries; management; recruitment; variability; vendace.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on six original articles, which will be referred to by their Roman numerals (I-VI). Some additional data are also presented.

I   Marjomäki, T. J. Analysis of the spawning stock-recruitment relationship of vendace (*Coregonus albula* (L.)) with evaluation of alternative models, additional variables, biases and errors. Ecology of Freshwater Fish (accepted manuscript)

II   Karjalainen, J., Auvinen, H., Helminen, H., Marjomäki, T. J., Niva, T., Sarvala, J. & Viljanen, M. 2000. Unpredictability of fish recruitment: interannual variation in young-of-the-year abundance. Journal of Fish Biology 56: 837-857.

III   Marjomäki, T. J., Auvinen, H., Helminen, H., Huusko, A., Sarvala, J., Valkeajärvi, P., Viljanen, M. & Karjalainen, J. 2004. Spatial synchrony in the inter-annual population variation of vendace (*Coregonus albula* (L.)) in Finnish lakes. Annales Zoologici Fennici 41 (in press)

IV   Marjomäki, T. J., Kirjasniemi, J. & Huolila, M. 1995. The response of fisheries to decline in the vendace (*Coregonus albula* (L.)) stock of Lake Puulavesi, Finland. Archiv für Hydrobiologie. Special Issues: Advances in Limnology 46: 421-428.

V   Marjomäki, T. J. Comparison of harvest strategies for a vendace population with highly variable recruitment. Manuscript. 21 p.

VI   Marjomäki, T. J. & Huolila, M. 2001: Long-term dynamics of pelagic fish density and vendace (*Coregonus albula* (L.)) stocks in four zones of a lake differing in trawling intensity. Ecology of Freshwater Fish 10: 65-74.

RESPONSIBILITIES OF TIMO J. MARJOMÄKI IN THE JOINTLY WRITTEN ARTICLES OF THIS THESIS

II   The article is based on an original idea by prof. Juha Karjalainen who also analysed the density and growth data and wrote the article. T. J. Marjomäki did not take part in collection or preparation of larval data. He took part in statistical analysis of spatial distribution and growth of larvae as well as mortality. He was responsible for the analysis of the relationship between abundances of larvae at different stages and recruitment, and cowrote the discussion and conclusions concerning the above mentioned responsibilities.

III   T. J. Marjomäki was responsible for the idea, data analysis and majority of the manuscript preparation. The population data were collected and prepared for analysis by the author and coauthors as stated in Table 1 in III. The discussion was written jointly.

IV   T. J. Marjomäki was responsible for the idea, data collection and analysis and most of the manuscript preparation. The discussion was written jointly.

VI   T. J. Marjomäki was responsible for the idea, data collection and analysis and manuscript preparation. The coauthor assisted in collection and preparation of the data.

1   INTRODUCTION

"Erittäin suurta vähenemistä eivät vanhat kalastajat sano olevan huomattavissa muikun suhteen, ehkäkin sitä yhä useammalla pyydyksellä pyydystetään. Sillä perin huonoja kalansaalisvuosia kerrottiin aina 40-20 vuotta sitten olleen, jos taas oli hyviäkin eli samoin kuin nytkin on laita. "[1]

A. T. (1901): Kalastuksista Puulavedellä.

"From the earliest times, a characteristic feature in all branches of the fishing industry has been fluctuations in the respective yields from year to year."

Johan Hjort (1914): Fluctuations in the great fisheries of northern Europe.

Thus, the interannual fluctuation of yield has been and is still a central characteristic of both ocean and freshwater fisheries. Hjort (1914) realised that the reason for this is the spectacular variation in annual reproduction success, which leads to variation in recruitment (= number of fish of a cohort that have survived to certain age, the abundance of the earliest age at which a cohort can effectively be estimated, usually the youngest age that they enter a fishery (Myers 1998)). Hence, from the viewpoint of sustainable management of fisheries, it is essential to gain an understanding of the central question of population dynamics: Why do animal populations fluctuate as they do? (Royama 1992). For fish populations the question can be focused on the crux of the recruitment problem: to determine the magnitude and cause of density dependent and density independent components of mortality during egg, larval and juvenile stages (Myers 1995). This target illustrates well the complex nature of the recruitment process. Firstly, the causes of mortality may be multifarious,

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[1]   Regarding vendace, the old fishermen have not noticed a very great decrease, although it is being fished with ever increasing number of gears. Because it has been observed that very poor fish catch years occurred 40-20 years ago, though good years as well, that is, in the same way as presently. (Translation by T. J. Marjomäki)

A. T. (1901): On fisheries in Lake Puulavesi

some of them regulated by population density, and some density independent determined by more or less unpredictable factors external to population. Secondly, compensatory processes can potentially occur at one or more stages of the prerecruit phase and different stages are subject to different sources of density independent and density dependent mortality (e.g. Paulig 1973, Fogarty 1993).

Considering population regulation by density dependent processes and fisheries management, the most important issue to understand is the relationship between spawner abundance and subsequent recruitment (e.g. Myers 2001). Despite the fact that it is seldom clearly detectable from the time series due to a high level of unpredictable variation (e.g. Fogarty et al. 1991), this relationship sets the limits for overfishing and determines the level of compensatory density dependence in prerecruit mortality (Mace 1994, Myers et al. 1994). (Compensatory density dependence is a feedback from population density that counteracts a population change and therefore acts to stabilise population by increasing survival and/or growth during a population decline and decreasing them during population increase, opposite to the depensatory case (Royama 1992). For fisheries, the consequences of over or under estimating compensation and compensatory reserve are serious. These include risk of population decline, unnecessary spending of monetary resources, and unnecessary restrictions on fishery and energy generation (Rose et al. 2001).

The variability of recruitment, and thus also yield, is a major source of uncertainty in fisheries management having wide-ranging influences on the fisheries system (as discussed by Sipponen 1999). The nature of this unpredictable variation sets margins on the fisheries from the biological subsystem. For the fisheries to be sustainable, large recruitment variation demands flexibility and adaptability of the socioeconomical subsystem, the ability to withstand or absorb the variation. These preconditions must be recognised also by the political administrative subsystem in its actions to ensure adaptability. On the other hand, fishing itself can affect the biological subsystem and hence its own scope of action. Fishing can drive the dynamics of the resource by inducing a major component of the mortality and regulate the spawning stock level and competition. Therefore, it is important to understand the extent that harvesting strategy and magnitude of fishing determine the dynamics and especially the interannual variability of yield (e.g. Laevastu & Favorite 1988, Haddon 2001).

However, despite often being viewed as a nuisance by fisheries and researchers of population regulation, the interannual recruitment variability in general, and occasional strong pulses of recruitment in particular, may also be of crucial importance for persistence of populations in a stochastic environment (Fogarty 1993 and references therein).

For vendace (*Coregonus albula* (L.)), the most important target of commercial fisheries in Finnish inland waters, the large variation in recruitment has been demonstrated based on age determination from scales as early as 1919 by T. H. Järvi (Järvi 1919). In vendace, being a short lived species, the variation is reflected strongly on yield (Viljanen 1988a). Besides theoretical interest, recruitment variation is also an issue for the fisheries. According to an inquiry

by Salmi (1998) Finnish commercial inland fishers considered the variability of fish stocks to be their greatest difficulty. The fishers have adopted several strategies to cope with this variability, such as regulation of fishing effort, changing fishing method, target species and fishing grounds, combination with other incomes, and diversifying by forward integration closer to the needs of consumers *etc.* (*e.g.* Salmi et al. 1999, Sipponen et al. 1999).

Due to long a tradition of vendace population monitoring and research, several typical characteristics of population variability can be outlined. One of the main features is the high degree of unpredictability, which implies the effect of external factors (e.g. Viljanen 1988a). An abundant year-class emerges typically once in every two to four years. Many associations between recruitment and environmental factors have been suggested (e.g. Järvi 1942, Auvinen 1988, Helminen & Sarvala 1994). Another typical feature is the occasional appearance of long-term sequences of very poor year-classes (e.g. Järvi 1942) in larger areas synchronously (Valkeajärvi et al. 2002). Various reasons, from fluctuation of predator stocks (Auvinen 1994, Heikinheimo 2001, Valkeajärvi et al. 2002, Valkeajärvi & Marjomäki 2003) to natural cyclicity *e.g.* solar activity (Lind & Peiponen 1988), have been suggested to cause this. An interesting feature, in conflict with the strong effect of external factors, and merely implying strong regulation, is the tendency for cyclical variation, especially a two year cycle (e.g. Hamrin & Persson 1986, Helminen et al. 1993a, Auvinen et al. 2000). Asymmetrical intraspecific competition has been suggested to be the reason for this (Hamrin & Persson 1986). Considerable intraspecific competition is unquestionable as the growth of vendace is strongly density dependent (Viljanen 1986, Helminen et al. 1993a, Marjomäki & Kirjasniemi 1995, Valkeajärvi & Bagge 1995, Auvinen et al. 2000). Overall, the density dependent growth and persistence of the populations confirm (Shepherd & Cushing 1990, Royama 1992) that despite the large random variation density dependent regulation also plays a role in vendace population dynamics.

Fishing has been suggested to affect year-class fluctuation of vendace (e.g. Auvinen 1987, 1994, Salojärvi 1987, Valtonen & Marjomäki 1988, Helminen 1994, Helminen et al. 2002). Its most extreme manifestation, recruitment overfishing, has been demonstrated to cause a prolonged decline in the heavily exploited stock of Lake Pyhäjärvi (southwest Finland) (Sarvala & Helminen 2002) and the need for a precautionary principle in harvesting has been called for (Helminen et al. 1997). The above mentioned two year cyclicity has been suggested to be typical of strongly exploited populations, and the break of the cycle could be due to decline in the exploitation rate (Auvinen 1994, Helminen 1994). The stock-recruitment relationship has been suggested to be dome shaped by many authors (Auvinen 1978, Viljanen 1988a, Valtonen & Marjomäki 1988, Salojärvi 1991a, Salmi & Huusko 1995 a, b). Hence, It has also been suggested that by optimising the spawning stock level one could dampen the fluctuations or increase the probability of an abundant year-class (e.g. Valtonen & Marjomäki 1988, Salmi & Huusko 1995 b).

2   OBJECTIVES

This study analyses the characteristics and causes of the variability of vendace recruitment and its effects on and interactions with vendace harvesting.

Firstly, the focus was on the dependence of the vendace recruitment process on density (population regulation) and more or less unpredictable external factors. The specific issues addressed were:

i) timing and density dependence of mortality of prerecruit larvae and juveniles,

ii) existence and scale of spatial synchrony in interannual recruitment variation which implies the effect of external factors and

iii) relationships between spawning stock and recruitment. In this context, unpredictability, parameter and model uncertainties and methodological biases were analysed.

Further, recruitment variation gives rise to a bidirectional question concerning vendace harvesting:

i) From the direction of fish population, how are large population fluctuations reflected in the dynamics of fisheries? The treatment of this question is intentionally simplistic aiming only to outline some general margins determining the relationship between stock density and fishing effort. Thorough socioeconomical analysis is beyond the scope of this study.

ii) From the direction of fishers, the aim was to use modelling to analyse the impact that different stock size dependent harvest strategies would have on the stock dynamic and their own scope of action.

Finally, the intention was to deduce some preconditions that the stock fluctuations and adaptability of fisheries impose on fisheries assessment and management, in order to improve sustainability of fisheries.

3 MATERIALS AND METHODS

The general aspects of the materials and methods used in this study will be presented here. Certain detailed elements are given in each of the original papers.

3.1 Study lakes

Papers I, IV, and VI are based solely on data collected since 1984 from Lake Puulavesi in central Finland (Fig. 1). Lake Puulavesi covers an area of 325 km^2. The data were collected from a 200 km^2 sector of the lake (Fig. 1 in VI). Lake Puulavesi is oligotrophic, with a total phosphorus content of 3-7 µg l^{-1} and colour content of 15-20 Pt mg l^{-1}. The pelagic fish assemblage consists mainly of vendace and smelt (*Osmerus eperlanus* (L.)), whereas the populations of perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* (L.)) in pelagic areas are negligible. The lake has been stocked with brown trout (*Salmo trutta* L.), landlocked salmon (*S. salar* L.), pikeperch (*Sander lucioperca* (L.)) and whitefish (*Coregonus lavaretus* (L.) *s.l.*) during the study period.

The vendace data for paper II were collected from lakes Pyhäjärvi (SW Finland), Puruvesi (Hummonselkä and Harvanselkä), Paasivesi, Pyhäselkä, Onkamo, and Kitka (Fig. 1). Details on hydrological and limnological characteristics, and on vendace are given in Table I in II.

The data for paper III were collected from 21 Finnish lakes or lake basins (Table 1, Fig. 1).

TABLE 1   Study lakes for paper III, years of population data, and data source. Lakes in Fig. 1.

Lake	Population data from years			Data sources
	Spawning stock biomass	Newly hatched larvae	Recruitment	
Yli-Kitka	70-90	95-98, 99[1]	71-91	Salmi & Huusko (1995a), II
Kiitämö	70-90		71-91	Salmi & Huusko (1995a)
Kirpistö	71-90		71-91	Salmi & Huusko (1995a)
Muojärvi	70-90		71-91	Salmi & Huusko (1995a)
Kuusamojärvi	71-90		71-91	Salmi & Huusko (1995a)
Kostonjärvi	76-90		77-91	Salmi & Huusko (1995a)
Kerojärvi	74-90		75-91	Salmi & Huusko (1995a)
Irnijärvi	70-90		71-91	Salmi & Huusko (1995a)
Oulujärvi	72-88		73-89	Salojärvi (1991b)
Lentua			84-94	Huusko & Sutela (1998a)
Suomunjärvi	74-86, 88-92, 94-02		75-86, 88-92, 94-02	Viljanen et al. 2003
Pohjois-Konnevesi	78-98		85-99	P. Valkeajärvi, unpublished data
Etelä-Konnevesi	71-00		71-97	Valkeajärvi & Marjomäki (2003)
Onkamo	80-96		80-97	Viljanen (1988a), Auvinen et al. (2000), II
Paasivesi		80-85, 93, 96-98, 99-02[1]	85-98	II
Puruvesi, Hummonselkä		89-98, 99-02[1]	77, 79, 83-84, 87-88, 90-97	II
Puruvesi, Harvanselkä		92-98, 99-02[1]	77-97	P. Valkeajärvi, unpublished data
Pyhäjärvi, south-east Finland	77-89[2]	89-98, 99-02[1]	77-90	Auvinen & Auvinen (1994)
Puula	82-96		83-95, 96[1]	I
Päijänne, Tehinselkä	83-00[1]		82-96	P. Valkeajärvi, unpublished data
Pyhäjärvi, south-west Finland	80-00[1]	85-97, 98-02[1]	71-96, 97-00[1]	Helminen et al. (1997)

[1] previously unpublished data
[2] population fecundity estimate
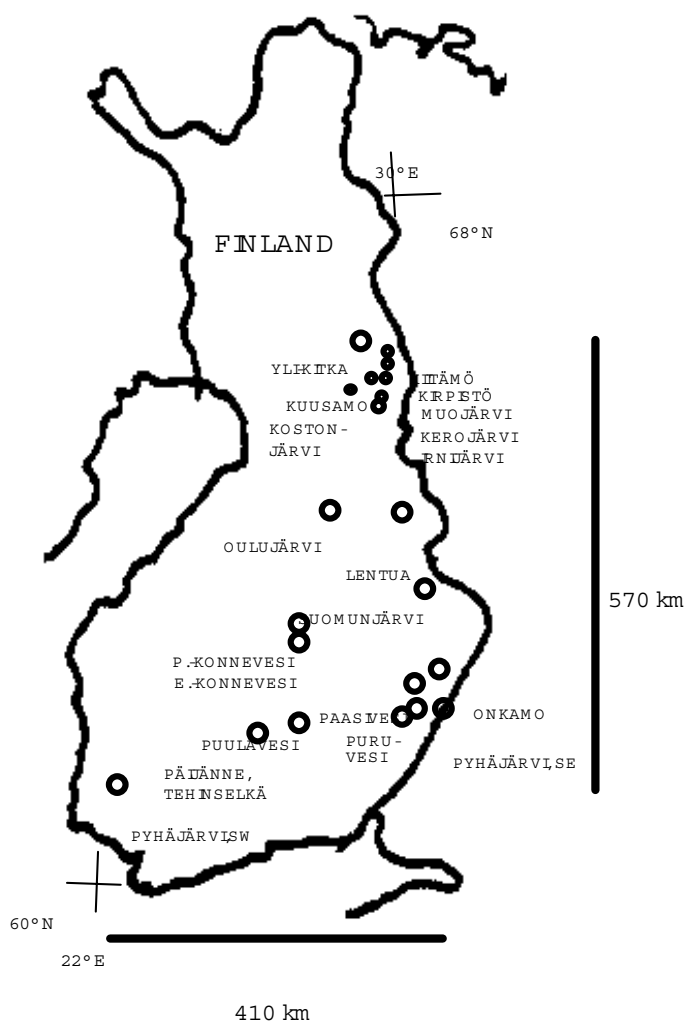
FIGURE 1   Study lakes.

3.2   Vendace abundance

3.2.1   Larval density and mortality (II, III)

The total number of vendace larvae was estimated using consistent sampling procedures and equipment (Karjalainen et al. 1998) in all lakes except Lake Konnevesi. A stratified random sampling design was applied (II). Samples were collected from four horizontal strata (depth zones). Zone 1, shallow water from shoreline to a depth of 0.5 m, samples gathered with a tube net. Zone 2 (0.5-1 m), defined according to 0.5 and 1 m depth curves, samples gathered with Bongo nets attached to a boat. Zone 3 (1-2 m), defined according to 1 and 2 m depth curves, samples gathered as in zone 2. Zone 4 covered the central pelagic area deeper than 2 m, and samples were gathered as in zones 2 and 3, except for lakes Puruvesi and Paasivesi where larval samples were taken from the vertical depth layers 0-1 and 1-2 m with a pair of Bongo nets pushed in front a vessel

and from the depth layers 2-3, 3-4 and 4-6 m with Bongo nets pulled behind the vessel. Within each sampling stratum samples were randomised around the lake. The start point of each tow was randomised. The nets were towed along a zigzag route between inner and outer borders of the zone in zones 1-3. In zone 4, 1X1 km randomly sampled squares determined the borders of each tow. All fish caught were preserved in the field with 1:1 mixture of 70 % ethanol and 1 % formalin.

In all zones, the volume of each haul was measured by a flowmeter and catches were converted to sample abundance per 100 m^3 according to the volume of each haul. To estimate total number of larval vendace in lakes Pyhäjärvi, Onkamo and Kitka, pelagic surface (from 0-0.6 m below the surface) densities from these lakes were multiplied by factor of 2, which was based on the vertical distribution data from the pelagic zones of lakes Puruvesi and Paasivesi.

Larval sampling started in the first week after ice-off and the sample schedule followed the arrival of spring. Mortality between first week and third week after ice-off was estimated directly from total abundance estimates.

The fish were counted and their species identified in the laboratory (Karjalainen et al. 1992). Total lengths and preserved fresh masses of the larvae were measured from random subsamples of the population samples. The growth rate between the first and third week after ice-off was estimated (II).

In Lake Konnevesi, larval sampling was carried out with a shore bag seine (mesh size 1 mm) from 1984 to 1998 in 13 fixed sites in the littoral area around the lake. The samples were collected in May about one week after ice-off. In each site three hauls were done (about 100 m^2 haul^{-1}) (Valkeajärvi & Bagge 1995). Since 1999 bongo netting has been carried out with a method consistent with the other lakes.

3.2.2 Spawning stock and recruitment estimates (I, II, III)

Number of young-of-the-year vendace recruitment indices after the first growing season in autumn-winter, and spawning stock indices in the previous autumn, were produced by various methods described in detail in references in Table 1 and II. Most commonly the estimates were based on yield per unit effort and random catch samples from seine fishing. Exceptionally, in Lake Puruvesi and partly in Lake Pyhäjärvi (SW Finland) the estimates of recruitment were based on a regression of fish length after the first growing season against abundance (Helminen et al. 1993a). In Lake Konnevesi the indices were estimated from autumn gill net catch per unit effort (Valkeajärvi & Marjomäki 2003).

Absolute abundance estimates of recruits (individuals ha^{-1}) and spawning stock biomass (kg ha^{-1}) for lakes Pyhäjärvi (SW Finland) Puruvesi and Paasivesi were calculated by the depletion method (Carle & Strub 1978, Helminen et al. 1993b, Auvinen & Jurvelius 1994). In Lake Puulavesi the recruitment and spawning biomass indices were converted to absolute (ha^{-1}) estimates by a ratio between the indices and absolute density estimates from echo sounding (I, details in Marjomäki & Huolila 1995).

3.2.3 Pelagic fish density in Lake Puulavesi (VI)

Since 1986, the pelagic fish density in Lake Puulavesi was estimated annually using echo sounding. The data were collected with a sphere calibrated SIMRAD EY-M echo sounder and a 70-24-F single-beam transducer (technical details in Marjomäki & Huolila 1995 and VI) and analysed with the Hydroacoustic Data Acquisition System (HADAS, Lindem Data Acquisition). The system produced fish density estimates and target strength distribution using the modified Craig & Forbes (1969) method.

The survey was carried out during four nights in mid August from 2.5 h after sunset to 1 h before sunrise. Fish echoes were very seldom detected in areas shallower than 10 m. Therefore, the analysis was restricted to areas with bottom depth deeper than this. The density estimation was carried out according to two way stratified sampling design. The first stratification was based on different basins. Second, eight of the basins were further stratified by depth structure into 10-20 m deep and >20 m deep areas. The echo sounding transect routes were set into different strata according to location possibilities, sailing safety and coverage of the deeper parts of the stratum.

The echo sounding estimate of fish density (individuals ha^{-1}) in a depth stratified basin was calculated by area weighted mean of mean densities of the two depth strata. For an unstratified basin, a simple average fish density was used. The mean density of a certain >10 m deep zone of the lake consisting of many surveyed basins was estimated by a >10 m deep area weighted mean of mean densities in different basins (details and equations in VI).

3.3   Vendace fishing data from Lake Puulavesi (I, III, IV, VI)

3.3.1 Data sources

In 1984-1996, seine fishing yield and effort data were obtained from the daily fishing records of 4-13 and annual postal inquiries of 22-28 seining units, the coverage being 55-75 % of the seining units. Data on domestic and recreational fishing were obtained by annual postal inquiry sent to a random sample of >100 households which had purchased fishing licences for the lake, the coverage being >10 % of all domestic and recreational fishers using equipment requiring local license (IV). The trawling data were obtained from daily fishing records and interviews with 1-3 trawling units and postal inquiry to 1-3 units, the coverage being 100 %. The statistics for commercial gill netting were obtained by postal inquiries and personal interviews.

To assess the response strategies of the fishers to yield fluctuation, and the limits for their operation, an additional postal inquiry was sent to all trawling and seining units and commercial gill net fishers for vendace in Lake Puulavesi at the beginning of 1998, the percentage of response being 100, 70 and 100, respectively. Previously unpublished results are presented in this thesis.

3.3.2 Fishing statistics

In the analysis of the fishery response to decline in the vendace stock (IV) the average effort (E) of the summer (May-August) and autumn (September-December) seining units, as well as subsistence gill net fishers was estimated by

$$E = \Sigma\, f * n^{-1}$$

where

  $\Sigma\, f$ = the sum of efforts of separate fishers
  n = the number of fishers

  The unit of effort in summer and autumn seining was one seine haul, in winter seining a 100 m of haul and in gill net fishing one gill net day. The average yield per unit effort (YPUE) was estimated by

$$YPUE = \Sigma\, Y * (\Sigma\, f)^{-1}$$

where

  $\Sigma\, Y$ = the sum of yields of separate fishers
  $\Sigma\, f$ = the sum of efforts of separate fishers.

The YPUE and f were calculated separately for two commercial gill net fishers for the period June-October.
  One hectare swept by trawl was used as a unit of trawling effort. Only the marketable yield of the trawl was taken into account, and monthly YPUE and fishing effort were calculated for the period June-September. If fishing was started after the beginning of June due to late ice-off or if there were periods of no fishing because of equipment breakdown, the effort data were corrected for whole month periods.
  In VI, year in the yield and effort statistics were determined from August 15 to August 14 of the following year. Total effort of all trawling units was used as the annual index of trawling intensity. The YPUE of trawl (kg ha^{-1}) in August-September was calculated from daily fishing records of one trawling unit fishing in a certain zone of the lake and another for the other two trawling zones. The YPUE was also divided into young-of-the-year and older fish by their proportions in trawl catch samples. The YPUE for autumn seining was calculated separately for each seining unit and converted relative to the maximum.
  In I and VI the vendace population biomass index was based on the average standardised autumn YPUEs of different seining units. The standardisation was done to remove the effect of seine width and different cod-end structures (Marjomäki & Huolila 1995). The relative change in biomass

from year to year was then estimated by the ratio of mean YPUEs in consecutive years for the seining units that fished in both years.

A simplistic graphical model called here "The Sustainable Operation Window" was developed to outline the margins affecting a fishing enterprise's ability to counteract stock fluctuations by effort adjustment (Fig. 2). The window was defined as a two dimensional set of the realisable pairs of x = (yield per unit effort) and y = (daily fishing effort where revenue is greater than costs). The essential variables defining the frames of this window are maximal potential daily fishing effort, maximal constant daily market demand, fish price and fixed and variable costs of fishing.
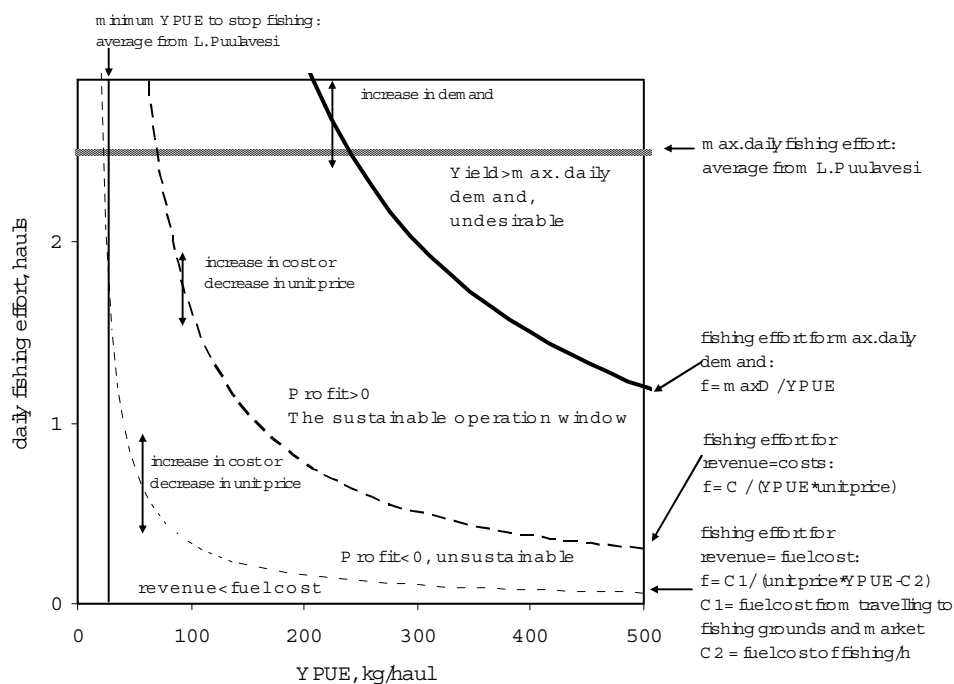
FIGURE 2   The components of The Sustainable Operation Window. The equations used are given by each component. YPUE = yield per unit effort, C = cost, f = effort.

A parameter set collected from the fisheries in Lake Puulavesi for 1997 and some values considered typical of vendace fishing were used to illustrate the shape of the operation window of trawl, seine and gill net fishing enterprises. The Lake Puulavesi parameters were collected by a postal inquiry sent to all the trawl and seine and commercial gill net fishers on the lake. The statistics of trawling are based on 2 trawling units, those of seining on 9 units with at least 15 % of annual income from fishing, 7 of which fished in winter also, and those of gill netting to 5 fishers. The average values of different variables were used in generating the operation windows.

The annual fixed costs of a fishing unit were estimated as

$$C_{fix} = C_{lic} + 0.2 \, \Sigma(C_i \, p_i)$$

where

C_{lic}=cost of fishing licences

$\Sigma(C_i{}^*p_i)$=sum of the values of fishing property items weighted by
percentage of their fishing use.

The estimates of fish price were based on interviews with fishers and the seasonal variation of price (e.g. Finnish Game and Fisheries Research Institute 1998). The price of gill net catch was higher due to larger size of fish, consumer oriented marketing and value gained from roe separation.

3.4 Recruitment models (I, II, III)

3.4.1 Statistical analysis

The linear and three nonlinear models by Cushing (1971), Ricker (1954) and Beverton & Holt (1957) (I) were applied to the spawning stock-recruitment data (I, III), first week-third week after ice-off larval abundance data and third week larval abundance-recruitment data (II).

The random component ε of the models was assumed to be log-normally distributed, so that

$$\ln(y)=\ln[f(x)]+ \varepsilon, \; \varepsilon \sim N(0,\delta^2).$$

The parameters of the ln transformed models were estimated using the iterative least squares method. The fitting and comparison of the models was accomplished following the procedures described by Iles (1994). The judgement of the suitability of the model was also based on the significance and the conditions for acceptability (Table 1 in I) of the parameter estimates.

For Lake Puulavesi data (I), the Spearman correlation coefficients between additional variables and recruitment, as well as the residuals of S-R models were calculated. In cases of significant correlation the additional variable was incorporated in the S-R model assuming multiplicativity of the effects. Two types of the coefficient of determination r^2 were calculated for every model fitted (I), the standard r^2 relative to constant recruitment and r^2 relative to the H_0-hypothesis of the proportional S-R model. Both r^2 were also adjusted for the number of parameters in each model.

3.4.2 Simulation exercises (I)

The biases introduced by time series and measurement errors were evaluated by Monte Carlo simulation. The dynamics of an age structured vendace population model including density dependent growth (details in I) was simulated using the Ricker and Cushing recruitment functions with various recruitment model parameter sets. The random components of the recruitment

model (ϕ) were assumed to be independent and log-normally distributed with mean=0 and s.d.=1.3. In order to keep the maximum number of recruits at a realistic level and the distribution of values of ϕ symmetrical, the range of the values of ϕ was limited to ± 2.0 (range of e^{ϕ} from 0.135 to 7.39) by forcing any values > 2 and < -2 to 2 and -2, respectively.

The measurement errors of spawning biomass (S) and recruitment (R) were assumed multiplicative and the estimates S_e and R_e were simulated from the simulated "exact" values by

$$S_e = S^* e^{\tau} \qquad \tau \sim N(0, \delta^2_{\tau})$$
$$R_e = R^* e^{\upsilon} \qquad \upsilon \sim N(0, \delta^2_{\upsilon}).$$

It was assumed that τ and υ are independent of each other. Three levels of $\delta_{\tau} = \delta_{\upsilon}$ were applied.

The simulation was started from the initial values of variables typical for Lake Puulavesi. With each combination of S-R model parameters (3 sets) and measurement error level (3 levels), at least 10 000 S and R data sets of 128 years were simulated. The first 100 years were used to "warm up" the simulator so that in year 101 the values of the population state variables were independent of their initial state. The parameters of both the Ricker and the Cushing S-R functions were then estimated for the next 14 and 28 years from linearised models by linear least squares regression, and the parameter estimates and s.e. of estimates were stored. Also, the estimated residual sums of squares of the models were compared with each other and with the linear recruitment model by F-test. Over compensation was inferred if the estimate of β in the Ricker model was positive and either the sum of squared errors was lower for the Ricker than the Cushing model or the Cushing model parameter γ was negative. The percentiles of at least 10 000 estimates of recruitment model parameters and test results were compared.

3.5   Analysis of spatial synchrony in population variation (III)

Young-of-the-year recruit density in autumn-winter, spawning stock biomass indices in autumn and abundance of newly hatched vendace larvae in spring were assembled from 21, 17 and 7 lakes or lake basins, respectively for the period from 1970 to 2002 (Table 1, Fig. 1).

The data analysis closely followed the methods used by Myers et al. (1997a). Prior to the analysis, all the time series of vendace population indices were ln-transformed. The Pearson product moment correlation coefficient was used as an index of synchrony in interannual variation for each pair of time series i and j which overlapped temporally by at least five years. For 17 recruitment series, the density dependent components from the recruitment (R) series were removed by fitting linear proportionality, the Cushing (1971) or the Ricker (1954) recruitment model, depending on which produced the lowest

error mean square, to ln(R) by iterative least squares fitting and correlated the residuals from these regressions. Lag one autocorrelation of residuals was also calculated and, in the case of Pyhäjärvi eastern Finland, a significant negative autocorrelation was removed by regression before calculating the model residuals.

Separately for each population index, the distribution of the mean correlation was simulated, assuming random variation of the time series by producing 5 000 sets of data of normally distributed random numbers, temporally matching the real data. Then, all the correlations for pairs i and j and their mean were calculated. The significance of observed mean correlations of population indices were then evaluated against the simulated distribution assuming random variation, i.e. no synchrony.

A simple estimate of the spatial scale of synchrony in two time series is the distance over which their correlation $r_{i,j}$ is reduced by a factor e^{-1}, i.e., the exponential decay rate or the e-folding scale (Myers et al. 1997). To estimate this, the following model was fitted by iterative least squares:

$$r_{i,j} = r_0 * \exp(-D * v^{-1})$$

where r_0 is the correlation between two populations at zero separation, v is the e-folding scale and D is the distance between the populations in kilometres (D_T), the north-south vector (D_N) or east-west vector (D_E) of this distance. Max(r_0) = 1 assuming no measurement error in time series. If the estimated r_0 was greater than one the fitting was repeated by forcing r_0=1.

Also, to take into account that some correlation-distance relationships might have a "shoulder", the following model was fitted

$$r_{i,j} = r'_0 * \exp(-0.5 * (D * v^{-1})^2)$$

where v' is the standard deviation of normal distribution.

The analysis was repeated for selected data where dispersal of vendace or its predators was considered improbable (see Table 1 in III).

Mean air temperature from nine weather stations (data from Finnish Meteorological Institute) during the first four weeks after the ice break date in a close by lake (data from Finnish Environment Institute) was used as an index of temperature conditions affecting prerecruit vendace. The data used were from years 1974-1989. The treatment and analysis of mean temperature data were similar to that of vendace data except that temperature data were not ln-transformed.

3.6 Comparison of harvest strategies (V)

Three different harvest strategies for a trawl type fishery, 1) constant revenue, 2) constant effort and 3) an intermediate autoregulative strategy aiming at reduction of revenue variation, each incorporating three alternative minimum threshold levels of monthly revenue to stop fishing were compared by applying Monte Carlo simulation.

An age structured population model, updated at the discrete time units of one month, was applied. The model structure incorporated density dependent growth rate during summer months and weight loss during winter, age specific instantaneous natural mortality, size dependent value of fish and instantaneous fishing mortality as a function of size dependent catchability. Fishing effort which was dependent on revenue per unit effort (U_m) in the beginning of each month

$$f = a * U_m^{-b} \qquad \text{if } U_m > U_T$$
$$f = 0 \qquad \text{if } U_m \bullet U_T$$

where U_T = threshold level of U_m. Three threshold levels were used: 20, 40 and 80 revenue units hour^{-1} of trawling. Three different values for b were considered:

> b=0 =>f=a   constant effort strategy, revenue relative to U
> b=0.5   increasing f with decreasing U, slower decrease in revenue than in U
> b=1 =>revenue=a   semi constant revenue, increase in f with decrease in U.

The number of recruits was simulated by the Ricker and Cushing recruitment functions. Also, the negative dependence between consecutive recruitment was simulated by including a hypothetical dependence into the S-R relationship. The random component of the recruitment ε was assumed to be log-normal with mean 0 and standard deviation of 0, 0.6 or 1.2. The range of the values of ε was truncated to ± 1.7 in order to keep the maximum number of recruits within the range observed in nature.

The criteria for comparing performance of different strategies were: the mean annual revenue, the coefficient of variation of revenue, mean and coefficient of variation (C.V.) of spawning population biomass, the proportion of years when spawning population is below 200 kg km^{-2}, mean and C.V. of recruitment, mean and C.V. of annual effort, maximum monthly effort and maximum theoretical effort needed to apply a certain strategy. One possible tradeoff between mean revenue (ρ) and its variation (S.D.=standard deviation) was illustrated by an objective function (O)

$$O = \text{mean}(\rho)*(1-\lambda) - \lambda*\text{S.D.}(\rho), \qquad \text{(Quinn et al. 1990)}$$

where λ = 0.5.

The number of recruitment sequences where $r_t > r_{t+1} < r_{t+2} > r_{t+3} < r_{t+4} > r_{t+5}$ (t=1...100) was used as index of tendency for two year cyclicity of recruitment. The results were evaluated against the expected number of sequences (8) in a sequence of normally distributed random variables.

With each parameter combination 150 years were simulated. The simulator was allowed to "warm up" the first 50 years after which the state

parameters were independent of the initial values. The values of the criterion variables were recorded for each run. The procedure was repeated 500 times and the medians of these values, each resembling a 100 year sequence, were used in analysis. This was repeated with different levels of fishing effort or target constant revenue and the dependence of the criterion variables on the mean annual income was analysed. Zero discount rate was used in all cases.

4 RESULTS AND DISCUSSION

4.1 The recruitment process in vendace

In this section the current knowledge on the vendace recruitment process is reviewed and the results in papers I, II and III are evaluated in relation to this. A selection of field studies analysing the association between various factors and recruitment from time series with correlation/regression methods is summarised in Fig. 3. Both significant and insignificant tested associations are presented but considering the representativeness of the data the possibility of publishing bias (e.g. Knight 2003) must always be kept in mind. When evaluating these associations, the findings of experimental studies and detailed field studies on the ecology of prerecruit vendace are presented.

First, the correlative approach commonly used in recruitment studies is briefly evaluated. Then, the studies examining the level and interannual mortality variability of vendace during different prerecruit life stages are presented. Next the roles of density dependent and independent processes in population dynamics, and hypotheses and theory of their operation mechanisms are discussed in more detail. Finally, conclusions and suggestions for further studies are given. The effects of fishing are discussed in section 4.2.

4.1.1 Correlative studies: approaches, weaknesses and interpretation

A correlative empirical approach has been widely used in analysis of fish recruitment variation, also in the case of vendace (Fig. 3). To begin with, it is important to note that the correlations measure association and thus can not be viewed as a test of a previously stated hypothesis. It does not demonstrate "cause and effect". At best, correlations serve as a basis for establishing a future hypothesis (Sissenwine 1984). Further, considering statistical testing of hypotheses, it must be noted that typically high residual variability in recruitment severely limits the power of tests (Hinrichsen 2002) .

In correlative studies of vendace recruitment, two different approaches have been used concerning recruitment process (Fig. 3): the external factors have been correlated either directly with the index of recruitment (R) or with the index of prerecruit survival ($S_{prerecruit}$).

A weakness of the first approach is that, besides being obviously a function of many other essential factors, recruitment is always a function, being possibly strongly nonlinear, of the population fecundity (or spawner abundance as its index). This may be, among measurement errors, a significant source of recruitment variation masking the effects of other factors and should be always included if possible (Myers 1998).

In the second approach, studying the prerecruit (between spawning in the autumn and the recruitment in the next autumn-winter) survival, the effect of spawning stock is taken into account. In Fig. 3 this class of studies includes firstly the studies where the survival is estimated directly from density estimates at various life stages. In that case, strong density dependence of survival can still affect the evaluation. A source of severe bias in this method is the fact that the dependent variable is a function of the independent variable (survival=density(t2)*density(t1)$^{-1}$). Thus, measurement error in independent variable induces artificial negative dependence between the abundance estimates and survival, implying compensatory mortality. A second group is formed by studies where the density dependence in a recruitment process is modelled by a spawning stock (S)-recruitment (R)-model. (These models of the form R=f(S) can always be transformed to estimate survival by dividing the equation by S). Yet, this approach is not without problems either. Firstly, the S-R model fitting typically suffers from considerable model and parameter uncertainty (I). Secondly, the parameter estimates of certain models and parameter combinations are likely to suffer from biases caused by measurement errors (Walters & Ludwig 1981, Kehler et al. 2002, I) and the time series nature of the data (Walters 1985, Royama 1992, I). Due to these biases, compensatory density dependence can be overestimated severely (I).

Prerecruit survival in different life stages has been analysed by estimating the association between densities in different life stages by linear correlation (Fig. 3) and various models describing the density dependence in survival (II). Concerning the interpretation of linear correlation analysis, it should be noted that low significance of correlation coefficient may emerge as a consequence of two different phenomena: either high level of unexplained variation in survival (error variance) or weak association between the variables (low covariance), which itself may be due to strong density dependent regulation and low level of unpredictable variation. Further, as in S-R models, these results suffer from bias by measurement error of the independent variable (the former of the two life stages compared) (e.g. Bradford 1992). The bias from the time series nature of the data may also be involved as long as the density in a certain life stage (x-axis) depends on some previous value of the lifestage (y-axis). Success of the analysis will also depend on the range of the initial abundances (e.g. Hutchings & Myers 1994).
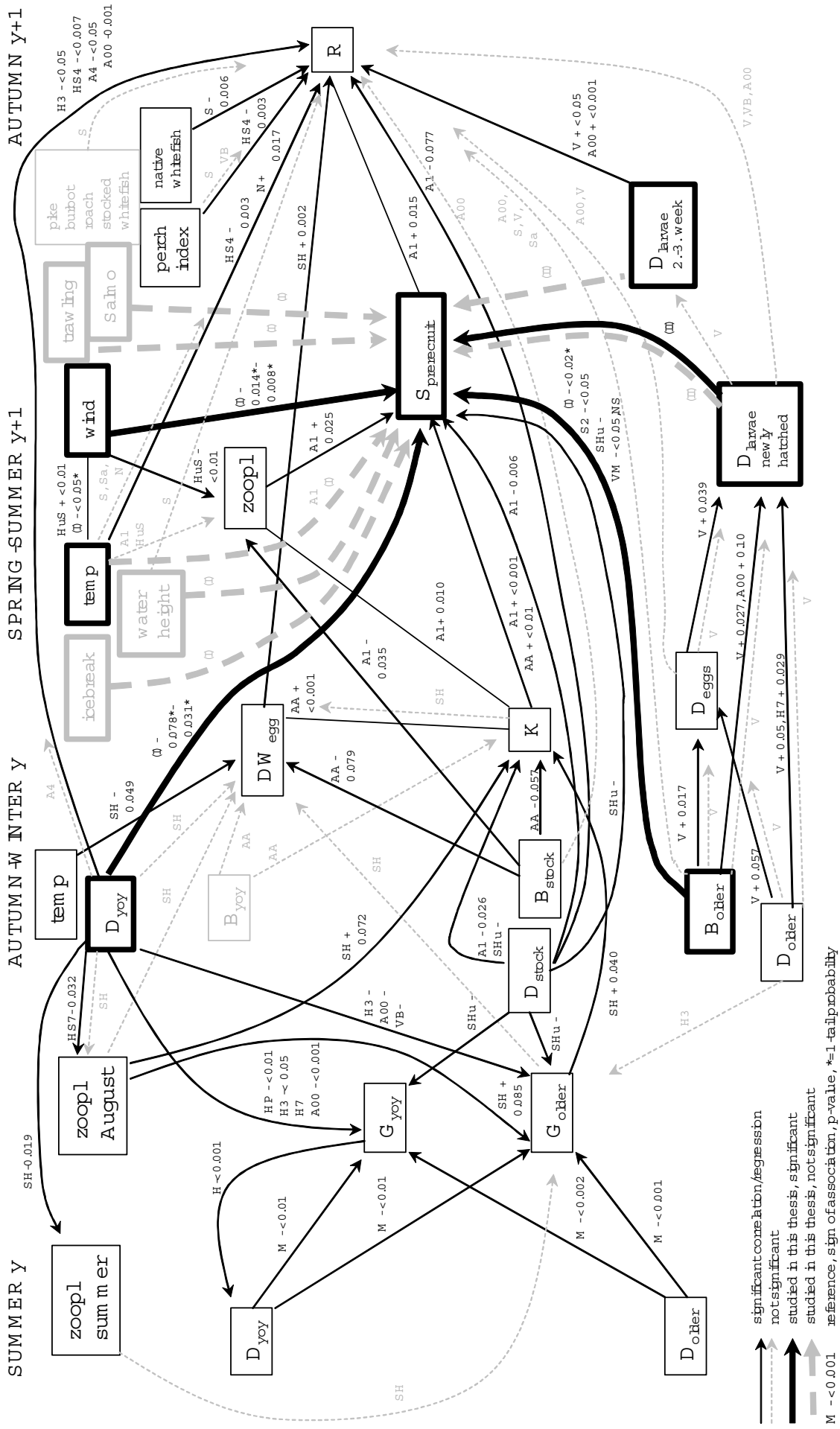
FIGURE 3 A selection of analysed associations between factors potentially linked to recruitment of vendace in field data. In boxes: B=biomass, D=density, DW=dry weight, G=growth, K=condition, $S_{prerecruit}$=survival, temp=temperature, zoopl=zooplankton. References: A1= Auvinen 1988, A4= Auvinen & Auvinen 1994, AA=Auvinen et al. 2000, A00=Auvinen et al. 1994, H3=Helminen et al. 1993a H7=Helminen et al. (1997) HP=Hamrin & Persson 1986, HS4=Helminen & Sarvala 1994, HS7= Helminen & Sarvala 1997, HuS= Huusko & Sutela 1998b, M=Marjomäki & Kirjasniemi 1995, N=Nyberg et al. 2001, S=Salojärvi 1991a, S2=Salojärvi 1991b, Sa=Salonen (1998), SHu=Salmi & Huusko 1995a & b, SH=Sarvala & Helminen 1995, V= Viljanen 1988b, V = Viljanen 1988, VB=Valkeajärvi & Bagge 1995, VM= Valtonen & Marjomäki 1988.

The comparison of the variability or unpredictability in mortality in different life stages is rendered difficult by the fact that these estimates always also include the effect of measurement errors in the component of the estimate (Bradford 1992, Myers & Cadigan 1993a, b, Mertz & Myers 1995, Bradford & Cabana 1997).

Various reasons can complicate the estimation of the effects of environmental factors on survival. Many factors can vary simultaneously in nature, often exhibiting interactive (nonadditive) effects on recruitment (Rose & Summons 1992). Also, monitoring can often be unrepresentative of long term conditions (Rose et al. 2001). Bradford (1992) and Mertz & Myers (1995) have concluded that any environmental variable that is to serve as a proxy for mortality must be very tightly correlated with mortality if there is to be a significant correlation between the proxy variable and recruitment. Finally, many relationships between mortality and environmental factors may be nonlinear (Shepherd et al. 1984).

4.1.2 Prerecruit mortality and its variability

In this section, the importance of mortality during different prerecruit life stages in determining recruitment is evaluated. The emphasis is on estimation of stage specific mortality and its variability and potential, or indications of density dependence in mortality. The life stages considered and their durations are: egg, from spawning in autumn to hatching in spring around the time of ice break; the period from hatching to two to three weeks of age was considered to represent larval stage; the period from third week to recruitment in autumn represents the late larval - juvenile stage.

From spawning to hatching

Nissinen (1972) suggested direct proportionality between spawning stock and deposited egg number. Later Viljanen (1988b) demonstrated that the spawning biomass, number of deposited eggs and newly hatched larvae were strongly and significantly correlated (Fig. 3) and directly proportional (cf. Fig. 3 in Viljanen 1988b). Significant linear association between spawner biomass or density and the abundance of newly hatched larvae has been found also by Helminen et al. (1997) and Auvinen et al. (2000) (Fig. 3). These findings imply no clear density dependence of mortality during this stage. Evaluating from the r^2, the predictability of larval density from spawning stock has been low in some lakes, but in some cases very high (r^2=0.32-0.38 in Onkamo (Viljanen 1988b, Auvinen et al. 2000), 0.58 in Pyhäjärvi SW (Helminen et al. 1997) and 0.84 in Suomunjärvi (Viljanen 1988b).

The observations by e.g. Kamler et al. (1982) and Wilkonska & Zuromska (1982, 1988) imply that mortality is related to egg quality which implies the possibility of delayed density dependence. Its potential causes and consequences will be discussed later in section 4.1.3.

Mortality of vendace eggs has been estimated both in laboratory and field conditions (Zawisza & Backiel 1970, Nissinen 1972, Kamler et al. 1982,

Zuromska 1982, Wilkonska & Zuromska 1982, 1988, Viljanen 1988b, Viljanen & Koho 1991, interpretation from data in Fig. 3A in Auvinen et al. 2000). These studies showed that survival is typically low, only a few percent, and in natural conditions the interannual variation is often high. The mortality is especially high between fertilization and the time of attainment of the eyed egg stage and in the beginning of hatching (Viljanen & Koho 1991).

Thus, although the published estimates of mortality during the whole period from spawning to hatching in nature are sparse, they imply high and variable mortality and, therefore, strong potential for determination of recruitment. Due to the long duration of this stage, small differences in daily mortality rates caused by e.g. differences in incubation temperature (Koho 2002) and timing of formation of ice cover and melting of ice (Nyberg et al. 2001), predation intensity, and oxygen concentration (Koho 2002) *etc*. can become significant.

From first to third week after hatching

The association between the densities of newly hatched and two to three weeks old larvae has been found to be low (Viljanen 1988b) (Fig. 3). This implies, according to Viljanen (1988b), that most of the larval mortality is concentrated in a relatively short period in early development supporting Hjort's (1914) critical period concept. Taking into account the different interpretations of correlation analysis (section 4.1.1.), Viljanen's results can also be interpreted to imply very high unpredictability of mortality. The results of Huusko (1998) and II support these conclusions.

In II, the average proportional mortality from first to third week after hatching in five lakes was 65 % with the lake specific averages ranging from 64 to 95 %. Typically, the interannual variation of mortality was high (Table 2). The coefficient of variation of mortality was 0.76 for pooled data from four lakes. Neither the between lake differences in mean mortality (ANOVA) nor in C.V. (pairwise t-test with Bonferoni correction) were significant.

The value of ln(mean daily mortality) for vendace, -2.21 (Table 2), is consistent with the typical values from -5 to -1 of larvae for freshwater and marine fishes reviewed by Bradford & Cabana (1997). However, the index of interannual variation in mortality, ln(variance), of vendace was much higher than expected from its ln(mean), being among the highest observed (see Bradford & Cabana Fig. 17.3a). This applies also to the lake specific values. Assessing by the equation of Mertz & Myers (1995) this result is unlikely to be due to bias from the effect measurement errors on variance estimates.

No indications of compensatory density dependence of mortality, i.e. higher mortality at high initial larval density, were found during this period in different lakes (Spearman r, all 1-tailed $p>0.25$) (Fig. 4) or in combined results from all lakes (Fisher's test for aggregated p-values, 1-tailed $p>0.33$). Further, the data did not imply depensatory mortality. Viljanen 1988b found no association between larval abundance and their density.

TABLE 2 Mean, interannual standard deviation (S.D.) and coefficient of variation (C.V.) of the instantaneous total mortality in lakes Paasivesi, Hummonselkä (Puruvesi) , Harvanselkä (Puruvesi) and Onkamo during the period from first to third week after ice-off (hatching), from third week to autumn and the whole period. Period lengths were assumed to be 14, 150 and 164 days, respectively. Data as in Fig. 5 in II.

Period	Variable	Paasivesi	Hummon-selkä	Harvan-selkä	Onkamo	All data
Week 1 - week 3	Z during the period					
	Mean	1.42	1.34	1.87	1.61	1.54
	S.D.	1.15	0.74	1.33	1.47	1.16
	C.V.	0.81	0.55	0.71	0.91	0.76
	Daily Z					
	Mean	0.10	0.10	0.14	0.12	0.11
	ln(Mean)	-2.29	-2.35	-2.01	-2.16	-2.21
	ln(Var)	-5.00	-5.88	-4.71	-4.51	-4.98
Week 3 - autumn	Z during the period					
	Mean	4.65	1.29	0.94	1.97	2.36
	S.D.	2.99	1.16	1.21	0.90	2.27
	C.V.	0.64	0.90	1.30	0.46	0.96
	Daily Z					
	Mean	0.031	0.009	0.006	0.013	0.016
	ln(Mean)	-3.47	-4.76	-5.08	-4.33	-4.15
	ln(Var)	-7.83	-9.72	-9.64	-10.23	-8.38
Week 1 - autumn	Z during the period					
	Mean	6.07	2.63	2.81	3.58	3.90
	S.D.	2.79	1.23	1.01	1.96	2.35
	C.V.	0.46	0.47	0.36	0.55	0.60
	Daily Z					
	Mean	0.037	0.016	0.017	0.022	0.024
	ln(Mean)	-3.30	-4.13	-4.07	-3.82	-3.74
	ln(Var)	-8.14	-9.77	-10.17	-8.85	-8.49
Number of years		8	7	5	9	29

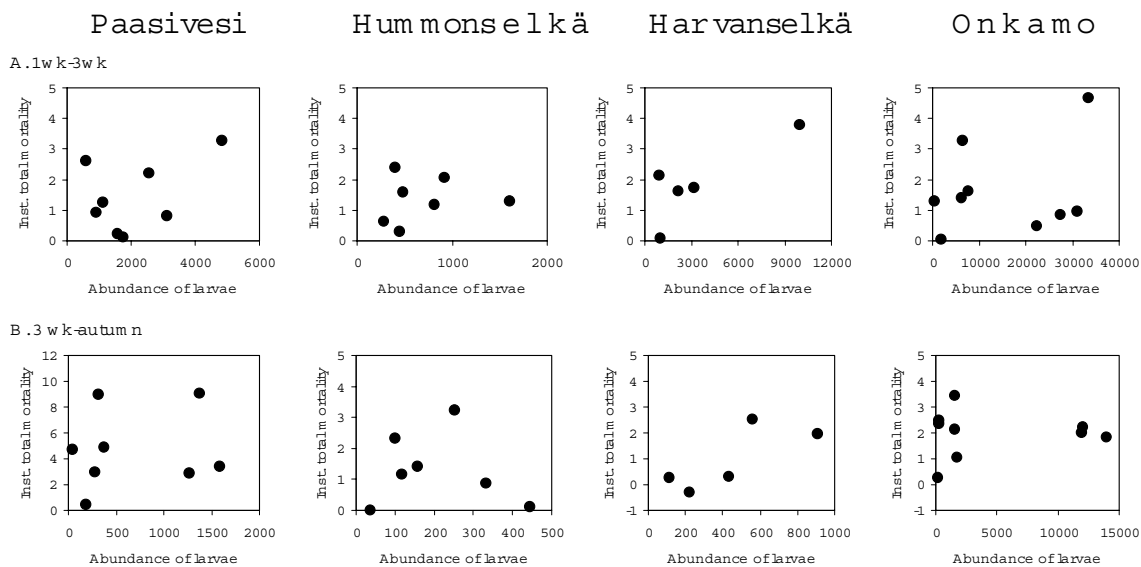Paasivesi   Hummonselkä   Harvanselkä   Onkamo

FIGURE 4   The relationship between the instantaneous total mortality and larval abundance (individuals ha^{-1}) in the beginning of the period A) from first to third week after hatching B) from third week to recruitment autumn. Standard error of the mortality estimate is typically <<0.2.

From third week to recruitment in autumn

The predictability of recruitment from density of larvae a few weeks old has been high in certain lakes (Viljanen 1988b, Auvinen et al. 2000) (Fig. 3). However, in many lakes, the mortality during this period has been highly unpredictable (II). The average instantaneous total mortality from third week to autumn estimated from the data in II was 2.36 and the coefficient of variation was at the same level as in the previous period. The average mortality in Lake Paasivesi during this period was significantly higher than in the other lakes (II) and also higher than during the larval period in this lake (MANOVA, p<0.05) which may be due to high predatory mortality as suggested by Auvinen et al. (2001).

The ln(mean daily mortality), -4.15, was on the level typical for juvenile fishes, from -6 to -3 (Bradford & Cabana 1997). As with the newly hatched larvae, the variation of mortality was again higher than expected by the model of Bradford & Cabana (1997) but consistent with their idea of constant C.V. Thus, significant potential for determination of recruitment also occurs during this period. The importance of the juvenile stage in causing variability of mortality has been suggested e.g. by Smith (1985) but see Myers & Cadigan 1993a & b for demersal fish.

Presumably most of the vendace mortality occurs in the beginning of this period. The high variability may be connected with differences in duration of the early high mortality period. Due to temperature induced variability in growth rate the length of the high mortality period can be extended in some years (Helminen & Sarvala 1994). However, regular observations by vendace fishers of sudden strong declines in 0+ vendace density as late as in July-August

indicate potential for high mortality throughout the first summer. In order to gain more understanding on the mortality of vendace during this period, methods for monitoring vendace density during the whole first summer of life should be developed. These could include e.g. joint use of horizontal echosounding and standardised trawl type gear.

No significant compensatory density dependence in mortality was detected (Fig. 4) in any lake (Spearman r, all p>0.05, 1-tailed) or in the combined results of all lakes (Fisher's test for aggregated p-values, 1-tailed p>0.20). Further, no indications of depensatory mortality were found. Density dependence in mortality has not been documented in earlier studies either, but the association between density and growth (Hamrin & Persson 1986, Viljanen 1986, Helminen et al. 1993a, 1997, Marjomäki & Kirjasniemi 1995) (Fig. 3) suggests that potential for density dependent predation mortality occurs.

No significant negative dependence was found between mortalities during the period from the first to third weeks and from third week to autumn in different lakes (all p>0.09, 1-tailed), or in the combined data (Fisher's test for aggregated p-values, 1-tailed p>0.25). This implies that variation in stage specific mortality is not greatly compensated for during the later stage.

It can be concluded that, although the daily mortality after hatching was highest during the first few weeks (II), as high and unpredictable cumulative mortality, and therefore potential for determination of recruitment also occurred at a later stage and presumably also during the egg stage as also suggested by Auvinen et al. (2000). This supports the general view of several authors (e.g. Sissenwine 1984, Anderson 1988, Peterman et al. 1988, Bradford 1992, Mertz & Myers 1995 and Bradford & Cabana 1997) that considerable variability in fish mortality can occur after the first feeding period of young fish larvae, and that all prerecruit stages can contribute significantly to variation in recruitment. The stage (or stages) over which cumulative mortality is most variable is likely to be the stage over which recruitment variability is determined (Sissenwine 1984, Pepin & Myers 1991). This is not yet fully assessed in case of vendace.

The question of the relative importance of density-dependent and density-independent mortality at different stages remained unsolved as well. Major part of the data in II was from the low stock period and, therefore, the conclusions concerning density-dependence should be verified with data containing larger range of newly hatched densities.

For most species, it is unclear at what stage density dependent and density independent mortality occurs (Myers 2001). The general pattern that the primary source of variability in recruitment is the enormous interannual variability in density independent mortality during the egg and larval stages has been suggested (e.g. Houde 1987, Leggett & DeBlois 1994), but Myers (2001) notes that considerable density dependent mortality can occur at different stages in different species. The question of timing of density dependent mortality is important as there is growing evidence that density dependent mortality in later stages can dampen the variability generated by the earlier stages, and act to finely adjust recruitment levels (Gulland 1965, Myers & Cadigan 1993ab, Bailey 1994, Leggett & DeBlois 1994, Bradford & Cabana 1997).

The relative importance of the two types of mortality at each life stage may also determine the variability in survival at different population densities (Myers 2001).

Myers et al. (1995) and Liermann & Hilborn (1997, 2001) have considered depensation a very rare phenomenon or not strong enough to be important in a population's dynamics (but see Shelton & Healey 1999).

4.1.3 Density-dependence in vendace recruitment process

4.1.3.1 Determination of population fecundity

Population fecundity is strongly connected to spawning biomass (assuming constant sex ratio). Yet, the relationship between biomass and population density is not linear because the vendace growth is strongly density dependent (Fig. 3) due to food competition. For example, in Lake Puulavesi the average weights of age 1+ vendace were 13 g and 21 g during the periods of high and low stock densities, respectively (Marjomäki & Huolila 1994). The compensatory effect of density on biomass growth is somewhat enhanced by size specific fecundity being negatively density dependent (Marjomäki 1992, Sarvala et al. 1992). This means that in dense populations the egg number per female weight unit is lower than in sparse populations. Yet, for vendace, the proportional effect of numerical changes in fecundity is typically minor (e.g. Marjomäki 1992, Sarvala et al. 1992), and the dynamic range of spawning populations is typically high. So, the spawning biomass and population fecundity are typically highly correlated, but not exactly linearly related. The assumption of spawning biomass, being sufficient proxy for population fecundity, has been increasingly criticised recently (Marshall et al. 1999 and references therein).

Indications of earlier maturation in fast growing vendace has also been detected (Sarvala et al. 1992), also marginally enhancing the fecundity of sparse populations.

The density dependence of post recruitment natural mortality, which would also affect the dependence of spawning biomass on density, has not been observed directly but is highly probable as predation mortality is strongly connected to prey fish size (reviewed in Rose et al. 2001).

Thus, it can be concluded that determination of vendace population fecundity is clearly a compensatory process. Gurney and Nisbet (1980) have shown that if the birth rate (in this case fecundity) is dependent upon age and total population size, a sufficient condition for the population stationary state local stability is simply that mortality and the per capita birth rate (fecundity) are compensatorily density dependent. Thus, only these processes are needed for population regulation. However, these feedbacks alone are not usually large enough to effectively stabilise recruitment (Craig & Kipling 1983, Koslow 1992, Koslow et al. 1995, Trippel 1995).

4.1.3.2 The effects of spawning stock and previous year-class density on recruitment

Although no indications of density dependence in survival were found in analysis of larval and juvenile life stages (section 4.1.2), many analyses relating vendace spawning stock (S) and recruitment (R) suggest compensatory density dependence (Valtonen & Marjomäki 1988, Salojärvi 1991a, Salmi & Huusko 1995 a & b, I) (Fig. 3). To be precise, it must be noted that the S-R relationship also includes the above described (section 4.1.3.1) density dependence of size specific fecundity and therefore the compensation in the S-R relationship does not solely imply density dependent survival.

The compensation in post hatching stages was studied in II. In only one lake out of five significant compensation was found when relating first week larval density and recruitment.

A possible reason for the fact that the compensation manifests itself when the whole period between spawning and recruitment is considered is due to compensation arising from complex relationships among multiple processes operating in multiple life stages (Paulik 1973). These small, typically undetectable, density dependent changes can combine to result in significant compensatory responses (e.g. Rothschild 2000, Rose et al. 2001).

In many vendace S-R analyses, it is assumed that a model sufficient to describe the density dependence is the Ricker (1954) curve with a decreasing right hand limb implying over compensation (e.g. Valtonen & Marjomäki 1988, Viljanen 1988a, Salmi & Huusko 1995a & b). Yet, statistical evaluations imply considerable uncertainty about the best model. In Lake Puulavesi (I), the fit of the compensatory models by Ricker, Cushing (1971) and Beverton & Holt (1957) to the data was equally poor. Also when fitting the Ricker or Cushing models to data from 17 lakes (III), the best fit was gained as often by either model. Thus, the data do not support the general applicability of an over compensatory S-R model for all vendace stocks. Theoretically, over compensation is most likely to appear in the densest populations but further evaluation of the population density required to induce over compensation is impaired by the lack of absolute density data for many populations. Evaluation of the amount of compensation in the S-R relationship is further complicated by measurement and time series errors (I).

The slope of the S-R relationship in a low spawning population level and larval density is a measure of stock exploitation resilience and target for much analysis. In many cases it has been difficult to detect any decrease in recruitment with decreasing spawning stock, due to compensation. This has led to a debate concerning if it is essential to include the effect of spawning stock in recruitment analysis (e.g. Myers & Barrowman 1996, Gilbert 1997, Myers 1997, Hilborn 1997). Due to its occasional stock recessions, vendace has provided good opportunities to detect the effect of an increasing S-R relationship in low population levels. It was demonstrated in II that generally high larval abundance was needed to produce a high number of recruits. The positive dependence between spawning stock size and recruitment has been demonstrated by Helminen et al. (1997, 2002). Also, Salonen (1998) and

Valkeajärvi & Marjomäki (2003) detected that strong year-classes emerged from reasonably large spawning stocks.

Other than the spawning stock, the previous year-class strength (Helminen et al. 1993a, Helminen & Sarvala 1994, Auvinen 1994, Auvinen & Auvinen 1994, I) and total population size in previous autumn (spawning stock + juveniles) (Salmi & Huusko 1995a & b) have also been found to be in negative association with recruitment or prerecruit survival (Fig. 3).

Mechanisms for compensatory mortality

The analyses of associations in field data do not reveal the mechanisms operating in compensatory mortality. However, they serve as catalysts in formation of hypotheses for possible mechanisms. For vendace, the central hypotheses are based on food competition. Firstly, mortality can be due to competition between prerecruits themselves. The density of the spawning sub population, *via* population fecundity, regulates the initial larval density and the level of competition. Secondly, mortality can be due to delayed effects of previous year competition. Both mechanisms may operate in different years or simultaneously, making their separation difficult in field data.

Food competition between prerecruits in larval and post larval stages may cause density dependent mortality (Auvinen 1978, Salojärvi 1987) either directly by starvation or by increased predation due to slow growth. Karjalainen (1992) and Koho & Viljanen (1998) showed, in cage experiments and in the laboratory, that both starvation mortality and growth of vendace larvae are dependent on larval density. However, vendace larvae are fairly resistant to direct starvation (Karjalainen 1991) and carrying capacity is large in comparison with typical food consumption of larvae (Karjalainen 1992, Koho & Viljanen 1998). Further, it was concluded in II that the number or total area of nursery places did not restrict recruitment. On the other hand, there are interannual differences in the quantity and quality of planktonic food for the larvae, and Huusko (1998) concluded that starvation was probable in certain years. Generally for fish, little unequivocal evidence of a causal link between the availability of food during the larval period and larval survival and/or recruitment has been reported (Leggett & DeBlois 1994). Moreover, in those cases where evidence does exist, the magnitude of the effect appears small.

Helminen et al. (2002) and Koho (2002) have recently emphasised the significance of predation as the primary cause of death in slower growing vendace larvae, instead of starvation. According to a "bigger is better" hypothesis, larger fast growing larvae are less vulnerable to predation than smaller ones (e.g. Miller et al. 1988, review by Leggett & DeBlois 1994). Size dependent mortality of vendace larvae has been demonstrated indirectly by Helminen & Sarvala (1995) based on increase in myomere count during the larval period. Also, Huusko (1998) documented a certain amount of size dependent predation mortality in vendace larvae, but the most intensive reduction in larval density and the period of high proportion of vendace in predator diet failed to coincide.

There are many possible mediating mechanisms for delayed density dependent mortality i.e. the reducing effect of previous year-classes on prerecruit survival (Ward & Larkin 1964, Townsend 1989, Levy & Wood 1992, Walters & Woodey 1992). For vendace, two main mechanisms have been proposed. Firstly, the reproductive output can be affected either quantitatively or qualitatively by competition during the growing season prior to spawning (for vendace Hamrin & Persson 1986, Helminen et al. 1993a, generally e.g. review by Rose et al. 2001 and references therein). In Fig. 3 this is illustrated by the following chain of associations: dense stock -> severe food competition -> slow growth and condition with deterioration of some essential quality components in the eggs which are indicated by low dry weight -> low survival of the larvae (e.g. Auvinen & Auvinen 1994). The negative association between population abundance and plankton food has been observed in nature during the growing season (Sarvala & Helminen 1995, Helminen & Sarvala 1997) (Fig. 3), and egg quality has been shown to determine larval size and survival (Dabrowski et al. 1987, Wilkonska & Zuromska 1988). However, Koho (2002) estimated by simulation that egg dry weight alone is insufficient to determine larval survival. Some delayed density dependent mortality may take place in the egg stage, as Kamler et al. (1982) and Wilkonska & Zuromska (1982, 1988) have shown that egg survival is dependent on egg quality. This phenomenon has been demonstrated also for e.g. Baltic herring (*Clupea harengus membras* L.) (Laine & Rajasilta 1999). In herring, high egg dry weight, which corresponds to the total protein content of eggs, was not beneficial but triacylglycerol and cholesterol levels were suggested to determine mortality.

The second mechanisms of delayed density dependence in vendace is based on the idea that planktivory in the previous growing season affects the food production for larvae in the following spring (Auvinen 1988, Huusko 1998). A supporting association between high autumn abundance and next spring zooplankton density has been found by Auvinen 1988 (Fig. 3). This mechanism can work in synergy with the first.

The young-of-the-year juvenile fish of the previous year have a central role in both of these delayed regulation mechanisms. This is obvious firstly because of their significant proportion in the total density of short lived species such as vendace. Secondly, because of juvenile competitive dominance (Hamrin & Persson 1986), the effect of age 0+ fish on competition has been suggested to be even higher than what might be expected solely from their numerical proportion. However, Marjomäki & Kirjasniemi (1995) found no clear evidence supporting juvenile dominance in determination of the growth of the 0+ and older vendace in a certain lake, where numerical dominance of 0+ was not apparent every year. There, older fish affected their own growth and 0+ growth (Fig. 3), and judging from the estimated competition parameter estimates, their effect on growth was much higher that that of 0+. Contrary to Hamrin & Persson (1986), adult competitive dominance has been suggested by Aass (1972) and Sandlund et al. (1991).

Independent of the possible competitive dominance, the importance of age 0+ fish in competition and determination of delayed mortality is self evidently higher the lower the density of older fish in the population. Concerning the

effect of competition between the older fish themselves in delayed density dependence, it should be noted that their delayed effect through competition and direct effect through determining larval density are simultaneous, and therefore unassessible by correlative analysis.

A phenomenon suggested to be a consequence of the delayed effect of the previous year-class is the tendency towards two year oscillation of and negative autocorrelation in vendace recruitment time series (Hamrin & Persson 1986). Yet, it must be emphasised that delayed density dependence is not their necessary precondition. Generation cycles, i.e. cycles with a period of roughly one generation (Godfray & Hassell 1987, Knell 1998) can, under certain conditions, be directly due to positive association between population fecundity and recruitment. Nissinen (1972) suggested that the reproduction of an abundant year-class gave rise to a new abundant one in a vendace stock where the post spawning mortality was so high that a single year-class was responsible for the majority of reproduction. Townsend et al. (1990) showed by modelling that, for high adult mortality levels, accidentally starting two year cycle could prevail for years in roach population maturing at two years of age, and Myers et al. (1998) demonstrated that a four year cycle in sockeye salmon (*Oncorhynchus nerka* (Walbaum)) could result from a stable mode excited by stochastic forcing, and the increase in harvest rate increased the cyclicity. Tendency towards two year cyclicity was also found in a vendace population model without any delayed density dependence (V) in the case of low average spawning population caused by high mortality. However, Helminen et al. (2002) demonstrated that delayed density dependence was essential in order to mimic the strong two year fluctuation observed in Lake Pyhäjärvi vendace. This is in accordance with the idea that delayed density dependence can reinforce cyclic patterns, which can lead to a particularly strong and persistent cycle (Townsend 1989, Townsend et al. 1990, Helminen 1994, Myers et al. 1997b).

In order to evaluate the effect of the previous year-class on prerecruit survival, the effect of spawning biomass was removed by modelling in papers I, and III. In Lake Puulavesi (I), weak statistical support for the negative effect of the previous year-class on prerecruit survival was gained. However, in only one of 17 vendace stocks (III) a statistically significant negative autocorrelation prevailed in the residuals of recruitment after removal of spawning stock effect. Generally the hypothesis of negative autocorrelation was not supported (Fisher's test for aggregated p-values, p=0.40). Thus, it seems that the delayed effect of the previous year-class can not be considered a very typical regulator of vendace population dynamics. Yet, due to the uncertainties and biases in S-R modelling (I), short time series and the possible correlation structures between S_{t-1} and R_{t-1} this result must be considered preliminary and needs more detailed analysis.

Cannibalism, resulting in strong density dependent feedback, has been documented for a variety of fish species (Smith & Reay 1991) and suggested to cause oscillation in recruitment (e.g. Henderson & Corps 1997). Cannibalism of eggs and newly hatched larvae is an alternative hypothesis to competitive interactions in explaining the negative association between recruitment and both spawning stock and previous year juvenile densities by one simple

mechanism. It was firstly suggested for vendace by Nordqvist (1942). However, cannibalism of vendace has only been detected by Huusko & Sutela (1992), despite many extensive studies on vendace feeding (cf. e.g. Hamrin & Persson 1986). Yet, cannibalism may be difficult to detect as the period may be short. It may be only typical for lakes where most of the larval population occupies the pelagic zone (Karjalainen et al. 2002) and the larvae may be identifiable for only a short time after ingestion.

4.1.4 The role of density independent factors

Many results indirectly imply significant roles of density independent factors external to the population in determining vendace recruitment.

Firstly, the unpredictable variation in prerecruit mortality (II) was large (section 4.1.2).

Secondly, the standard error of the estimate (S.E.) in the density dependence models (I, III: average 1.3, mode 1.2, range from 0.5 to 3) was high in comparison with estimates from other fish stocks (e.g. Hightower & Grossman 1985, Mertz & Myers 1996, Hinrichsen 2001). Note, however, that S.E. also includes the effects of measurement errors, which may be important in total variation (Mertz & Myers 1995), and that S.E. as an index of interannual variation is also dependent on how representative the S-R model is of the true relationship (Rose et al. 2001).

Thirdly, the recruitment dynamics synchrony of isolated populations can be regarded as evidence of the effects of external factors on the dynamics (Moran 1953). Regrettably, the amount of spatial correlation can not be used as an index of the magnitude of external effects, as the signals can be filtered by the system in a complex manner as shown for isolated populations by Greenman & Benton (2001). In vendace, the recruitment success in close by lakes has been found to be synchronised (Salmi & Huusko 1995a & b, III). However, the scale of this synchrony was short, only a few hundred kilometres (III), although the scale of spatial correlation of environmental forcing agents is typically in thousands of kilometres (e.g. Myers et al. 1997a). It was shown in III that the effective scale of correlation of these agents can be short especially along the north-south axis. This is based on the assumption that a significant proportion of the recruitment determination occurs during a short period and the difference of timing of this period is in weeks due to differences in the time of ice break and hatching times.

Associations between certain factors and recruitment or prerecruit survival have been searched for in many studies (Auvinen 1988, Salojärvi 1991b, Helminen & Sarvala 1994, Valkeajärvi & Bagge 1995, Nyberg et al. 2001, I), and some statistically significant correlations have been found (Fig. 3). Yet, the possibility of spurious correlations is always high in this type of analysis (Shepherd et al. 1984, Myers 1998) and therefore the causal mechanism of the association should be established. Bradford & Cabana (1997) reminded us that in order to gain truly predictive relationships between an environmental factor and year-class strength, the variable has to affect survival over a large fraction of the prerecruit period.

Many meteorological variables have been correlated with recruitment as they determine the match or mismatch of the spatial and/or developmental status of the prerecruits with those of the optimal conditions of different critical factors, e.g. prey availability, in different life stages (Match-mismatch hypothesis by Cushing 1972). Nyberg et al. (2001) suggested that the ability to match the hatching with the optimal "spring window" is lower for autumn spawning species such as vendace than for spring spawners, leading to higher variability of recruitment of autumn spawners than spring spawners.

Temperature is an important regulative factor in all life stages of vendace. It can affect the quality of sexual products *via* its effect on food production during the growing season (Kamler et al. 1982, Wilkonska & Zuromska 1988), and regulate the metabolic rates and survival of eggs (Zuromska 1982, Viljanen & Koho 1992) and larvae (Koho et al. 1991, Koho 2002). The development of temperature after hatching also determines the succession of zooplankton and thus prey availability for the young larvae. The effect of temperature in prerecruit survival is complex as the optimums may be very different in different life stages as emphasised by Koho (2002). Positive association between recruitment and spring temperature has been detected in field studies by Helminen & Sarvala 1994 (Fig. 3) who suggested that the effect is based on an increase in the duration of the larval stage vulnerable to predation mortality (for "Stage duration" hypothesis see review by Leggett & DeBlois 1994). Also, Nyberg et al. (2001) found a positive correlation between the year-class strength and water temperature during larval hatching in an eutrophic lake. Interestingly, the increase of water temperature after that had a negative effect on recruitment. They suggested that this was due to increased predation by warmwater species, which emphases the complexity of the effect of temperature.

The relative effect of density independent factors in population dynamics and therefore also population variation should be greater at the limits of a species range (Myers 1998, 2001). This is supported by observations of vendace dynamics at different latitudes. In his study of the northernmost Finnish vendace population of Lake Inari, Salonen (1998) considered that the summer temperature is an important determinant of year-class strength. On the other hand in Sweden, near the southern limit of vendace distribution, winter temperature largely regulated the recruitment (Nyberg et al. 2001). There, the coldest winters with late ice-break were associated with the strongest year-classes and very early ice-break or no ice-formation resulted in weak year-classes.

Another climatic factor associated with prerecruit survival of vendace (I) (Fig. 3) and many other fishes (Mertz & Myers 1995) is wind forcing. The causal mechanism may be the effect of wind on zooplankton density or the feeding success of the larvae as demonstrated for vendace by Huusko and Sutela (1998b). The effect of turbulence/stability on food availability and mortality of fish larvae has been demonstrated by e.g. Lasker (1981) (stability hypothesis), Peterman & Bradford (1987) and Cury & Roy (1989).

Fish community structure may affect vendace recruitment. Negative correlation between perch stock index and recruitment (Helminen & Sarvala

1994) (Fig. 3) or prerecruit survival (Valkeajärvi & Marjomäki 2003) has been detected. The effect of perch is most probably by predation as perch has been shown to feed on vendace larvae and juveniles (e.g. Huusko & Sutela 1992, Huusko et al. 1996, Tolonen 2000). The effect of predation may already be significant during the incubation of eggs (Zuromska 1982, Kamler 1982). The relationship between predator density and vendace dynamics may, in many cases, be too complex to be revealed by linear correlation due to a functional relationship of predator and interspecific competition (Heikinheimo 2001). The synchronous low stock period in southern parts of Finland (III) may partly indicate the effect of synchronous dynamics of perch stocks on vendace. This emphasises the need for monitoring the fish community more widely in order to understand the dynamics of certain species.

The effect of stocked salmonids (*Salmo salar* and *S. trutta*) in prerecruit survival of vendace was studied in I. No significant correlation was found. This was consistent with previous suggestions by Valkeajärvi et al. (1997) who suggested that the stocking density of salmonids in relation to number of young-of-the-year vendace in Lake Puulavesi is not high enough to induce significant mortality. In certain lakes with higher salmonid stocking densities and lower larval vendace densities the predation has been considered sufficient to deplete the young-of-the-year vendace and prolong stock recession (e.g. Valkeajärvi et al. 1997, Vehanen et al. 1998, Auvinen et al. 2001).

An association between naturally reproducing whitefish and vendace year-class has been detected by Salojärvi (1991b) (Fig. 3). He suggested that this may be due to food competition by whitefish causing vendace mortality. However, in some cases this association might be caused by the opposite causality. E.g. Valkeajärvi & Bagge (1995) have shown that whitefish stock increased during the periods of low vendace stock.

4.1.5 Conclusions and suggestion for future research

Exceptionally high levels of variation caused by unpredictable density independent factors can be considered typical of prerecruit mortality of vendace. Density dependent compensatory mortality also occurs, but its regulatory effect on recruitment variation is typically of less importance. These findings are consistent with the interpretations from life history theory. Vendace can be considered as an opportunistic species by the classification of Winemiller & Rose (1992) based on fecundity, juvenile survivorship and age of maturity. Rose et al. (2001) suggested that opportunistic strategists have low to intermediate compensatory reserve and show less compensation than the equilibrium strategists. Because opportunists inhabit highly variable environments (for vendace e.g. the feeding conditions in spring) and seldom approach environmental carrying capacity, they show high interannual variation with the highest proportion of density independent variation.

The generally high importance of unpredictable factors does not mean that the dynamics is always highly stochastic. The heavily exploited lakes Pyhäjärvi SW (Helminen & Sarvala 1997), Onkamo (Auvinen et al. 2000) and Pyhäjärvi SE (Auvinen 1994) with two year oscillation imply strongly to density driven

dynamics, whether compensatory or not, in certain low levels of population abundance.

Many different populations of vendace, in the context of different kinds of communities, ecosystems and fisheries, have been studied extensively in order to find out why a particular population fluctuates as it does. This has been a fruitful approach in so far as different mechanisms can dominate in determining the fluctuation in different lakes, and progress in understanding these fluctuations could be achieved only step by step and lake by lake (Helminen et al. 2002). Yet, deductions from these lake specific rather short recruitment time series are always impaired by the possibility of e.g. spurious association determining the further course of the analysis, low power of statistical tests to reveal weak but maybe common associations, unrepresentativity of the time series of typical state, range and combinations of essential factors, methodological biases *etc*. Thus, gaining species and larger level ecological understanding on population dynamics demands for generalisations from the vast data base from these studies. Therefore, along with detailed lake specific and experimental studies one should increasingly apply synthetic an approach in the analysis of these databases with modern meta analytical methods that explicitly account for sampling and measurement error, as suggested by Myers (2001). With these methods for example the following questions should be analysed further:

1. What are the typical levels, variations and density dependence of survival in all prerecruit stages from spawning to recruitment. Especially, field observations on mortality between spawning and hatching should be assessed.

2. What are the maximum reproductive potential and level of compensation in vendace S-R-relationship.

3. What is the role of delayed density dependence in regulation of recruitment process of vendace.

4. What are the relative effects of density dependent and density independent factors, and variability of recruitment, in relation to latitude of the population.

4.2 Harvesting and stock variation - interactions

In this section, commercial vendace fishing is analysed in relation to temporal stock variability. First, the observations on adaptation of fishers to stock fluctuation are analysed in the context of a simple model that sets boundaries for sustainable operation. Then, the effects of different fishing strategies on stock and revenue variation, and risk of stock collapse are studied by a simulation model. Finally, a case study monitoring the effects of intensive trawl fishing in a lake is presented.

4.2.1 The response of vendace fishers to stock variation

4.2.1.1 Observed response

Fishing efforts of the types of fishing for vendace in Lake Puulavesi, commercial trawling, semicommercial (part time commercial) and subsistence seining, and commercial and subsistence gill netting were monitored during decline of the yield per unit effort (YPUE) of vendace (IV).

The part time commercial and subsistence seine and subsistence gill net fishing effort declined with the decline in their YPUE, which had a compensatory effect on change in stock. The average decline in effort appeared to be mainly due to fishers ceasing fishing totally one by one while some others decreased their effort only marginally until YPUE was very low. No clear attempts to maintain yield by increasing fishing effort were detected.

One commercial trawling enterprise and a gill net fisher first increased their fishing effort as YPUE declined trying to ensure regular yield. Theoretically, this introduced a depensatory effect upon stock change. Later they reduced their effort as YPUE declined to an unprofitable level, which had a compensatory effect. The other trawling unit and gill net fisher responded in the same manner as the seine and recreational gill net fishers, i.e. with decreasing effort as YPUE declined.

The tendency of trawling enterprises to stabilise their yield during the stock decline by increase in effort has been described also by Jurvelius et al. (1992) in Vuoksi water course. In their interview of Finnish vendace fishers, Sipponen et al. (1999) found that full time commercial vendace fishers increased their effort during stock decline whereas the effort of part time commercial fishers changed little. Sipponen & Valkeajärvi (2002) studied the response of commercial trawlers in Lake Päijänne. During the periods with lowest stock abundance, trawling effort decreased considerably and shifting to whitefish stocks helped to maintain trawling and survival of fishing enterprises. During the high stock period the market situation effectively regulated trawling effort. When the abundance and catches increased, trawlers reduced their daily fishing hours because the marketable catch was caught in a shorter time. Thus, these responses resembled that of some Lake Puulavesi fishers in that the maximum effort was applied in some intermediate stock level. In Lake Inari, Salonen

(1998) noted that, despite the decline in stock, fishing effort remained high for some time, as great capital investment gave rise to a great need to go fishing.

Depensatory fishing mortality has also been suggested e.g. for certain Pacific salmon fisheries (Peterman 1980, Eggers & Rogers 1987, Ricker 1987, Cass & Wood 1994).

4.2.1.2 A graphical model for the response of fishing effort to stock change: "The Sustainable Operation Window"

A simplistic graphical model is used here to conceptualise some of the boundaries affecting the ability of a fisher to counteract the stock and revenue fluctuations by effort adjustment and thereby sustain his operation profitability. The shape of the window for different fisheries is compared with their observed response. The boundaries are derived from Lake Puulavesi fishing statistics and some hypothetical economic parameters considered typical of vendace fisheries (Table 3). In the case of an individual fisher in a particular lake the parameters may differ considerably from this example depending on particular costs and unit price which depend on the equipment used, location of fishing grounds, local market demand *etc*. However, the results are not very sensitive to the economical parameter values at any realistic parameter levels. Nonetheless, it must be emphasised that the analysis must be considered generally qualitative.

The operation window for trawl fishing (Fig 5A) suggests that fishing enterprises are able to and forced to adjust their effort due to stock fluctuations. First, they have to limit their effort during high stock periods due to limited market demand (also e.g. Sipponen & Valkeajärvi 2002). Second, they have to increase fishing during stock decline in order to maintain profitability. The lower limit of stock to stop fishing depends on the unit price of fish and costs. Continuing fishing in unsustainable situation can be desirable from the point of view of the market contacts (e.g. Sipponen et al. 1999). Also, a high fixed cost due to recent large investments can make fishing cessation difficult even when the stock is not high enough to ensure profitability.

The YPUE can vary considerably between different enterprises (e.g. due to gear dimensions or quality of fishing grounds) and this also has an effect on their response (shaded areas of high and low catchability (q) in Fig. 5AS). During the high stock period, an enterprise with high catchability (e.g. due to large gear or good fishing grounds) capable of catching several hundreds of kilograms in hour must limit its effort considerably due to limited market demand. The enterprise is then able to increase the effort easily during quite considerable stock decrease. In case of occasional low stock, the enterprise can carry on fishing in unsustainable areas due to profits gained during a profitable period. If the catchability of an enterprise is low, its ability to adjust effort is more limited. Even during the high stock period, the fishing effort must be kept high and the border of sustainability is reached with much smaller relative decrease in YPUE than with high catchability gear (assuming the same cost structure for both). Thus certain overcapacity of effort during the high stock period is a prerequisite for survival during low stock.

The operation window for summer-autumn seining (Fig. 4B) reveals the reason for decline in seine effort with stock decline in Lake Puulavesi. There, the average YPUE of the traditional mostly part time commercial seining was only 20 kg haul^{-1} in the years of highest stock levels (Fig. 1 in IV), which is an unsustainable level assuming any realistic cost structure. Thus, any decrease in stock from its maximum will make some fisher cease fishing. However, during the last decade, two new seining enterprises capable of sustained operation have emerged there. Their sustainability is based firstly on higher catchability due to large gear capable of sweeping large areas, ensuring considerably higher YPUE than with traditional gear. Secondly, the costs are low due to the fact that the hydraulically powered gear is operable by one man instead of 2-3 as in traditional seining. The need for limiting effort due to limited market demand is only an issue for these two enterprises with the largest gear.

The maximum potential fishing effort is an essential boundary of the window for winter seine fishing (Fig. 5C). Although it is theoretically possible to fish up to 2 hauls a day, no enterprise in Lake Puulavesi (Table 3) considered it practical. So in practise the potential for effort adjustment is very limited. Only the two above mentioned enterprises with large gear and one man have been capable of sustained winter fishing during the last decade.

The window for commercial gill netting (Fig. 5D) is effectively limited by daily market demand. The gill net fishers rely more on direct marketing to consumers to get higher prices. In the case of abundant stock, effort is effectively limited by the rate of fish removal from nets by one man, which is on average 110 kg d^{-1} (range from 50 to 200). This limit also depends greatly on the size of the fish, and may even decline more in high stock due to smaller fish size during high stock. The figure predicts that at a typical YPUE level, less than 2 kg gill net^{-1} d^{-1}, sustainability is only possible with close to maximal effort. This prediction, however, depends greatly on the unit price of fish, as the price in many cases can be even higher due to roe separation, smoking *etc.* refining processes which decrease the sustainable YPUE lower limit.

The analysis also emphasises the fact that the minimum stock level for sustained operation is variable and depends on the price of fish and cost of fishing as well as technical innovations. The increase in price and decrease in costs make fishing profitable at ever lower stock level and *vice versa*.

The graphical presentation is admittedly simplistic as many important aspects affecting strategies and flexibility of fishers e.g. social involvement (Salmi et al. 1998), possibility of forward integration by small scale processing and marketing directly to consumers (Salmi et al. 1998, Toivonen 1998) and nonmonetary individual benefits (Anderson 1980, Sipponen et al. 1999) are not included. There are also several economic issues not included in this approach but which may affect the shape of the window considerably. First of all, the price of fish was assumed to be independent of the YPUE. In reality, due to increase in market demand and size of fish with stock decline, the unit price will also increase (e.g. Jurvelius et al. 1992), thus increasing the profitability of fishing and decreasing the need for increase in effort. The market demand from one fisher may also be negatively dependent on YPUE due to fish size and regionally larger supply during a high stock period. This decreases the market

demand curve in high YPUE increasing the need for effort reduction. The monthly salary was assumed fixed i.e. independent of fishing hours. This means that the salary per hour will decrease with increasing effort. This can make the fishers reluctant to increase their fishing during stock decline but seek other sources of income. When refining the economical analysis, a discount rate should also be taken into account. A detailed analysis of these economic issues is beyond the scope of this study.

TABLE 3   Lake Puulavesi fisheries statistics for 1997 and other parameters (see footnotes for sources) used in generation of Fig. 5.

| Variable		Trawl	Summer seine	Winter seine	Gill netting
Number of cases		2	9	7	5
Effort regulated					
based on YPUE, % of fishers		100	100	0	40
Labour, persons	average	2	2	2	1
	min-max	2-2	1-3	1-3	1-2
Maximum daily					
market demand, kg	average	500	400	750	77.5
	min-max	500-500	100-500	500-1000	77.5
Minimum YPUE to					
stop fishing,	average	47.5	17.5	40	1
kg unit effort^{-1}	min-max	35-60	0-50	0-100	1-1
Maximum daily effort	average	5	4.4	1.7	51
	min-max	5	2-10	1-2	30-80
Fishing months in year[1]		5	6	4	3
Working days in month[2]		25	25	25	30
Unit price of fish[3], € kg^{-1}		1.5	1.5	2	3
Costs					
Various fixed, € a^{-1}		6500	2000	2000	2000
Salaries[4], € month^{-1} man^{-1}		2100	2100	2100	2100
Fuel					
Other than fishing, € d^{-1}		25	25	25	25
Fishing, € effort^{-1} 16		3	0	1	0

[1] typical values based on fishery bookkeeping
[2] full time fisher assumed to operate 6 d per week except in gill netting 7 d per week
[3] interviews of fishers and Finnish Game and Fisheries Research Institute (1998)
[4] average monthly salary in Finland 1997
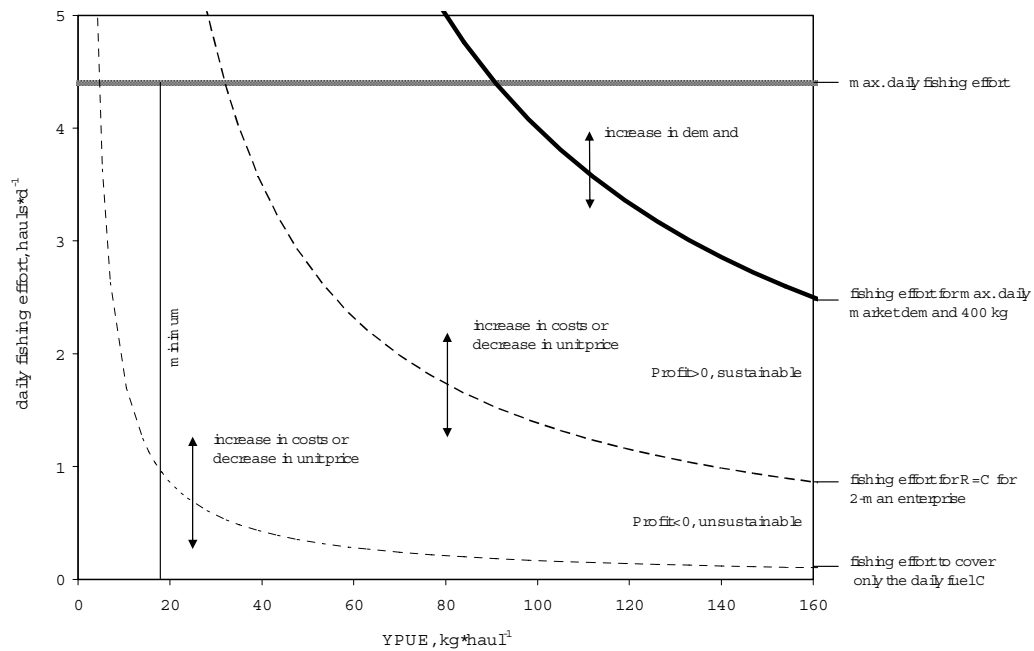
46

A. Trawl
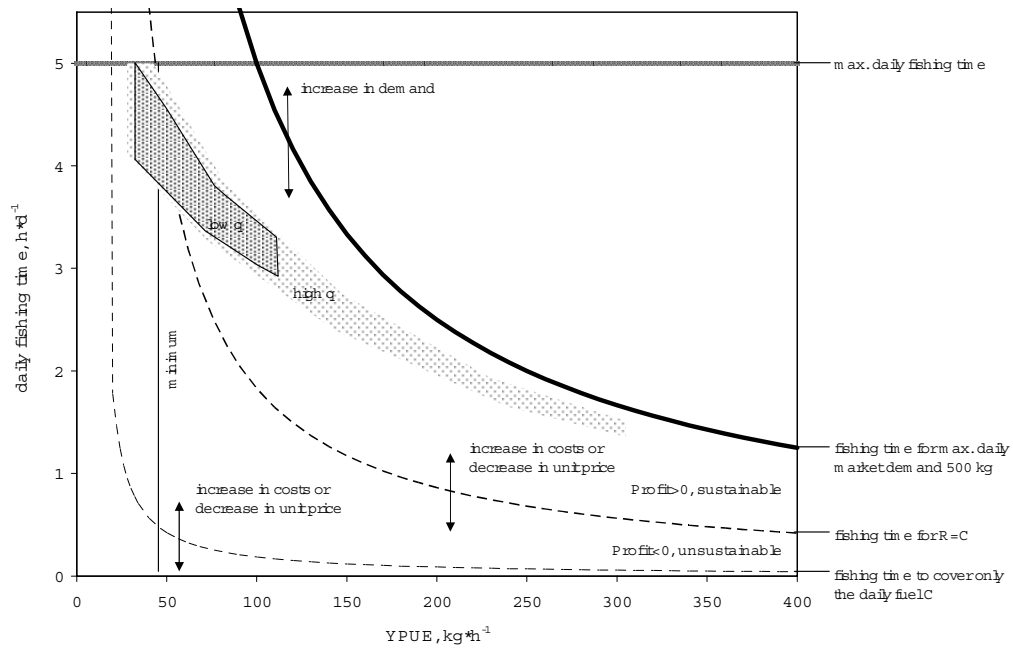
B. Summer-autumn seine

FIGURE 5   "The Sustainable Operation Window" determining the pairs of yield per unit effort (YPUE) and daily fishing effort satisfying the conditions profit (revenue (R)-cost (C))>0, yield•maximal daily market demand and effort•maximal daily effort. A. trawling, B. summer-autumn seining, C. winter seining and D. gill netting. Refer to Table 3 for values of parameters used. Continued on the next page. q = catchability.
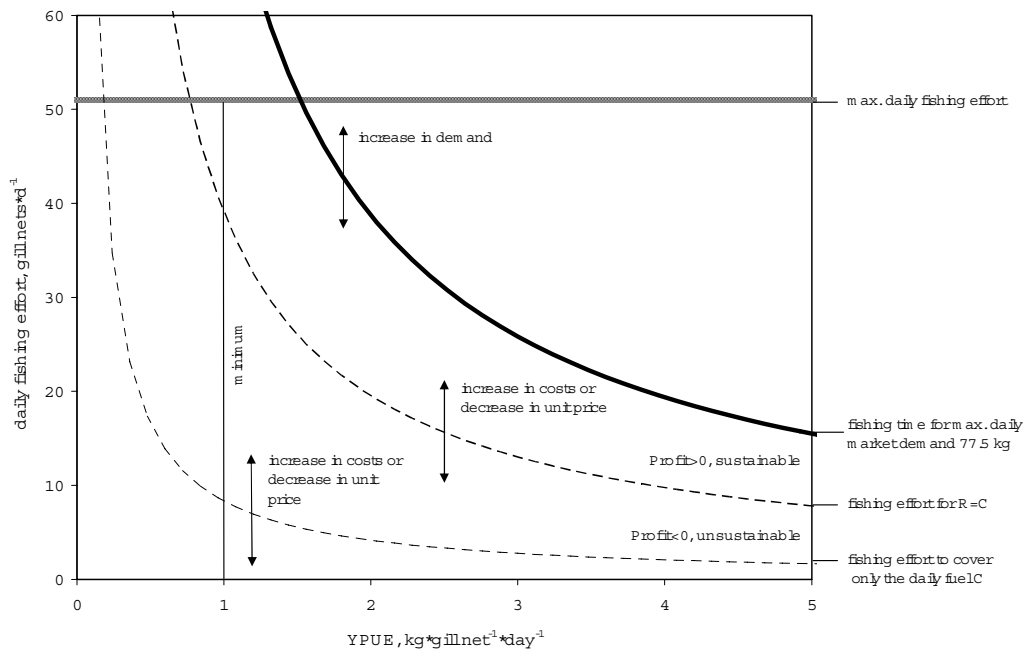
C. Winter seine
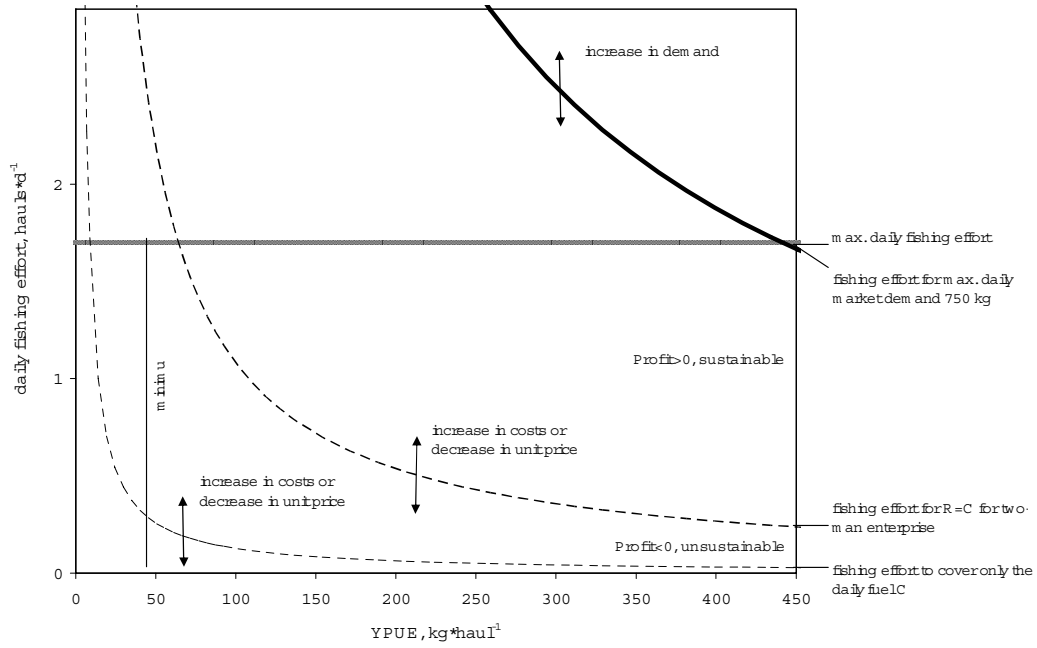
D. Gill nets

FIGURE 5   Continued from the previous page.

4.2.2 Comparison of harvest strategies for variable vendace population: a simulation approach

Given the premise that the ability of the vendace fisheries and markets to absorb the high natural variability in yield and revenue is limited, flexible harvest strategies aiming at lower interannual variability compared with that of the stock were analysed (V). Constant effort strategy represented the reference strategy where variation of annual revenue is proportional to stock value. The strategy aiming at constant revenue was the other extreme. A strategy where fishing effort is moderately increased with decreasing stock served as an intermediate between the extremes and was considered to represent the typical autoregulative vendace fisheries. Despite its ability to maximise the average yield and revenue, the constant stock size strategy was not included because it also maximises the interannual variability (e.g. Ricker 1958, Allen 1973, Gatto & Rinaldi 1976). Three different levels of fishing shutdown threshold were incorporated into the basic strategies.

In case of high recruitment variability, the qualitative performance of different strategies was not sensitive to the studied examples of S-R relationships, the Ricker and Cushing relationship either with or without negative dependence between consecutive recruitments.

In the case of low fishing shutdown threshold, the constant effort strategy performed best and the constant yield strategy worst concerning the objectives of maximum mean annual revenue, maximum mean efficiency (mean revenue/mean effort), and low risk for low spawning biomass, the indicator of the risk of collapse of fisheries. The interannual variability of revenue increased with the increase in mean annual effort and mean revenue up to the maximum revenue and beyond in all model combinations. For the constant effort strategy, the revenue variation was already high at low mean revenue levels. For the strategy aiming at constant revenue, variation was low at low mean revenue level but increased rapidly with increasing revenue. The intermediate strategy produced promising tradeoffs of moderate mean revenue with low variation and low risk to reproduction at a certain mean revenue level close to the maximum. The performance of the strategies by criterion of variation in effort was naturally opposite to revenue variation as the revenue stability was gained by increasing effort variability.

When the threshold level of fishing shutdown was increased the differences in performance of the strategies decreased. Importantly, the variability of revenue at a certain mean revenue increased for every strategy, thus limiting the scope for trading off mean revenue and its variability. On the other hand, the increase in threshold decreased the risk of low spawning stock. The threshold, due to being a "boom and bust" stopping rule of highly nonlinearly compensatory nature was also demonstrated to cause instability to the dynamics.

The results were qualitatively the same as above for the case of lower recruitment variability but naturally the coefficients of variation of revenue and effort and risks of low spawning stocks were lower.

Increased tendency for two year cyclicity was detected for all the studied strategies when the effort (and thus mortality) was high enough to keep the spawning population in a steeply increasing section of the S-R curve (see section 4.1.3.2 for closer discussion of cyclicity).

Thus, the results imply that the possibility of adjusting fishing effort autoregulatively as described in paper IV (section 4.2.1.1) can be beneficial when the market demand of fish limits the operation. The precondition for successful effort adjustment is a low enough number of fishing enterprises so as not to over exploit the stock easily during decline. Some threshold regulation to protect spawning stock may also be necessary despite the fact that it may somewhat decrease the scope of effort adjustment by the fishers. The results are in accordance with the other studies where mixed strategies of effort adjustment to stabilise supply and thresholds were combined (e.g. Walters 1975, Ruppert et al. 1985). However, as emphasised in V the choice of optimal harvesting strategy for different vendace stocks is a question of balancing various costs, benefits and risks weighted by their specific utilities. This question requires further study.

4.2.3 Effect of trawling on dynamics of pelagic fish stocks: a case study

An 11 year time series of hydroacoustic fish density estimates and yield and effort statistics in four zones of Lake Puulavesi were compared in an attempt to reveal the effects of intensive trawl fishing on fish density and yield (VI).

The comparison was based on the assumption that no such migrations between zones occur that would considerably affect the population dynamics in different zones. This assumption is supported by the studies on vendace migrations (Viljanen 1978, Valkeajärvi 1983, Jurvelius et al. 1995, Auvinen et al. 2002.) and indirectly by the differences in growth in different zones in Lake Puulavesi (VI).

The comparison revealed no detrimental effects of trawling on pelagic fish stocks. First, the abundant year-classes and the stock decline were detected in the same years in every zone giving correlation between the dynamics of the zones. Further, the acoustic estimates of fish density and the growth of fish implied no decrease in fish density in the most intensively trawled zones in comparison to less intensively exploited, in fact an increase. However, the interannual variation of fish density was higher, although not significant statistically, in the most intensively exploited zones which is in accordance with the theory of exploitation (e.g. Beddington & May 1977) and the predictions of the simulation study (V). Finally, no clear decrease was found in yield per unit effort of trawl or pelagic fish density with increase in trawling effort.

Thus, the results suggest that the compensatory processes in vendace population dynamics have so far been effective enough to compensate for the increase in fishing mortality in terms of average densities and yields. The synchrony in interannual variation, however, implies that the recruitment is determined largely by external factors, which is in agreement with III. The results partly contradict the results of Auvinen (1987, 1994) from Pyhäjärvi, southeast. There, strong year-classes emerged more often, and with high

tendency for two year cyclicity, in an intensively fished zone of a lake than in a zone of minor fishing pressure. According to Auvinen (1994) this was due to strong density dependent regulation by intraspecific factors directly or indirectly through community level changes by intensive fishing. However, a severe decline in late 1980s occurred in both zones implying an external cause, in this case an increase in predatory perch.

The results suggest that trawling, despite its indirect fishing mortality to young-of-the-year vendace passing through cod-end (Suuronen et a. 1995) has not played a major role in their large and unpredictable (II) total mortality. The fact that large areas of the lake have served as natural reserves (e.g. Roberts & Polunin 1991) for young-of-the-year vendace may partly explain this. The distribution of juvenile vendace and its spatiotemporal overlap with trawling effort is currently unknown and should be assessed in different lakes before the effect of trawl on their mortality can be assessed.

Although covering several vendace generations, the study period was short in comparison with longer term changes e.g. in fish community level, whether due to fishing or environmental factors, and frequency of rare environmental effects.

The fact that positive dependence has been suggested between larval density and recruitment in low spawning stock (II) calls for precaution if fishing will be increased in the future. Continuous monitoring of both trawled and non trawled zones will be needed to separate the detrimental effects of fishing as early and indisputably as possible from other sources of variability.

5   CONCLUSIONS FOR VENDACE FISHERIES ASSESSMENT AND MANAGEMENT

This study has highlighted the following biological bases for vendace fisheries management: First, the interannual variability in recruitment of vendace is typically great and to a large extent determined by unpredictable external factors. Second, generally high uncertainty exists about the functional form and parameters of the spawning stock-recruitment relationship. Yet, clear evidence of poor recruitment from the smallest spawning stocks and larval abundances have been found which call for precaution as the basic principle in vendace harvesting.

Under these biological conditions, optimisation of fishing mortality or spawning stock in order to achieve high level recruitment with small interannual variation is hardly a realisable option. Thus, the sustainability of full time commercial vendace fisheries demands for the possibility to adjust fishing effort in order to level the yield and revenue fluctuations. This adjustability is only possible if a) the capacity of effort of individual fishing enterprise is high and b) the number of enterprises harvesting a population is so low that the increase of effort during decline does not easily endanger the productivity of the stock. An alternative strategy of yield adjustment worth studying might be e.g. switching between several stocks (Muje et al. 2003).

The possibility of effort adjustment demands stock assessment to provide those responsible for fisheries management with information of a) the minimum allowed spawning stock level to secure adequate recruitment together with risk assessment accounting for the various types of uncertainties in this information and b) an estimate of the long term sustainable yield with the tolerable level of interannual variation and the maximum allowed potential fishing effort (number of commercial fishing enterprises). These tasks require, in the case of highly variable recruitment, long term monitoring of the populations at various life stages with proper assessment of the precision of the monitoring methods.

A prerequisite for vendace fisheries management according to these suggestions is rearrangement of the present fishing license system in lakes

which consist of a mosaic-like structure of fishing rights ownership by several independently operating statutory fishing associations (see e.g. Sipponen et al. 1999). The total amount of licenses for commercial harvesting of a population must be based on the productivity of the population in the context of the ecosystem. This is not the case at present. Thus, there is demand for cooperation of the stakeholders, comanagement and consideration of ecosystem based management.

The point of view of this study concerning the inland fisheries system was limited to the nature and certain consequences of the biological variability of the resource. Multidisciplinary approaches are needed to assess the significance and applicability of the results in the broader context of the whole inland fisheries system.

Acknowledgements

First, I want to thank my supervisors prof. Tapani Valtonen who turned on my interest in fish and especially vendace population dynamics and Juha Karjalainen who gave me the possibility to stay tuned despite of occasional drop-out feelings. Many discussions with Juha have extended my understanding on the early life history of fishes.

Discussions with cowriters have been most illuminating. Discussions with many other groups have had deep impacts on my thinking as well. Especially, I want to thank all who have attended the meetings of the "national vendace working group". Communication in the multidisciplinary INSURE-project group has been inspiring as well. Collaboration with Dr. Juha Jurvelius has been very educating. The atmosphere and activities in our working room have prevented the things from getting too scientific.

I am indebted to many fishers in Lake Puulavesi for their endless motivation to provide me with data. From them I have also learned many secrets of behaviour of vendace and the viewpoints of the fishers.

I thank for cooperation the Employment and Economic Development Centre for south Savo, Fisheries Services, Mikkelin kalatalouskeskus, Fisheries Region of Puula and the statutory fisheries associations there and the municipal communities of Hirvensalmi, Kangasniemi and Mikkeli (formerly Mikkelin maalaiskunta).

Markku Raatikainen's help has been invaluable in various tasks during the years. Without Markus Huolila's disinterested hobbyism on echosounding the field work would have been impossible. Osmo Rätti's navigational skills were crucial in planning and starting of the nightly echo-sounding surveys in the pre GPS age. I am indebted also to Juha Lilja, Tapio Keskinen, Jussi Kirjasniemi, Mikko Koivurinta, Osmo Pitkänen, Jari-Pekka Pääkkönen and the technical, office and library staff of my department as well as staff of the universities of Joensuu and Turku and the Finnish Game and Fisheries Research Institute for a myriad of types of services and assistance.

The language in the original papers was checked by prof. Roger Jones, Dr. Roy Siddall and Mrs Riitta Wilmot. The language in this summary was checked by Dr. Daniel White.

My greatest thanks go to my family and relatives for their care and support.

This study was financially supported by the municipalities of Hirvensalmi, Kangasniemi and Mikkelin maalaiskunta, the Fisheries Region of Puula, Employment and Economic Development Centre for south Savo, Finnish Cultural Foundation/Central Finland, the Academy of Finland - research programme on Sustainable Use of Natural Resources (SUNARE).

"Of making many books there is no end, and much study wearies the body"

     Ecclesiastes 12: 12

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YHTEENVETO

Muikun, Coregonus albula (L.), vuosiluokkien runsauden vaihtelu ja sen vaikutukset kalastukseen

Tässä väitöskirjassa tutkittiin muikun rekryyttimäärän (=vuosiluokan runsaus ensimmäisen elinvuoden syksyllä tai talvella) vuosien välisen runsaudenvaihtelun ominaispiirteitä ja syitä sekä tarkasteltiin vaihtelun vaikutuksia kalastukseen ja sen säätelyyn ja toisaalta kalastuksen heijastumista vuosiluokkavaihteluun. Tutkimus kuuluu kalabiologian ja kalatalouden tieteenalaan.

Muikunpoikasten keväisen kuoriutumisen ja syksyisen rekrytoitumisen välisen jakson kuolevuuden sekä kutukannan ja siitä seuraavana syksynä seuraavan rekryyttimäärän välisen riippuvuuden analyysit osoittivat, että muikun rekrytoitumista edeltävän kuolevuuden vuosien välinen vaihtelu on erittäin suurta. Jaksolla jäänlähdön jälkeiseltä viikolta kolmannelle viikolle poikasten päiväkohtainen keskimääräinen kuolevuus oli noin 10 % ja tämän jälkeisellä jaksolla noin 1 %. Molempien jaksojen jaksokohtainen kokonaiskuolevuus ja sen vaihtelevuus olivat kuitenkin samaa suuruusluokkaa, joten myös jälkimmäinen jakso on merkittävä vuosiluokan suuruuden määrääjänä. Kuolevuus johtuu merkittävältä osalta populaation tiheydestä riippumattomista ulkoisista tekijöistä. Tässä tutkimuksessa havaittiin Puulavedellä yhteys voimakkaiden kevätkesän tuulien ja poikasten suuren kuolevuuden välillä. Ulkoisten tekijöiden suurta merkitystä vuosiluokkavaihtelun säätelijänä osoittaa myös havaittu lähellä toisiaan sijaitsevien muikkujärvien vuosiluokkavaihteluiden samarytmisyys eli synkronia.

Puulaveden aineistosta analysoitiin tarkemmin populaatiodynamiikkaan ja kalastuksen säätelyyn keskeisesti vaikuttavaa kutukannan biomassan ja rekryyttimäärän välistä riippuvuutta sekä tarkasteltiin riippuvuuden määritysmenetelmään liittyviä virhelähteitä. Puulaveden kutukanta-rekryyttiriippuvuuden havaittiin olevan kompensatorinen (= kutukannan kasvaessa jälkeläistuotto kutukannan yksikköä kohden, esim. jälkeläisiä/kg kutukaloja, pienenee). Rekryyttimallin muotoa ja parametrien arvoja koskeva epävarmuus oli suurta. Regressioanalyysiin perustuva tiheysriippuvuuden tutkimusmenetelmä on harhainen aineiston mittausvirheiden ja aikasarjaluonteen vuoksi; monessa tapauksessa menetelmä yliarvioi kompensoivan prosessin suuruutta.

Säkylän Pyhäjärvellä havaittiin poikasten kuoriutumisen ja rekrytoitumisen välisen jakson kuolevuuden olevan kompensatorista. Sen sijaan neljässä muussa tutkitussa populaatiossa merkittävää kompensaatiota ei havaittu. Vastakuoriutuneiden poikasten määrän ja rekrytoituvan vuosiluokan runsauden välillä todettiin kuitenkin olevan positiivinen yhteys, mikä korostaa riittävän kutukannan varmistamisen merkitystä kalastuksen säätelyn reunaehtona.

Puulavedellä havaittiin viitteitä edellisen vuosiluokan runsauden negatiivisesta vaikutuksesta seuraavan vuosiluokan runsauteen. Tämän mekanismin on arveltu aiheuttavan muikulle tyypillistä vuosiluokkavaihtelun kaksivuotissykliä. Simulaatiomallin avulla osoitettiin, että muikkujen kuolevuuden kasva-

essa, esim. kalastustehon kasvaessa, vuosiluokkavaihtelun kaksivuotissyklisyyden todennäköisyys kasvaa. Tämä tapahtuu myös silloin, kun edellinen vuosiluokka ei vaikuta seuraavan runsauteen.

Voimakas vuosiluokan runsaudenvaihtelu aiheuttaa suurta kalastettavan kannan vaihtelua. Kalastuksen säätelyn kehittämisen kannalta on tärkeätä tuntea, miten eri kalastajaryhmät reagoivat tähän vaihteluun ja toisaalta miten kalastusstrategia ja pyynnin intensiteetti vaikuttavat populaatiodynamiikkaan. Puulaveden kalastusta koskeva aineisto, graafinen mallitarkastelu sekä muiden tutkijoiden havainnot osoittavat, että varsinkin tehokkailla pyydyksillä kuten troolilla kalastavat ammattikalastajat joutuvat säätelemään pyyntiponnistustaan saaliin tasaamiseksi. Kalastajat lisäävät pyyntiään kalakannan heiketessä ja lopettavat pyynnin kokonaan kannan pudotessa kannattavan pyynnin takaavan tason alapuolelle. Simulaatiomallin avulla jäljiteltiin pyyntistrategiaa, jonka tavoitteena oli jonkin verran vähentää myyntitulon vuosien välistä vaihtelua kalastusta säätelemällä. Strategia tuotti kompromissin, jossa yhdistyi lähes yhtä suuri vuotuinen myyntitulo kuin vakioituun pyyntiponnistukseen perustuvassa strategiassa, vakioponnistusstrategiaa pienempi vuosien välinen vaihtelu sekä pienempi kutukannan romahtamisen riski kuin vakioitua myyntituloa tavoittelevassa strategiassa. Tulon vaihtelu kuitenkin kasvoi kaikilla em. strategioilla pyyntiponnistuksen kasvaessa.

Puulaveden erilaisilla troolausintensiteeteillä kalastettujen alueiden pitkäaikaisseurannassa ei havaittu tehokkaan kalastuksen vaarantavan ulappakalakantoja. Runsas vuosiluokka syntyi kaikilla alueilla samoina vuosina, ulappakalojen tiheys ja yksikkösaalis pysyivät kaikilla alueilla keskimäärin samalla tasolla riippumatta kalastuksen intensiteetistä. Nämä havainnot osoittavat epäsuorasti kompensaatiomekanismien merkitystä muikun kannanvaihtelun taustalla.

Ammattikalastuksen mahdollisuus sopeutua muikkukannan voimakkaaseen epäennustettavaan vaihteluun kalastusta säätelemällä edellyttää ammattikalastajamäärän säätelyä. Kalastajamäärän on oltava muikkukannan tuottavuuteen nähden niin pieni, ettei ylikalastustilannetta ja kalastuksen voimakasta rajoitustarvetta synny helposti, kun pyyntiponnistus kasvaa kannan pienetessä. Muikkukadon todennäköisyyttä voitaneen pienentää ja kannan elpymistä kadosta nopeuttaa minimikutukantaan perustuvalla pyynnin säätelyllä. Näiden säätelymenetelmien käyttöönotto edellyttää kuitenkin järvikohtaista tietoa muikkukannan tuottavuudesta sekä kutukannan ja rekryyttimäärän välisen riippuvuuden luonteesta. Järvikohtaisen ammattikalastuslupien määrän suhteuttaminen muikkukannan tuottavuuteen edellyttää myös lupajärjestelmän kehittämistä.

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