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Spatial synchrony in the inter-annual population variation of vendace (*Coregonus albula* (L.)) in Finnish lakes

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We analysed the spatial scale of synchrony in the inter-annual variation of vendace population indices from time-series of 21 Finnish lake basins. We detected significant positive correlation between lakes in the variation of abundance of young-of-the-year recruits, residuals of a density dependence model for recruitment, newly hatched larvae and spawning stocks. The spatial scale of correlation was typically 100–300 km and anisotropic, being shorter along the north–south vector of distance than along the east–west vector. The outcomes did not change when the data were restricted to rule out cases with a possibility of dispersal between populations. The scale and anisotropy structure of synchrony in mean temperature during the four week period after the local ice break date closely resembled that of the vendace population indices. Regionally correlated exogenous factors synchronise the recruitment variation either directly or perhaps also through environmentally induced synchrony in predator stocks. The effective scale of correlation for these factors, especially along the north–south axis, can be short if a large proportion of the prerecruit mortality occurs during a short period and the timing of this period at different latitudes varies by weeks due to differences in time of ice break and vendace hatching.

Introduction

Regional synchrony in the dynamics of local populations is common in animal populations (e.g. Kendall *et al*. 2000 and references therein), including many marine and freshwater fish species (Myers *et al*. 1997). Three main mechanisms have been suggested to cause this phenomenon: (1) regionally correlated exogenous factors such as weather conditions (Mackenzie 1952, Moran 1953, Hanski 1991, Royama 1992, Ranta *et al*. 1995), (2) the dispersal of individuals between populations (e.g. Finerty 1980, Hanski & Woiwod 1993, Holmes *et al*. 1994, Ranta *et al*. 1995) and

(3) trophic interactions from nomadic predators (Ims & Steen 1990, De Roos *et al.* 1991) or pathogens (Shepherd *et al.* 1988, Myers 1993). Lake-dwelling freshwater fish populations are suitable for analysing the pure effect of regional stochasticity as the cause for synchrony for two reasons. Firstly, populations are often effectively isolated, in the same way as island populations of terrestrial animals (Grenfell *et al.* 1998), which rules out dispersal-dependent causes of synchrony. Secondly, due to the possibility of age-determination in fishes, separation of different year-classes is possible. This gives a possibility to measure directly the population growth in numbers by reproduction (= recruitment) and also potential to filter out the density-dependent components of the population variation related to spawning stock or previous year-classes.

Vendace (*Coregonus albula* (L.)) is a short-lived coregonid fish species commonly occupying pelagic areas of large lakes and brackish waters in northern Eurasia. Considerable interannual variation in recruitment and prolonged periods of low abundance are typical of its populations. Several mark-recapture studies have shown that the migrations of vendace between separate basins within one lake are non-existent or minor (Viljanen 1978, Valkeajärvi 1983a, Jurvelius *et al.* 1995, H. Auvinen unpubl. data). Thus, dispersal of vendace between adjacent lakes to an extent that would influence population dynamics is improbable. The same minimal migration applies also to perch (*Perca fluviatilis*) (Nissinen 1975, Valkeajärvi 1983b), a common natural predator of vendace in lakes. Despite extensive surveys (e.g. Valtonen *et al.* 1988, 2001), no pathogens or parasites capable of inducing considerable mortality of vendace have been found.

According to several analyses, factors intrinsic to populations, such as spawning stock, density of larvae or previous year-class strength, typically explain only a minor fraction of the interannual variation in vendace recruitment estimates (e.g. Viljanen 1988a, Karjalainen *et al.* 2000, Marjomäki 2003). Apart from measurement error the observed large unpredictable variation can be caused by various environmental and biotic factors affecting the prerecruit mortality. The period mostly determining the year-class strength occurs during the first few weeks after larval hatching (Viljanen 1988a, Huusko & Sutela 1998a, Auvinen *et al.* 2000, Karjalainen *et al.* 2000) which takes place around ice break in spring (Karjalainen & Viljanen 1992). Järvi (1942) suggested that weather conditions during spawning and/or hatching affect recruitment success. Thereafter, statistical support from lake-specific studies has been gained for the effect of spring temperature (Auvinen 1988, Helminen & Sarvala 1994) and wind forcing (Marjomäki 2003). If regionally correlated environmental factors significantly affect the recruitment of vendace, synchronous variation in closely-spaced populations should occur as suggested by Salojärvi (1987). Indeed, significant correlations of recruitment variation in adjacent lakes have been documented (Salmi & Huusko 1995a, 1995b). In the absence of dispersal, the spatial scale of population synchrony (the relation between intensity of synchrony and distance between populations) should resemble that of the relevant forcing agents (e.g. Sutcliffe *et al.* 1996, Williams & Liebhold 2000).

Vendace is the main target of professional fishing in Finnish lakes. Synchronous stock fluctuation due to environmental factors may have important applications for management of its fisheries. Theoretically, a fisherman harvesting unpredictably fluctuating fish stocks could reduce his uncertainty of income by harvesting several adjacent stocks in turns (Muje *et al.* 2004). Large-scale synchronous variation of harvestable stocks might, however, render this goal difficult to achieve.

In this paper, we analyse the time-series of indices of recruitment, spawning stock biomass and newly hatched larval abundance of vendace collected from Finnish lakes. We aim to determine the synchrony in variation between lakes and to estimate its spatial scale. First, we use all the available data and second, a selection of the data where the possibilities of dispersal of vendace or its predators are ruled out as completely as possible to show that the synchrony is due to regionally correlated environmental factors. As an example of spatial synchrony in environmental factors, we also compare the scale of synchrony with that for temperature during the first few weeks after ice-break.

Material and methods

Sources of data

We used time-series of estimates of the young-of-the-year recruit density indices in autumn-winter, spawning stock biomass indices in autumn and abundance of newly hatched vendace larvae in spring from 21, 17 and seven lakes or basins, respectively (Table 1, Figs. 1 and 2) for the period from 1970 to 2002. The majority of the recruitment and spawning stock data was from the 1980s and most of the larval abundance data from the 1990s. Recruitment and spawning stock indices were mostly based on catch per unit effort and catch sample data, but in some cases also on hydro-acoustic surveys and removal methods (Helminen *et al.* 1993a). The abundance estimates of newly hatched larvae are mainly based on bongo-net sampling with uniform equipment and procedures which are described in Karjalainen *et al.* (1998), except for lake Konnevesi (Valkeajärvi & Marjomäki 2004). The methods are described in detail in the data sources listed in Table 1.

As an index of temperature conditions affecting prerecruit vendace, we used mean air temperature from nine weather stations during the first four weeks after the ice break date in a lake close to each station (data from Finnish Environment Institute). Air temperatures were measured at nine weather stations (Finnish Meteorological Institute) and ice-break dates (Finnish Environment Institute) were taken from lakes near each weather station. The data used were from 1974–1989. The weather stations (Fig. 1) and their neighbouring lakes were: Kokemäki, Pyhäjärvi (southwest Finland); Lahti, Päijänne (Vääksy); Lappeenranta, Saimaa (Lauritsala); Tampere, Näsijärvi; Mikkeli, Saimaa; Joensuu, Höytiäinen; Kuopio, Kallavesi; Kajaani, Oulujärvi and Kuusamo, Poussunjärvi.

Data analysis

We followed closely the methods used by Myers *et al.* (1997) in their meta-analysis in order to ensure comparability of results. Prior to the analysis, we ln-transformed all the time-series of vendace population indices. We used Pearson product–moment correlation coefficient (cross-correlation with lag zero) 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 data sets, we removed the spawning stock dependent components from the recruitment (R) series by fitting to ln(R) data one of the following spawning stock–recruitment models

$$\ln(R_t) = \ln(\alpha S_{t-1}) \text{ linear proportionality} \quad (1)$$

$$\ln(R_t) = \ln(\alpha S_{t-1}{}^{\gamma}) \text{ Cushing (1971)} \quad (2)$$

$$\ln(R_t) = \ln[\alpha S_{t-1}\exp(-\beta S_{t-1})] \text{ Ricker (1954)} \quad (3)$$

where S_{t-1} is the spawning stock biomass index in autumn $t - 1$ and α, β and γ are model parameters. The fitting was accomplished by iterative least squares. The model which produced the lowest standard error of estimate was selected. If $\gamma < 0$ implying overcompensation, the Ricker model was always used. If $\gamma > 1$ and $\beta < 0$ implying no compensatory density dependence, the linear model was always used. The residuals (observed $\ln(R_t)$ – expected $\ln(R_t)$) from these regressions were then used in correlation analysis.

We also calculated lag one auto-correlation of the residuals and, in the case of Pyhäjärvi, southeast Finland, we removed a significant negative auto-correlation with regression

$$\ln(R_t) = \ln(f(S_{t-1})) - \rho R_{t-1} \quad (4)$$

before calculating the model residuals.

For each population index separately, we simulated the distribution of the mean correlation assuming random variation of time-series by producing 5000 sets of data of normally distributed random numbers, temporally matching the real data. Then we calculated all the correlations for pairs i and j and their mean. The significance of certain observed mean correlation of population indices were then evaluated against the simulated distribution assuming random variation.

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

Table 1. Study lakes, years of population data, the density-dependence model used, standard error (S.E.) of estimate for ln(R) from the model and data source. Lakes are represented in Fig. 1. The lakes marked with an asterisk (*) were included in the data selected to rule out the possibility of dispersal.

Lake	Population data from years			Density dependence model	S.E. of estimate of density dependence model	Data sources
	Spawning biomass	Newly hatched larvae	Recruitment			
Yli-Kitka*	70–90	95–98, 99[1]	71–91	Ricker	0.54	Salmi & Huusko (1995a), Karjalainen *et al.* (2000)
Kiitämö*	70–90		71–91	Cushing	1.06	Salmi & Huusko (1995a)
Kirpistö	71–90		71–91	Ricker	1.13	Salmi & Huusko (1995a)
Muojärvi	70–90		71–91	Cushing	0.82	Salmi & Huusko (1995a)
Kuusamojärvi*	71–90		71–91	Cushing	1.09	Salmi & Huusko (1995a)
Kostonjärvi*	76–90		77–91	Linear	1.42	Salmi & Huusko (1995a)
Kerojärvi	74–90		75–91	Ricker	1.20	Salmi & Huusko (1995a)
Irnijärvi*	70–90		71–91	Cushing	1.37	Salmi & Huusko (1995a)
Oulujärvi*	72–88		73–89	Ricker	0.82	Salojärvi (1991)
Lentua*			84–94			Huusko & Sutela (1998a)
Suomunjärvi*	74–86, 88–92, 94–02		75–86, 88–92, 94–02	Linear	3.01	Viljanen *et al.* (2004)
Pohjois-Konnevesi	78–98		85–99	Cushing	1.47	P. Valkeajärvi unpubl. data
Etelä-Konnevesi*	71–00	84–98, 99–02[1]	71–97	Ricker	2.42	Valkeajärvi & Marjomäki (2004)
Onkamo*	80–96	80–85, 93, 96–98, 99–02[1]	80–97	Ricker	1.95	Viljanen (1988a), Auvinen *et al.* (2000), Karjalainen *et al.* (2000)
Paasivesi*		89–98, 99–02[1]	85–98			Karjalainen *et al.* (2000)
Puruvesi, Hummonselkä		89–98, 99–02[1]	77,79, 83–84, 87–88, 90–97			Karjalainen *et al.* (2000)
Puruvesi, Harvanselkä*		92–98, 99–02[1]	77–97			Karjalainen *et al.* (2000)
Pyhäjärvi, SE Finland*	77–89[2]		77–90	Cushing & R_{t-1}	0.84	Auvinen & Auvinen (1994)
Puulavesi*	82–96		82–95, 96[1]	Ricker	1.39	Marjomäki (2003)
Päijänne, Tehinselkä*	83–00[1]		82–96[1]	Ricker	1.70	P. Valkeajärvi unpubl. data
Pyhäjärvi, SW Finland*	80–00[1]	85–97, 98–02[1]	71–96, 97–00[1]	Cushing	0.61	Helminen *et al.* (1997)

[1] Unpublished data.

[2] Population fecundity estimate.

e^{-1}, i.e., the exponential decay rate or the *e*-folding scale (Myers *et al.* 1997). To estimate this, we fitted by iterative least squares the model

$$r_{i,j} = r_0\exp(-D\nu^{-1}) \qquad (5)$$

where r_0 is the estimate of correlation between two populations at zero separation, ν is the estimate of *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. Theoretically, $\max(r_0) = 1$ assuming no measurement error in the time series. If the estimated r_0 was greater than one, the fitting was repeated by forcing r_0 to unity. To take into account that some correlation-distance-relationships might have a "shoulder", we fitted the model (Myers *et al.* 1997)

$$r_{i,j} = r'_0\exp(-0.5(D\nu'^{-1})^2) \qquad (6)$$

where r'_0 is the estimate of correlation between two populations at zero separation and ν' is the standard deviation of normal distribution. In model fitting the correlations were not weighted by the fraction of the years for which the two time-series had overlapping data.

The analysis was repeated for selected data where dispersal of vendace or its predators should be improbable (Table 1). From each pair of connected lakes the one with most recruitment observations was included, except for the lake chain Kiitämö, Kirpistö, Muojärvi and Kuusamojärvi where the two most remote were included.

The treatment and analysis of mean temperature data were similar to that of vendace data except that temperature data were not ln-transformed because it was assumed (central limit theorem) that the mean of 112 observations (four weeks × six daily observations four hours apart from each other) should closely follow a normal distribution.

Results

We found significant positive mean correlation (all 1-tailed $p < 0.1$) in inter-annual variation of all analysed population indices for vendace (Table 2). The removal of the dependence of recruitment from spawning stock biomass and previous year-class level had no noticeable effect on mean correlation (Residual in Fig. 2). This was also the case if comparing only the 17 lakes with both recruitment and residual series. For the full data, the mean correlation was highest in variation of larval densities and lowest in spawning stocks. The variation in correlation coefficients was large and contained a considerable number of negative values.

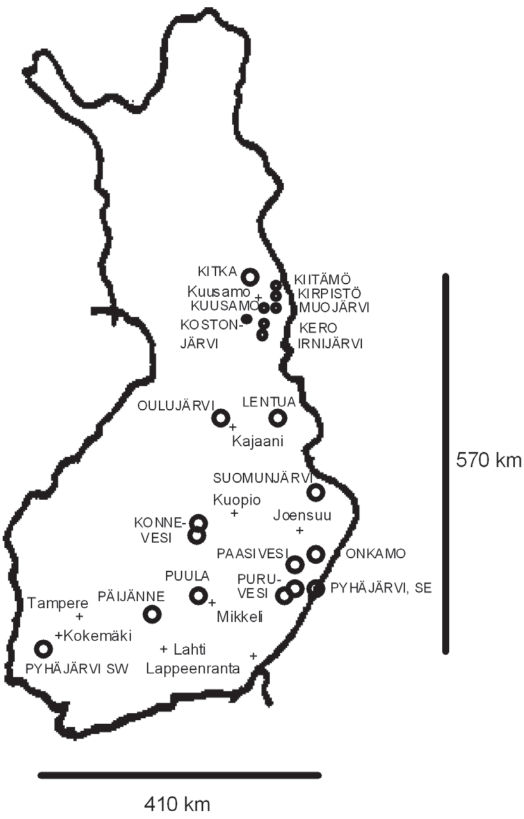


Fig. 1. Locations of the vendace populations (circles) and weather stations (crosses) used in the analysis.

In northern Finland, the synchrony in recruitment seems to be largely due to very low recruitment in certain individual years e.g. 1972, 1977, 1980 and 1990 (Fig. 2). For example, the recruitment in Kostonjärvi correlated significantly (all $p < 0.013$) with that of Kiitämö, Kerojärvi and Irnijärvi. Also, all the inter-lake correlations between Yli-Kitka, Kirpistö, Muojärvi and Kuusamojärvi were significant at the level

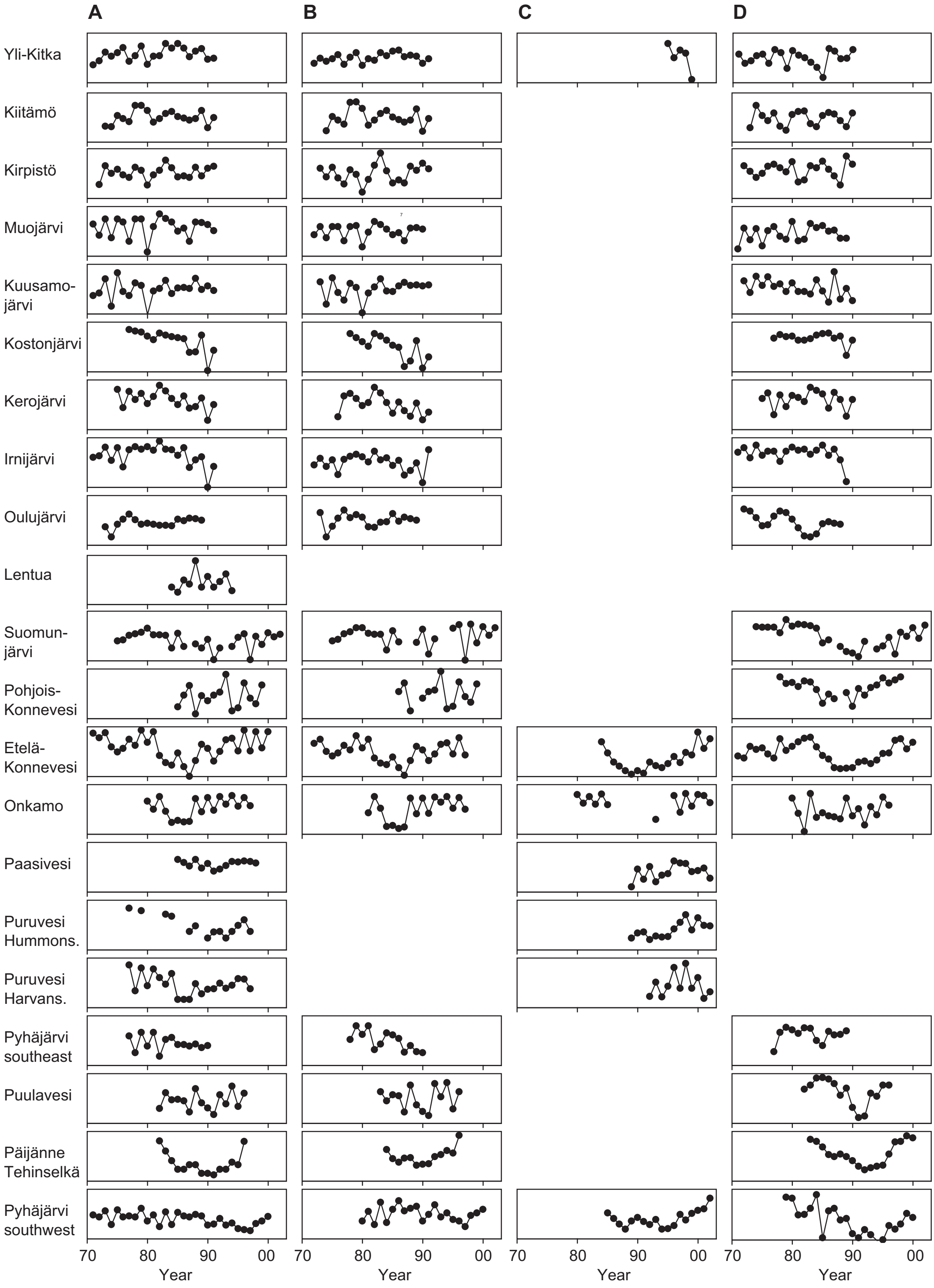


Fig. 2. Time-series of (**A**) ln(recruitment), (**B**) residuals of the density dependence model, (**C**) ln(newly hatched larvae) and (**D**) ln(spawning stock biomass or fecundity estimate) used in the analysis; *y*-axis scale arbitrary.

$p < 0.07$. The correlation in southern Finland seemed to be mostly due to a longer sequence of sparse year-classes around the end of the 1980s (Fig. 2). For example, a series of sparse year-classes occurred in the middle of the 1980s in Onkamo, Etelä-Konnevesi, and Harvanselkä (Puruvesi) and in the beginning of the 1990s in Paasivesi, Hummonselkä, Pyhäjärvi southeast, Päijänne and Pyhäjärvi southwest. A decline in recruitment also took place during the 1980s in certain northern Finnish stocks, causing most of the correlations between stocks from southern and northern Finland.

Regarding the total distance between populations, the estimates of the parameters representing the spatial scale of synchrony, ν and ν', were typically from 100 km to about 300 km (Table 3 and Fig. 3) for every population index. The estimated correlation of populations at distance zero, r_0 and r'_0, were from about 0.2 to 0.7, being highest for newly hatched larvae and lowest for the spawning stocks. The scale of synchrony in every population index seemed to be anisotropic, i.e. scale was dependent on the direction. Along the north–south vector of distance, the scale of synchrony was much shorter than along the east–west vector. Thus, the temporal variation of populations in the same latitude was rather synchronous and the synchrony vanished rapidly as the latitude changed.

There were only minor differences in the results when comparing the full data and the selected data where dispersal was ruled out (Tables 2 and 3, Figs. 3 and 4). The mean correlations for the selected data were significant differing only slightly from those for the full data. Further, the parameters r_0 and r'_0 for both full and selected data were very similar. Most of the high correlations mentioned above were between lakes that are not closely connected. Thus, it can be concluded that the observed correlation was not due to dispersal of vendace.

The scale of synchrony in four week mean temperature after local ice break date closely resembled that of the vendace population indices (Table 3 and Fig. 5). Furthermore, the same type of anisotropy structure was present.

Discussion

Our results indicate that regionally correlated environmental factors synchronise spatial variation of vendace populations, as suggested by Salojärvi (1987). The results are consistent with the findings in all studies on freshwater fishes that the scale of synchrony of recruitment is rather short, only up to a few hundred kilometres (e.g. Myers *et al.* 1997, Grenouillet *et al.* 2001). This was considered to be contrary to expectations by Myers *et al.* (1997) as lakes, like the oceans, are exposed to weather systems with a scale of synchrony of about 1000 km in terms of the annual average values. In Finland, the average temperatures are

Table 2. The mean with 5% and 95% percentiles of Pearson correlation coefficient for population indices of vendace. The *p* values are based on simulation.

Population index	Pearson correlation Mean	Percentile 5%	Percentile 95%	*p* 1-tailed	*n*
Full data					
Recruitment	0.16	–0.40	0.75	< 0.001	210
Residual from density-dependence model	0.14	–0.42	0.71	< 0.001	133
Newly hatched larvae	0.26	–0.58	0.70	< 0.004	20
Spawning biomass	0.12	–0.43	0.68	< 0.001	136
Selected data where dispersal is ruled out					
Recruitment	0.16	–0.31	0.65	< 0.001	120
Residual from density-dependence model	0.14	–0.46	0.65	< 0.002	78
Newly hatched larvae	0.15	–0.59	0.69	< 0.09	14
Spawning biomass	0.11	–0.48	0.66	< 0.004	78

Table 3. The parameter estimates and their standard errors (S.E.) for the models $r_{i,j} = r_0\exp(-Dv^{-1})$ (Model 1) and $r_{i,j} = r'_0\exp[-0.5(Dv'^{-1})^2]$ (Model 2) for vendace recruitment, residuals of density-dependence models for recruitment, abundance of newly hatched larvae and spawning stock biomass and mean air temperature from different weather stations during the first four weeks after the ice break date in a lake near the station.

Data	$r_{i,j}$	D	Model	r_0	r'_0	S.E.	v	v'	S.E.	n
Full										
	Recruitment	Total distance	1	0.33		0.07	264		90	210
			2		0.36	0.06		105	24	210
		North–south vector	1	0.50		0.10	57		21	210
			2		0.41	0.07		46	13	210
		East–west vector	1	0.16		0.03	> 10 000		> 10 000	210
			2		0.16	0.03		> 10 000	> 10 000	210
	Resid. of model	Total distance	1	0.35		0.08	213		80	133
			2		0.30	0.06		160	43	133
		North–south vector	1	0.50		0.12	52		23	133
			2		0.48	0.09		29	7	133
		East–west vector	1	0.18		0.05	400		423	133
			2		0.15	0.04		358	346	133
	Newly hatched	Total distance	1	0.63		0.17	245		132	20
			2		0.55	0.12		223	69	20
		North–south vector	1	0.67		0.22	108		72	20
			2		0.52	0.13		94	40	20
		East–west vector	1	0.41		0.16	249		252	20
			2		0.36	0.12		215	140	20
	Spawning stock	Total distance	1	0.20		0.07	459		319	136
			2		0.18	0.05		325	126	136
		North–south vector	1	0.22		0.06	327		193	136
			2		0.20	0.05		231	77	136
		East–west vector	1	0.12		0.04	> 10 000		> 10 000	136
			2		0.12	0.03		> 10 000	> 10 000	136
Selected data where dispersal is ruled out										
	Recruitment	Total distance	1	0.24		0.07	676		540	120
			2		0.16	0.04		> 10 000	> 10 000	120
		North–south vector	1	0.29		0.07	294		137	120
			2		0.34	0.07		87	26	120
		East–west vector	1	0.16		0.04	> 10 000		> 10 000	120
			2		0.16	0.03		> 10 000	> 10 000	120
	Resid. of model	Total distance	1	0.30		0.11	340		206	78
			2		0.28	0.08		218	72	78
		North–south vector	1	0.43		0.13	115		63	78
			2		0.35	0.09		96	36	78
		East–west vector	1	0.14		0.06	> 10 000		> 10 000	78
			2		0.14	0.05		> 10 000	> 10 000	78
	Newly hatched	Total distance	1	0.61		0.31	194		158	14
			2		0.49	0.18		200	97	14
		North–south vector	1	0.95		0.67	45		39	14
			2		0.69	0.34		40	22	14
		East–west vector	1	0.35		0.25	162		244	14
			2		0.28	0.17		179	186	14
	Spawning stock	Total distance	1	0.29		0.13	272		182	78
			2		0.24	0.09		230	90	78
		North–south vector	1	0.27		0.10	247		170	78
			2		0.25	0.07		196	82	78
		East–west vector	1	0.11		0.07	> 10 000		> 10 000	78
			2		0.11	0.05		> 10 000	> 10 000	78

Continues

Table 3. Continued.

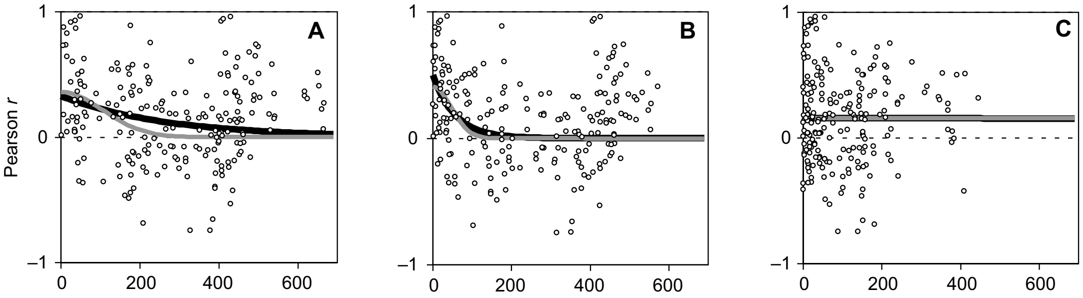
Data	$r_{i,j}$	*D*	Model	r_0	r'_0	S.E.	*v*	*v*′	S.E.	*n*
Four-week-average temperature										
		Total distance	1	1*			237		42	36
			2		0.82	0.14		207	36	36
		North–south vector	1	0.81		0.15	197		67	36
			2		0.67	0.09		178	38	36
		East–west vector	1	0.36		0.14	1 408		4 559	36
			2		0.36	0.10		361	342	36

* estimate > 1, forced to 1

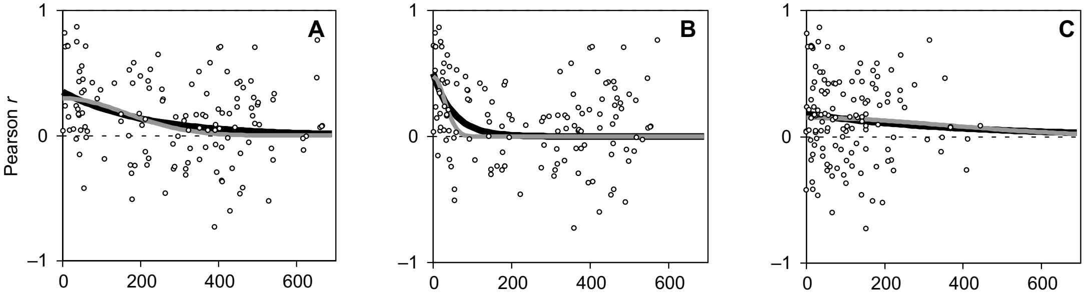
strongly correlated throughout the country even at the time scale less than monthly. Yet, the scale of correlation of essential environmental factors may be quite short considering that the most important period for determination of recruitment is typically a few weeks only and that the temporal difference in the occurrence of this period at different latitudes can also be in weeks. Further, the shorter this period is, the lower the average spatial correlation of the environmental factor, as the average temporal overlap of this period between locations diminishes. In our data, for ice break that triggers hatching, the average time difference between the southernmost and northernmost stations was about three weeks (range in different years from less than two to more than four weeks). Thus, our results emphasise that when comparing the scale and level of spatial synchrony of the populations with that of environmental factors, knowledge of the basic ecology of the species is essential for determining the length and possible anisotropic timing of the essential period for environmental correlation. This has implications for the debate on the possible different scales of correlation when either dispersal or regional stochasticity is the cause (e.g. Hanski & Woiwod 1993, Ranta *et al.* 1995, 1999, Sutcliffe *et al.* 1996, Haydon & Steen 1997, Lande *et al.* 1999, Swanson & Johnson 1999, Koenig 2001).

Our data do not identify which particular environmental factors are important causes of synchrony. Different factors and their combinations may be crucial in different years. However, the resemblance of the regional scale and anisotropy structure of synchrony in vendace and temperature data, together with the previously found correlations between meteorological factors and vendace recruitment (e.g. Auvinen 1988, Helminen & Sarvala 1994, Marjomäki 2003) and various studies demonstrating the effect of weather agents on feeding success of vendace larvae (e.g. Auvinen 1988, Huusko & Sutela 1998b) suggest that the synchronising factors are mostly meteorological. Myers *et al.* (1997) hypothesised that differences in trophic relationships, especially predation, may decrease the scale of synchrony in freshwater ecosystems in comparison with oceans. However, we expect that non-dispersing predators may also synchronise prey dynamics, if the variation in populations of predators is synchronised by environmental factors. Perch is occasionally an important predator of prerecruit vendace (Huusko & Sutela 1992) with the potential to affect recruitment significantly (Auvinen 1994, Helminen & Sarvala 1994, Heikinheimo 2001, Valkeajärvi & Marjomäki 2004). Its recruitment success has been shown to be strongly associated with many environmental factors, especially temperature (Koonce *et al.* 1977, Craig 1987, Lehtonen & Lappalainen 1995). Spatial correlation in year-class strengths of perch populations, possibly due to climatic factors, has also been found (Lappalainen *et al.* 1996). The fluctuations of the predatory perch subpopulations are slower than those in vendace, with high abundance typically supressing vendace recruitment for several years (e.g. Valkeajärvi & Marjomäki 2004). Thus, perch population fluctuations could be partly responsible for the vendace stock recessions in the 1980s and 1990s. During that period, the perch stocks were exceptionally abundant in certain lakes (Auvinen 1994, Heikinheimo *et al.* 2002, Valkeajärvi & Marjomäki 2004). Some

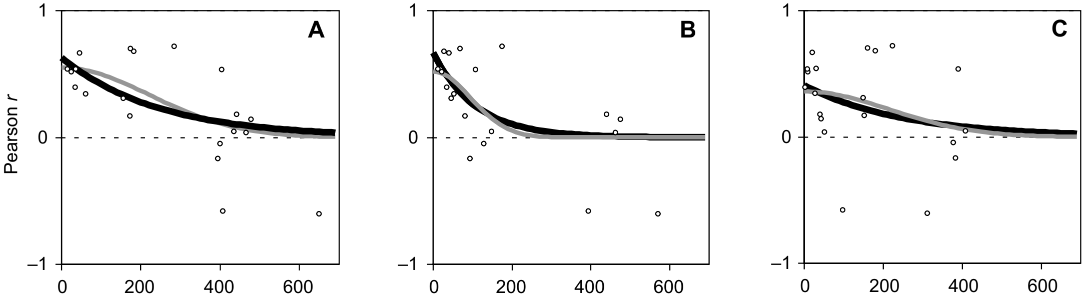
Recruitment



Residuals of density-dependence model



Newly hatched larvae



Spawning stock

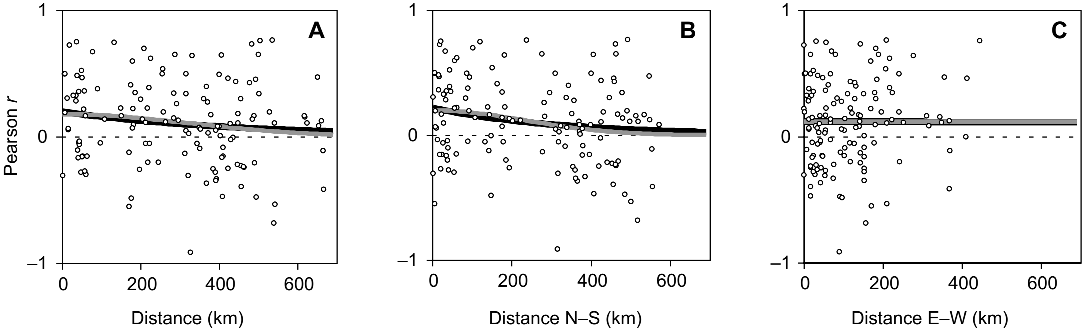


Fig. 3. Correlation of recruitment, residuals of the density dependence model, newly hatched larvae and spawning stock, between pairs of vendace stocks versus (**A**) distance, (**B**) north–south and (**C**) east–west vector of distance between the stocks. Fits of the models $r_{i,j} = r_0\exp(-Dv^{-1})$ (black curve) and $r_{i,j} = r'_0\exp[-0.5(Dv'^{-1})^2]$ (grey curve).

synchrony, comparable to dispersal of predators, might emerge from anthropogenic factors, such as regional trends in fishing mortality or stockings of predatory fishes. However, Valkeajärvi *et al.* (2002) did not consider them responsible for the vendace stock recession in southern Finland.

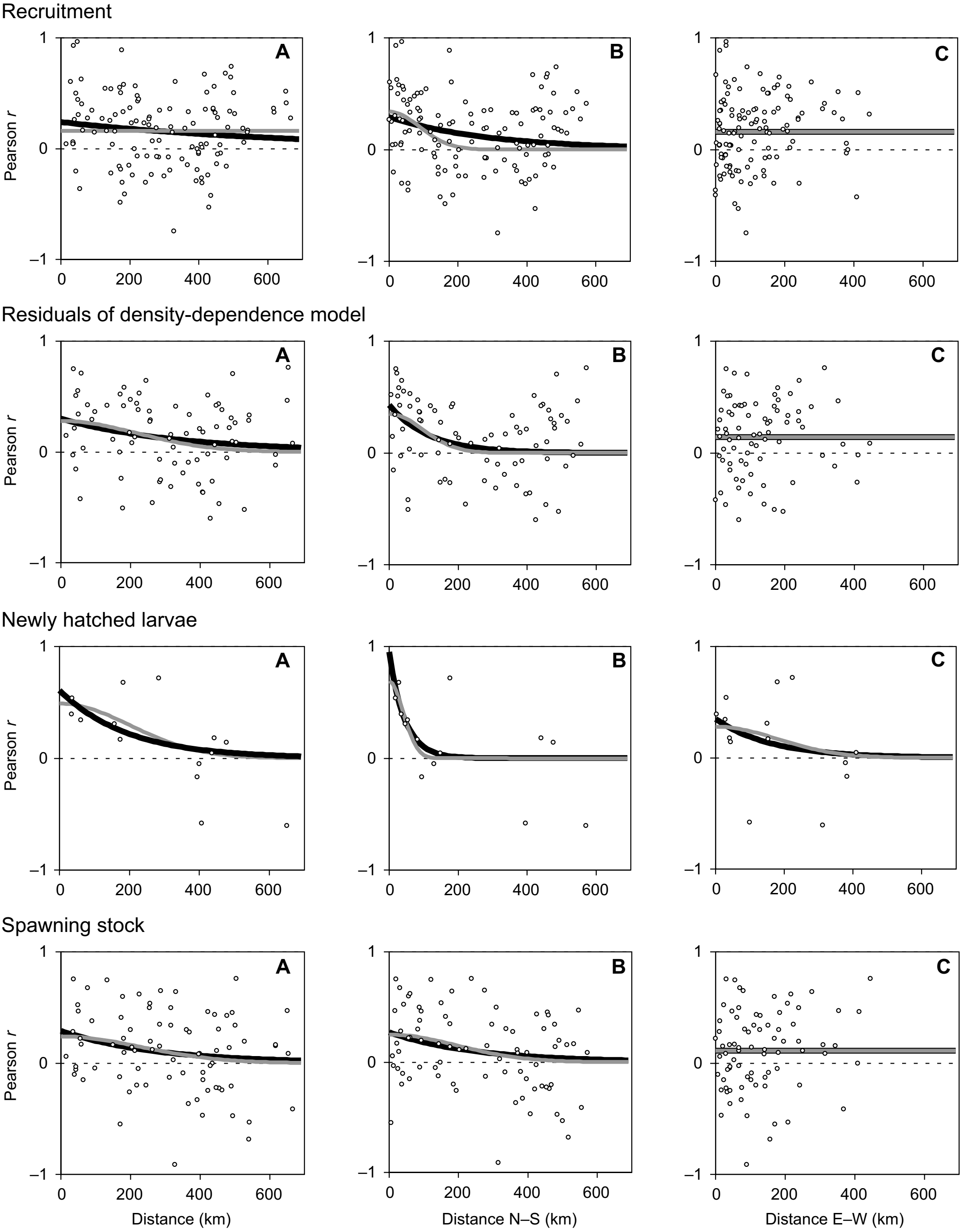


Fig. 4. As in Fig. 3 but for the selected data with no possibility of dispersal (lakes marked with an asterisk (*) are listed in Table 1).

Moran's theorem states that the spatial correlation of population variation will equal the environmental correlation in populations with identical linear dynamics (Moran 1953, Royama 1992). If the population dynamics is non-linear the effectiveness of an environmental factor in

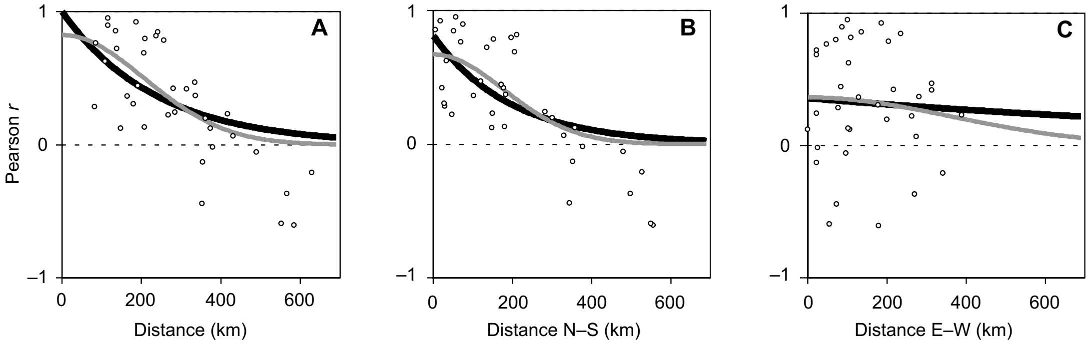


Fig. 5. Correlation between mean temperature during four week period after the local ice break date at pairs of weather stations versus (**A**) distance, (**B**) north–south and (**C**) east–west vector of distance between the stations. Curves as in Fig. 3.

synchronising populations depends strongly on the structure of the underlying deterministic population dynamics, especially the tendency towards cyclicity (Grenfell *et al.* 1998, Ranta *et al.* 1998, 1999, Greenman & Benton 2001). In non-cyclic population models, the population synchrony is generally lower than that of the environmental factor, as the synchronising effect is filtered by the model (Greenman & Benton 2001). This reduction in correlation depends on the statistical distribution and variability of the factor. In cyclic populations, on the other hand, correlation enhancement between populations is possible through phase-locking (Ranta *et al.* 1998, 1999), even in the case of no dispersal (Greenman & Benton 2001). Vendace recruitment has been suggested to be non-linearly dependent on spawning stock (e.g. Valtonen & Marjomäki 1988, Viljanen 1988a, Salojärvi 1991) and two-year cyclicity has been detected in certain selected sequences of recruitment time series of vendace (Hamrin & Persson 1986, Helminen *et al.* 1993b, Auvinen 1994, Auvinen *et al.* 2000). In our data, there were sequences of same-phase two-year oscillation in Etelä-Konnevesi, Puruvesi Harvanselkä, Pyhäjärvi southwest and Pyhäjärvi southeast in the late 1970s–early 1980s and in Etelä-Konnevesi and Onkamo and Puulavesi in the 1990s. The removal of density dependence from the recruitment data had no noticeable effect on the magnitude or spatial structure of the synchrony. The unpredictable variation around the density dependence models was very high in the majority of populations (Table 1), the average standard error of estimate being 1.3. This high level of unpredictability strengthens the view that the population dynamics of vendace are largely driven by external, density-independent factors and explains why the spatial correlation structure was similar in recruitment including density-dependent effects and the series of model residuals. It should be noted, however, that correct removal of density-dependence is always disturbed by considerable model and parameter uncertainty and biases from measurement and time series errors (Marjomäki 2003).

As expected, the spawning stock dynamics were somewhat synchronous in the presence of recruitment synchrony. Vendace is a short-lived species (e.g., Viljanen 1986) so recruitment variation significantly affects the spawning stock. In our data, taking spawning stock biomass as an index of harvestable stock, despite the average correlation being positive, at a scale of 100 km, many negative correlations between adjacent populations occurred. Thus, potential for reducing vendace yield variation by interlocked use (Muje *et al.* 2004) of several vendace stocks exists. One theoretical question, requiring closer analysis, is how fishing affects the level of synchrony between spawning stocks. If there were significant differences in mean and temporal variation of fishing mortality between adjacent populations, these might effectively act against the synchronising effect of environmental agents.

Synchrony in variation of density of newly hatched larvae was higher than in other indices. Partly the synchrony in newly hatched larvae arises because their densities depend on the spawning stock densities (e.g. Viljanen 1988b) which are themselves synchronised. Some mortality associated with environmental factors may also have taken place between spawning in autumn and larval sampling in spring. Part of the explanation for the high correlation may lie in the fact that the data for the newly hatched larvae were typically from populations that were recovering from recession and thus had increasing larval densities. The effect of increasing spawning stock could not be removed because spawning stock data were lacking in the majority of cases. Also, the time series were typically short, so that reliable removal of serial correlations was not possible. Thus, the results must be considered preliminary. Nevertheless, the synchronous recovery of these populations does itself stand as evidence of synchrony in population dynamics due to exogenous factors.

A severe obstacle in any comparison of synchrony in population indices and environmental factors is the fact that the expected value of the observed correlation between two variables and its variance depends on the level of measurement error of these variables (Koenig 1999, Lande *et al.* 1999, Buonaccorsi *et al.* 2001), or more precisely on the ratio between their true variation and measurement error variation (signal-to-noise-ratio = *S*/*N*). Low *S*/*N* leads to correlation biased towards 0 and renders the measurement of scale difficult. In the case of low *S*/*N*, the expected correlation would be close to 0 and its random variation high, even in the extreme case of correlating two data sets derived from monitoring the same population. In densities of newly hatched and recruiting vendace, the true variation (strength of signal) has been high as many stocks have undergone collapses and recoveries during the study period. The variation of spawning stock is typically lower and therefore these series may have lower *S*/*N*-ratio as well. The level of random variation has been estimated in the case of density of newly hatched larvae (Karjalainen *et al.* 2000). The 95% confidence level of mean of ln(density) was typically less than mean ± 10%. In many cases, according to simulation results (T. J. Marjomäki unpubl. data), the precision of recruitment and spawning stock indices is lower than that and they are, therefore, more vulnerable to bias. However, large measurement error might also introduce false positive correlation of variation under certain conditions. This might happen if the measurement error itself is dependent on some large scale environmental agent, for example if the catchability of the gear used in population density monitoring depends on wind forcing or water temperature, although we do not consider this a likely bias with our data.

In conclusion, regionally correlated environmental factors, most probably meteorological, synchronise the variation in vendace stocks directly or through environmentally-induced synchrony in predator stocks. This strengthens the view that density-independent factors are important in determining vendace recruitment. The geographical scale of synchrony, especially along the north–south axis, is short, which is consistent with the short period for recruitment determination of vendace and the timing of that period varying between latitudes.

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