

Environmental effects on the recruitment dynamics of coregonids from the Petchora River

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Stock-recruitment processes in four coregonid species, *Coregonus lavaretus pidschian*, *C. peled*, *C. albula maris-albi* and *C. autumnalis*, from the Petchora River were investigated. The dynamics of density-independent mortality for the 0-group of each species were reconstructed using stock-recruitment models and compared with environmental factors including average monthly water surface temperature, average monthly water level, monthly total length of open sunshine, ice thickness during winter months, and date of steady ice cover setting. The results of a stepwise variable selection analysis showed that 68.7% to 95.1% of the recruitment variability is due to perturbations in environmental conditions. The primary factor influencing pre-recruitment mortality is insolation. Less important, but still significant, factors are water temperature and water level.

Introduction

Determination of the environmental factors controlling the year-class strength of fish populations is very important for the development of empirical methods dealing with recruitment prediction. Analyses of the role of environmental factors on fish reproduction processes are often reduced to searching for relationships between characteristics of the hydro-physical regime and some indices of final abundance of fry (Salojärvi 1982, Rijnsdorp *et al.* 1992, Nilssen *et al.* 1994). However, it is obvious that the accuracy of such methods is low because of indirectness and non-linearity of the relationships.

Direct comparisons of recruitment abundance (or of some abundance indices) with the dynamics of environmental characteristics often fail (e.g., Zykov 1981, Salojärvi 1982, Sharov 1987). One may expect to obtain more reliable results from comparing the dynamics of environmental factors with those characteristics of population dynamics processes controlled by environmental conditions in a direct way (Tang 1985, Kriksunov and Sharov 1987, Stocker and Noakes 1988, Schweigert and Noakes 1991). Hence, it would appear preferable to analyze independent elements of the recruitment process, such as density-dependent and density-independent components of mortality.

that successful description of the recruitment process for whitefish, vendace and peled is achieved by using the Ricker's function:

$$R(E) = E \times \exp[-(\alpha E + \beta)T] \quad (1)$$

whereas for Arctic cisco it was necessary to use a modified form of Eq. 1:

$$R(E) = E \times \exp[-(\alpha E^c + \beta)T] \quad (2)$$

where R is recruitment (cohort abundance at time T), E is initial abundance of the generation, proportional to the spawning stock, β is density-independent mortality, α is density-dependent coefficient, and T is the pre-recruitment period.

It should be taken into account that the models given above express only average relationships. The interannual recruitment fluctuations may be a reflection of environmental effects, modifying the existing relationships between parent stock and recruitment through the changes in intensity of the mortality process. Fry survival, having the main role for cohort abundance, is determined by values of density-dependent (αE) and density-independent (β) mortality rates. Keeping in mind the biological meanings of the parameters, the density-dependent mortality rate α can be treated as conservative and rather constant one, whereas the density-independent mortality rate β reflects perturbations in environmental factors and is subject to considerable year-to-year fluctuation. It can be suggested that deviations of recruitment abundance from values predicted by the model are mediated mainly by the interannual variability of parameter β .

Using the time series of population fecundity and recruitment, the dynamics of the density-independent mortality rate over the period under consideration can be reconstructed by a rearrangement of Eq. 1 as follows:

$$\beta_i = \ln(E_i/R_i)/T - \alpha E_i \quad (3)$$

The resulting values of parameter β are presented in Table 2.

The most significant factors influencing the recruitment processes of the Petchora coregonid fishes can be determined from comparison of reconstructed dynamics of density-independent mortality rates with environmental characteristics. The latter are represented by: average monthly water surface temperature (TEMP), average

monthly water level (in cm) (LEV), monthly total length of open sunshine (in hours) (SUN), ice thickness during winter months (in cm) (ICE), and date of steady ice cover setting (IS). Available hydro-climatic data are referred to three geographical points. One of these is located near the river mouth, i.e. at the feeding ground of fry (hereafter FG), and other two points are located about 300 and 600 km upstream, i.e. at the spawning grounds of coregonids (hereafter SG1 and SG2).

Analysis of relationships between environmental factors and density-independent mortality rate was performed in two steps. Firstly, pair correlation coefficients were calculated. However, paired comparisons are not always informative but often result in a distorted picture of relationship structure. As a rule, the risk of spurious correlations is much higher than the significance tests show (Walters and Collie 1988). The reasons for this are the existence of auto-correlative properties in many time series and the complex structure of relationships between hydro-climatic fac-

Table 2. The reconstructed dynamics of density-independent mortality rate (β).

Year	Whitefish	Peled	Arctic cisco	Vendace
1960			0.0046	
1961			0.0489	
1962	0.0582		0.0550	
1963	0.0597		0.0602	
1964	0.0639		0.0574	
1965	0.0693		0.0625	
1966	0.0704		0.0603	
1967	0.0699		0.0570	
1968	0.0697		0.0544	0.0514
1969	0.0712		0.0533	0.0488
1970	0.0666	0.0878	0.0580	0.0543
1971	0.0693	0.0867	0.0608	0.0550
1972	0.0611	0.0774	0.0614	0.0515
1973	0.0710	0.0817	0.0601	0.0514
1974	0.0744	0.0801	0.0622	0.0549
1975	0.0757	0.0736	0.0589	0.0580
1976		0.0742	0.0488	0.0537
1977		0.0787	0.0655	0.0567
1978		0.0855	0.0622	0.0659
1979		0.0851	0.0653	0.0612
1980		0.0790	0.0614	0.0622
1981		0.0776	0.0586	0.0565
1982		0.0916		0.0638
1983		0.0859		0.0554
1984				0.0554

tors. The latter can lead to significant correlations between the variable of interest and a wide set of interdependent characteristics although the real impact is due to only one of them. Secondly, stepwise variable selection technique was used. This technique consists of entering the variables into a regression model only in cases when it can be demonstrated that they make a significant contribution to the variance of the analyzed characteristic.

Results and discussion

Despite the apparent vagueness of the coefficients of pair correlation between the density-independent mortality rates of the Petchora coregonids and the environmental factors (Table 3), some general conclusions can be drawn from them. The success of fry survival during the compensatory

phase is determined by environmental conditions not only over the period of density-dependent regulation but also during the period of spawning and egg incubation (Table 3). Apparently, in the case of vendace and peled, the principal impacts on fry mortality are due to environmental conditions in the spawning season. In connection, it is of interest that there is a strong resemblance in some morpho-ecological features of these two species (Lebedeva 1974).

In Table 4, the regression models are shown that express the results of the application of the stepwise variable selection procedure. Correlation matrixes of the independent variables indicate that multicollinearity between them is not prominent and does not considerably affect the relationships structure (the highest correlation coefficient between independent variables is $r = -0.365$). In all cases the mean values of the residuals did not differ significantly from zero, and the calculated

Table 3. Pair sample correlations between reconstructed values of density-independent mortality rate (β) and environmental factors. In parentheses the statistically significant coefficients ($p < 0.05$) are shown. FG, SG1, and SG2 denote feeding ground and spawning grounds, to which environmental data refer.

Water temperature		Sep.	Oct.	May	Jun.	Jul.	Aug.
Whitefish	FG	-0.31	-0.45	(-0.89)	0.07	-0.31	0.10
	SG1	-0.35	-0.14	-0.16	-0.13	-0.45	0.15
	SG2	-0.12	0.07	(-0.67)	-0.27	-0.49	0.32
Peled	FG	-0.54	-0.20	0.49	-0.37	-0.11	(-0.59)
	SG1	-0.39	0.21	0.04	-0.20	0.03	-0.52
	SG2	0.13	0.25	0.32	-0.11	-0.01	-0.58
Vendace	FG	0.47	-0.19	-0.20	-0.13	-0.10	-0.26
	SG1	0.35	0.10	0.16	0.17	-0.11	-0.19
	SG2	0.49	0.28	0.31	0.17	-0.20	-0.23
Arctic cisco	FG	-0.16	-0.10	-0.55	(0.48)	0.12	0.36
	SG1	-0.29	0.03	0.32	0.34	0.14	0.38
	SG2	-0.22	-0.16	-0.01	0.29	0.20	(0.47)
Ice thickness		Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Whitefish	SG1	(0.57)	0.20	0.52	(0.60)	(0.63)	0.37
	SG2	0.02	0.34	-0.03	0.31	0.32	-0.06
Peled	SG1	0.12	0.09	0.09	-0.12	0.16	0.45
	SG2	0.05	-0.35	-0.30	-0.27	-0.29	-0.08
Vendace	SG1	-0.17	-0.01	-0.11	-0.14	0.01	0.30
	SG2	-0.34	-0.29	-0.32	-0.41	(-0.56)	-0.45
Arctic cisco	SG1	-0.03	0.04	0.31	0.38	0.39	0.21
	SG2	-0.25	-0.05	-0.06	-0.01	-0.01	-0.34

Continued

Table 3. Continued.

River water level		Sep.	Oct.	Nov.	Dec.	Apr.	May.	Jun.	Jul.
Whitefish	FG	−0.05	−0.07	−0.31	0.02	0.18	−0.07	0.25	0.20
	SG1	−0.04	−0.11	−0.35	−0.49	−0.31	−0.08	0.21	0.34
	SG2	−0.06	−0.11	−0.30	−0.47	0.02	−0.10	0.21	0.46
Peled	FG	−0.14	(−0.55)	0.14	−0.05	−0.37	−0.01	−0.29	−0.12
	SG1	−0.22	−0.36	−0.28	−0.04	−0.10	−0.02	−0.25	0.03
	SG2	−0.26	−0.45	−0.39	0.01	−0.19	−0.02	−0.26	0.01
Vendace	FG	0.06	−0.02	0.05	0.25	−0.16	0.31	−0.47	0.03
	SG1	0.04	0.14	−0.25	0.42	0.10	0.24	−0.42	−0.16
	SG2	−0.18	0.10	−0.15	0.20	0.17	0.20	−0.34	0.20
Arctic cisco	FG	0.03	0.02	0.26	−0.10	(0.44)	(0.46)	−0.09	−0.28
	SG1	0.04	0.00	−0.24	−0.22	0.03	0.42	−0.15	−0.30
	SG2	0.06	0.12	−0.01	0.12	0.30	0.38	−0.15	−0.25
Duration of open sunlight		Sep.	Oct.	Nov.	Apr.	May.	Jun.	Jul.	Aug.
Whitefish	FG	0.15	0.20	−0.12	0.07	−0.21	0.19	0.03	−0.01
	SG1	0.23	0.20	0.02	0.22	(−0.58)	0.03	0.15	−0.31
	SG2	−0.22	0.24	0.26	−0.12	−0.33	0.03	−0.18	−0.03
Peled	FG	−0.24	−0.38	−0.33	−0.10	0.08	−0.31	−0.10	−0.47
	SG1	(−0.60)	−0.49	−0.38	0.29	0.17	−0.44	−0.46	−0.18
	SG2	0.11	−0.03	−0.36	−0.04	0.26	−0.42	0.05	−0.28
Vendace	FG	−0.39	−0.30	−0.06	0.19	−0.43	−0.21	−0.21	−0.41
	SG1	(−0.62)	−0.28	(−0.52)	0.06	0.27	−0.14	−0.08	−0.11
	SG2	−0.36	0.09	0.07	0.47	0.10	−0.21	−0.22	−0.25
Arctic cisco	FG	0.34	0.02	−0.02	−0.23	−0.40	0.24	−0.21	0.21
	SG1	0.31	0.30	0.03	0.02	(−0.59)	0.04	0.03	0.04
	SG2	−0.25	−0.10	0.20	−0.02	−0.42	0.09	−0.08	0.11

values of skewness indicated that the distribution of residuals were close to normal. Thus, the application of linear regression models for description of changes in fry mortality rates within the observed range of the analyzed parameters appears to be valid. The regression equations explained from 68.7% (for peled) to 95.1% (for vendace) of the mortality rate variance (the values for Arctic cisco and whitefish were 75.6% and 90.1%, respectively). From these results, it seems apparent that the success of peled fry survival is determined mainly by environmental conditions at spawning (their effect explains 65.2% of mortality variance). The impact of these conditions on vendace fry is smaller but still important (47.8% of variance), whereas their effect on whitefish fry is insignificant (< 1% of variance) and the mortality of Arctic cisco fry depends only on hydro-climatic conditions during the spring. This trend is thoroughly

consistent with the schedule of the spawning time of Petchora coregonids (peled-vendace-whitefish-Arctic cisco) (Solovkina 1962). It appears that the shorter the time interval that separates spawning from relatively constant winter conditions, the less is the influence of environmental factors at spawning on the recruitment process.

Auspicious effects of winter conditions are due mainly to the establishment of an optimal thermic regime for egg incubation. For coregonid fishes such a regime is provided by water temperatures ranging from 0 to 2 °C (Meshkov and Lebedeva 1977, Lebedeva 1981, Chernyaev 1981, Zuromska 1982a, Lebedeva *et al.* 1985, Zhukinsky 1986). It is known that an increase in temperature at the early stages of embryogenesis leads to delay and even halting of development (Chernyaev 1981, 1990, Zhukinsky 1986). For whitefish from Lake Erie, Lawler (1965) reported that an earlier decrease of

temperature in autumn to the level of 0.5 °C was one of the necessary factors for the emergence of a strong year-class. A similar, although not prominent, relationship also occurs in the case of the Petchora whitefish. Apparently, the date of steady ice cover setting in this situation can be treated as an indicator of stable water temperature decrease, for which the direct measurement entails considerable errors (Eckmann *et al.* 1988).

In situations in which the thermic regime is close to optimal (as is probably true for the

Petchora basin), other environmental factors become dominant for egg survival and fry viability (Zuromska 1982b). The stepwise regression analysis reveals the water level at early stages of egg development as one of factors controlling recruitment success. The effect of this factor is probably due to subsiding of ice onto the ground when water level is low (Venglinsky and Tyaptirgyanov 1981, Sorokin 1981). Zhukinsky (1986) pointed out that during the first months of embryogenesis the eggs of coregonid fishes are very sensitive to pressure.

Table 4. The regressions between density-independent mortality rate and environmental factors (*see* text for abbreviations) together with correlation matrixes of the independent variables. First and second indices placed by factor abbreviation indicate location and month, to which the hydro-climatic data refer.

Peled

$$\beta = 0.121972 - 1.02 \times 10^{-4} \times \text{SUN}_{\text{SG}, 9-11} - 4.3 \times 10^{-5} \times \text{LEV}_{\text{SG}, 10} - 4.6 \times 10^{-5} \times \text{SUN}_{\text{SG}, 7}$$

(R^2 adjusted = 0.687)

Correlation matrix

	$\text{SUN}_{\text{SG}, 9-11}$	$\text{LEV}_{\text{SG}, 10}$	$\text{SUN}_{\text{SG}, 7}$
$\text{SUN}_{\text{SG}, 9-11}$	1.000	-0.046	-0.020
$\text{LEV}_{\text{SG}, 10}$		1.000	-0.135
$\text{SUN}_{\text{SG}, 7}$			1.000

Vendace

$$\beta = 0.092973 - 1.65 \times 10^{-4} \times \text{SUN}_{\text{SG}, 9} - 5.4 \times 10^{-5} \times \text{LEV}_{\text{SG}, 1} - 2.43 \times 10^{-4} \times \text{ICE}_{\text{SG}, 3} + 6.5 \times 10^{-5} \times \text{SUN}_{\text{SG}, 4} - 1.5 \times 10^{-5} \times \text{LEV}_{\text{FG}, 6}$$

(R^2 adjusted = 0.951)

Correlation matrix

	$\text{SUN}_{\text{SG}, 9}$	$\text{LEV}_{\text{SG}, 1}$	$\text{ICE}_{\text{SG}, 3}$	$\text{SUN}_{\text{SG}, 4}$	$\text{LEV}_{\text{FG}, 6}$
$\text{SUN}_{\text{SG}, 9}$	1.000	-0.076	0.055	-0.243	0.231
$\text{LEV}_{\text{SG}, 1}$		1.000	-0.177	-0.237	-0.109
$\text{ICE}_{\text{SG}, 3}$			1.000	-0.365	0.211
$\text{SUN}_{\text{SG}, 4}$				1.000	0.160
$\text{LEV}_{\text{FG}, 6}$					1.000

Whitefish

$$\beta = 0.070962 - 1.13 \times 10^{-4} \times \text{SUN}_{\text{SG}, 9} + 9.5 \times 10^{-5} \times \text{IS} + 3.84 \times 10^{-4} \times \text{ICE}_{\text{SG}, 3} - 1.03 \times 10^{-4} \times \text{SUN}_{\text{SG}, 5}$$

(R^2 adjusted = 0.909)

Correlation matrix

	$\text{SUN}_{\text{SG}, 9}$	IS	$\text{ICE}_{\text{SG}, 3}$	$\text{SUN}_{\text{SG}, 5}$
$\text{SUN}_{\text{SG}, 9}$	1.000	-0.083	0.001	-0.072
IS		1.000	-0.167	-0.181
$\text{ICE}_{\text{SG}, 3}$			1.000	0.037
$\text{SUN}_{\text{SG}, 5}$				1.000

Arctic cisco

$$\beta = 0.073183 - 7.3 \times 10^{-5} \times \text{SUN}_{\text{SG}, 5} + 1.6 \times 10^{-5} \times \text{LEV}_{\text{FG}, 5}$$

(R^2 adjusted = 0.756)

Correlation matrix

	$\text{SUN}_{\text{SG}, 5}$	$\text{LEV}_{\text{FG}, 5}$
$\text{SUN}_{\text{SG}, 5}$	1.000	0.120
$\text{LEV}_{\text{FG}, 5}$		1.000

Furthermore, ice subsiding in the riverside zone leads to decreased oxygen supply and, as a consequence, to a decrease in the viability of eggs (Venglinsky and Tyaptirgyanov 1981).

According to the regression equations, the most important factor affecting the success of new generations of Petchora coregonids is the insolation factor (it explains more than 50% of variance in each case). At the spawning period the effect of sunlight on fry survival is positive in all cases. However, at the final stages of embryogenesis, during hatching and in the larval phase the influence of insolation is less important. For peled, whitefish, and Arctic cisco it is slightly positive, whereas for vendace it is actually negative. Zhukinsky (1986) reported that light could cause damage to coregonid eggs through photo-chemical transformations of proteins, nucleic acids and lipids, which are components of cell membranes. In the experiments of Popov and Zotin (1961) the process of hatching of the Svir whitefish embryos proceeded faster in darkness than under illumination. On the other hand, for northern waters, where temperature at the end of embryogenesis is rather low, light energy could be the main factor regulating the rate of development. The time of hatching as well as the rate of phyto- and zooplankton development at nursery grounds of coregonids was determined by the intensity of sun illumination (Chernyaev 1981, 1990). In addition, the only parameter that ensures seeking and seizing of forage particles by early larvae is visual stimulus (Volkova 1981, Kugaevskaya and Sergienko 1985, Radenko and Terentyev 1989).

Thus the discrepancy in opinions concerning the role of sunlight in the development of coregonid fishes at early stages of ontogenesis evidently reflects a duality in mechanisms of its influence. The prevalence of one or another effect is related to the specificity of adaptive reactions of the populations.

In the case of the coregonids of the Petchora basin the positive influence of solar radiation at spawning time on the survival of eggs and fry can be established for populations of vendace, peled and, to a lesser extent, whitefish. For vendace and peled the illumination regime at the spawning season is the most important factor of all the environmental characteristics analyzed. Mechanism of the positive effect may consist of intensification of egg pigmentation under higher illumina-

tion (Zhukinsky 1986). Strongly pigmented eggs are most resistant to the effects of abiotic factors and produce the most viable larvae (Lebedeva 1974, 1981, Ghalaktionova 1983).

By contrast, reactions to the insolation factor during spring can differ. Evidently, for the vendace population the negative effects predominate; this is confirmed by the positive relationship of fry mortality to open sun duration at spawning grounds in April and the negative relationship to ice thickness in March (since ice hampers the penetration of sunlight to the lower water layer). An opposite situation occurs for whitefish: the relationship of the density-independent mortality rate to ice thickness in March is positive, whereas that with open sun duration in May (the hatching time) is negative. The auspicious effect of the illumination factor is also observed for Arctic cisco fry.

According to information from the literature concerning the early ontogenesis of coregonid fishes, embryos hatching at relatively late stages of individual development come to mixed foraging early (Kugaevskaya 1983). On the other hand, it is known that vendace larvae hatch having the most incomplete development of morphological features (Lebedeva 1974). Perhaps this explains the predomination of direct effects of solar radiation over indirect ones (through food resource development) in this case. Later, when embryogenesis processes are completed, the availability of planktonic organisms probably becomes the main factor that controls fry survival. This is confirmed, in particular, by a negative relationship between parameter β values and water level in June.

The correlation between new generation abundance and water level at the feeding period of fry has often been pointed out for the Petchora basin and other water systems (Ghaltzova 1974, Ivanova 1977, 1985, Zamyatin *et al.* 1981, Sharov 1987). The auspicious effect of high water level is commonly thought to be related to the covering of floodlands by water and the formation of a broad shallow-water zone with highly abundant phyto- and zooplankton, along which the fry drifts downstream (Bogdanov 1986). However, when the impacts of several environmental factors are studied simultaneously, as in the stepwise variable selection method, the results show that the role of this factor in the reproduction of the Petchora coregonids is not very prominent and in some

cases (e.g., Arctic cisco) can even be negative. The abundance of planktonic organisms is determined by a whole set of external factors, of which water level is not necessarily the most important. For example, the survival rate of vendace fry is positively related to water level, but that of Arctic cisco, whitefish, and peled fry is related to the duration of open sun.

The results presented demonstrate the close relationship of density-independent mortality of fry with environmental conditions. In some cases, an almost full statistically valid explanation of recruitment variability caused by external factors can be given. Moreover, the relationships revealed are not in contradiction with field and experimental observations. Nevertheless, it is essential to keep in mind that only strong pulsations of environmental factors can cause notable changes in fry mortality. Therefore, the results could be improved if longer and more variable time-series were available. In addition, we had to restrict the analysis to only those environmental characteristics for which data records exist. Perhaps, there would be some shift in the relationship structure if other important factors, such as water quality, sedimentation pattern etc., were incorporated.

Apart from some new information about ecology of coregonids reproduction, the results obtained allow for clearer understanding of coregonids population dynamics as a whole. Being the populations with complex age composition, they react notably to considerable pulsations of density-independent mortality only. Every such pulsation would generate a transient process in population dynamics. As these environmental impacts are irregular in regard of strength and time, population dynamics of coregonid fishes seems to be a consequence of transient processes with different duration (Kriksunov *et al.* 1992).

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References

- Bogdanov V.D. [Богданов В.Д.] 1986. [Role of the Lower Ob flood-lands in nursery conditions of Coregonids larvae]. In: *Biological Problems of the Northern Region*. Proc. XI All-Union Symp. Yakutsk, Suppl. 4: 12–13. [In Russian].
- Chernyaev G.A. [Черняев Г.А.] 1981. [The peculiarities of temperature and light effects on embryogenesis of Lake Baikal Coregonids]. In: *Proc. 2 All-Union Conf. Biol. Biotech. Rearing Coregonids*, pp. 22–25, Petrozavodsk. [In Russian].
- Chernyaev G.A. [Черняев Г.А.] 1990. [Ecological and physiological peculiarities of reproduction and development of coregonid fishes]. *Ph.D. Thesis*, Moscow. 46 pp. [In Russian].
- Eckmann R., Gaedke U. & Wetzlar H.J. 1988. Effects of climatic and density-dependent factors on year-class strength of *Coregonus lavaretus* in Lake Constance. *Can. J. Fish. Aquat. Sci.* 45: 1088–1093.
- Ghalaktionova E.L. [Галактионова Е.Л.] 1983. [Respiration intensity and viability of embryos and larvae in different populations of peled (*Coregonus peled*) in relation with egg pigmentation level]. In: *Problems of early ontogenesis of fish*. Proc. III All-Union Conf., pp. 143–145, Kaliningrad. [In Russian].
- Ghaltzova M.Z. [Гальцова М.З.] 1974. [The vendace of Chud Lake]. *Izv. GosNIORC* 83: 77–88. [In Russian].
- Ivanova N.V. [Иванова Н.В.] 1977. [The influences of environmental factors on stock size of the Petchora vendace]. In: *Biological resources of the White Sea and inland waters of Northern Europe*. Proc. 10 Sess. Sci. Cons., pp. 94–95, Syktyvkar. [In Russian].
- Ivanova N.V. [Иванова Н.В.] 1985. [Modern conditions of natural reproduction of the Petchora vendace]. In: *Ecology and reproduction of freshwater Salmonid fishes in the White and Barentz Sea basin*, pp. 121–128, Murmansk. [In Russian].
- Kriksunov E.A. & Sharov A.F. [Криксунов Е.А. & Шаров А.Ф.] 1987. Modelling of reproduction and analysis of autooscillatory rhythm system in population dynamics of short-cycle fishes. *Zhurnal obshchey biologii* 48: 259–268 [In Russian with English summary].
- Kriksunov E.A., Bobyrev A.E. & Sharov A.F. 1992. Self-sustained oscillations in fish population dynamics. *Russ. J. Aquat. Ecol.* 1: 115–123.
- Kugaevskaya L.V. [Кугаевская Л.В.] 1983. [The variability among coregonid embryos at hatching, and timing of active feeding stage occurrence]. *Ryb. khoz.* 10: 36–40. [In Russian].
- Kugaevskaya L.V. & Sergienko L.L. [Кугаевская Л.В. & Сергиенко Л.Л.] 1985. [Ecological requires of Coregonid larvae to several environmental factors]. In: *Proc. 3 All-Union Conf. Biol. Biotech. Rearing Coregonids*, pp. 85–89, Tjumen. [In Russian].
- Lawler G.H. 1965. Fluctuations in the success of year-classes of whitefish populations with special reference to Lake Erie. *J. Fish. Res. Board Can.* 22: 1197–1227.
- Lebedeva O.A. [Лебедева О.А.] 1974. [Ecological and morphological specificity of Coregonids individual development.]. *Ph.D. Thesis*, Moscow. 20 pp. [In Russian].
- Lebedeva O.A. [Лебедева О.А.] 1981. [Ecological tolerance of Coregonids at early stages of life.]. In: *Proc. 2 All-Union Conf. Biol. Biotech. Rearing Coregonids*, pp. 13–16, Petrozavodsk. [In Russian].

- Lebedeva O.A., Zavyalova M.N. & Philippova G.P. [Лебедева О.А., Завьялова М.Н. & Филиппова Г.П.] 1985. [The study of peled early ontogenesis in industrial, natural, and laboratory environment]. In: *Proc. 3 All-Union Conf. Biol. Biotech. Rearing Coregonids*, pp. 96–99, Tjumen. [In Russian].
- Meshkov M.M. & Lebedeva O.A. [Мешков М.М. & Лебедева О.А.] 1977. [The specificity of individual development rate among Salmonid species]. In: *Evolution of animals individual development rate*, Moscow, Nauka: 200–216. [In Russian].
- Nilssen E.M., Pedersen T., Hopkins C.C.E., Thyholt K. & Pope J.G. 1994. Recruitment variability and growth of Northeast Arctic cod: influence of physical environment, demography, and predator-prey energetics. *ICES mar. Sci. Symp.* 198: 449–470.
- Popov A.V. & Zotin A.I. [Попов А.В. & Зотин А.И.] 1961. [The dependance of Salmonids and Coregonids embryos hatching on some environmental factors]. *Ryb. khoz.* 11: 22–28. [In Russian].
- Radenko V.N. & Terentyev P.V. [Раденко В.Н. & Терентьев П.В.] 1989. [The influence of temperature and light on peled larvae]. In: *Peled Coregonus peled* (Gmelin, 1788) (Pisces: Coregonidae), Moscow, Nauka: 228–230. [In Russian].
- Rijnsdorp A. D., Van Beek F. A., Flatman S., Millner R. M., Riley J. D., Giret M. & De Clerck R. 1992. Recruitment of sole stocks, *Solea solea* (L.), in the North-east Atlantic. *Neth. J. Sea Res.* 29: 173–192.
- Salojärvi K. 1982. Spawning ecology, larval food supplies and causes of larval mortality in the whitefish (*Coregonus lavaretus* L.). *Pol. Arch. Hydrobiol.* 29: 159–178.
- Schweigert J. F. & Noakes D. J. 1991. Forecasting Pacific herring (*Clupea harengus pallasii*) recruitment from spawner abundance and environmental information. In: *Proc. Int. Herring Symp., Anchorage, Alaska, USA*: 373–388.
- Sharov A.F. [Шаров А.Ф.] 1987. [The investigation of population dynamics of fishes with short life-span by using of stock-recruitment models]. *Ph.D. Thesis*, Moscow. 176 pp. [In Russian].
- Solovkina L.N. [Соловкина Л.Н.] 1962. [Fishes of medium and lower stream of the Usa River]. In: *Fishes of the River Usa basin and their food resources*, Moscow-Leningrad, Academic Press: 88–135. [In Russian].
- Sorokin V.N. [Сорокин В.Н.] 1981. [The problems of natural reproduction of Arctic cisco in Lake Baikal.]. In: *Proc. 2 All-Union Conf. Biol. Biotech. Rearing Coregonids*, pp. 136–138, Petrozavodsk. [In Russian].
- Stocker M. & Noakes D.J. 1988. Evaluating forecasting procedures for predicting Pacific herring (*Clupea harengus pallasii*) recruitment in British Columbia. *Can. J. Fish. Aquat. Sci.* 46: 928–935.
- Tang Q. 1985. Modification of the Ricker stock recruitment model to account for environmentally induced variation in recruitment with particular reference to the blue crab fishery in Chesapeake Bay. *Fish. Res.* 3: 12–21.
- Venglinsky D.L. & Tyaptirgyanov M.M. [Венглинский Д.Л. & Тяптиргьянов М.М.] 1981. [The specific aspects of natural reproduction and commercial exploitation of coregonid and salmonid stocks in Extreme North lakes with unstable hydrological regime]. In: *Proc. 2 All-Union Conf. Biol. Biotech. Rearing Coregonids*, pp. 116–118, Petrozavodsk. [In Russian].
- Volkova L.A. [Волкова Л.А.] 1981. [Some peculiarities of feeding behavior of Arctic cisco in Lake Baikal]. In: *Proc. 2 All-Union Conf. Biol. Biotech. Rearing Coregonids*, pp. 35–37, Petrozavodsk. [In Russian].
- Walters C.J. & Collie J.S. 1988. Is research on environmental factors useful to fisheries management? *Can. J. Fish. Aquat. Sci.* 45: 1848–1854.
- Zamyatin V.A., Krokhalevsky V.P., Polymsky V.N. & Shumilov I.P. [Замятин В.А., Крохалевский В.П., Польшский В.Н. & Шумилов И.П.] 1981. [Stock status and problems of fisheries management of Coregonids in the River Ob basin]. In: *Proc. 2 All-Union Conf. Biol. Biotech. Rearing Coregonids*, pp. 122–124, Petrozavodsk. [In Russian].
- Zhukinsky V.N. [Жукинский В.Н.] 1986. [The influence of abiotic factors on variability and viability of fish in early ontogenesis]. Moscow, Agroprom Press. 254 pp. [In Russian].
- Zuromska H. 1982a. Conditions of natural reproduction of *Coregonus albula* (L.) and *Coregonus lavaretus* (L.). *Pol. Arch. Hydrobiol.* 29: 1–28.
- Zuromska H. 1982b. Egg mortality and its causes in *Coregonus albula* (L.) and *Coregonus lavaretus* (L.), in two Masurian lakes. *Pol. Arch. Hydrobiol.* 29: 29–70.
- Zykov L.A. [Зыков Л.А.] 1981. [The population dynamics peculiarities and effectiveness of stocking activities, applying to peled in Lake Yendyr]. In: *Proc. 2 All-Union Conf. Biol. Biotech. Rearing Coregonids*, pp. 125–129, Petrozavodsk. [In Russian].

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