

**EFFECTS OF ENVIRONMENTAL FACTORS,
ESPECIALLY TEMPERATURE,
ON THE POPULATION DYNAMICS OF
PIKEPERCH (*Stizostedion lucioperca* (L.))**

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Academic dissertation in Fisheries Science

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ABSTRACT

The effects of environmental factors on the population dynamics of pikeperch (*Stizostedion lucioperca* (L.)) were analysed in the coastal areas of the northern Baltic Sea and in three lakes. The thesis is a summary from seven articles based on long-term data collected mainly by different Finnish and Estonian institutes. The studied abiotic factors were air and water temperature, water level and salinity, secchi disk depth, wind velocity and distribution, and the duration of winter. The main studied biotic factors were length and abundance at age 0, and year-class strength and yields during subadult and adult stages.

The study revealed that the most important environmental factor affecting the population dynamics of pikeperch was temperature. Water temperature had positive effects on annual abundances, growth, year-class strengths and yields. Mortality during the first winter was shown to be dependent on size, but the ranks of year-class strengths were already established by the end of July during the first growing season. The results further suggest that the size-dependent winter mortality should be higher after cold than warm summers. The strong dependence on temperature is also seen in similar year-class strength variations over different pikeperch populations. Strong year-classes were born during warm summers and weak ones during cold summers. Other studied environmental factors had little or no effects on the population dynamics. This was probably due to the fact that the interannual variations in these factors were within suitable levels and hence had no clear effects on year-class strengths.

Pikeperch, as a warm water species, seems to benefit from predicted climate warming based on the several positive effects of temperature on population dynamics. The results suggest stronger year-classes and higher yields for pikeperch in a warmer climate. However, based on current knowledge, it is not possible to evaluate the potential changes in interactions among abiotic and biotic factors which might occur and which could cause unexpected surprises in the future.

LIST OF ORIGINAL PUBLICATIONS AND AUTHOR'S CONTRIBUTION

The thesis is a summary and discussion of the following articles, which are referred to by their Roman numerals in the text:

- I** Kjellman J., Lappalainen J. & Urho L. 2001. Influence of temperature on size and abundance dynamics of age-0 perch and pikeperch. *Fish. Res.* (In press).
- II** Lappalainen J., Erm V., Kjellman J. & Lehtonen H. 2000. Size-dependent winter mortality of age-0 pikeperch (*Stizostedion lucioperca*) in Pärnu Bay, the Baltic Sea. *Can. J. Fish. Aquat. Sci.* 57: 451-458.
- III** Lappalainen J., Erm V. & Lehtonen H. 1995. Pikeperch, *Stizostedion lucioperca* (L.), catch in relation to juvenile density and water temperature in Pärnu Bay, Estonia. *Fish. Manage. Ecol.* 2: 113-120.
- IV** Kjellman J., Lappalainen J., Urho L. & Hudd R. Early determination of perch and pikeperch recruitment in the northern Baltic Sea. (Submitted manuscript).
- V** Lehtonen H. & Lappalainen J. 1995. The effects of climate on the year-class variations of certain freshwater fish species. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. *Can. Spec. Publ. Fish. Aquat. Sci.* 121: 37-44.
- VI** Lappalainen J. & Lehtonen H. 1995. Year-class strength of pikeperch (*Stizostedion lucioperca* L.) in relation to environmental factors in a shallow Baltic bay. *Ann. Zool. Fennici* 32: 411-419.
- VII** Lappalainen J., Lehtonen H., Böhling P. & Erm V. 1996. Covariation in year-class strength of perch, *Perca fluviatilis* L. and pikeperch, *Stizostedion lucioperca* (L.). *Ann. Zool. Fennici* 33: 421-426.

Author's contribution in articles:

- I** The article was planned jointly. Jakob Kjellman analysed the data and wrote the first version of the manuscript.
- II** The idea of the article was author's. Author made the statistical analyses and wrote the first version of the manuscript.
- III** The article was planned jointly. Author analysed the data and was mainly responsible for the writing.
- IV** The idea and planning of the article was joint. Jakob Kjellman analysed the data and wrote the first version of the manuscript.
- V** The idea of the article was Hannu Lehtonen's, but the article was planned together. The author carried out the analyses, and Hannu Lehtonen was mainly responsible for the writing.
- VI** The idea of the article was author's. Author made the statistical analyses and wrote the first version of the manuscript.
- VII** The article was planned jointly. The author analysed the data and wrote the first version of the manuscript.

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1. INTRODUCTION

1.1. Environmental factors and population dynamics of fish

Environmental factors are suggested to be the main source making noise to the recruitment data for several fish species (Shepherd et al. 1984, Rothschild 1986, Myers 1998). Often the studied abiotic factors have been climatological, such as air temperature, winds or precipitation. The most significant of these is undoubtedly temperature (Shepherd et al. 1984, Myers 1998). This is due to two obvious links. First of all, a strong coupling in temperatures between atmosphere and shallow water basin like the Baltic Sea exists (e.g. Alenius 1989, Heino 1994), and secondly, because fish are poikilothermal animals their body temperature follows closely that of water.

Changes in water temperature affect either directly or indirectly the physiology and behaviour of fish (Coutant 1987). Fish seek temperatures where the amount of energy available for movement, growth and development of gonads is in optimum (Fry 1971). This is possible because fish have well-developed thermoreceptors (Murray 1971). Fish also exhibit ontogenetic shifts in thermal niche. For many species the selected temperatures in larval and juvenile stages are higher than in adult stages (Coutant 1987). Therefore larval and juvenile fish are often found in shallow waters in littoral zones and sheltered bays (Urho et al. 1990). Characteristic for these habitats are not only higher water temperatures but more frequent food supplies (Frankiewicz et al. 1996).

Generally, mortality is at its highest at the early life stages. At the same time the susceptibility to changes in environmental factors is at its lowest. Therefore an episodic change in an essential environmental factor can cause high mortality among larval and juvenile fish (Rutherford & Houde 1995, Karås 1996). After entering to exogenous feeding the risk of mortality reduces while the juvenile fish grow. Fast-growing juveniles have usually lower mortality rates than slow-growing ones (Pepin & Myers 1991). This is due to better mobility of larger juveniles, opportunities to find food and to escape from predators (e.g. Pepin 1991). On the other hand, increased activity of larger juveniles can also increase contact rates with predators and may even result in higher mortality compared with smaller juveniles (Rutherford & Houde 1995).

In northern latitudes increased mortality also occurs during the first winter. For several fish species, often in laboratory conditions, winter mortality has been shown to be dependent on size (Post & Evans 1989, Huusko & Eironen 1995, Kirjasniemi & Valtonen 1997). Hence the growth rate and the size of juvenile at the end of the first growing season should be closely related to possible size-dependent mortality during the first winter. In addition to the size of the juvenile also the duration of winter is important. The longer the winter the more severe winter mortality of the same size (Johnson & Evans 1991). Since the duration of winter increases towards north while the duration of growing season decreases, the overall levels of winter mortality should also increase (Shuter & Post 1990).

According to Shepherd et al. (1984) three potential causes for variations in recruitment of fish stocks are generally involved. These are:

- 1) environmental factors (climate, tidal conditions etc),
- 2) the abundance of the parent stock as a whole (the stock-recruitment effect), and
- 3) the abundance of predators on, or competitors, of the pre-recruit stages (ecological interactions).

Further Shepherd et al. (1984) suggested that the environmental factors are likely to affect fish stocks via four principal processes, which are:

- 1) direct physiological effects,
- 2) disease,
- 3) feeding, and
- 4) predation.

Any of these may result in either direct mortality or sublethal reduction in performance.

Environmental factors covary over large areas (Malcher & Schönwiese 1987, Heino 1994, Myers et al. 1997). So if the fish stocks are affected by these environmental factors, the stocks should also fluctuate similarly over different areas (Shepherd et al. 1984). Recent analysis of long-term data has shown this for many species among several populations (Myers et al. 1995, Myers et al. 1997, McKinnell & Karlström 1999).

The relationships between environmental factors and biotic variables, such as abundances, year-class strengths or yields, have been generally studied with correlation and regression analyses (Svärdson & Molin 1973, Buijse & Houthuijzen 1992). The use of these methods has the potential danger that the obtained relationships, even though statistically significant, are spurious, e.g. meaningless.

Therefore two widely used approaches are 1) to formulate hypothesis *a priori* based on earlier findings, or 2) to evaluate the possible spuriousness of the relationships *posteriori*. The possible spuriousness has been estimated by comparing the obtained results with other similar studies with the same or closely related species. It is also typical that a possible cause and effect mechanism is postulated, but any mechanisms cannot be proved based on these analyses.

1.2. Pikeperch

In the present thesis the relationships between environmental factors and the population dynamics of pikeperch (*Stizostedion lucioperca* (L.)) are studied. Pikeperch can be characterized as a warm water species with preferred temperature from 24 up to 29°C (Hokanson 1977). It belongs to family Percidae (195 species) and to genus *Stizostedion* (5 species) (Nelson 1994, Song et al. 1998). Two other Percidae species, perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* (L.)), are also common in the same northern waters as pikeperch (Collette & Banarescu 1977). More closely related four *Stizostedion* species are found in eastern and southern Europe (*S. volgensis* (Gmelin) and *S. marina* Cuvier), and in North America (walleye (*S. vitreum* (Mitchill)) and sauger (*S. canadense* (Smith))) (Collette & Banarescu 1977).

Of the Percidae family most intensively studied are the commercially important species like perch, yellow perch (*Perca flavescens* (Mitchill)), pikeperch and walleye. All these species show large annual variations in stock sizes, year-class strengths and in yields (Neuman 1974, Willemsen 1977, Koonce et al. 1977, Lehtonen et al. 1996). This has led to similar aimed studies to search the possible reasons behind the variations. Several extensive studies, particularly with perch and walleye (Neuman 1974, Böhling et al. 1991, Buijse et al. 1992, Karås 1996, Baccante & Colby 1996), have inspired to search analogous relationships also with pikeperch. One should note, however, that walleye and pikeperch are not as closely related as perch and yellow perch (Thorpe 1977, Faber & Stepien 1998, Song et al. 1998). According to reviews by Marshall (1977) and Hokanson (1977) large differences can be found between the two *Stizostedion* species in tolerances to several environmental factors. Thus, the results obtained with walleye probably cannot be directly applied to pikeperch.

Among the first studies of climatic effects on pikeperch is the work by Svärdsen & Molin (1973). They showed that the growth rates of pikeperch depend on temperature and that the growth declines towards north in six lakes in Sweden. They further showed that the year-class strengths correlated positively with air temperature and that the year-class strengths fluctuated in the same way between two lakes, Lake Mälaren and Lake Hjälmaren. Others have shown that the environmental factors causing variations in year-class strengths of pikeperch lists, for example, the sum of degree days over 14°C (Willemsen 1977), high summer temperatures (Buijse & Houthuijzen 1992), low water temperatures in early spring and subsequent rapid increases in water temperatures (Buijse et al. 1992), and wind direction and speed during the spawning period (Woynarovich 1963). Kirjasniemi & Valtonen (1997) showed the presence of size-dependent winter mortality for pikeperch in a laboratory study. Svärdsen & Molin (1973) even speculated that the ultimate factor creating dominant year-classes might be mortality during the first winter in Scandinavia. However, only few studies have dealt with winter mortality of pikeperch in natural habitats (Willemsen 1977).

Pikeperch is important both in recreational and commercial fisheries, but the annual yields are highly variable (Svärdsen & Molin 1981, Buijse 1992, Buijse et al. 1992, Lehtonen et al. 1996). Attempts have been made to stabilise these variations with different management measures such as juvenile stockings. Yet no stabilisation has been noted (Buijse et al. 1994), even though stockings have increased catches in some lakes (Sutela & Hyvärinen 1998). Unfortunately high annual variations in stock sizes can lead to overfishing and may even collapse fish stocks (Swartzman et al. 1983, Colby & Lehtonen 1994). Collapses have been noted also for pikeperch. According to Colby & Lehtonen (1994) pikeperch stocks in several lakes collapsed during 1940 - 1970. This coincides with the period of declining air temperatures, and replacement of cotton nets by nylon ones.

Majority of the pikeperch populations studied here are situated near to the northern limits of the species range. The preferences for warm waters and, on the other hand, lower than optimal temperatures in the northern Europe should promote the effects of climatic factors on population dynamics of pikeperch. Environmental

factors, especially temperature, are more important at the limits of distribution range than near the centre (Planque & Frédou 1999). According to Myers (1998) an obvious advantage of the nearness to the northern limits is that the influences of environmental factors are generally simple enough to be understood. Further, if the mortality during the first winter is the ultimate factor creating dominant year-classes in Scandinavia as suggested by Svårdson & Molin (1973), it should stand out in the present materials.

1.3. Objectives of the thesis and original articles

The main objective here is to evaluate the importance of environmental factors on the population dynamics of pikeperch. The primary emphasis is put on the first year of life, and on the beginning of the first growing season. Since the studies began within the climate change programme "SILMU" initiated by the Academy of Finland (III, V-VII), the possible effects of temperature on pikeperch populations were estimated first (V, VI, Lappalainen & Lehtonen 1997, Lappalainen et al. 1997). It was predicted then that air temperatures will rise by 3 - 7°C by the year 2100 in northern Europe (Carter et al. 1995, IPCC 1995), which probably has great effects on wind patterns, precipitation and evaporation rates, stream flows and water levels, and certainly on water temperatures (Elo et al. 1998).

Even though Shepherd et al. (1984) pointed out three potential causes influencing recruitment (see

the list in Chapter 1.1.), only the effects of environmental factors were studied (I-VII). The evaluation of the two other causes, stock-recruitment effects and ecological interactions, were beyond the initial scope within the "SILMU" programme. However, no stock-recruitment relationships have been noted for pikeperch (Willemsen 1977, Buijse et al. 1992, Mooij 1996), while the possible effects of ecological interactions are discussed later in Chapter 3.

The present thesis focuses on pikeperch, even if perch was also studied in most of the articles (I, IV-VII). The first two articles included evaluate the effects of environmental factors on pikeperch during the first year of life (I, II). Articles III and IV combine the abundance estimates during the first year of life with the subsequent yields and year-classes in subadult and adult stages. In articles I-IV the effects of water temperature on growth and abundance of age-0 pikeperch were studied. The timing of sampling was, however, different. Sampling was performed either during the first growing season (I, IV), or after it in autumn (II, III) (Fig. 1). In articles V and VI the relationships between several environmental factors and year-class strength variations were evaluated, whereas in the last article (VII) no environmental factors were studied, but the study only focused on the variations in year-classes between species and populations.

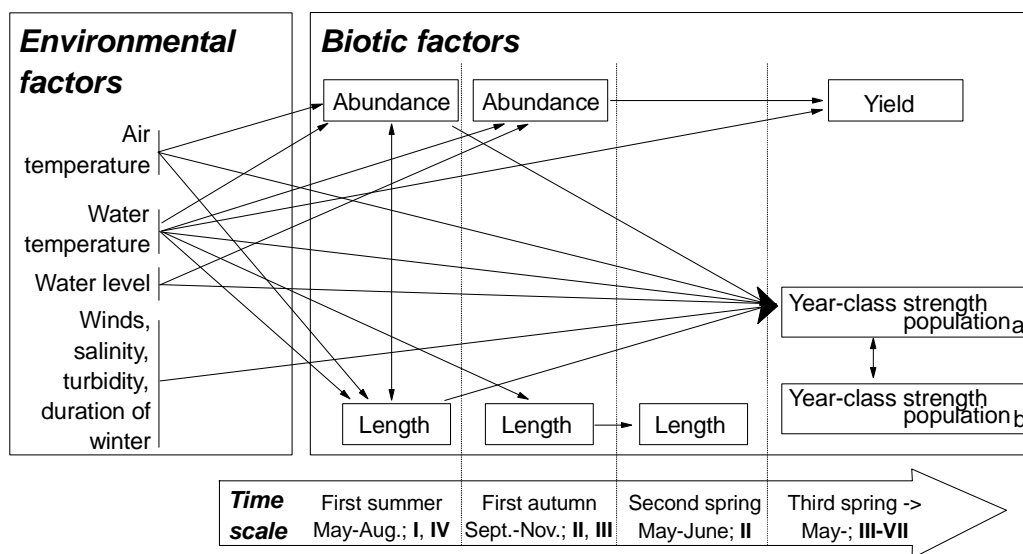


Fig. 1. Overview of the studied relationships. Bold Roman numerals refer to each article.

The specific objectives in each of the seven articles were:

- to evaluate the validity of size and abundance estimates obtained with a beach seine (**I**),
- to study the size-dependent winter mortality of age-0 pikeperch (**II**),
- to study the factors affecting abundances at autumn and subsequent yields (**III**),
- to evaluate the relative weights of both size and abundance at age 0 on the formation of year-class strengths of perch and pikeperch (**IV**),
- to estimate the effects of environmental factors on year-class strength variations of four species in several populations (**V**),
- to evaluate the effects of environmental factors on year-class strength variations in one pikeperch population (**VI**), and
- to compare the year-class variations of pikeperch and perch between species and in relation to geographical distance (**VII**).

To achieve the specific objectives the size and abundance estimates at age 0 were compared with the number of day, air and water temperature during the first growing season (**I**). In article **II** it was hypothesised that if winter mortality is dependent on size, all factors affecting the length at age 0 will also affect winter mortality. The purpose was two-sided in article **III**. First the effects of mean monthly water temperature and water levels on abundance in autumn were analysed. Thereafter the autumn abundances and water temperatures were compared with the subsequent yields in commercial catches. In article **IV** interactions among abundance and size of age-0 pikeperch, duration of first winter, and year-class strength were studied. The last three articles focused on environmental factors and year-class strength variations of pikeperch (**V-VII**).

The present thesis has four specific aims, which are:

- 1) to evaluate the effects of water temperature on length, growth and abundance of age-0 pikeperch during the first growing season (**I-IV**),
- 2) to study the link between the abundance at age-0 with the subsequent year-class strengths and yields (**II-V**),

- 3) to study the effects of environmental factors on the year-class strength variations (**IV-VII**), and
- 4) to summarize for the effects of environment factors on the population dynamics of pikeperch in the northern parts of its distribution range.

2. MATERIAL AND METHODS

2.1. Study areas

The study area covers the Baltic coastal waters between latitudes 55 – 61°N and lakes Lohjanjärvi, Mälaren and Hjälmaren (Fig. 2). In the northern part of the study area in the Bothnian Sea, the salinity of the surface water is up to 3 - 5 ‰ and in the southwestern coast of Finland 5 - 6 ‰. There is no tide in the Baltic and the water level mostly depends on winds and air pressure. In shallow inlets and bays temperatures of 20 - 25°C are reached almost annually. The coastal waters are normally ice-covered for 3 - 4 months in southwestern Finland, and more than 6 months in the northernmost parts of the Baltic Sea. The interannual variations in ice cover are small in the northern Baltic, while ice-free winters occur outside the archipelago in southwestern Finland. Pärnu Bay and Lake Lohjanjärvi are generally ice-covered an average of 140 days each winter.

Four coastal pikeperch populations were studied more closely: Laajalahti Bay (**I**), Vanhankaupunginlahti Bay (**I, IV-VII**) and Vartiokylänlahti Bay (**I**) in Finland and Pärnu Bay (**II, III, VII**) in Estonia. The three Finnish bays are all situated closely to each other in the waters off Helsinki. The distance between the most distant bays, Laajalahti Bay and Vartiokylänlahti Bay, is about 13 km. Laajalahti Bay, 5.25 km², is the largest of the bays, while Vanhankaupunginlahti Bay and Vartiokylänlahti Bay are smaller, 5.04 km² and 3.34 km², respectively. All are relatively shallow with a mean depth of 1.4 - 2.4 m and a maximum depth of < 5 m. Pärnu Bay is the largest of these bays, 340 km². It is situated in the northeastern Gulf of Riga. The greatest depth is 8 m in the central part of the bay.

The water salinity in Vanhankaupunginlahti Bay (0 - 3 ‰) is lower than in the two other bays (3 - 6 ‰) off Helsinki, especially during the peak discharges of the Vantaanjoki River. The mean monthly Secchi disk depth varies from 47.7 cm (SD = 22.2, n = 35) in June to 28.6 cm (SD = 13.6, n =

36) in August. Salinity variation in Vanhankaupunginlahti Bay is similar to that in Pärnu Bay. Near the outlet of the River Pärnu water salinity varies from 0 - 0.8‰ to 5.5‰ during spring and autumn, respectively. Both Laajalahti Bay and Vanhankaupunginlahti Bay have been slowly recovering from high loads of nutrients, whereas the water quality in Vartiokylänlahti Bay has been good during the whole study period (Pesonen et al. 1995).

2.2. Environmental data

The meteorological data, daily mean air temperature (°C), wind velocity (m s⁻¹), and precipitation (mm), were obtained from the Finnish Meteorological Institute (I, IV-VI). The data on the formation, duration, and melting of the ice and also the water level measurements were obtained from the publications of the Finnish Institute of Marine Research (IV, V). Water temperature, water salinity and Secchi disk transparency data were obtained from the City of Helsinki, Centre for the Environment (I, VI). The effects of water temperature on lengths and abundances of perch and pikeperch were estimated based on the modelled daily water temperature in waters off Helsinki (I, IV), whereas the daily water

temperature measurements were available in Pärnu Bay (II, III).

In articles I and IV daily water temperature estimates were based on modelled values. This approach was chosen because water temperature was measured only approximately once a week. Another reason for modelling was that the water measurements in different bays were not from the same days. Therefore the daily water temperatures at all the three bays were estimated with a dynamic model based on mean air temperature at Kaisaniemi weather station (60°10', 24°57'):

$$WT_t = a + WT_{t-1} + b * (AT_{t-1} - WT_{t-1}) \quad (1)$$

where WT_t presents water temperature at day t , AT_t is the air temperature at Kaisaniemi weather station, a and b are constants. The constants were estimated using the method of minimum sum of squares. The modelling showed that the daily water temperatures for the years 1982 - 1989 could be estimated with reasonable accuracy ($r^2 = 0.87 - 0.92$). The models gave similar results when estimated with independent data in years 1990 - 1993 ($r^2 = 0.85 - 0.94$; I).

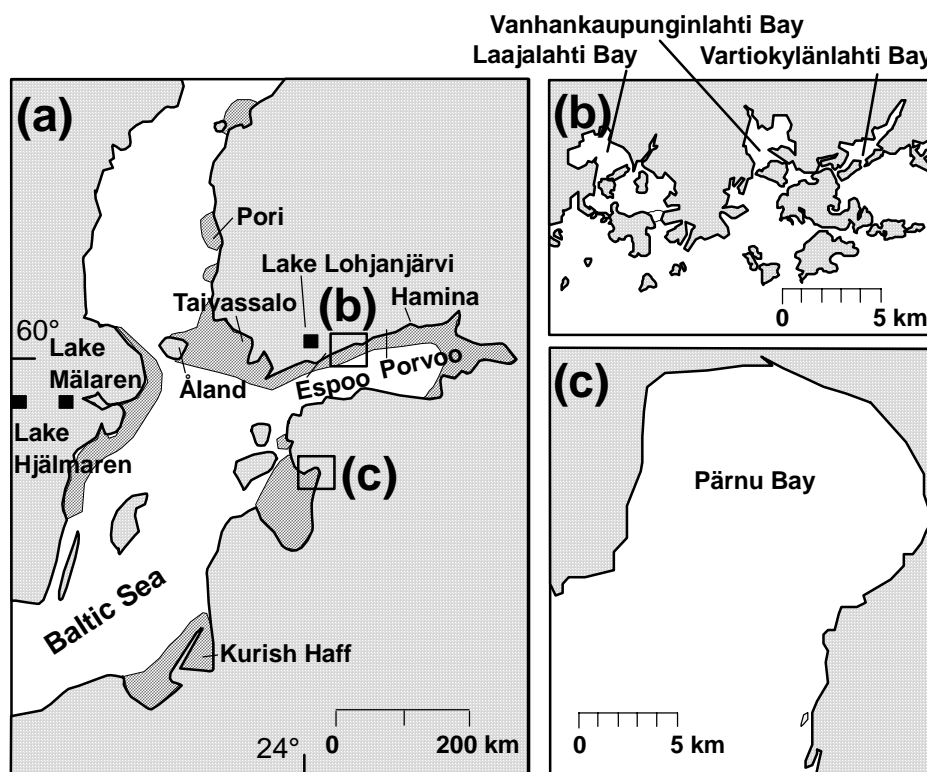


Fig. 2. (a) Locations for used pikeperch materials. Two areas, (b) waters off Helsinki and (c) Pärnu Bay, were studied in more detail. (a) Pikeperch occurs in the shaded area in the Baltic Sea (Lehtonen et al. 1996).

The effects of water temperature on length and abundance were studied using a degree-days (DD) over a certain threshold temperature (Buijse & Houthuijzen 1992, **I**, **II**, **IV**). This was calculated as:

$$DD = \sum_{i=1}^D (WT - TH), WT \geq TH \quad (2)$$

where D is the previous day of capture, i first day when $WT \geq TH$, WT is daily water temperature and TH the threshold value. In articles **I** and **II** several different threshold values were analysed, 10 - 15°C and 10 - 16°C, respectively, while in article **IV** only one threshold value of 10°C was used.

2.3. Fish data

The fish materials were obtained from the City of Helsinki (**I**, **IV**), from the Estonian Marine Institute (**II**, **III**, **VII**) and from the Finnish Game and Fisheries Research Institute (**IV-VII**). The data for Lake Mälaren and Lake Hjälmaren were obtained from Svärdsen & Molin (1973), and that for Kurish Haff from Gaygalas & Gyarulaytis (1974) (**VII**).

Beach seine was used in percid sampling in the water off Helsinki (**I**, **IV**) and juvenile trawl in Pärnu Bay (**II**, **III**). The beach seine was 2.5 m deep and had an arm length of 10.5 m. The mesh size was 5 mm and 1 mm at the cod end. The seine was set approximately 20 m from a boat or the beach, and thereafter pulled by hand towards the boat or the beach with ropes. In Pärnu Bay juvenile trawling took place in August-October and in May and the beginning of June (**II**, **III**). The length of ground rope was 22 m and the mesh size 6 mm at the cod end.

Age-0 fishes were conserved in 4% formaldehyde in the field and later counted and measured for total length (TL) (mm) in laboratory (**I**, **IV**). The lengths were reported as means and standard deviations for each haul and species. In each bay 10 stations were hauled 3 - 4 times per summer. Average length was calculated weighting the reported mean length with the number of juveniles in each haul. In Pärnu Bay the mean lengths and abundances were based on catches in one day (**II**, **III**). Length was measured as standard lengths (SLs) to the nearest mm. Abundances were expressed as the mean number of age-0 pikeperch in the juvenile trawl per half an hour. Length distributions were available at age 0, whereas only minimum, mean and maximum lengths were

known at age 1. Age-0 pikeperch were distributed to 10 length groups based on their standard length (**II**).

Subadult and adult pikeperch samples were collected from both commercial pikeperch catches and from the test fishings preceded by the Finnish Game and Fisheries Research Institute (**IV-VII**). Samples were taken during the spawning period in May and June with gill nets. The gill nets were monofilament nets 30 m in length and 1.8 m in depth with a mesh size of 45 mm. The fyke net samples of pikeperch were obtained from commercial catches in Vanhankaupunginlahti Bay (**VI**).

2.4. Calculation of year-class strength

The year-class strengths of pikeperch were calculated in 12 populations according to the method of Svärdsen (1961) and adjusted by Neuman (1974) (**IV-VII**). For the analysis pikeperch were aged from scales. The year-class strength was calculated in almost all cases from the annual catch sample of 100 - 300 fish. The relative year-class strengths were estimated stepwise beginning with calculation of the age-group distribution percentage in the yearly samples. Thereafter, the mean age distribution percentage for each age-group during the entire period was established. In the next step, the various year-classes in different years were expressed as percentages of this mean age distribution. The relative year-class strengths were the mean of these percentages (e.g. Böhling et al. 1991).

The most important prerequisite for this method is that all fish samples are collected using the same equipment in different years. All pikeperch were collected with similar gill nets. The second prerequisite is that the variation in natural mortality after the first year of life is low, as has been noted in many studies concerning pikeperch (Deelder & Willemsen 1964, Willemsen 1977, Van Densen & Grimm 1988, Sonesten 1991). The use of this method also presupposes that the fish collected have been hatched in the same area and that the larvae and juveniles remain in the nursery area or near it during the first summer. Pikeperch fulfil these requirements because the homing behaviour towards the same spawning areas is well developed and the juveniles leave the nursery area in late summer or in autumn (Lehtonen & Toivonen 1987, Urho et al. 1990).

The advantage of the method is that no estimations of the mortality are needed if all the other above-mentioned prerequisites are fulfilled. The disadvantage is that if the annual growth of the fish varies greatly, the method could overestimate the relative year-class strength in rapidly growing year-classes. This error was minimised by using only year-class indices based on catches from at least three-year-long periods (IV-VII). In article IV the youngest and oldest age-groups to be included in calculations were also estimated based on the lowest c.v. (Hudd et al. 1996). This method or modifications of it has been used recently by Wyatt (1988), Böhling et al. (1991) and Lehtonen et al. (1993).

The relative year-class strengths were estimated from samples in two gears in Vanhankaupunginlahti Bay (VI). The gill net samples ($n = 4080$) were collected during 1977 - 1994 and the fyke net ($n = 3638$) samples during 1980 - 1991. The year-class strengths were calculated from age-groups 2 - 8 and 3 - 9 in gill nets and in fyke nets, respectively. The comparison showed that both gears gave similar estimates from the relative year-class strengths in Vanhankaupunginlahti Bay during the years 1973 - 1986 ($r = 0.90$, $p < 0.0001$, $n = 14$; both log-transformed).

2.5. Statistical analysis

Several statistical analyses such as correlation, partial correlation and regression analysis were used in included articles (I-VII; Table 1). The year-class strengths were ln-transformed to achieve normal distributions in articles V-VII. Because in article IV

Spearman rank correlation analysis was used no ln-transformations were needed. The possibility of spurious relationships were reduced by carefully evaluating the rationality of the used environmental factors. The basic assumption was that the matching of environmental and biotic factors should be as close as possible both spatially and temporarily (I-VI). Furthermore, the more precise and accurate estimates should also yield higher statistical significances. Such an approach was used in article I, in which the relationships between growth and time, air temperature and water temperature were studied. On the other hand, since the most emphasis was put on annual differences in all the articles (I-VII), even an annual index of environmental factors may be used and could reveal the underlying relationship between the studied factors.

The statistical level of significance was usually set at $p \leq 0.05$. The exact p-values and descriptions of the statistical methods are found from the original articles (I-VII). The word "effect" as used here indicates only that the analysis was found significant. The possible mechanisms behind could be either direct but also indirect affecting though some other underlying factor. Thus, even though not always used, the word "effect" should be read as "potential effect" or "possible effect".

Table 1. Summary of used statistical methods in original articles (I-VII). DD_x is temperature sum over certain (x) threshold temperature and YCS is relative year-class strength.

Article	Estimation	Statistical methods	Variables
I	Effects of water temperature on lengths, growth and CPUE	Spearman correlation, general linear models, nonlinear regression	Length, abundance, DD ₁₀ , time
II	Size-dependent winter mortality	Spearman correlation	Lengths at age 0 and age 1
	Juvenile growth	Spearman correlation	Length at age 0 in autumn and DD ₁₀ -DD ₁₆
	Effects of duration of winter	Partial Spearman correlation	Deviations from length differences between age 0 and age 1 against duration of ice cover
	Effects of water temperature on the proportion of different sized juveniles at first autumn	Logistic regression	Proportion and DD ₁₅
III	Effects of environmental factors on autumn abundances	Pearson correlation	Abundance, water temperature and level
	Factors affecting to yields	Regression analysis	Abundance and water temperature
IV	Effects of water temperature on length, CPUE	Nonlinear regression	Size, abundance, DD ₁₀
	Effects of water temperature sum on YCS	Spearman correlation	YCS, DD ₁₀
	Partial relationships	Partial Spearman correlation	Deviations of abundance, size, DD ₁₀ on 31 July and YCS
V	Effects of environmental factors on YCSs	Pearson correlation	YCS, air temperature, wind velocity, precipitation, formation, duration and melting of ice cover
VI	Effects of environmental factors on YCSs	Pearson correlation, partial correlation, regression	YCS, winds, water temperature, level, salinity, and transparency
VII	Annual differences, similarities and variations in YCSs of perch and pikeperch	Mann-Whitney U-test, Kendall's coefficient of concordance, cluster analysis	YCS
	Effects of distance	Pearson correlation	YCS, distance between populations

3. RESULTS AND DISCUSSION

3.1. Effects of first summer on population dynamics

3.1.1. Temperature

3.1.1.1. Abundance

The significance of first growing season on the population dynamics of pikeperch was obvious (**I-VII**). The most important environmental factor was temperature (**I-VI**). An apparent increase in significances among different temperature estimates was found from air temperature to water temperature, and to water temperature sums estimated as degree-days over a certain threshold (**I-VI**). The higher the value for the accumulated degree-days, the more abundant pikeperch juveniles leading to higher yields and stronger year-classes (**III-VI**, Willemsen 1977, Buijse & Houthuijzen 1992).

Willemsen (1977) and Buijse et al. (1992) found no stock-recruitment relationship for pikeperch in Lake IJssel. This was seen as statistically nonsignificant correlations between spawning stock and abundance of age-0 pikeperch in August (Buijse et al. 1992), between larval abundance and juvenile abundance, and between larval abundance and commercial catches (Willemsen 1977). On the other hand, summer water temperatures were positively correlated with autumn abundances (**III**, Buijse et al. 1992), and autumn abundances were positively correlated with commercial catches both in Lake IJssel (Willemsen 1977) and in Pärnu Bay (**III**). In another lake in the Netherlands, in Lake Tjeukemeer, no relationship existed between spawning stock and larval abundances of pikeperch in May and June, but the larval abundances were positively related with autumn abundances (Mooij 1996). Thus, all these results suggest that no direct relationship exists between the spawning stock and larval abundances of pikeperch, but abundances during the late larval stages should be correlated with the abundances in autumn. The results further suggest that water temperature has strong positive effects on larval survival, because summer (**I**) and autumn abundances (**III**) were positively correlated with water temperature during the larval stages.

The failure to show the stock-recruitment relationship is a fishery management problem. Intuitively such a relationship must exist, at least at

the lower stock sizes (Colby & Lehtonen 1994, Myers et al. 1994), but the stochastic effects of temperature cause huge annual variations in larval mortalities. No stock estimates for pikeperch were available, but the results here (**I-VI**) and elsewhere (Willemsen 1977, Buijse et al. 1992, Mooij 1996) suggest that if the negative effects of temperature on larval survival could be taken into account, similar stock-recruitment relationship for pikeperch should emerge as has been showed for other fish species (e.g. Salojärvi 1992, Planque & Frédoou 1999).

Water temperatures during June and July had the strongest positive effects on the coming year-class strength, while those in May seemed to have no effects (**IV-VI**). This is in accordance with the knowledge of the timing of spawning of pikeperch (Svärdson & Molin 1973). Usually pikeperch starts to spawn in late May or early June when water temperature has reached 10 - 14°C (Hokanson 1977, Sonesten 1991, Colby & Lehtonen 1994, Lappalainen et al. 1997). During warmer springs the onset of spawning is earlier than during colder ones (Erm 1981, Salminen et al. 1992). The onset of spawning matches rather closely with the lowest temperature (8°C) where the normal development of embryos is possible, and to optimal temperature (12°C) where the highest number of normal embryos is hatched (Muntyan 1967). The rate of development of eggs and early larval growth also depends on temperature (Muntyan 1967, Geldhauser 1992).

Even though mortality was not studied here, the steadily stabilizing decline after the peak abundance found in article **I** was most likely caused by the decrease in natural mortality as the juveniles grew (Fig. 3). Some part of the decline may be due to outward migration of age-0 pikeperch or due to gear avoidance (**IV**). Similar declines have been noted for several fish species including pikeperch during the first growing season (Beyer 1989, Pepin 1991, Salojärvi 1992, Houde & Zastrow 1993, Dörner et al. 1999). As the body size increases, instantaneous natural mortality decreases (Miller et al. 1988, Pepin & Myers 1991, Rice et al. 1993, Houde 1997). The results in articles **I-IV** fit very well to the theory of stage-specific survival as suggested by Houde (1997). During larval stages in June (e.g. early summer) instantaneous mortality of pikeperch is higher than weight-specific growth, which means that biomass is decreasing. Later on when the mortality reduces sufficiently as the juveniles grow the weight-specific growth surpasses the mortality,

and the biomass starts to increase. According to Houde's theory, this should also match with the establishment of the year-class strength, e.g. the period from late June to late July for pikeperch (Fig. 3).

The year-class strength of pikeperch was established in Lake IJssel in August (Buijse et al. 1992), whereas the same was noted in Vanhankaupunginlahti Bay in late July (IV). Necessarily there is no discrepancy between the two studies due to different sampling periods. Buijse et al. (1992) had no abundance estimates for July and only three year data for abundance in June, while

we (IV) had reliable abundance data only for the late July. So more frequent sampling in both sites during summer months might have yielded similar results. Because the spawning of pikeperch and the rate of development of eggs and early larval growth are all positively correlated with water temperature (Muntyan 1967, Erm 1981, Sonesten 1991, Geldhauser 1992, Salminen et al. 1992), the period for the highest larval mortalities should be earlier and the duration of this period shorter in the southern populations than in the northern populations.

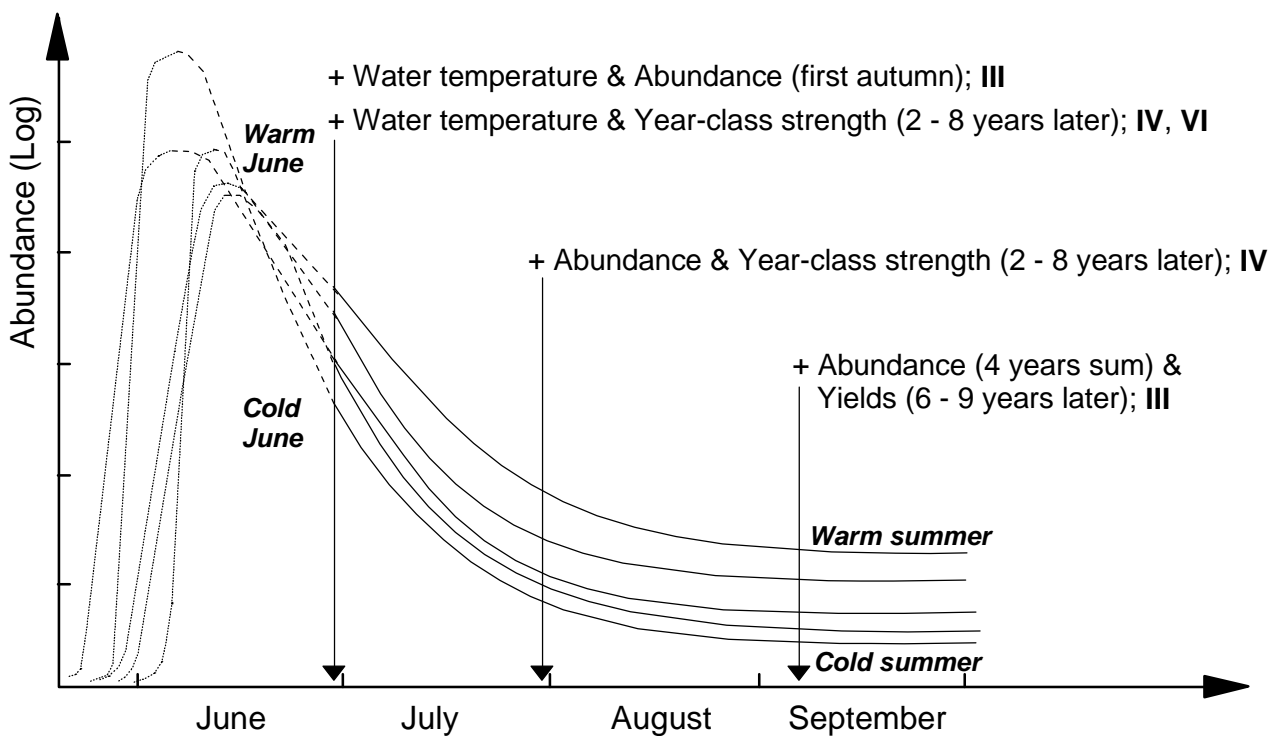


Fig. 3. Positive correlations found between water temperature during the first summer and different abundance variables. The timing of these correlations is marked with arrows. Each line, divided to dotted, hatched and solid parts, shows hypothetical changes in abundances during different summers in respect of water temperature. Dotted part presents increases in abundances as larvae are still hatching, hatched part shows period for highest mortalities, and solid part presents observed declines in abundances (I). Bold Roman numerals refer to each article.

3.1.1.2. Length and growth

During warm summers age-0 pikeperch grows faster and the sizes obtained by the end of growing season are greater (I, II; Fig. 4a; Buijse & Houthuijzen 1992, Ruuhijärvi et al. 1996). According to several authors (Erm 1962, Erm 1981, Ruuhijärvi et al. 1996, Hansson et al. 1997a), most of age-0 pikeperch are nonpiscivorous in waters near the northern distribution range. The late shift to larger fish prey could be due not only to cold waters, but also to the lack of suitably sized fish prey. In Finland, almost all fish larvae are still too large to be potential prey for juvenile pikeperch several weeks after hatching (Urho 1994). The main shift to piscivory, therefore, appears to occur during the second growing season in waters near the northern limits of pikeperch distribution (Erm 1981, Ruuhijärvi et al. 1996, Hansson et al. 1997a). In more southern localities, such as in Lake IJssel, age-0 pikeperch > 10 cm TL are able to prey on smelt (*Osmerus eperlanus* (L.)) during the first growing season (Buijse & Houthuijzen 1992). Since piscivorous pikeperch grow more rapidly than planktivorous pikeperch even at same water temperature (Van Densen 1985a, Mooij & van Nes 1998), the large differences found in mean lengths between Lake IJssel and Pärnu Bay, especially between 350 - 500 degree-days (Fig. 4b), could be due to different proportion of piscivorous (Lake IJssel) and planktivorous (Pärnu Bay) pikeperch. The same has been found also in some lakes in the Netherlands where annual variations in the proportion of planktivorous and piscivorous pikeperch cause considerable variations in mean lengths attained during the first growing season (Van Densen 1985a, Van Densen 1985b, Van Densen et al. 1996, Mooij & van Nes 1998).

Diet of age-0 pikeperch was not studied here, but it is known that larval pikeperch are planktivorous (Erm 1962, Erm 1981). Pikeperch spawn in Pärnu Bay in early June. Until early July, the primary food items for age-0 pikeperch are small-sized zooplankton (*Copepoda* nauplii and adults), while from July to September food consists mainly of tiny sand goby larvae (*Pomatoschistus minutus* (Pallas)) and larger macroinvertebrates, such as *Neomysis integer* Leach and *Corophium volutator* (Pallas) (Erm 1962, Erm 1981). On two of the three studied bays off Helsinki the total biomass of zooplankton was positively correlated with water temperature (Pellikka & Viljamaa 1998). This implies that during warm summers the abundances and

biomasses of both age-0 fish and zooplankton are higher that during cold ones (I, Pellikka & Viljamaa 1998). On interannual basis, however, the effects of food must be rather small. Otherwise it could be very difficult to explain the positive correlations between growth and water temperature (I, II), water temperature and abundance (I, III), and also the positive correlations between growth and abundance (I, IV) with the year-class strength (IV). These findings are in accordance with Mooij et al. (1994). They concluded that in most years the growth rate of 0+ planktivorous fish, such as perch, pikeperch, ruffe, bream (*Abramis brama* (L.)) and roach (*Rutilus rutilus* (L.)), was not food limited. The only exception was piscivorous pikeperch. The variation in growth rate of piscivorous pikeperch could be explained by the higher availability of smelt in warmer years.

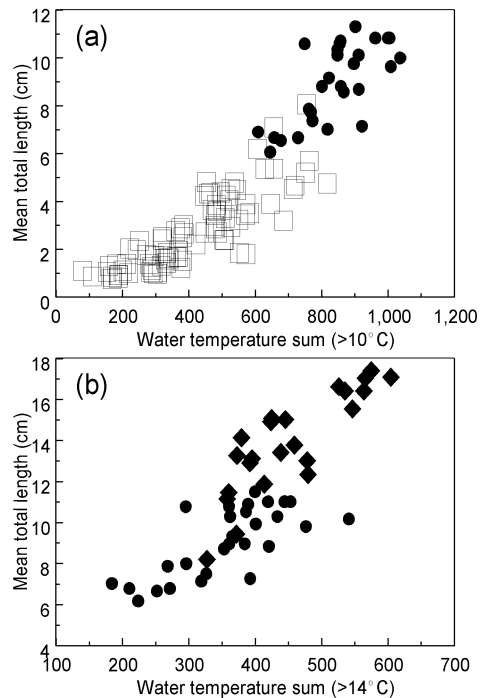


Fig. 4. (a) Comparison of mean lengths of age-0 pikeperch in relation to water temperature in three bays off Helsinki (open boxes; I) and in Pärnu Bay (black circles; II); and (b) in Pärnu Bay (black circles; II) and in Lake IJssel (black diamonds; Buijse & Houthuijzen 1992).

The effect of diet is seen indirectly in length distributions and skewnesses during the first autumn (II). The onset of piscivory usually results in positively skewed length distributions, which later on changes from positive to negative indicating main shifts in feeding from zooplanktivory to piscivory (Van Densen 1985b, Buijse & Houthuijzen 1992, Van Densen et al. 1996). Though the skewnesses and mean lengths were not correlated either in Pärnu Bay (II) or in Lake IJssel (Buijse & Houthuijzen 1992), a significant negative correlation was found when these two data sets were combined ($r_s = -0.43$, $p < 0.05$, $n = 52$; Fig 5; see also Van Densen et al. 1996). In Pärnu Bay, but also in Finland, the length distributions of age-0 pikeperch are usually positively skewed after the first growing season (II, Ruuhijärvi et al. 1996), suggesting that the main shift to piscivory occurs during the second growing season.

Density-independent factors seem to rule over density-dependent ones in the studied populations of pikeperch in the Baltic Sea. However, the situation may be different in lakes at least in certain years. In Finland pikeperch occurs naturally in lakes larger than 10 ha (Lappalainen & Tammi 1999). In Lake Hiidenvesi, located in southern Finland (lake area 30.3 km², Tallberg et al. 1999), after the very warm summer 1999 abundances of age-0 pikeperch were several times higher than after the colder summer 1998 (Olin & Ruuhijärvi 2000, Lappalainen et al. unpubl.). In October 1999 age-2 pikeperch were found to be cannibalistic eating age-0 juveniles (Vinni unpubl.). This is in accordance with the findings in Sulejow and Bautzen reservoirs (Dörmer et al. 1999, Frankiewicz et al. 1999). In Sulejow reservoir substantial cannibalistic behaviour was observed in years with a high number of age-0 pikeperch (Frankiewicz et al. 1999), whereas in Bautzen reservoir the largest age-0 pikeperch started to eat their slow-growing conspecifics in August (Dörmer et al. 1999). The results (IV-VII) suggest that the cannibalism probably does not disturb the importance of temperature on year-class strength variations in the studied northern waters, but could stabilise the variations as noted in Sulejow reservoir (Frankiewicz et al. 1999).

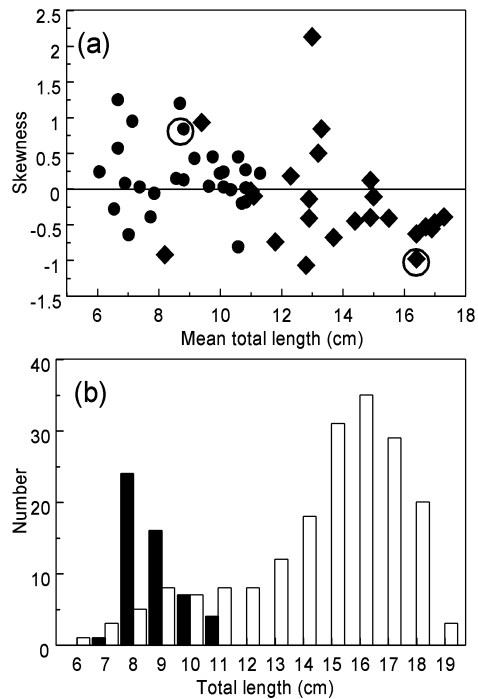


Fig. 5. (a) Skewness of length distributions in relation to mean total length (cm) of age-0 pikeperch in Pärnu Bay (black circles; II) and in Lake IJssel (black diamonds; Buijse & Houthuijzen 1992). (b) Examples of positive and negative length distributions in Pärnu Bay (black bars; skewness = 0.84, $n = 52$, September 1961; II) and in Lake IJssel (open bars; skewness = -0.94, $n = 188$, September 1988; Buijse & Houthuijzen 1992). Skewnesses of these two years are encircled in (a).

3.1.2. Other environmental factors

Besides temperature only winds had some effects on the coming year-class strengths. The mean wind velocity alone had no effects on year-class strengths (V, Buijse et al. 1992), but when both the direction and duration of the winds were considered, the effects of winds were noted (VI). Calculated wind indices were negatively correlated both with the year-class strength and water temperature. Such an effect alone could decrease growth and increase mortality, explaining the observed negative correlation. Viitasalo et al. (1995) found that southwesterly winds correlated negatively with total zooplankton biomass in a relatively open outer archipelago off the Hanko peninsula on the southwest coast of Finland. Although those results cannot be generalized to cover semienclosed areas

such as Vanhankaupunginlahti Bay, the food shortage could be among possible factors causing the negative correlations found between the year-class strength and the wind indices in July (VI).

Episodic changes in environmental factors have been found to cause mortality and affect the year-class strengths of perch (Karås 1996). Here these changes were not studied mainly due to the lack of sufficient daily data. Some indication of detrimental effects of short-term changes on year-class strength was found in Vanhankaupunginlahti Bay (VI). In 1971 the year-class strength of pikeperch was weaker than could be expected based on either temperature or wind indices. In the same year the salinity was highest with a mean value of 4.92 ‰ (SD = 0.36, n = 6) in June in 1971, while being 3.01 ‰ (SD = 1.42, n = 68) during the rest of the study period in 1972 - 1990. According to laboratory study by Klinkhardt & Winkler (1989) the mortality of eyed pikeperch eggs increased almost linearly from 0.7 ‰ where mortality was lowest to 6.7 ‰ where no eggs were alive. Therefore the high salinity levels in 1971 may have increased egg mortality either directly or indirectly.

Variations in water levels during the spawning period of pikeperch had no effects on either the juvenile abundance in autumn in Pärnu Bay (III) or on the year-class strengths in Vanhankaupunginlahti Bay (V). In lakes, however, water level variations have been shown to be positively correlated with the year-class strength of pikeperch (Svärdson & Molin 1973, Koonce et al. 1977). In the Baltic Sea, spawning areas of pikeperch occur in bays and river inlets at 1-3 m depths (Sonesten 1991). The water levels do not normally drop low enough in the Baltic Sea so that the pikeperch eggs could dry. When the water levels are low, the potential effects of waves increase, although in semienclosed inlets and bays the influence of waves on eggs is smaller than in more exposed areas.

The results obtained in article V suggest that the water transparency (measured as secchi disk depth) was low enough and hence had no marked effects on survival and subsequent abundances and year-class strengths. Nevertheless, notable effects might have emerged if the variations had been larger, especially if the water transparency had been greater. According to Svärdson & Molin (1973 and ref. therein) high turbidity may protect the larvae from predators during the first 3-4 days when the larvae move up and down in the water column. In a laboratory experiment direct sunlight has been

found to cause increased mortality during the larval stage of pikeperch (Woynarovich 1960). In another experiment walleye larvae from hatching to 17 days old were more evenly distributed, showed greater average swimming speeds, faster growth rates and improved gas bladder inflation in turbid waters than larvae cultured in clear water exposed to reduced light intensity (240 lux) (Rieger & Summerfelt 1997).

Most of the studied environmental factors were strongly connected with each other. Therefore it is not generally a simple task to estimate the true effects of each of the studied factor on population dynamics. However, the obtained results suggest that first the effects of temperature should be taken into account with suitable statistical methods. When this is done the strongest effects should be searched during the larval and juvenile stages in June and July.

3.1.3. Covariations in pikeperch populations

The year-class strength variations of pikeperch are similar in different populations, and the resemblances in year-classes are higher the closer the populations are situated to each other (VII). At distances less than 300 km 5 statistically significant correlations were found out of 8, and the relationship between the distance and the variations in year-class strengths between populations was negative (VII). These findings support the hypothesis that large-scale weather variations, mainly via water temperature, synchronize the variations in year-class strengths (V, VII). It is difficult to find any alternative biotic or abiotic factor which could act in a uniform manner over large areas (Shepherd et al. 1984). The possible mechanism behind these similarities lies in the positive correlations between abundances and water temperatures (I), and between abundances and subsequent year-class strengths (IV).

Myers et al. (1997) found the spatial scales of recruitment to be 50 km and 500 km for freshwater and marine species, respectively. The shorter scale in freshwater was hypothesised to be caused by predation. Although the scales (VII) were not studied analogously as in Myers et al. (1997) between species or habitats (freshwater vs. marine, brackish water), it is obvious that the scales for pikeperch are closer to that for marine species than for freshwater species.

The distances in year-class covariations are much lower than the same scales in air

temperatures, which covary from 1000 to 2000 km between climatic stations (Malcher & Schönwiese 1987, Heino 1994, Myers et al. 1997). In the study of Malcher & Schönwiese (1987) annual temperatures were correlated together instead of summer temperatures. This is important because correlations are lower between summer than annual mean temperatures (Heino 1994) and, on the other hand, summer temperatures have most influence on the variations of year-class strength of pikeperch. Furthermore, the location of the climatological reference station also affects the correlations between stations, at least in Finland (Heino 1994).

3.2. Effects of first winter

Winter mortality of age-0 pikeperch is dependent on size in Pärnu Bay (**II**). Size-dependent winter mortality has also been found in laboratory experiments (Huusko & Eironen 1995, Kirjasniemi & Valtonen 1997). In the laboratory wintering success of age-0 pikeperch was dependent mostly on the energy reserves and not on the amount of food available during the winter (Kirjasniemi & Valtonen 1997). On the other hand, the energy reserves, e.g. lipid content, vary among juvenile pikeperch during the first autumn depending on the diet quality, which has been found to affect survival expectations in laboratory (Kirjasniemi & Valtonen 1997). Generally the weight-specific fat content (lipid) increases with size, while the weight-specific standard metabolism declines (Conover 1992).

In the laboratory, pikeperch as long as 4.7 - 4.9 cm (TL) were able to survive through the winter, and only among juveniles longer than 5.5 - 6.0 cm was mortality very low (Huusko & Eironen 1995, Kirjasniemi & Valtonen 1997). In Pärnu Bay the smallest pikeperch juvenile found after the first winter was 6.2 cm (TL), even though juveniles < 6.0 cm were abundant during several autumns (**II**). These results are in accordance with the laboratory experiments, at least concerning minimum lengths. The findings in Pärnu Bay also suggest winter mortality for longer juveniles than has been found in laboratory or in outdoor ponds (**II**, Huusko & Eironen 1995, Kirjasniemi & Valtonen 1997, Hansson et al. 1997b).

The effects of duration of ice cover on the size-dependent winter mortality of pikeperch were contrary to our expectations (**II**). Longer winters appeared to reduce the size-dependent mortality when the effects of varying lengths at age 0 were accounted for. Possibly the depletion of energy

reserves could have increased during winters with exceptionally early melting of ice cover leading the age-1 pikeperch to cope with subnormal (low) water temperatures in reduced food levels.

No direct effects of winter on year-class strengths were detected (**V**), even when the effects of water temperature were scaled out from the abundance (**IV**). This was probably due to the strong dependence of growth and abundance on summer temperatures (**I-IV**). However, because the proportion of different-sized juveniles in autumn was dependent on summer temperatures, the winter mortality should be higher after cold than warm summers (**II**), especially because both growth and abundance were correlated with summer water temperature (**I-IV**). Therefore, in general, after warmer summers larger and more abundant juveniles should lead to lower winter mortality, and the opposite after colder ones.

The failure to show the effects of winter on year-class strengths could be due to the data used (**IV**, **V**). First, no abundance estimates were available either in autumn or spring, so that the actual changes in abundances could not be evaluated during the winter. Second, the year-classes were estimated on a relative basis, which is probably not as accurate an estimate as it should be to be able to detect the possible effects of winter. Further, the duration of winter was based on ice data, which might not be the best possible estimate to describe the severity of winter (see also **II**). Therefore, if reliable abundance estimates had been available both after the first growing season in the autumn and in the second spring, the possible negative effects of winter on year-class strengths could have been detected.

On the relative basis summer temperature had a more pronounced effect on the year-class strength than the duration of winter (**IV**, **V**). This seems to contradict against the speculations by Svärdsön & Molin (1973) that the ultimate factor producing dominant year-classes may be winter mortality. However, this does not mean that winter mortality does not exist. On the contrary, because size was positively related to abundance (**I**, **IV**), the size-dependent winter mortality (**II**) may be substantial and increase with latitude due to decreasing temperatures during the first summer (Shuter & Post 1990, Lappalainen & Malinen 2001) without being significantly correlated with the year-class strengths within a population.

3.3. Behavioural aspects

The lack of knowledge of the behaviour of age-0 and age-1 pikeperch is marked. If the behaviour was known in more detail, the estimation of the validity of the results obtained with the beach seine and trawling would have been easier (I-IV, Urho 1997). What is known is that yolk-sac larvae of pikeperch occur in open-water areas near the edge of littoral vegetation (Hudd et al. 1984). Older larvae are also found among vegetation, but the highest densities are still near the edge of vegetation at depths of 0.5 - 2 m (Hudd et al. 1984, Urho et al. 1990). Afterwards increased abundances of pikeperch towards deeper waters in midsummer and earlier in warmer summers have been reported (Urho et al. 1990, Mikheev & Pavlov 1993).

In the littoral zone maximum abundance of pikeperch larvae was found at lengths of about 18 mm, although some pikeperch shorter than 10 mm were also caught (I). In August a decreasing correlation between water temperature and lengths suggested movements towards deeper waters at a size 40 - 70 mm. These lengths can be associated with dietary shifts from zooplankton to larger food items (e.g. Ruuhijärvi 1988, Van Densen et al. 1996). Generally habitat shifts into the vegetated littoral zone have been attributed to shelter seeking and predator avoidance (Mittelbach & Chesson 1987, Diehl & Eklöv 1995), whereas increased swimming activity towards deeper waters has been connected with the decrease of inshore food resources (Mikheev & Pavlov 1993, Wang & Eckmann 1994).

Maximum lengths of pikeperch were about 1 cm bigger in samples collected with juvenile trawl in Pärnu Bay in the second spring than in the first autumn (II). Some parts of these differences could be due to growth and sampling, but also to behaviour aspects. Trawling may have excluded longest juveniles during autumn if they migrated earlier to wintering areas or moved to areas where they could not be sampled (c.p. Erm 1981, Lehtonen & Toivonen 1987, Frankiewicz et al. 1996). Immigration of juveniles seems unlikely, because the nearest population of pikeperch exists in Matsalu Bay, which is more than 80 km from Pärnu Bay. Several studies have shown that pikeperch are rather stationary and their migrations are usually short (Erm 1981, Lehtonen & Toivonen 1987, Hansson et al. 1997b).

Almost nothing is known of the wintering behaviour of pikeperch during the first winter. The behavioural aspects can be, however, very important. For example, southern white perch (*Morone americana* (Gmelin)) were more active and consumed more stored energy than native northern yellow perch in a laboratory experiment (Johnson & Evans 1991). According to Johnson & Evans (1991) this behavioural difference explained partly higher mortality rates of white perch during the winter. Garvey et al. (1998) assumed that direct or indirect effects of predation caused the observed size-dependent winter mortality for largemouth bass (*Micropterus salmoides* (La.)). The indirect effects were due to predation risk, which may have forced the juveniles to move to suboptimal habitats leading to increased energy depletion.

3.4. Climate change and pikeperch

Pikeperch, as a warm water species, seem to benefit from climate warming based on the several positive effects of temperature on population dynamics (I-VI, Lappalainen & Lehtonen 1997, Lappalainen et al. 1997). Warming will extend the duration of the first growing season (Lappalainen et al. 1997). Longer and warmer summers will increase growth rates and reduce mortality during the first summer and winter (I, II). Longer and more abundant age-0 pikeperch (I-IV) also suggest stronger year-classes and higher yields in future catches (Lappalainen et al. 1997).

All the positive effects of water temperature on population dynamics suggest that the distribution area of pikeperch will shift northwards in Finland in warmer climates (Lappalainen & Lehtonen 1997). In lakes natural dispersal occurs slowly, so the expansion will probably need introductions into new waters. At present, due to the economic value of pikeperch, and high annual stocking rates, the expansion seems more likely than for other species with lower value (Lappalainen & Lehtonen 1997). The range of extension, however, depends mostly on the rate of warming, but several other factors act simultaneously. These factors, for example, account for the duration of ice cover. Present simulations (Elo et al. 1998) suggest that the duration of ice cover will shorten, which was found to have negative effects on the wintering age-1 pikeperch (II). On the other hand, greater mean lengths due to better growth during warmer summers will probably compensate for the negative effects of reduced duration of ice cover.

Here the importance of diet was indirectly shown through growth and length distributions (I, II). In Pärnu Bay and the three bays in the coastal areas in Finland, lengths and growth were positively related with water temperature (I, II). However, the relationship between length and temperature (I) should not directly be used to estimate the lengths in future climates with higher temperatures, because the possible switch to piscivory even during the first growing season will increase growth more than based only on water temperature (Fig. 4b; c.p. Mooij et al. 1994). An open question is if there are suitable-sized prey species so that the main shift to piscivory is possible even as early as during the first summer, and further, when this shift could occur in the future. Many unexpected changes by the interactions with other species are also likely to occur.

4. CONCLUSIONS AND FUTURE RESEARCH NEEDS

The most important environmental factor affecting the population dynamics of pikeperch was water temperature (I-VI). Other environmental factors had little or no effects on dynamics (III-VI). Water temperature had positive effects on abundances, growth, year-class strengths and yields (I-VI). Mortality during the first winter was shown to be size-dependent (II), but the ranks of year-class strengths were established already during the first growing season (IV-VI). The results, however, suggest that the size-dependent winter mortality should be higher after cold than warm summers (II). The strong dependence on temperature is also seen in similar year-class strength variations over populations (VII).

The achieved results suggest the following relationships between temperature and studied biotic factors (I-VII). In warm waters larvae and juveniles grow faster and their mortality is lower than in colder waters resulting in stronger year-classes and yields (Fig. 6). The year-class strength of pikeperch is established already during the late July. The size-dependent winter mortality may be severe, but the positive relationship between abundance and size efficiently masks the possible negative effects of winter on year-class strengths.

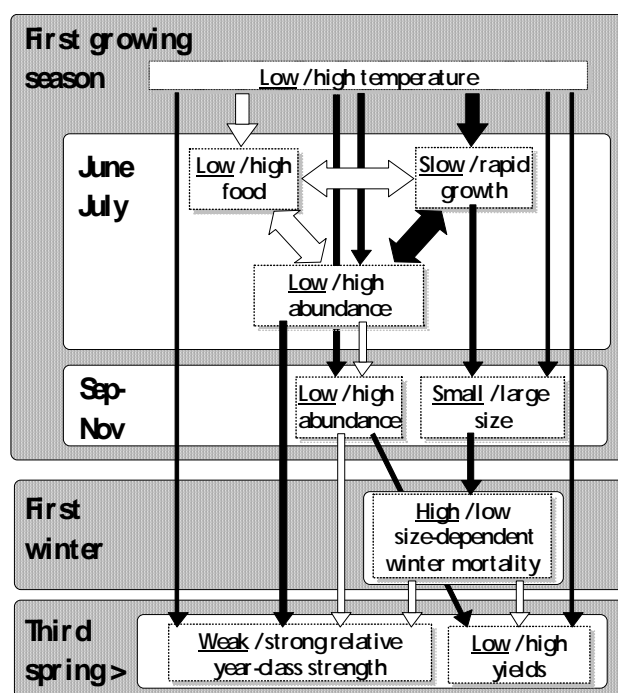


Fig. 6. Schema of major relationships among water temperature and biotic factors. The relationships marked with solid arrows have been found to be significant (I-VII). The food or links marked with white arrows were not studied in the present thesis, but can be suggested to be also significant based on the results obtained here. The wider the arrow the more important the link.

The results here warrant two major topics for the subsequent research to get a clearer picture of the components affecting the population dynamics of pikeperch. The first and most obvious one is to focus on factors causing mortality during the critical two months after hatching (June and July). This evaluation should contain intensive fish and water sampling both in the littoral and pelagic zones. To evaluate the potential trophic interactions the stomach contents of caught species should also be analysed. The second research topic should be a more thorough analysis of the levels of natural mortality of pikeperch during the first winter. This could be studied with a frequent sampling both during the first autumn and next spring. Such an analysis should yield estimates for the total mortalities based on changes in abundances during the first winter.

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