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Biology and exploitation of pikeperch, *Stizostedion lucioperca* (L.), in the Baltic Sea area

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In the Baltic Sea, there are considerable environmental gradients from north to south and from littoral areas to the open sea. These gradients include both abiotic (e.g. salinity and temperature) and biotic parameters (e.g. prey and predator abundances). The Baltic Sea thus forms a variable, and with respect to salinity, extreme, environment for a typical limnetic and warm water species like pikeperch. It is forced to spawn in shallow inlets, estuaries and bays where salinity is lower and temperature higher than in exposed areas. Pikeperch occur mainly in eutrophicated archipelagoes and bays where the spring and summer temperatures are high. It has expanded its distribution in recent decades, in response to increased coastal eutrophication. Pikeperch is also favoured by high summer temperatures, as shown by a positive correlation between temperature and year-class strength. Pikeperch populations are heavily affected by human disturbances and exploitation. In many areas it is economically the most important species. The effects of intensive fishery on pikeperch populations are largely unknown, as is the ecological significance of pikeperch as a piscivorous predator.

1. Introduction

The Baltic Sea is neither an ocean nor a lake but a large brackish water basin. There are considerable environmental gradients from north to south and from estuaries, bays and littoral areas to the open sea. These gradients include both abiotic parameters (e.g. salinity and temperature) and biotic parameters (e.g. prey and predator abundances). Thus the Baltic Sea constitutes an extreme environment for maintainance of both marine and freshwater organisms, among them pikeperch, *Stizostedion lucioperca* (L.). According to archeological findings pikeperch immigrated from the Caspian–Black Sea region into the Baltic Sea area about 6 000 years ago, during the Ancylus lake period (Lönnberg 1898). Since then, pikeperch have spread widely in the Baltic, and in recent years its local abundance has increased significantly due to coastal eutrophication (see reviews by Hansson 1985 and Hansson & Rudstam 1990). The objective of this study is to review the existing literature on pikeperch in the Baltic Sea and make

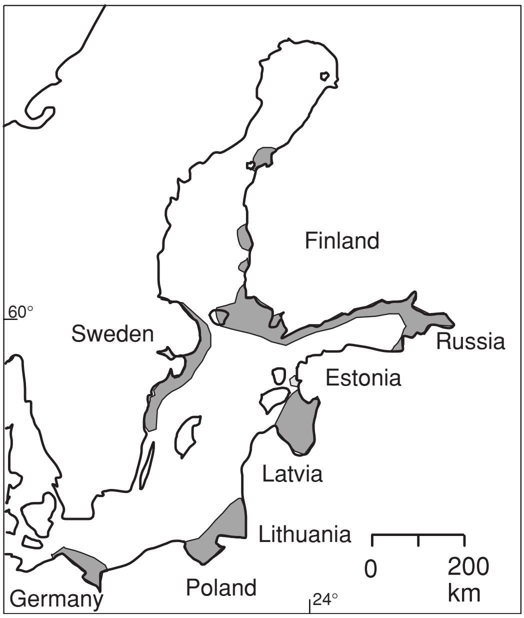

Fig. 1. Areas in which strong pikeperch populations occur. Pikeperch may occur outside the shaded areas but only in minor populations.

some comparisons with freshwater populations in the same geographical region.

2. Distribution and characteristics of pikeperch habitats

Pikeperch is locally abundant in coastal and littoral areas in almost the entire Baltic with exception of the northernmost areas, exposed coasts and the most saline parts of the South-West Baltic Sea (Fig. 1). The densiest populations occur in the oligohaline bays which are usually more or less eutrophicated. The preferred habitats for young and adult pikeperch are the pelagic or open areas of sheltered coastal localities close to the shoreline (Repecka & Mileriene 1991, Thiel 1991, Winkler *et al*. 1994). High water temperatures and algal blooms can cause local fish kills, as reported from the southern Baltic Sea (Virbickas *et al*. 1974, Kell & Noack 1991). The westernmost native pikeperch population on the South-West Baltic occur in Saaler Bodden near Rügen island. Pikeperch may live at salinities > 12‰ (Sonesten 1991) but probably only rarer. Occassionally pikeperch are caught even in Öresund and near Bornholm (Otterström 1912, 1933) which indicates that adult pikeperch can tolerate relatively high salinities (9–10‰) in the western Baltic Sea. However, early life stages are not able to survive in this area. Salinities exceeding 2.5–3‰ (Deelder & Willemsen 1964, Kukuradze 1974) are too high for normal development. But this fact is not in agreement with observations in the Baltic Sea. According to a review by Klinkhardt and Winkler (1989), fertilization and egg development is possible at 10‰. It seems that there is a short critical period for early larval stages and they can survive only at salinities < 4.5–4.75‰ (Olifan 1945). Areas with such salinities are potential spawning areas for pikeperch. However, pelagic larvae may be transported by currents to areas having salinities higher than 5‰.

3. Fecundity, spawning and development of larvae and juveniles

In general, pikeperch attain sexual maturity in the Baltic Sea between 2–5 years of age, the bulk of individuals at the age of 3–4 years (Virbickas *et al*. 1974, Winkler *et al*. 1989). In general, males mature one year earlier and with a smaller body size than females (Filuk 1955, Wiktor 1962, Virbickas *et al*. 1974, Winkler *et al*. 1989). Due to the lower growth rate, pikeperch mature generally later in the northern Baltic (4–5 years of age) (Erm 1981b). Erm (1981b) reported that the pikeperch in the Pärnu Bay (Estonia) is partly a portion spawner. The fecundity of pikeperch is positively correlated over a large range with the size of the females (Table 1). In general, the fecundity of the Baltic Sea pikeperch seems to be higher than in freshwater populations (Filuk 1962, Virbickas *et al*. 1974). The fecundity of a 45 cm female seems to be similar between the compared populations. Significantly lower fecundity for Vistula Bay (Filuk 1962) and the Saaler Bodden (Winkler *et al*. 1989) might be a temporal compensatory effect of dense population under conditions of food shortage (Samohvalova 1982, Winkler 1991a).

Spawning of pikeperch generally takes place in late April–early May in the southern Baltic Sea (Filuk 1962, Gaygalas & Gyarulaitis 1974, Virbickas *et al*. 1974, Winkler *et al*. 1989) and in late May–June in the northern Baltic Proper and the Gulf of Finland (Erm 1976, Lehtonen 1987). According to Virbickas *et al*. (1974), and Lappalainen and Lehtonen (1995), spawning begins at temperatures from 10°C, while Filuk (1961), and Gaygalas and Gyarulaitis (1974) reported 12–14°C as the lowest temperatures for spawning.

To be able to reproduce and form viable populations, pikeperch depend on areas where water warm up early in the spring/summer. Thus, successful reproduction and development of larvae and juveniles occur mainly in sheltered archipelagoes and bays (Erm 1981a, Lehtonen 1983). In many parts of the Baltic Sea suitable (low) salinities are found only in such areas. Another feature typical to areas inhabited by pikeperch is turbid water, which is known to favour larval development (Woynarovich 1960). This kind of turbid, inner archipelago waters, have become more common due to eutrophication which has resulted in the establishment of strong populations in areas where the species was relatively rare in the last century (Toivonen 1966, Hansson 1985, Hansson & Rudstam 1990). For example, Winkler *et al*. (1994) demonstrated that there is a positive correlation between the biomass of zooplankton and the number of young-of-the-year juvenile pikeperch. The turbidity caused by eutrophy is an indication of a high level of primary and secondary production. Furthermore, pikeperch is known as a well adapted fish species to prey under conditions of low light intensity (Ali *et al*. 1977). In these respects, the biology of pikeperch in the Baltic Sea is similar to that described from freshwater habitats (Deelder & Willemsen 1964, Sonesten 1991). Pikeperch spawn in the Baltic Sea under lentic conditions, only a smaller proportion of the species use slightly lotic areas in river mouths as spawning grounds (Gaygalas & Gyarulaytis 1974). The depth of spawning grounds range between 0.7–2.5 m (Filuk 1962) or 1–3 m (Virbickas *et al*. 1974, Lehtonen & Lappalainen 1995).

Virbickas *et al*. (1974) gave a detailed description of spawning and larval development of pikeperch in the Kuronian Lagoon. According to them, pikeperch begin their spawning activities before sunrise. The males build nests of 0.5 m in diameter, at a depth of 5–10 cm on sandy grounds. However, females can lay their eggs also on stones, roots of waterplants and other hard substrates, for example on artificial spawning substrates. Filuk (1955) reported that pikeperch laid eggs on dead zebra mussel (*Dreissena polymorpha*) shells. The highly sticky eggs are laid in 3–4 layers (Virbickas *et al*. 1974). Typical to pikeperch both in the Baltic Sea and lakes is that males guard the eggs until their hatch. The larvae live during the first two weeks post hatching near the bottom and then change their habitat from the benthic to the pelagic (Virbickas *et al*. 1974, Repecka & Mileriene 1991, Thiel 1991, Winkler *et al*. 1994).

The eggs of pikeperch from the Kuronian Lagoon have a diameter of 0.7–0.85 mm before and 1.02–1.67 mm after the fertilization (Virbickas *et al*. 1974). Depending on temperature, the larval development takes 5–9 days. The length of larvae after hatching range between 4.1–4.8 mm (Virbickas *et al*. 1974) or 3.9–4.5 mm (Erm 1981a). At the age of 2–5 days the larvae start exogenous feeding and their yolk-sacs are totally used after 10–12 days, at the length of 6.5–9 mm (Erm 1981a). In the Kuronian Lagoon the larvae feed on cyclops and nauplii for 14–15 days post hatching and then change their habitat from benthic to pelagic.

Table 1. Fecundity (1 000 eggs per female) of pikeperch from different localities of the Baltic Sea.

Locality	Age at maturity in years	Range of fecundity	Range of length (cm)	Fecundity of a 45 cm female	Ref.
Helsinki	4–5	34–901	37–64	220	(1)
Pärnu Bay	4–5	154–1 110	41–62	242	(2)
Kuronian Lagoon	3–4	24–1 227	39–79	260	(3)
Vistula Lagoon	3–5	64–2 957	42–84	216	(4)
		94–2 499	43–83	125	(5)
Greifswalder Bay	3–4	208–2 545	52–86		(6)
Darss-Zingster Bay	3–4	31–1 090	39–76	186	(6)

(1) Lehtonen (unpubl.), (2) Erm 1981a, (3) Virbickas *et al.*1974, (4) Lugovaja 1991, (5) Filuk 1962, (6) Winkler *et al.* 1989.

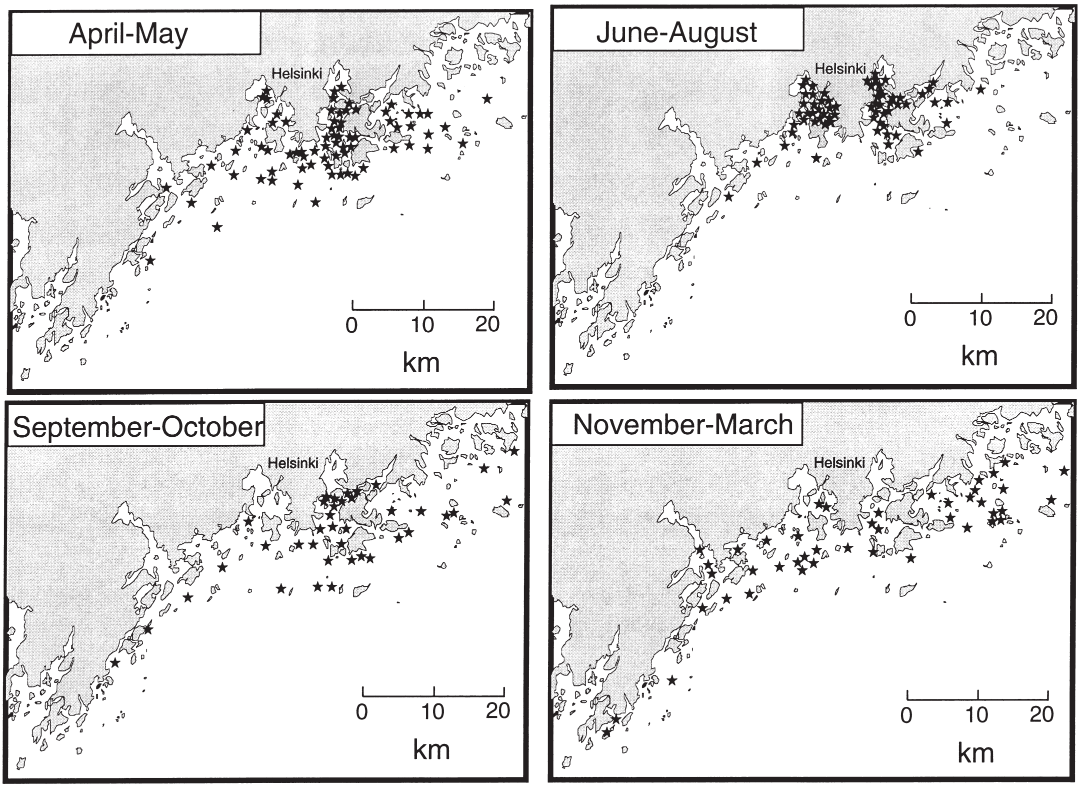

Fig. 2. Recaptures from pikeperch taggings in the Helsinki sea area, Finnish south coast fish were tagged in inlets of Helsinki during the spawning period. Each star represent one recapture. Note that there are many recaptures outside the area shown in the maps, particularly in winter and late autumn (Lehtonen 1977).

4. Migrations

Pikeperch occur in many more or less separate spawning populations along the coastal waters of the Baltic Sea (Toivonen 1968, Lehtonen 1983), but feeding and wintering migrations may cause populations to overlap (Lehtonen & Toivonen 1987). Soon after spawning, pikeperch females leave the spawning grounds while males guard the eggs. Feeding areas are usually situated in the vicinity of spawning grounds (Lehtonen & Toivonen 1987), but dispersal may be extensive under favourable temperature conditions (Segerstråle 1936, 1949). During warm summers young pikeperch disperse over large open water areas in the northern Baltic Sea, while in ”normal” summers they avoid open and relatively cold waters. The effects of temperature can also be seen in the dispersal of different pikeperch populations. In sheltered areas the water warms more than in the open coastal regions, and as a result the dispersal is more extensive when there is a large archipelago outside the spawning site (Lehtonen & Toivonen 1987). It is probable that food supply also influence the dispersal areas and activities of pikeperch (Winkler 1991a).

In autumn, pikeperch seek deeper waters where they stay over winter. Although pikeperch are active even during the cold period (Colby & Lehtonen 1994), they are probable relatively sedentary in winter (Segerstråle 1949). Locations of the wintering habitats are influenced by temperature and are usually in deeper water than the summer habitats (Winkler & Thieme 1978, Segerstråle 1983), what has also been found in lakes (Sonesten 1991). In the northern parts of the Baltic the winter habitats are usually situated offshore (Fig. 2), while in the lagoons of the southern Baltic most pikeperch overwinter in oligohaline sheltered bays and coastal areas. Migration to these areas takes place in early autumn (Henking 1923, Kraczkiewicz 1965). Older specimens, however, may overwinter in the Baltic Sea also in this area, and perform spawning migra-

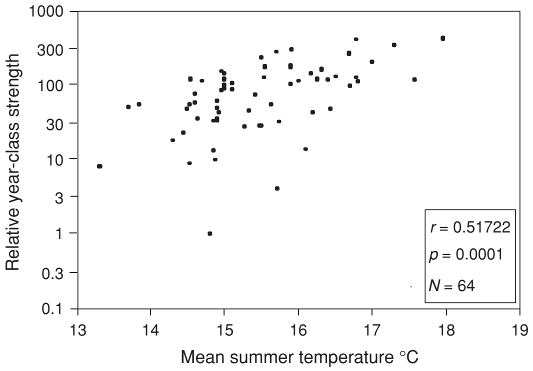

Fig. 3. The dependence of relative pikeperch year-class strength on summer mean temperature according to material collected from the Baltic Sea (Lehtonen & Lappalainen 1995).

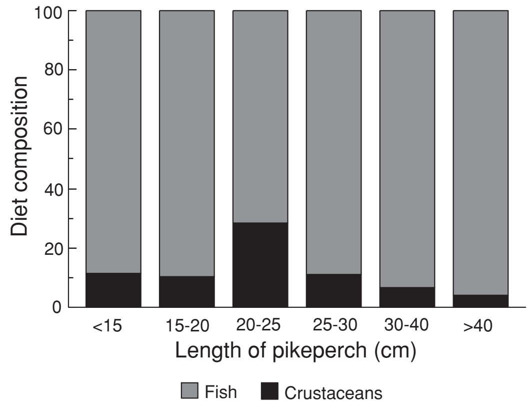

Fig. 4. Diet composition of pikeperch of different sizes in the Himmerfjärd Bay, northern Baltic Proper (from Hansson unpubl.).

tions to the sheltered bays in March or April of the following year. The distance between wintering and spawning areas is usually less than 30 km but may in some cases be even > 200 km (Lehtonen 1983). However, not all individuals of a pikeperch population perform migrations. The populations have a resident component (individuals which perform only movements) and a migrating component. Their proportions differ according to the localities where they live and the actual ecological conditions (Winkler 1992).

Despite the regular dispersal pattern, some fish may migrate differently. Winkler and Thieme (1978) reported that one pikeperch which was tagged and released in the Bay of Stettin was caught 9 months later in one of the Masurian lakes (Poland). That means that this specimen had crossed the open Baltic coast to Vistula Bay and migrated into fresh water.

5. Recruitment and year-class strength variation

In contrast to lakes, where spawning takes place in the shallows of open lakes (Sonesten 1991), Baltic pikeperch spawn entirely in estuaries, inlets and shallow bays. The optimal temperature for larval growth is 24–29°C (Hokanson 1977, Marshall 1977, Hilge 1990) but in the Baltic Sea such temperatures are seldom reached and the development occurs usually between 15–25°C. However, Kokurewicz (1969) suggested that larvae with the best condition coefficient favour temperatures between 12–16°C.

Fish populations living in extreme environments, e.g. pikeperch in the Baltic Sea, are vulnerable to even minor changes in their habitat (Colby & Lehtonen 1994). Accordingly, wide inter-annual variations in the year-class strength of pikeperch have been observed in various parts of the Baltic Sea (Gaygalas & Gyarulaytis 1974, Erm 1981b, Hahlbeck 1993, Lehtonen *et al.* 1993, Lappalainen *et al.* 1995, Lehtonen & Lappalainen 1995). A general feature throughout the range of pikeperch is that high summer temperatures exert positive effects on the year-class strength (e.g. Willemsen 1977, Svärdson & Molin 1981, Lehtonen *et al.* 1993, Lehtonen & Lappalainen 1995). Other factors influencing reproduction success in the Baltic Sea include, for example, winds and upwellings (Lappalainen & Lehtonen 1995), high water levels (Virbickas *et al.* 1974), salinity (Klinkhardt & Winkler 1989) and stones overgrown with colonies of zebra mussels (Virbickas *et al.* 1974). The strength of individual year-classes may vary more than 300-fold in the northern Baltic Sea as shown in Fig. 3 (Lappalainen & Lehtonen 1995). In Pärnu Bay, Estonia, a long-term monitoring of pikeperch year-classes and many environmental factors revealed a significant correlation between year-class strength and cumulative water temperature during the first four years of life (Lappalainen *et al.* 1995).

6. Interactions between pikeperch and other fish species

6.1. Diet

The feeding biology and ecology of pikeperch in the Baltic Sea is nearly the same as in freshwater habitats. The first food of larval pikeperch is small

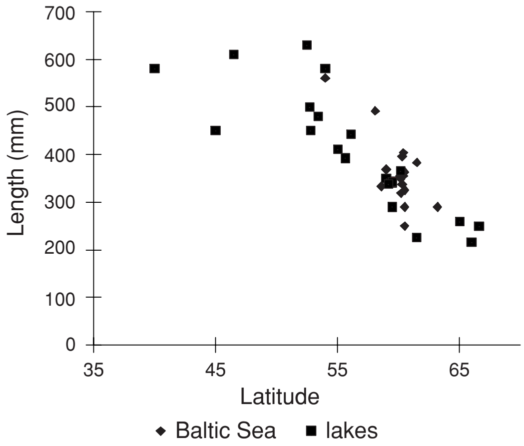

Fig. 5. Length of pikeperch at age 4, in the Baltic Sea and in lakes. Baltic data from Deelder and Willemsen (1964), Hansson (unpubl.), Karlström and Bergelin (1989), Lehtonen (1979, 1983, 1987), Lehtonen and Miina (1988), Määr (1947), Popova and Sytina (1977), Segerstråle (1983), Sellerberg (1976), Svärdson and Molin (1973) and Willemsen (1977).

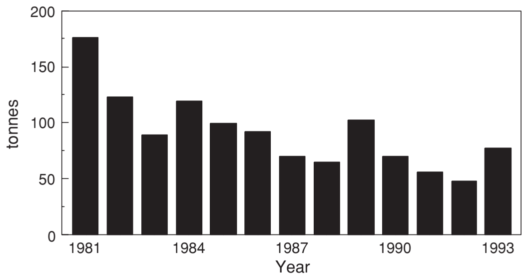

Fig. 7. Pikeperch catch from the Swedish commercial coastal fishery in 1981–1993 (Swedish Official Statistics).

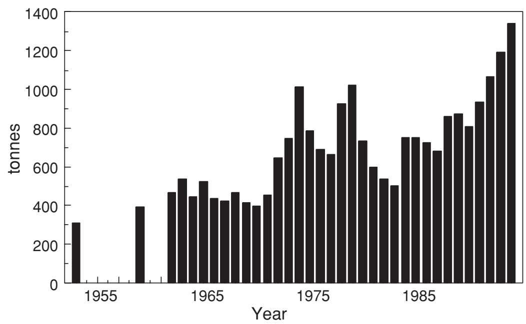

Fig. 6. Pikeperch catch from Finnish coastal fishery (commercial and recreational) in 1953, 1959 and 1962–1994.

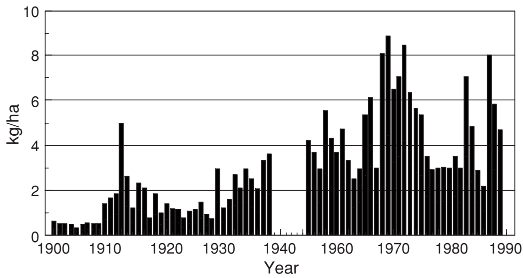

Fig. 8. Annual pikeperch catch per hectare from the commercial coastal fishery in the Bay of Stettin (Germany) in 1900–1938 and 1955–1989 (Germany and Poland) (Winkler 1991b).

zooplankton (Virbickas *et al.* 1974, Erm 1976). Pikeperch often become piscivorous in their first summer but fish may constitute a considerable proportion of the diet already when the pikeperch is 20–30 mm (Erm 1976, Thiel 1987, 1989, Lugovaja 1991). From this size and often for some years onward, mysid shrimps (*Mysis* and *Neomysis*) may be particularly important prey especially in circumstances where no fish larvae are available (Thiel 1987, 1989, Segerstråle 1949).

The piscivorous nature of pikeperch is demostrated in many studies by the dominance of fish in its diet from their second year of life (Fig. 4, Anttila 1971, Salmi 1982, Samohvalova 1982, Winkler 1989, Lugovaja 1991). Species composition of the prey varies between areas, but the most important species are perch, roach, smelt, ruffe, herring (*Perca fluviatilis*, *Rutilus rutilus*, *Osmerus eperlanus, Gymnocephalus cernuus* and *Clupea harengus,* respectively). In dense pikeperch populations, substantial cannibalism may also occur (Lugovaja 1991, Winkler 1989, 1991a). The feeding migrations of pikeperch from bays to the open sea in the southern Baltic Sea are an adaptation to avoid strong competition for food.

6.2. Effects of pikeperch predation and predation on pikeperch

A possible effect of predation is a decrease in the abundance of prey and this may result in intra- or interspecific food competition, provided that consumers are food limited. That adult pikeperch in lakes has the potential to influence the abundance of their prey have been shown in several studies (Holcík 1977, Linfield & Rickards 1979, Hickley 1986, Benndorf 1987, Persson *et al.* 1993), and Thiel (1987) suggested competition between young-of-the-year (YOY) pikeperch and perch in the Baltic Sea area. As discussed in Section 7, data on prey avail-

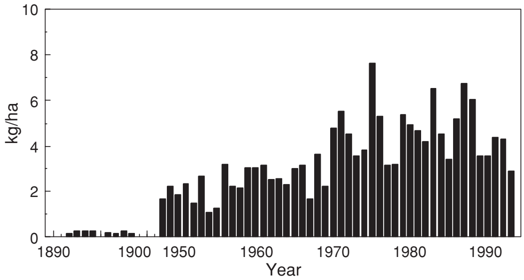

Fig. 9. Annual pikeperch catch per hectare from the commercial coastal fishery in the Darss-Zingster Bodden (Germany) in 1892–1900 and 1948–1993 (Winkler 1991b).

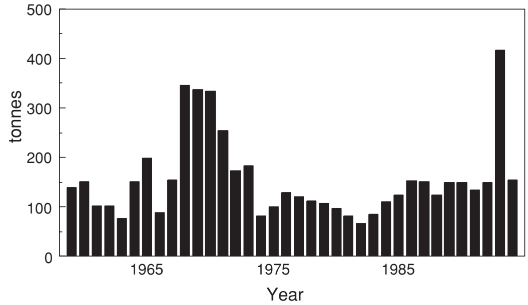

Fig. 10. Annual pikeperch catch from the commercial fishery in the Pärnu Bay (Estonia) in 1959–1994 (Vaike Erm, Estonian Marine Institute, unpublished).

ability for pikeperch are scarce and the same is true for data on the effects of predation by pikeperch. There are, however, observations of interannual variation within some areas indicating negative correlations between catches of pikeperch and other piscivorous species (perch and pike) (Lehtonen 1985, Winkler 1989, 1991b). Filuk (1962) and Ilenkova (1977) pointed out that there exists an inverse correlation between pikeperch density and the density of the main prey-species, the smelt. In lakes, such negative correlations have been interpreted as effects of predation by pikeperch (Svärdson & Molin. 1973), but interactions in the opposite direction may also occur as both pike and perch are predators on young pikeperch (Winkler 1989).

7. Growth

That the growth of pikeperch is influenced by temperature and the length of the growing season is obvious from a compilation of published data on lengths at various ages from waters at different latitudes (Fig. 5). From this graph, it is also clear that the Baltic Sea pikeperch has a "normal" growth for its latitude, or possibly a slightly faster one than in lakes, as suggested by Määr (1947) and Lind (1977). The available data does not allow any clear conclusions as to what extent the growth of pikeperch is limited by temperature and food, as data on prey availability are scarce. Furthermore, correlations between growth and temperature can be spurious, resulting from effects that the temperature might have on the production of prey organisms. That YOY pikeperch probably are food limited, usually reaching a length < 15 cm in the Baltic, is indicated by the high growth potential shown in the laboratory (Hilge 1990). Occassionally, however, much faster growth in the Baltic has been reported, e.g. YOY with a length of 19–24 cm in November (Hahlbeck 1993). Our general conclusion that, at least, juvenile pikeperch can be food limited in the Baltic, is supported by the *in situ* observation by Thiel (1989), that growth of YOY pikeperch is influenced by food availability. There are also observations indicating that food availability is limiting for the growth of adult fish (Filuk 1962, Samohvalova 1987, Lugovaja 1991, Winkler 1991a). The growth rates of pikeperch from several areas in the Baltic Sea are summarized in Table 2.

8. Exploitation

Pikeperch is economically one of the most important freshwater fish species in the nearshore waters of the Baltic Sea. The highest catches are taken along the South and South-West coast of Finland, the Pärnu Bay, the estuaries and lagoons of eastern Germany, the Stettin, Vistula and Kuronian Lagoons and certain Swedish archipelago areas in the southern Gulf of Bothnia and the northern Baltic Proper. There are records of recreational catches only from Finland, where the yield amounted to 816 tonnes in 1992. Regional catches from various areas of the Baltic sea are shown in Figs. 6–10.

There is a clear seasonal pattern in pikeperch fishing. The first peak in landings takes place in spring when pikeperch migrates from their overwintering areas to spawning grounds. The more important second peak in pikeperch landings takes place from September until November/December (Wiktor 1962, Ilenkova 1977, Lehtonen 1983, Winkler 1989). According to Virbickas *et al.* (1974), more

Table 2. Length of pikeperch at different ages in the Baltic Sea.

	Age in years										
Area	1	2	3	4	5	6	7	8	9	10	Ref.
Stettiner Haff/Pol.	169	300	405	510	610	645	665				(1)
Stettiner Haff/Ger.	161	345	442	515	570	640					(2)
Stettiner Haff	150	310	470	560	640	680	700	730	780	790	(3)
Greifswalder Bodden	169	308	437	538	610	664	710	728	747		(4)
Vistula Bay	122	237	367	448	508	549	604	639	680	730	(5)
Saaler Bay	152	286	386	464	520	566	606	628	638		(4)
Kuronian Bay	135	245	361	431	477	536	601	649	700	761	(6)
Pärnu Bay	106	203	291	372	461	513	570	618	652	689	(7)
Pärnu Bay	195	307	399	491	542	606	732				(8)
Bråviken	121	204	267	333	388	508					(9)
Himmerfjärden		236	313	369	415	440	448				(10)
Eastern G. Finland	96	210	286	330	400	474	540	568	636		(11)
Helsinki	98	186	294	357	425	485	570	620			(12)
Espoonlahti		173	254	354	421	449	445	425	559	575	(13)
Helsinki		188	258	319	382	400	416	442	488	512	(14)
Helsinki		197	282	349	391	414	425	459	501	521	(13)
Helsinki	98	186	294	357	425	485	570	620			(15)
Halikonlahti		210	260	338	375	387	387	409	407	428	(13)
Åland archipelago				396	380	388	397	409	440	465	(13)
Porvoo		185	269	355	396	421	470	531	551	610	(13)
Pernaja			403	404	415	429	449	485	526		(13)
Taivassalo		192	220	250	330	354	379	397	422	443	(14)
Taivassalo	90	195	233	325	372	366	383	397	415	436	(13)
Hamina			195	363	406	438	450	468	503	555	(13)
Pori			317	383	427	443					(13)
Maxmo	127	151	210	290	285	361	359	413	465	648	(13)

(1) Wiktor 1957, (2) Schlumberger 1962, (3) Neuhaus 1934, (4) Winkler 1980, (5) Filuk 1955, 1962, (4) Winkler 1980, (6) Virbickas *et al.* 1974, (7) Erm 1981a, (8) Määr 1947, (9) Sellerberg 1976, (10) Hansson (unpubl.), (11) Ilenkova 1977, (12) Seppänen 1970, (13) Lehtonen 1987, (14) Lehtonen 1983, (13) Lehtonen 1987, (15) Lehtonen 1979.

than 80% of the annual catch is taken in autumn. In the Russian part of the Vistula Lagoon the fishing of pikeperch is based primarily on fishes which migrate in autumn from the Baltic Sea to overwintering areas in the lagoon (Lugovaja 1992).

In all parts of the Baltic Sea the most used pikeperch fishing gears are gill nets. In second place are different kinds of trap nets. In some regions even seines (Filuk 1955, Gaygalas 1965) and trawls (Pruz 1924, Neuhaus 1934, Gaygalas 1965, Lehtonen 1979) are used. Recreational fishermen also catch pikeperch by angling, especially after the spawning season (Filuk 1955, Erm 1981a, Lehtonen 1983). These, and many other locally used methods may yield considerable catches of young pikeperch. The juvenile mortality of pikeperch has been high. For example, in the eel fyke net fishery in the Kuronian Lagoon (Gaygalas 1964, Virbickas *et al*. 1974). The cited authors give many examples which point out that especially trawling, dense meshed fyke nets and seining may increase the mortality of young pikeperch. Therefore, the use of some of those methods have been restricted.

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