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Fluctuations in year-class strength and growth of the vendace (*Coregonus albula* (L.)) in the small, mesohumic, oligotrophic Suomunjärvi, a lake in eastern Finland

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Year-class variation and growth of the vendace (*Coregonus albula* (L.)), the most important commercial freshwater fish species in Finland, was assessed in Suomunjärvi from 1974–2001 seine and gill net catches. We estimated the relative abundances and growth of the individual year-classes. The year-classes 1980, 1985, 1990, and 2000 were strong. There were often oscillations of year-class strengths, although the period of oscillation was not regular. Strong year-classes dominated catches for almost as long as they were present in the lake. The strongest year-class was about 300 times greater in size than the weakest. The growth of the year-classes varied considerably; the difference in growth rate between the strongest and weakest year class was about 2.5-fold. Comparison of the growth of a year-class with its strength showed a marked negative correlation ($p < 0.001$). The size of the whole stock (CPUE data) also had a negative effect on yearly growth ($p < 0.005$).

Introduction

Large variations in year-class strength and growth are typical of populations of the vendace (*Coregonus albula* (L.)) in Finnish lakes, and often the year-class strength oscillates in a regular pattern (Hamrin & Persson 1986, Viljanen 1986, 1988a, 1988b, Salojärvi 1987, Auvinen 1988, 1995, Sandlund *et al.* 1991, Helminen 1994, Turunen *et al*. 1998, Auvinen *et al*. 2000). One crucial problem is still our ignorance of the way in which the abundance of adults affects the strength and growth of the subsequent year-class.

The period of the year-class oscillation varies between populations, and some variation has also been found within the same population. In some lakes, the time period does not exceed two years, while in others it can be as long as five years. Three types of age-class cycles can be detected in Finnish lakes: (1) the catch is composed mainly of one-summer-old fish each year, indicating that a dominant age class is born every year (e.g. Pyhäjärvi, SW Finland), (2) the same year-class is dominant in the catch for two years (e.g. lake Puruvesi), and (3) the same year class is dominant in the catch for three to five years (e.g. lake Keitele).

There are several suggestions and hypotheses concerning possible reasons for these fluctuations, some of which point to the importance of abiotic factors and others to density-dependent self-regulation in the population (*see* Viljanen 1986). Recently, authors have stressed density-dependent regulation mechanisms in oscillating vendace populations (Hamrin & Persson 1986, Salojärvi 1987, Viljanen 1987, 1988a, 1988b, Helminen *et al*. 1992, 1993, 1997, Helminen & Sarvala 1994, Auvinen 1995, Auvinen *et al*. 2000), but opinions differ concerning how these mechanisms operate. Fishing seems to play an important role in maintaining a two-year cycle in stock fluctuations in Finnish lakes (Helminen *et al*. 1992, 1997, Auvinen 1995, Auvinen *et al*. 2000, Karjalainen *et al*. 2000). Auvinen (1995), studying the year-class fluctuation in vendace populations in areas subject to different fishing pressures, noted a distinct two-year cycle in the exploited part of the lake but not in the unexploited areas.

The growth of vendace in an individual lake can change very markedly between successive years, as reported by Järvi (1950), Svärdson (1966), Aass (1972), Nissinen (1972), Hamrin (1979), Lehtonen (1981), Viljanen (1986), Helminen *et al*. (1993), and Auvinen (1995). According to Järvi (1950), Svärdson (1966), Hamrin (1979), Viljanen (1988b), Helminen *et al*. (1993), and Auvinen (1995), these differences depend on intraspecific food competition. When a year-class is strong, growth is slow. When a year-class is weak, growth is rapid. It is not unusual for annual growth in length to fluctuate by 50%–100%, especially during the first year. Sometimes growth in length varied by more than a factor of two, and growth in weight varies by a factor of greater than ten between successive years (Viljanen 1986).

In this paper we describe the changes in year-class strength, year-class growth, and their interrelations, and the relations between yearly growth of the whole population and the size of the stock in Suomunjärvi from 1974 to 2001.

Study area, materials, and methods

The research was carried out in the mesohumic, oligotrophic Suomunjärvi in eastern Finland (63°08´N, 30°47´E) (area 650 ha, mean depth 5.7 m, max depth 27 m). The lake is covered by ice from early November to mid-May. Its main features have been described previously by Meriläinen (1978), Viljanen and Holopainen (1982), and Viljanen (1987).

The main fish species inhabiting the lake are vendace (*C. albula*, 30% of total biomass), perch (*Perca fluviatilis*, 27%), whitefish (*Coregonus lavaretus*, 14%), and roach (*Rutilus rutilus*, 12%) (Holopainen & Viljanen 1976). Catch statistics for both subsistence and recreational fishing were compiled by sending annual inquiries to all households that had taken out fishing licences. The total catch of all species in 1975–1983 was 1.6–5.1 kg ha^{-1}, of which 0.7–3.9 kg ha^{-1} was vendace. The average catch of vendace per hectare was about half the average for the 29 lakes in the Vuoksi watercourse (Auvinen *et al*. 1983). After 1983 no catch statistics were compiled.

Stock size and recruitment were estimated from material collected in Suomunjärvi by 12 experimental gill nettings in five randomly chosen areas in 1974 (mesh sizes 8, 10, 12, 14, 16, 18, 20, 22 mm, net length 30 m, height 1.8 m) and experimental seining (cod end 8 mm) in 1975–2001. Seining was conducted at the same time of the day in all years. Three to six randomly chosen permanent sites were used each year, plus a few extra randomly chosen sites in 1975–1987. The area swept by the seine was usually one hectare. Vendace in Suomunjärvi spawn under the ice in mid-December of their second autumn, when they have reached a total length of 8–14 cm. The maximum lengths of the year-classes at their oldest age were 14 to 24 cm.

The year-class strengths were estimated using catch-per-unit-effort (CPUE) statistics for the experimental seining (catch per tow). The CPUE data were also subjected to virtual population analysis (VPA) (Pope 1972). These were used together with age determinations to calculate the abundance of each age group. The natural mortality coefficient (M) for the first age group (0+) was taken to be 0.50, and that in the other age groups was assumed to be constant at 0.40 (Viljanen 1988b). The terminal fishing mortality was derived from the oldest age groups. The oldest individuals in our catches were usually at least five years old. The stock biomass was derived by multiplying the numbers in the different age-groups by the mean weight in each age group. The relative strength and relative growth of each year-class (all fish hatched in a given year) was calculated in relation to the mean value (100) for the years 1974–2001. The dependence of growth rate on strength of the year-class and on biomass of the total vendace population was estimated using a regression analysis based on the relative strength of each year-class, its relative growth, relative yearly growth of the whole population and the CPUE seine data. The number of annual hauls varied in the range 5–40 (average 11) in 1975–1987 and 3–4 in 1988–2001. Annual fish samples were taken from 3–6 seining hauls, each sample consisting of 200–500 fish, of which 30–100 were aged.

Results

The mean CPUE (seine-catch-per-tow) ranged from 0.6 (1991) to 54.4 kg (1979), and the total catch in 1975–1983 varied from 0.7 to 3.9 kg ha^{-1}. There were often oscillations of year-classes, although the period of oscillation is not usually the same; it can be 2, 3, or even more years (Figs. 1 and 2). Strong year-classes are almost always followed by weak year-classes, but weak year-classes may be followed by weak or strong year-classes. A very strong year-class can form the main catch for almost as long as it is subject to fishing. Examples are the 1980 year-class in catches from 1980 to 1984, the 1985 year-class from1985 to 1987, the 1990 year-class from 1990 to 1993, and the 2000 year-class from 2000 to 2001. The 1980, 1985, 1990, and 2000 year-classes were very strong, and the 1974, 1984, 1986, 1989, 1991, 1993, and 1999 classes were very weak. The strongest year-class for all years was 300 times the size of the weakest (Fig. 2). The differences between the year-classes were greatest during the first year of fish life.

The relative growth (length) of the year-classes varied considerably. The best growth rates were recorded by the year-classes of 1975, 1989, and 1992, while the poorest growth occurred in the year-classes of 1979, 1980, and 1985 (Fig. 3). The difference in growth rate between the best and worst year-classes was about 2.5-fold in length, and much more in weight. Year-class strength had a marked negative effect on growth of a year-class ($P < 0.001$) (Fig. 4). Similarly, the size of the whole stock (CPUE data) had a clear negative effect on yearly growth ($P < 0.005$) (Fig. 5).

Discussion

Catch-per-unit-effort (CPUE) data have been used extensively for stock assessment and are assumed to give a reliable index of population density if the assumptions about fishing gear and the spatial and temporal distribution of fish and fishing effort are correct (e.g. Richards & Schnute 1986). Comparison of CPUE and VPA data have shown that the two methods may be equally reliable for stock assessment purposes (Collie & Sissenwine 1983). These analyses also gave the same results in Suomunjärvi (Fig. 1), although VPA probably gives a more accurate indication of population size, especially at the ages of 0+ and one year, as vendace do not recruit fully into the seine hauls until between one and two years of age (*see* Viljanen 1988b). Various sophisticated methods have been presented for fine-tuning VPAs by reference to effort data to obtain more information on stock sizes and fishing mortality rates (Pope & Shepherd 1985). In the case of short-lived species, however, calculations of stock size performed by the VPA technique are particularly sensitive to variations in the assumed natural mortality coefficient (M) and associated estimates of fishing mortality (F) among the oldest age-groups, and especially the age-groups (F) in the final year.

According to the hypothesis presented by Viljanen (1986), the strength of a vendace year-class will be determined by: (1) autumn water conditions, which determine the development of the eggs at spawning grounds and hatching time, (2) the density and quality of the food available at the time of hatching and in spring, and (3) the size of the spawning stock, which determines intraspecific food competition and indirectly the condition, growth, and fecundity of the fish.

Hamrin and Persson (1986) suggested that short-term fluctuations in vendace populations

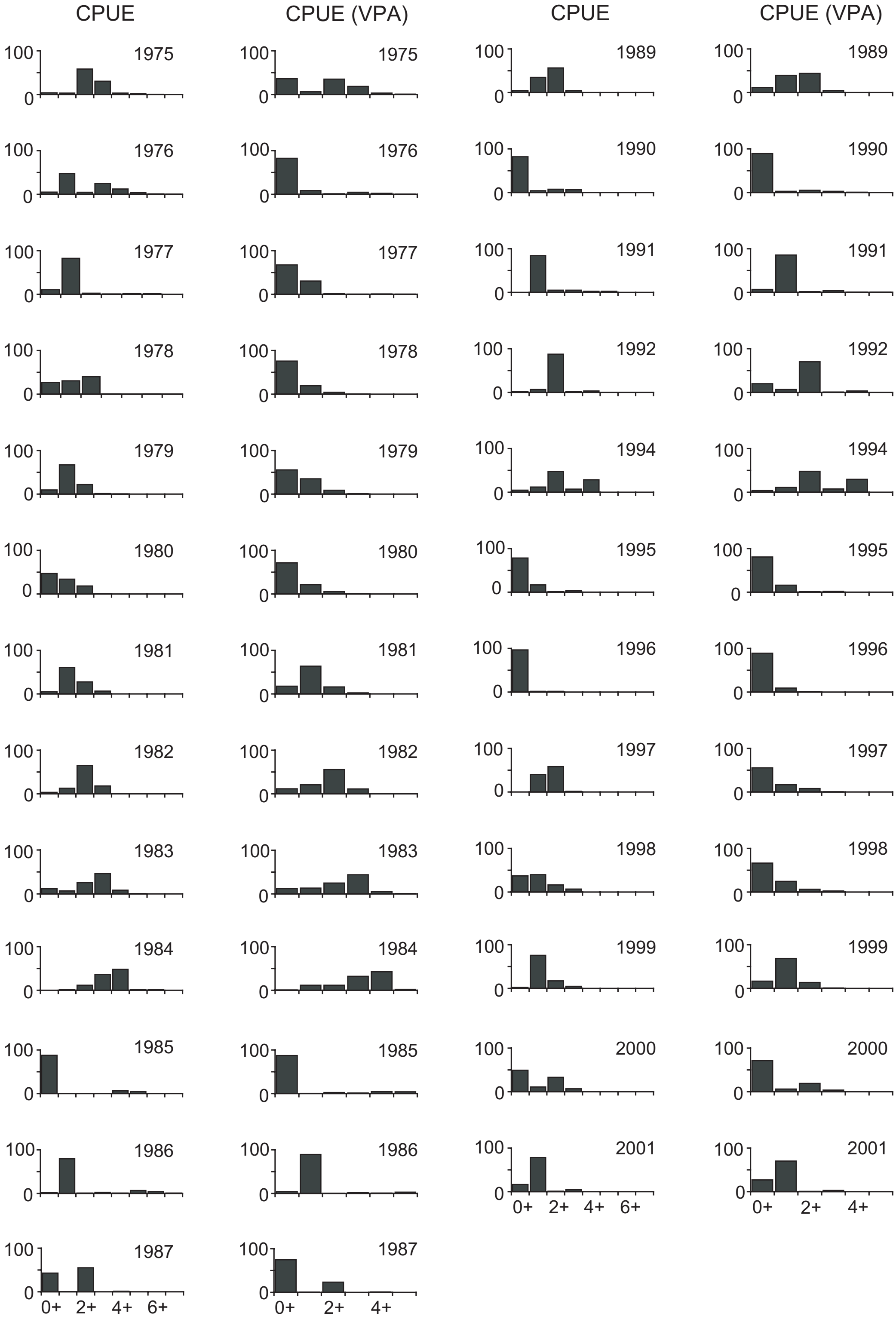

Fig. 1. Age distributions estimated by CPUE data and combined CPUE/ VPA-data from years 1975–2001 (*n* = 25) in Suomunjärvi, Finland.

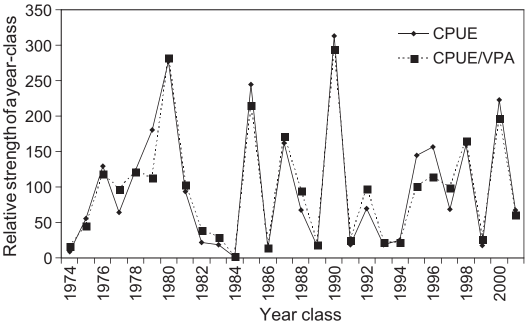

Fig. 2. Relative strength of the year-classes in 1974–2001 in Suomunjärvi. Mean = 100.

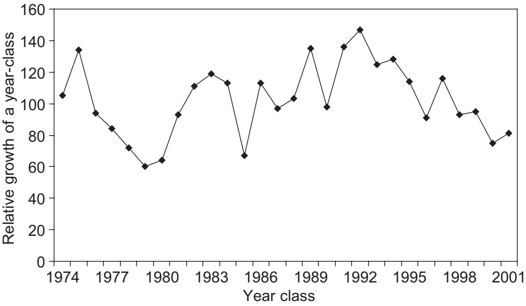

Fig. 3. Relative growth of the year-classes in 1974–2001 in Suomunjärvi. Mean = 100.

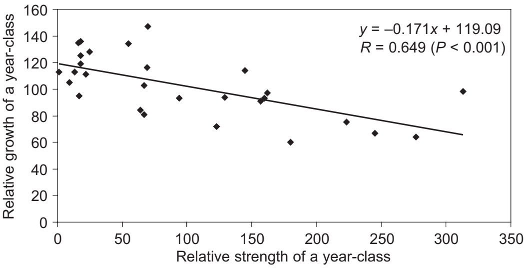

Fig. 4. Relationship between the relative growth of the year-classes and their strength in 1974–2001 in Suomunjärvi ($n = 28$).

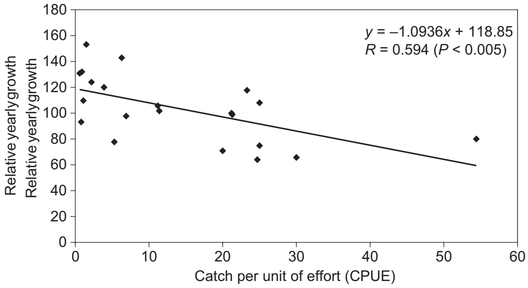

Fig. 5. Relationship between yearly growth and the estimated size of the whole stock (CPUE-data) in 1974–2001 in Suomunjärvi ($n = 28$).

are due to asymmetrical competition for food between age-classes, because fecundity varies with changes in the availability of food. This hypothesis is based on one central argument, that small vendace will have a competitive advantage during the summer due to their lower metabolic requirements and the low abundance and small mean size of available resources. The oscillation cycle is thought to occur because the individual size of one-year-old vendace belonging to a strong year class will be relatively small at the beginning of the summer due to high competition within the age-class. At the same time, as an effect of their high numbers during their first summer, they are competing actively with one-year-old vendace of the previous year-class, leading to a low reproductive output by the latter. One-year-old vendace in a strong year-class will therefore grow rapidly during the summer for two reasons (Hamrin & Persson 1986): (1) their own small size at the beginning of the summer and (2) low competition intensity from the small population of young from that year. This will result in a high reproductive output, so that each strong year-class will give rise to another strong year-class, and therefore a two year cycle.

According to Salojärvi (1987), this mechanism does not operate in Finnish vendace lakes. He suggests that the factors regulating the size of vendace populations can be divided into three groups: (1) regulation of fecundity, (2) starvation of larvae, and (3) predation. The impact of fishing compares favourably to the impact of predation. It is argued in this hypothesis that death of the larvae by starvation is the most important factor generating year-class fluctuations, while the other regulating factors tend rather to dampen the oscillations. It was concluded that one reason for the pronounced fluctuations in vendace populations was unbalanced fishing effort among years.

Variations in vendace year-class strength in Pyhäjärvi, SW Finland, in 1971–1990 were characterized by a two-year cycle of strong and weak year-classes, which implied density-dependent regulation, probably due to asymmetrical food competition between the age groups (Helminen *et al.* 1993, Helminen & Sarvala 1994, Helminen *et al.* 1997). The combination of abundance of piscivorous predators in the lake and of the warming of the water after the hatching of the larvae in spring determined the final year-class strength. Year-class sizes have remained very low since 1990, and the two-year cycle has been disrupted. The recruitment patterns observed in the vendace stock of Pyhäjärvi over the whole 26-year time series show the importance of spawning stock size, intraspecific competition, predator effects, and variations in the abiotic environment. The effect of the spawning stock could not be recognized as long as the population abundance fluctuated around a stable mean value and oscillations were largely determined by juvenile-adult competition (Helminen *et al.* 1997).

The data for Suomunjärvi (Viljanen 1988b) and Pyhäjärvi (Helminen *et al.* 1997) nevertheless suggest that high and low larval mortality can exist at both high and low larval densities (*see* also Karjalainen *et al.* 2000). Thus, larval mortality seems to depend not only on larval density but also on other factors such as the viability of the larvae, food conditions, or coexisting species (Viljanen 1988b, Huusko 1988, Huusko & Sutela 1992, Auvinen 1995, Sutela *et al.* 2002). According to results from seven vendace lakes in Finland, a high larval abundance is generally needed to produce a high number of recruits (Karjalainen *et al.* 2000). Larval abundance three weeks after ice break-up has an especially close positive correlation with the future strength of a year-class (Viljanen 1988b).

The two year cycle occasionally found in Suomunjärvi, where fishing pressure is low, is largely assumed to be determined by juvenile-adult competition. It has been shown in some lakes that the highest recruitment of vendace occurs when spawner abundance and larval abundance are both high and the lowest when the abundances are low, despite high variation in embryonic and post-embryonic mortality in the vendace (Karjalainen *et al.* 2000). However, it is noticeable in Suomunjärvi (Viljanen 1988a), lake Keitele (Valtonen & Marjomäki 1988), and Pyhäjärvi (Helminen *et al.* 1997) that a moderate spawning stock gives the best recruitment. Under favourable conditions, the highest recruitment may occur when the spawner abundance is high and a very strong year-class can form the main catch for almost as long as it is subject to fishing (Viljanen 1988a). A large, environmentally-induced variation in recruitment will tend to mask the stock-recruitment relationships at all spawning stock levels. The strongest year-class can have an abundance more than10 times greater than that of the weakest year-class (Viljanen 1986, 1988a, 1988b, Helminen 1994).

The absence of oscillations in some vendace populations at some periods can be explained by high interspecific competition, reduced intraspecific competition, changes in fishing, prolongation of mature life, and weather conditions. The growth rate of vendace, especially during the first growing season, has been found to have a negative correlation with cohort density and the size of the whole stock. This is a common feature in vendace populations (Hamrin & Persson 1986, Viljanen 1986, Helminen *et al.* 1993, Auvinen & Jurvelius 1994, Auvinen 1995), but it is not clearly distinguishable in all lakes (Viljanen 1986, Sandlund *et al.* 1991).

Conclusions

- The data on the percentage composition of catches suggest that there are often regular oscillations of year-classes, although the period of oscillation is not usually the same, and a very strong year-class can form the main catch for almost as long as it is subject to fishing.
- The strongest year-class was about 300 times larger than the weakest year-class.
- Differences in year-class strength were greatest during the first year.
- The difference in growth rate between the best and worst year-classes was about 2.5-fold.
- The growth of a year-class shows a close negative correlation with its strength.
- The size of the whole stock (CPUE data) has a very powerful negative effect on yearly growth.

— Because a strong year-class can dominate for many years and mask any regular oscillations in the rest of the population, it is possible that regular oscillations are more common in vendace populations than has been assumed previously.

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