

## POPULATION DYNAMICS OF WINDERMERE PERCH

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The history of the long-term studies of Windermere perch (*Perca fluviatilis* L.) is well recorded by Bagenal (1977) and there is no necessity to repeat it here. The main areas of interest throughout these studies have been factors which control recruitment and abundance (Le Cren 1965; Kipling 1976; Bagenal 1977; Le Cren et al. 1977; Craig et al. 1979; Craig 1980). This review looks briefly at some of the more recent analyses and interpretations of the changes that have occurred, and at the present level of understanding. The dynamics of a population of fish depend on how the individuals grow, reproduce and survive. The capacity of any organism to grow, reproduce and survive in a changing environment will depend on its ability to respond to these changes. This ability is limited by the organism's genetically determined powers of adaptation (both physiological and behavioural). Extensive knowledge about the responses of populations can be gained by studies conducted over a period of time. In this situation the changes in environmental conditions are brought about naturally although some conditions can be influenced by man. So far we have followed this system in Windermere. Initially in our study, the population of perch was severely perturbed by a fishery which removed a large proportion of the adult stock of fish (Worthington 1950). Since then the population has been monitored while it responded to the natural year-to-year changes in temperature and other factors. We are now in a position to make some fairly accurate predictions about the response of the population to certain environmental conditions. But these predictions are based largely on empirical correlations, and to make further progress we need to know more about the causal mechanisms involved. This will require experimental studies on the responses of individual fish; in particular their responses to temperature, the bioenergetics of their food use, and how they respond to the density of their own species.

Marking experiments have shown that there is little movement of perch between the north and south basins of Windermere, and perch do not migrate out of the lake so we are able to ignore immigration and emigration as factors in their population dynamics. In the analysis of population dynamics we are concerned with birth and mortality rates. Growth rates are also of importance in so far as they have a direct influence on the former two rates.

*Birth rate* is the number of offspring produced per female per unit of time. The *absolute fecundity*, i.e. the total number of eggs laid by a female perch, is related to the size of the fish. A regression of logarithm of absolute fecundity ( $F$ ) on the logarithm of length ( $L$ ) from data gathered in the years 1979, 1980 and 1981 gave:

$$\log F = 0.9754 + 2.5449 \log L$$

There has been a significant change in absolute fecundity of perch of the same size with time and this change has also been noted in pike (Bagenal 1973). For example a perch of 20 cm produced  $13\,100 \pm 700$  eggs during the period from 1944 to 1960 (Craig 1980), whereas the same-sized fish produced  $19\,300 \pm 1800$  eggs during the period from 1979 to 1981. Since egg production is related to the size of a fish, a faster-growing fish will be more fecund than a slow-growing fish of the same age. There has been a general tendency for growth rates of perch to increase from 1939 (when the study started) to the present (Fig. 1). A female hatched in 1955 was about 15.7 cm at three years of age (usual age of first maturity) and laid about 7600 eggs compared with a female (of the same age) hatched in 1968 which was about 20.2 cm long and laid about 19800 eggs. As perch get older, more and more energy is required for maturation of the gonads and this is at the expense of somatic (body minus gonad) growth (Craig 1977). Some very old fish do not have enough stored energy to develop an ovary. As the fish ages and gets larger more connective tissue develops within the ovary (Craig 1979) but the size of the egg increases (Craig 1974). It is possible that the size of an egg may influence the survival rate of the fish that hatches from it.

We are able, by means of the catches made in traps, to estimate the abundance of perch each year. The ages of the fish can also be determined so that we can trace the decline in the abundance in each successive year of fish that were hatched in any particular year. Such a group or brood is known as a *year class* or *cohort*. Data on the relative abundance of fish of any one cohort at each successive year can be converted into a mortality rate and it is convenient to express this as an annual instantaneous rate,  $Z$ ,

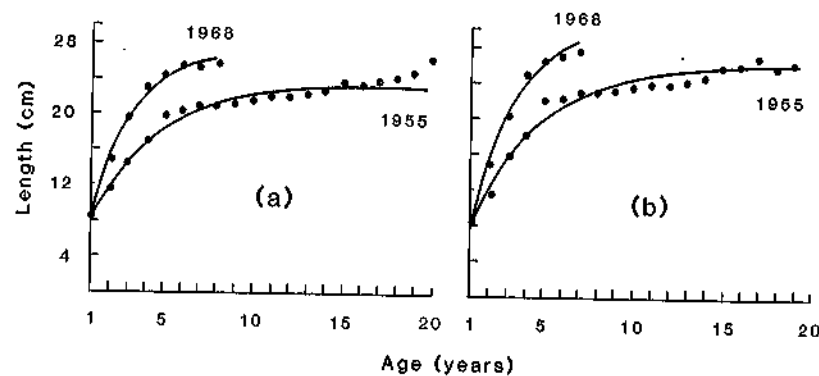


FIG. 1. Mean length (cm) against age of the 1955 and 1968 cohorts for (a) male and (b) female perch. Smoothed curves are shown derived from the best fitting von Bertalanffy growth curves.

where the number at age  $t+1$ ,  $N_{t+1}$ , depends upon the number at age  $t$ ,  $N_t$ . Thus

$$N_{t+1} = N_t e^{-Z}$$

Values of  $Z$  have been calculated for most cohorts of perch in Windermere over recent years (Craig et al. 1979). Catches over successive years and values of  $Z$  derived from them are shown for the 1955 and 1968 cohorts in Fig. 2. Adult mortality rates are remarkably constant throughout most of the life span of each cohort, as is known elsewhere (Alm 1951), but males have a consistently higher mortality rate than females. Females not only survive to a greater age but also have a greater ultimate length (Fig. 1); thus males and females have to be treated separately. Of particular interest is the difference in the mortality and growth rates between fish of the same sex but in different cohorts. Since 1955, the growth of perch has been well described by the simple equation of Von Bertalanffy (1938) given by:

$$L_t = L_\infty \{1 - e^{-K(t-t_0)}\}$$

where  $L_t$  = length at time  $t$ ,  $L_\infty$  = asymptote and thus ultimate length where, at least in theory (though rarely in practice), growth has ceased,  $K$  = rate at which the growth approaches the asymptote of the curve and

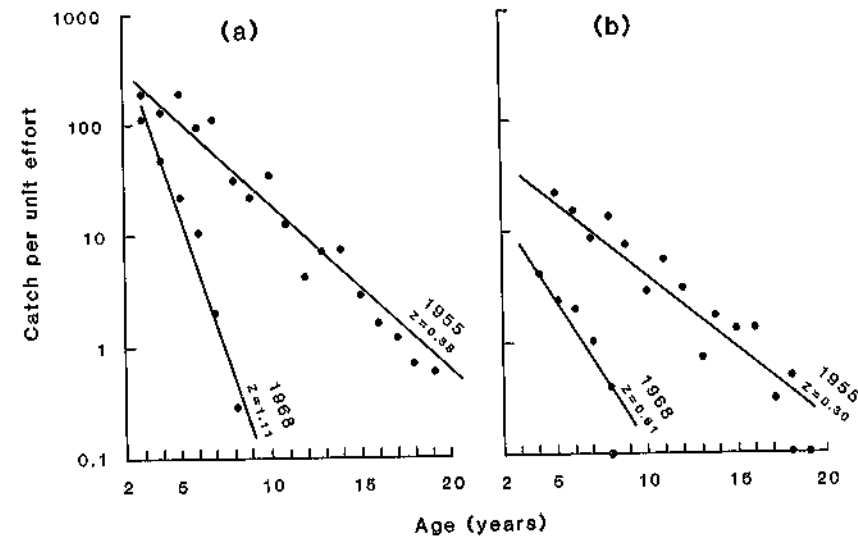


FIG. 2. Catch per unit effort (cpue) (perch caught in one trap over a whole season of 6 weeks) against age of the 1955 and 1968 cohorts for (a) male and (b) female perch; cpue is plotted on a logarithmic scale. Regression lines have been fitted to the points and mortality rates derived from these regressions are given in the figure.

$t_0$  = theoretical age at which  $L = 0$ . Craig (1980) has shown that  $Z$  is linearly related to  $K$  for cohorts of adult perch (Fig. 3). Beverton & Holt (1959) found a similar relationship among species within families of fish, rather than cohorts of one species. They suggest that the natural span of life is nicely adjusted to the time needed to complete the growth-pattern. The fast-growing perch soon become too big to be eaten by most of the predators in the lake, so other factors must be causing their deaths. Craig (1979) suggests that increased temperatures and a rich food supply speeds up growth and physiological ageing. Slow growth, the cause of which may be poor food supply or low temperatures or overcrowding or a combination of these, extends the life expectancy. Processes involved in physiological ageing are little understood and some fundamental studies need to be made in this area.

Although faster-growing fish in the adult stage have a higher mortality rate than slow-growing fish, the reverse is true during the early stages of their life (Fig. 4a). We are able to make an approximate calculation of juvenile mortality from estimating the difference between the number of eggs laid and the number of fish at age 2 years when first caught by the traps. It is likely that most mortality takes place in the first year of life, but as we have no way of estimating numbers at age 1 year, instantaneous mortality rates have been calculated over 2 years (from egg to age 2 years). Mortality rate decreases and growth increases with rise in temperature (Fig. 4b & c). Warm summers may produce more prey organisms for the young perch as well as increasing the latter's metab-

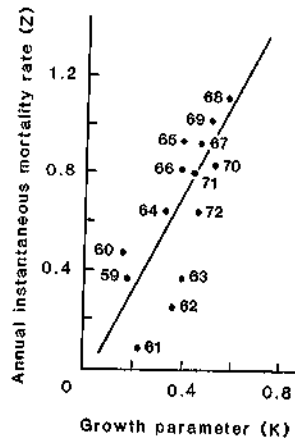


FIG. 3. Adult annual instantaneous mortality rate ( $Z$ ) plotted against the growth parameter ( $K$ ) from the von Bertalanffy growth equation, for male cohorts from 1959 to 1972. A regression line has been fitted to the points.

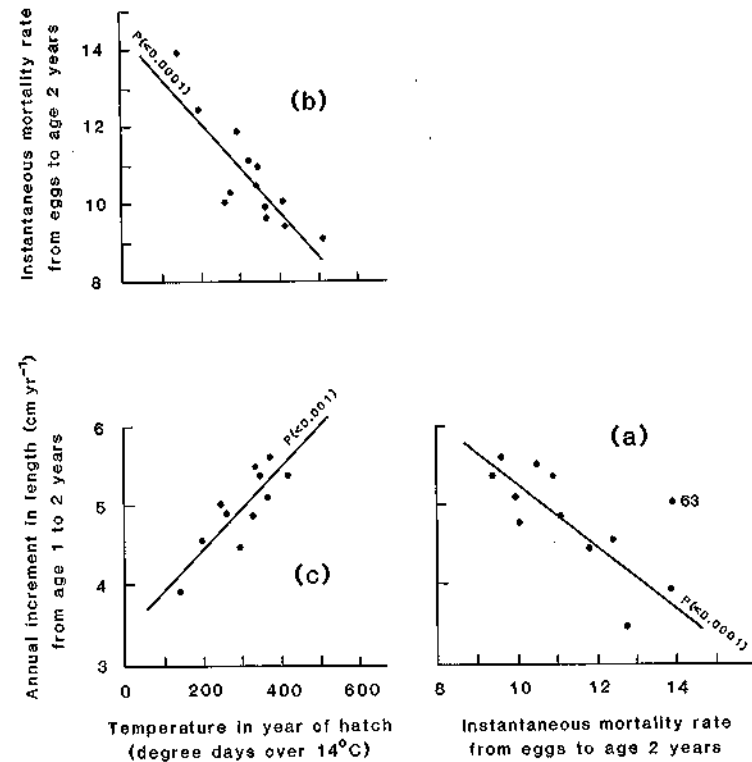


FIG. 4. (a) Annual increment in length ( $\text{cm yr}^{-1}$ ) from age 1 to 2 years plotted against instantaneous mortality rate over 2 years (from eggs to age 2 years). (b) Instantaneous mortality rate (from egg to age 2 years) plotted against an index of temperature (degree days above  $14^{\circ}\text{C}$ ). (c) Annual increment in length ( $\text{cm yr}^{-1}$ ) from age 1 to 2 years plotted against an index of temperature (degree days above  $14^{\circ}\text{C}$ ). The data for the figures are derived from cohorts from 1961 to 1972. Regression lines have been fitted to the data. Note in 4(a) that the 1963 cohort deviates from the line drawn. During the previous winter the lake became ice covered and many females were found reabsorbing their eggs in the spring. Thus fewer eggs than predicted were laid.

olism. These factors will increase their rate of growth which probably means the fish will be exposed to predators for a shorter period of time.

In order for populations to remain stable there is, in theory, a need for a relationship between birth rates and death rates. These rates must therefore be dependent on the density of the population. As the population density increases, death rate increases and birth rate declines.

Density-dependent factors include predation, which can be divided into cannibalism and predation by other species (Ricker 1954). Craig (1978) found that adult perch ate young perch (0+ years) and therefore the mortality rate of young perch is likely to be correlated with the abundance of adults. There is a paradox here as the number of eggs laid in spring is positively correlated with adult biomass, yet early survival is negatively correlated due to predation by their parents in the summer and autumn. Another important predator of perch is the pike (*Esox lucius* L.). The main effect of predation is in the perch's first year and is brought about by pike of the same age. Changes in birth and death rate result from changes in the availability of resources (food, habitat space) per individual in the population; physical environmental factors can also affect population abundance. This effect may be independent of population density or it may act in conjunction with density-dependent factors. Mortality rates of young perch are affected by water temperature (as discussed earlier) (Fig. 4b). Temperature also affects growth and thus biomass and fecundity. Le Cren (1958) closely correlated temperature and growth of Windermere perch.

The effect of the perch and pike fisheries in Windermere on perch abundance was to cause first a rapid and then a gradual decline in numbers even after the perch fishery ceased (Craig et al. 1979). Biomass did not decline as much as numbers, due to improvement in growth. Numbers and biomass of perch started to increase in the mid 1950s in the south basin due to strong cohort numbers (strengths) being produced during this time, but in the north basin increase in numbers and biomass occurred only in the late 1950s (over 10 years after the perch fishery in this basin ceased). The biomass of the 1959 cohort made up a large proportion of the total biomass in the north basin for most of the 1960s. (Fig. 5). (Note that the ordinate is on a logarithmic scale. Biomass is calculated for fish of 2 years or older.) After the production of this large cohort in the north basin, numbers declined through the 1960s but biomass reached a peak in 1962, fell slightly until 1964 and then remained stable (north basin mean =  $49 \pm 3$  tonnes (Mg)) until 1976. The biomass followed a similar pattern in the south basin but the 1955 cohort made a large contribution to the total biomass. Cohorts hatched in the early 1960s contributed very little to the total biomass as is shown by the 1962 cohort in Fig. 5. As the dominant 1959 cohort declined, later cohorts contributed more, as is shown by the 1966 and 1968 cohorts in the figure, and thus allowed the total biomass to remain stable.

It is very difficult to relate recruitment to environmental factors before this period of stable biomass, as Le Cren (1965) has pointed out. Kipling (1976) has shown a correlation between cohort strength and temperature and Le Cren (1955) showed that there is some synchrony between cohort strengths in different lakes. There was a stronger correlation ( $P < 0.001$ )

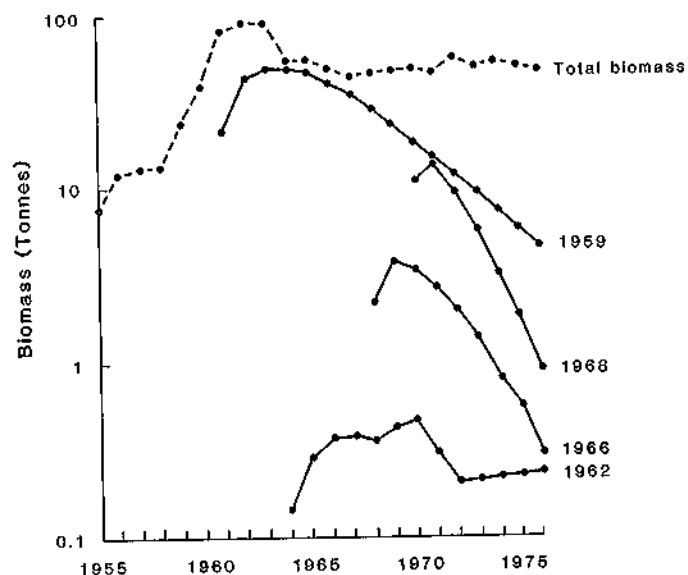


FIG. 5. Total biomass (tonnes) of adult perch (2 years or older) in the north basin of Windermere plotted against year from 1955 to 1976. Also given are biomass data for cohorts 1959, 1962, 1966 and 1968 contributing to the total biomass in the years where they are represented.

between the natural logarithm ( $\ln$ ) of cohort strength (at age 2 years) and temperature during the period of stable biomass compared with the period 1944 to 1958 ( $P < 0.01$ ). The negative correlation between  $\ln$  cohort strength and adult biomass was non-significant from 1944 to 1958 but highly significant ( $P < 0.001$ ) from 1959 to 1974. I postulate that the population had reached such a low limit in the 1950s that it was unable to respond to rapidly changing conditions. It needed the exceptionally warm years of 1955 and 1959 to break the barrier and 'flip' the perch population up to a high level again. There may well have been other coincident factors in 1959 (for example zooplankton crops suitably abundant and timed to help the quite exceptional fry survival). Perch in the north basin may not have been able to exploit the warm summer of 1955 due to heavy predation on the adult egg-laying stock by adult pike. The ratio of food consumed by the adult pike to biomass of adult perch present (available food) was far higher in the north basin than in the south basin (Fig. 6) at this time. Once the 1959 cohort had restored the situation, the population was able to respond to environmental factors and maintain stability. The recruitment of perch was found to be highly correlated ( $P < 0.001$ ) with the density of the cohort in relation to the pike cohort of

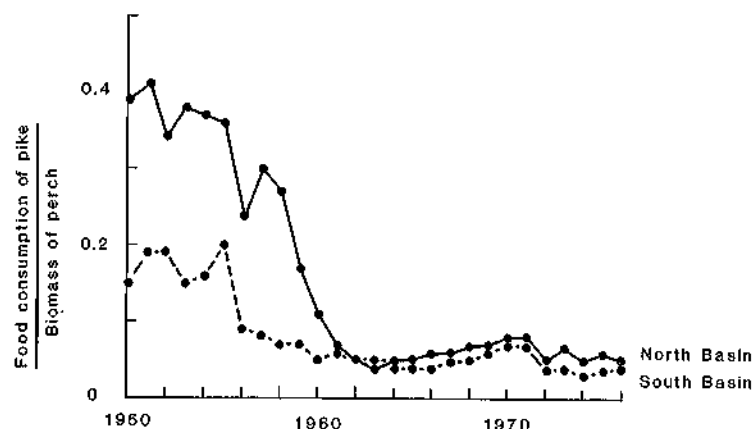


FIG. 6. The ratio of annual food consumption by pike (tonnes) /biomass of perch (tonnes) present plotted against year from 1950 to 1976 for the north and south basins of Windermere.

the same age. The best fit to the data was  $\ln$  cohort strength with  $\ln$  (cohort strength of perch/cohort strength of pike). Such a curved relationship implies that predation effects by pike increase as the ratio of prey to predator decreases. There were no significant differences between basins in this relationship between the two periods under consideration.

The relationship between the various factors affecting perch recruitment can be modelled by formulae of the form:

$$\ln y = b_0 + b_1 x_1 + b_2 x_2 + b_3 x_3$$

where  $y$  = cohort strength at age 2 years,  $x_1$  is a measure of temperature in year of hatch,  $x_2$  is biomass of adult stock in year of hatch,  $x_3$  is  $\ln$  (perch cohort strength/pike cohort strength) and  $b_0, b_1, b_2$  and  $b_3$  are constants.

The model was found to be an excellent fit to the data collected from 1959 to 1974 for both the north basin (the multiple correlation coefficient,  $r = 0.9882$ ) and the south basin ( $r = 0.9844$ ). Fig. 7 illustrates this model for the north basin of Windermere. It shows clearly how increase in temperature (a density-independent factor) increases cohort numbers, but an increase in predation, both by cannibalism of adult perch and predation by pike (density-dependent factors), decreases the number of perch reaching age 2 years.

In 1976 another quite unexpected twist to the story of perch in Windermere arrived in the form of a disease. (The primary pathogen of this perch disease has not yet been identified by fish pathologists (Bucke et al. 1979) although an epidemic appears to have moved over England from the south during the past twenty years.) Over 98% of the perch

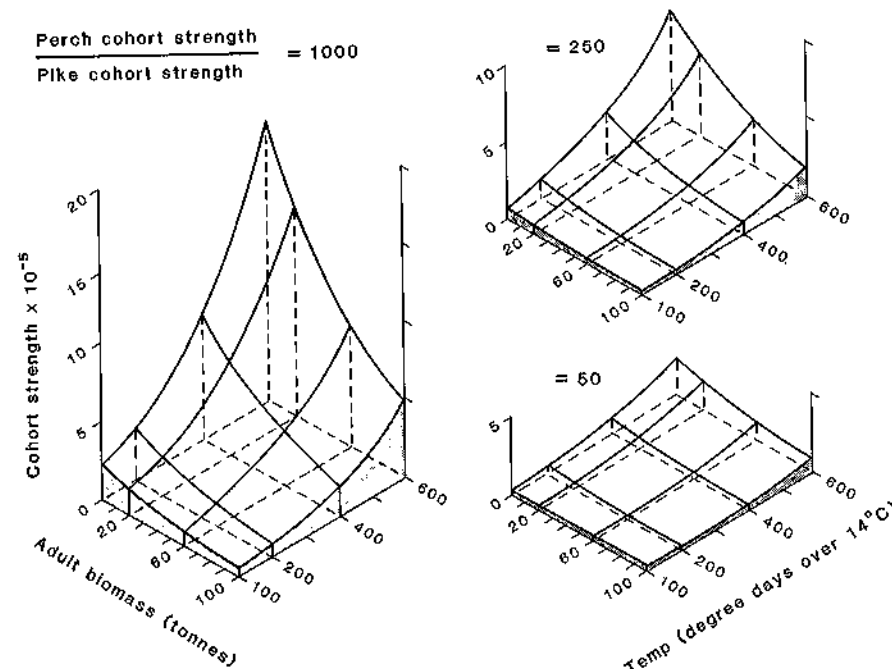


FIG. 7. Diagrams to illustrate the effect of adult biomass, temperature and pike on the cohort strength of perch at age 2. They are derived from simple models which are outlined in the text.

population in Windermere was killed as a result of the disease. Perch numbers have increased very little since 1976 until the present. In 1978 some female perch matured at only 2 years, but prior to this the youngest age of maturity had been 3 years. In the summer of 1981 about 30% of perch caught showed external signs of disease. Resistant strains will probably in time replace the original stock and when these and suitable environmental conditions return, as has been observed in other lakes, the population number may rise rapidly again. The residual stock is now greater than that which gave rise to the rapid increase in numbers in the late 1950s. It will be interesting to see if the population reaches and controls stability of biomass again but this could take another 15 to 20 years of observation.

The long-term study of the perch population has shown how flexible the population is and how it has behaved in different ways over successive periods of time since 1939. Through one of these periods it was possible to account for nearly all the variance in recruitment by a relatively simple

explanatory model and this has wide implications in fish population ecology. The outbreak of disease in 1976 resulted in another period of change. The reduction in numbers by natural causes formed a baseline for future studies (it started a natural experiment) and it is imperative for further understanding of animal population dynamics that the perch (and pike) populations should continue to be monitored.

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