Fresh water is the planet's most valuable natural resource and the challenge is to reconcile the needs for water in human activities with the requirements for healthy aquatic ecosystems. Management of this resource must be based upon the best available scientific knowledge, including the factors controlling water quantity, water quality and freshwater fisheries. All three areas interact and the IFE's research programme is directed towards understanding the key processes involved and then using this information to develop predictive models to aid the practical management of this vital, but fragile resource.

Programme 4 Freshwater Resources

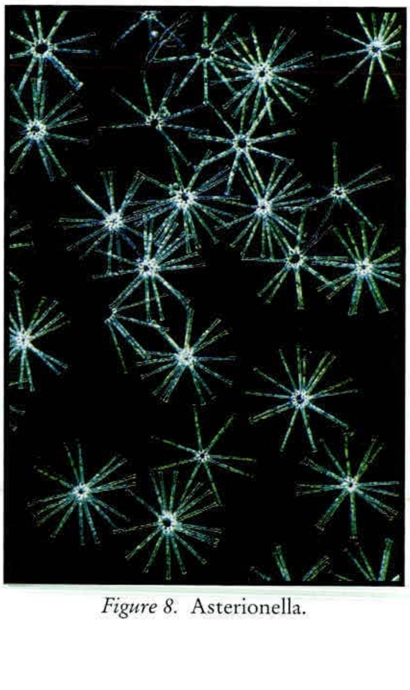


Figure 8. Asterionella.

Chaotic impacts of a dry winter on the phytoplankton of lakes

One of the most familiar and best studied features of phytoplankton ecology is the spring increase in temperate waters. The underpinning paradigm, much of which was assembled three or four decades ago through the work of John Lund at Windermere, is that the combination of winter recovery of *in-situ* nutrient concentrations and the increase in day length after the winter equinox offers an environment conducive to the growth and replication of planktonic algae. There is a small direct effect attributable to temperature rise but, in lakes as deep as Windermere, the progressive truncation of the depth of mixing as its heat content increases is crucial. The bloom continues until the algae are either limited by nutrients, eliminated by zooplankton grazers, killed by parasites, shed from suspension in a stagnating water column, or by a combination of these factors.

The main thrust of the more recent research into spring blooms has been to determine (i) why they are so regularly and characteristically dominated by very few species (usually of diatoms) and (ii) what factors are responsible for year-to-year variations in the eventual crop yield. In the lakes of the Windermere catchment, where continuous records of the changing composition of the phytoplankton now stretch back 52 years, the main participant is usually *Asterionella*, just as it was when John Lund began his studies, though other species of diatoms and various other algae are usually to be found in significant quantities. No two lakes produce identical populations and their maximal crops do not occur simultaneously. Nevertheless, enough is now known for it to be hypothesised that the key constraint on growth, after temperature, is the amount of light available to algae in suspension.

Figure 9. Grasmere.

Asterionella is one of the more efficient harvesters and converters of light energy, especially at low water temperatures and, provided an inoculum of cells persists in the water column, its ability to replicate faster than many of its so-called competitors and to initiate its increase earlier in the growing year is sufficient to anticipate its regular dominance.

Differences in its periodicity in the Windermere catchment are thus related principally to the site-specific physical conditions. In Windermere itself, *Asterionella* peaks during May, exceptionally in late April, after 13-15 replications (doublings). The maximum in the (deeper) north basin is generally about one week later than that in the south basin. In Esthwaite Water, which is rather smaller and shallower than Windermere, *Asterionella* generally dominates the spring peak that is reached at the end of March. The size of the maximal crop is similar to that in Windermere: simply, it grows earlier and, perhaps, faster in Esthwaite Water because, other things being equal, more of the lake volume is insolated and so, suspended algae are able to photosynthesise for a greater proportion of the day. The relationship in the smaller Blelham Tarn is similar to Esthwaite, and yet more favourable in Grasmere, but these two lakes are very susceptible to rapid flushing by discharges following heavy rainfall and runoff. *Asterionella* blooms in both, though with much greater interannual variation.

Differences in periodicity of phytoplankton are generally related to site-specific physical conditions.

The 1996 spring blooms in these lakes were all, to a greater or lesser extent, exceptional and mutually dissimilar. The events are supposed to be related, in site-specific ways, to the unusual hydrological conditions obtaining during the 1995-96 winter. After one of the wettest springs known, persistent high pressure systems over the UK blocked the normal westerly airstream and frontal systems, thus depriving the country of its regular precipitation.

Figure 10. Blelham Tarn.

These "continental" conditions also saw some low temperatures: all the lakes, even Windermere, experienced substantial periods of ice cover. So far as the winter-spring growth conditions for the phytoplankton in the lakes of the Windermere catchment were concerned, there were proportionate reductions in the displacement of inocula, while periods of inverse stratification modified the ability of water columns to suspend diatoms or to "dilute" the light income through the full water depth. The impacts on the phytoplankton were profound, distinctive and not altogether predictable.

In Grasmere, the spring bloom was the largest ever recorded in the lake. The late April maximum of Cryptomonad flagellates (2 300 ml^{-1}), with an abundant nanoplankton, achieved the phosphorus-determined carrying capacity. The response was attributable to a greater stock of algae being carried over through the winter. Diatoms failed to exploit the opportunity, mainly as a function of settling losses under ice, whereas the flagellated Cryptomonads escaped this particular constraint. Their acknowledged capacity to adapt to low winter light levels would have been an advantage, while low temperatures are protective in that they suppress the activities of potential consumers.

Lack of winter flushing in Blelham Tarn also contributed to the assembly of one of the largest (65 μg chlorophyll l^{-1}) and most persistent spring blooms (lasting until the end of June) observed in this lake. It was dominated throughout by the filamentous cyanobacterium, *Planktothrix mougeotii* (formerly *Oscillatoria agardhii* var. *isothrix*), with a maximum population of 381 mm ml^{-1}. This alga is more efficient than *Asterionella* as a light antenna but it grows very much more slowly and, usually, its numbers are depleted by winter flushing. The alga regulates its own buoyancy and, thus, offsets the sinking losses experienced by silicified diatoms. The persistence of a suspended, overwintering crop of *Planktothrix*, almost 100 times greater than normal, was sufficient to give the organism "pole position" in the 1996 race to dominance.

In the larger lakes, where even excessive winter inflows displace a relatively smaller proportion of the lake volume, the impact of a dry winter might be anticipated to be minimal. In fact, diatoms continued to dominate in Esthwaite Water, where the period of ice-cover was shorter. Nevertheless, it was the dry conditions which favoured the large, early and nearly pure bloom of *Asterionella* (maximum, 10 300 cells ml^{-1}, before the end of February!). With the silicon all but exhausted, the plankton became very diverse as other species tried to fill the void. Cryptomonads, *Closterium, Synura, Dinobryon* and *Uroglena* were among the expected participants but following the onset of stratification, filamentous cyanobacteria, *Anabaena* and especially *Aphanizomenon*, became overwhelmingly dominant.

The vast volume of Windermere tends to suppress any vagaries due to wet and dry periods. The crop sizes attained in 1996 were not the largest observed there; prior to the programme of restoration of the lake by phosphate-load reduction, the carrying capacity was rather higher. Nevertheless, in both the north and south basins, the crops emulated the lowered respective capacities, most likely as a consequence of the extended period of low flows and the retention of a larger inoculum of algae. In the North Basin the maximum in early May (14 μg chlorophyll l^{-1}) was dominated, as usual, by *Asterionella formosa* (5 600 cells ml^{-1}), with subsidiary masses of *Cryptomonas* spp., *Aulacoseira subarctica, Aulacoseira islandica* and *Fragilaria crotonensis*. The maximum was determined, also as usual, by exhaustion of the silicon and not by the amounts of phosphorus available. The net rate of increase of the *Asterionella* during April was also near normal (0.16 d^{-1}, as determined by temperature, daylength and underwater insolation). The difference was in the overwintering inoculum: the average concentration through January, 1996, was 1-2 cells ml^{-1}, whereas the long term average is almost an order of magnitude smaller (0.1–0.3 cells ml^{-1}). The difference may seem trivial but it is equivalent to three cell divisions and the opportunity to reach the silicon-determined capacity before the rates of cell loss (chiefly through sinking in a stagnating water column) began to suppress the size of the maximum actually achieved. Despite the volume difference, the dry year impacted just as surely on the phytoplankton dynamics in Windermere as in the smaller lakes.

The events described were, in their various ways, exceptional departures from a perceived norm. The explanations fit with what we believe to be distinctive species-specific performance abilities of the phytoplankton. Natural responses to extreme events improve our understanding of population dynamics and help us to grapple with the complexities of systems behaviour. In spite of all this, the events could not have been predicted. The biological outputs of a relatively minor perturbation in the system drivers belong to the realms of chaos theory.

Phytoplankton distribution and inorganic carbon

CO_2 is a highly dynamic resource in freshwaters

Within a lake the pH and concentrations of dissolved inorganic carbon and, in particular, carbon dioxide (CO_2), can vary with high frequency and large amplitude. These changes are driven by high rates of carbon uptake by photosynthetic organisms during the day and respiratory carbon production by the entire community during the night. During

Figure 11. Windermere.

Quite minor variations generate significant departures from the norm to enter the realms of chaos.

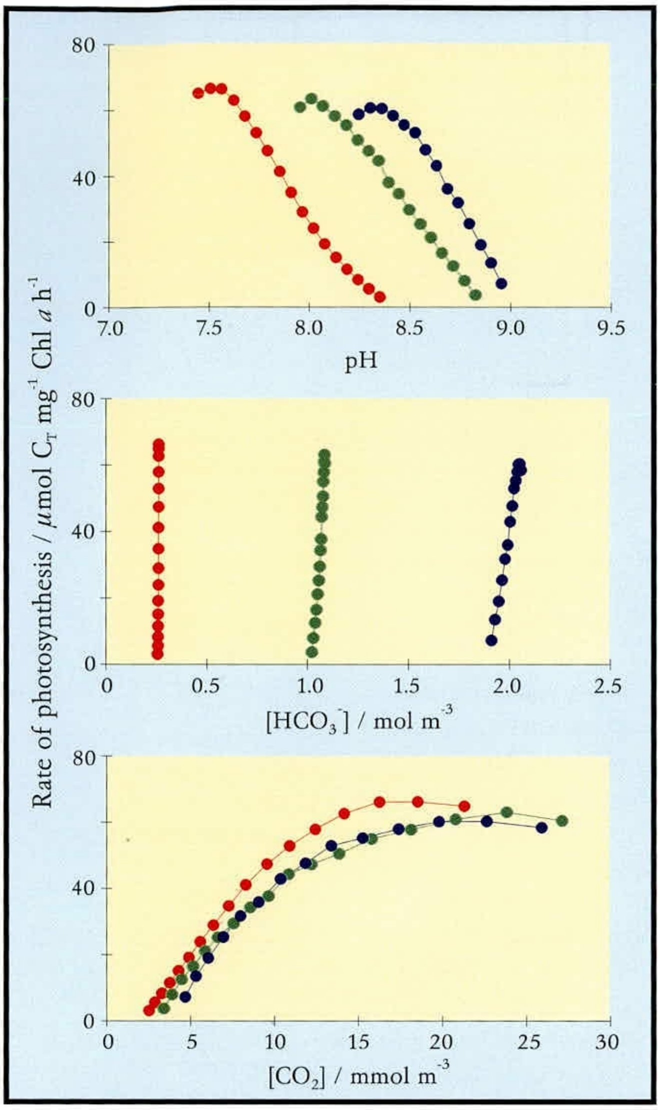


Figure 12. Measurements in media at three different alkalinities demonstrate that rates of photosynthesis by the chrysophyte Dinobryon sertularia are controlled by the concentration of CO_2.

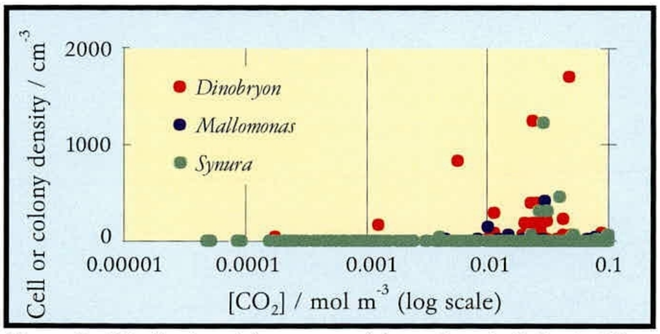


Figure 13. Distribution of three genera of chrysophytes in Esthwaite Water between 1984 and 1994 in relation to the concentration of CO_2.

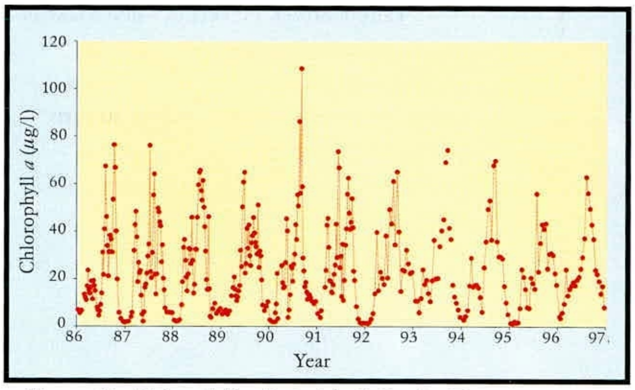
calm weather, especially when a lake is stratified, high pH values can be produced in the surface water and the [CO_2] can be reduced close to zero. Under these conditions, continued net photosynthesis will depend on the ability to use alternative sources of inorganic carbon such as bicarbonate (HCO_3^-).

Phytoplankton photosynthesis and CO_2

While CO_2 can be used by all aquatic photosynthetic organisms, not all can use HCO_3^- ions. One group of algae, the Chrysophyceae, appears to contain representatives that are unable to use HCO_3^- in photosynthesis. Rates of net photosynthesis by Dinobryon are independent of pH or HCO_3^-. Rather, they are controlled by the [CO_2] and are not possible once the [CO_2] falls below 3 mmol m^{-3} (Figure 12). This suggests that this group of algae may not be able to survive episodes of high pH and low [CO_2] which are common in productive lakes. This hypothesis can be tested by analysing long-term records of algal distribution and environmental conditions. Results for three genera of chrysophytes in one Cumbrian lake (Figure 13), support the hypothesis that their distribution is restricted by the availability of CO_2.

Water quality of Esthwaite Water

The concentrations of soluble reactive phosphate and chlorophyll *a* and depth of Secchi disc extinction showed there had been little improvement of the quality of surface water in Esthwaite since 1986, when phosphate stripping the effluent from Hawkshead sewage treatment works (STW) had been implemented. In fact the concentrations of total phosphorus had increased, on average, by 6.4 $\mu g\ l^{-1}$ in the period 1993/5 from those found in 1986/8. In the same period the soluble reactive phosphate concentrations in Black Beck, the main inflow, had decreased by an



Figures 14. Chlorophyll a (0-5m) in Esthwaite Water 1986-1996.

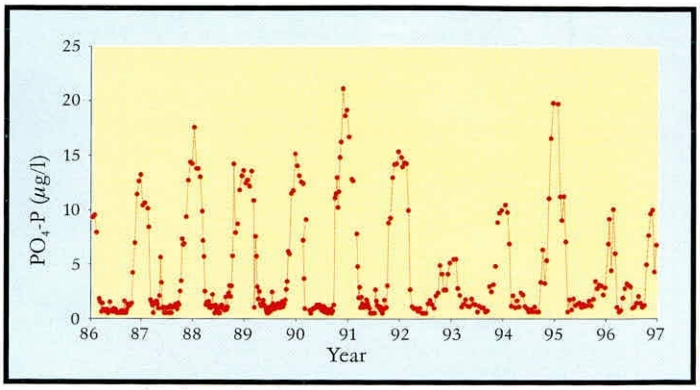


Figure 15. Phosphate phosphorus (0-5m) in Esthwaite Water 1985-1996.

average of 4.0 $\mu g\ l^{-1}$. The concentration of total phosphorus in the inflow remained unchanged.

The potential for surface sediments to supply phosphate to the overlying water was assessed by changes in the concentrations of alkali-extractable phosphate (AEP) in the upper 4 cm of sediment from 12 sites in the lake. Analysis of data from 1986 showed there had been a significant decrease in the average concentration of AEP but most of this was attributed to one site (site 9) affected by particulate material sedimenting from a fish rearing cage. If this site was eliminated from the analysis the concentrations of AEP in the sediments had not changed since 1986.

Given that phosphate stripping the effluent from Hawkshead STW was working efficiently, the sediment was not a net source of phosphate to the overlying water, and that phosphorus loads from minor inflows was negligible, the sustained poor quality of surface water must be maintained by additional sources of phosphorus to the lake. These are being investigated.

Improving water quality in Bassenthwaite Lake

Bassenthwaite Lake (Figure 16) has become more eutrophic (nutrient enriched) in recent years. This has led to concern over the survival of its vendace (*Coregonus albula*) population – one of only two remaining in the UK.

Assessing the nutrient load

The amount and sources of nutrients entering the lake were little understood until a detailed nutrient loading study was carried out in 1993. These data were interpreted using the IFE's dynamic lake model (PROTECH) which suggested that any management plans aimed at improving water quality should focus on reducing the phosphorus (P) load from the catchment. The total P load for 1993 was found to be about 16.7 tonnes. More than 40% of this came from STW discharges, while the remainder came from diffuse (non-point) sources (Figure 17).

Increased eutrophication has led to concern over the survival of vendace.

Figure 16. Bassenthwaite Lake – one of the larger waterbodies in the English Lake District.

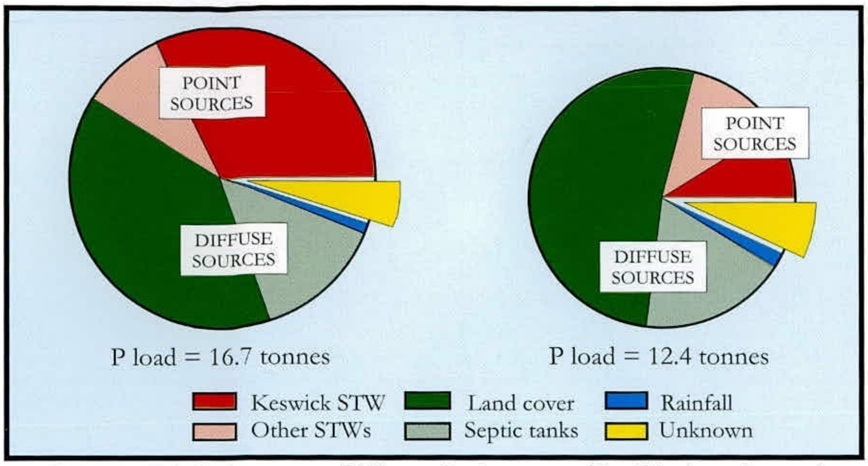


Figure 17. Relative importance of diffuse and point sources of P within the catchment of Bassenthwaite Lake, (a) before and (b) after the STW upgrade. Total P load is proportional to the area of each pie diagram.

Almost 20% of the phosphorus load to Bassenthwaite Lake may come from septic tanks.

Reducing the P load

More than 80% of the P load from STWs came from the main works at Keswick. This was upgraded in 1995, reducing the P output from this source by 80%, and the P load to the lake by 26%. As a result, non-point sources became relatively more important, accounting for almost 70% of the remaining P load to the lake (Figure 17). Any reduction in P load from these sources would require changes in farming or forestry practices within the catchment, or the provision of mains sewerage connections to premises currently served by septic tanks.

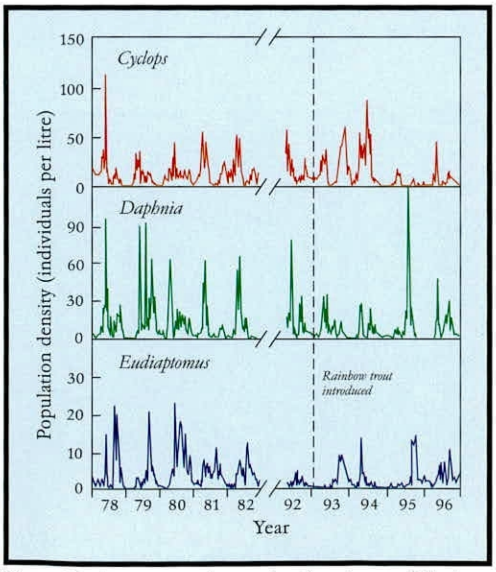


Figure 18. Long-term changes in abundance of Cyclops, Daphnia *and* Eudiaptomus *in Loch Leven, 1978-1996.*

Monitoring of Loch Leven zooplankton

The zooplankton community of Loch Leven, Kinross has been monitored since the late 1960s with the exception of a period during the 1980s when sampling became more sporadic. Zooplankton are an important component of the lake ecosystem as their grazing activities, particularly that of *Daphnia*, play a pivotal role in determining the overall abundance and species composition of the phytoplankton as well as being food for fish and indicators of trophic status. These years of accumulated monitoring data are an invaluable baseline for distinguishing long-term changes in Loch Leven from short-term temporal variations.

Crustacean zooplankton

Since 1971, the species composition has remained remarkably constant, with *Daphnia hyalina-galeata* and the cyclopoid copepod *Cyclops abyssorum* co-dominant. Normally the spring/early summer is characterised by maxima in both *Cyclops* and *Daphnia* numbers followed by smaller secondary peaks in the autumn. However, between 1993 and 1995 these species exhibited greater inter-annual variability in terms of their relative abundance, absolute concentrations and seasonality of occurrence (Figure 18). Instability in the plankton caused by measures to control P-loading (thereby limiting algal productivity) and by the stocking of rainbow trout were the factors linked to these changes. However, during 1996 the crustacean zooplankton reverted back to the patterns of abundance observed before 1993.

Rotifer zooplankton

In Loch Leven the rotifer zooplankton is a relatively diverse community with a total of 27 species recorded since the late 1970s. Six rotifer species generally dominate; *Keratella cochlearis, K. quadrata, Polyartha dolicoptera, Synchaeta kitna, Pompholyx sulcata* and

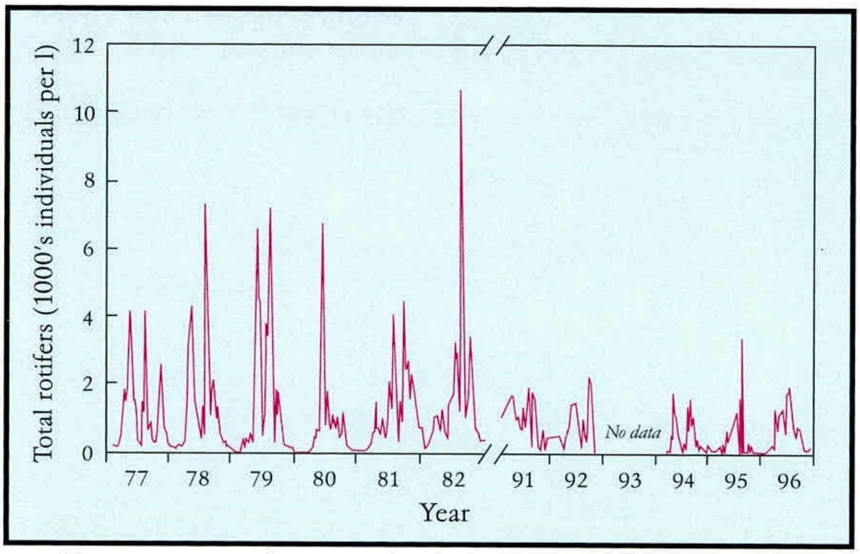


Figure 19. Long-term changes in total rotifer abundance in Loch Leven, 1977-1996.

Trichocerca pusilla. This species composition, like that of the crustacean zooplankton, remains one characteristic of nutrient-rich waters. However, total rotifer abundance declined in the period 1992-1996 compared to 1977-1982 (Figure 19). This reduction in the overall rotifer numbers suggests that the continuing programme of reducing the P load to Loch Leven is having some success in making the loch less eutrophic.

Loch Leven phosphorus reduction – the influences of catchment management and inter-annual weather variation compared

The problem

At a mean depth of just 3.9 m, uncoloured as against humic-stained, and only moderately flushed (*ca* 2 lake volumes per year), Loch Leven (Kinross, Scotland) is very efficient at converting its income of phosphorus (P) into planktonic algal biomass, especially if the *Daphnia* population fails (Figure 20). It has also received over many years, tonnages of nutrients such as nitrogen and silica as well as P, in run-off from rich agricultural land, and in outfalls of P-rich sewage and industrial effluents. Unsightly and sometimes toxic blooms of algae cloud the water (Figure 21), threaten biodiversity of emergent and submerged rooted vegetation and associated microflora and fauna. They are also thought to have contributed to decreased (trout) angling catches, although these may reflect a drop in angling effort rather than a significant fall in fish numbers. Algal material passing out of the lake can also lead to increased water treatment costs at downstream paper-mills (Figure 22).

Science underpinning the solution to the problem

The types, timing and abundance of planktonic algae, have been identified from the IFE's uninterrupted research since the late 1960s, on physical factors,

Loch Leven is very efficient at converting its phosphorus supplies into often troublesome algal blooms.

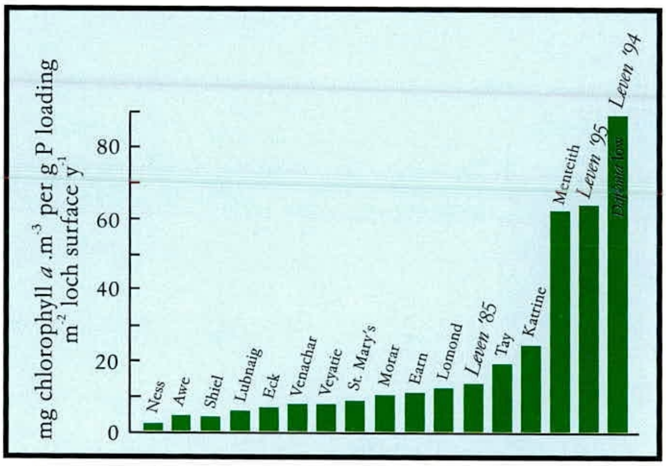


Figure 20. Loch Leven is amongst the most efficient of Scottish lochs in converting phosphorus supplies into algal biomass.

Figure 21. A particularly unsightly bloom.

Figure 22. Loch outflow leading to paper-mills relying on reasonable water quality.

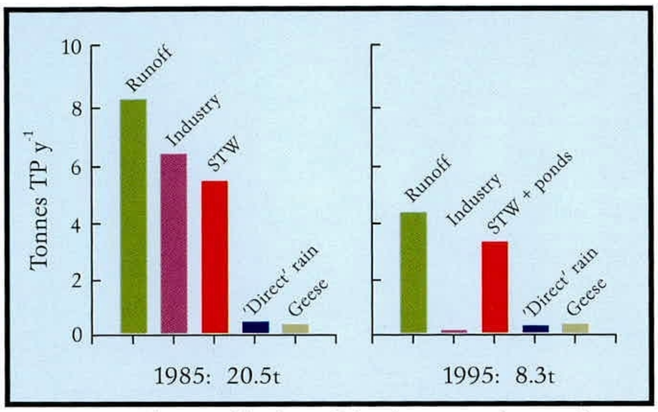


Figure 23. The annual loadings of phosphorus to Loch Leven form various sources: 1985 and 1995 compared.

Local authorities upgraded sewage treatment works on the basis of IFE's research findings and interpretation.

nutrient levels (and fluxes between catchment, loch, water, sediments and algae), and the zooplankton. Findings that phosphorus is the main *nutrient* limiting primary production, suggested that in order to reduce algal bloom developments, its inputs should be cut back significantly.

Results of the action taken

Local authorities implemented these recommendations and, indeed, the loadings measured in 1995 are considerably less than those recorded in 1985 (Figure 23). However, while much of the net decrease between the two years can be attributed to managed upgrades of sewage treatment works and eradication of the industrial effluent, the effect of contrasting rainfall regimes is considerable; much of the reduction in runoff-related P loading is due to the fact that only 890mm rain fell in 1995, compared with the 1250mm received in 1985. Nevertheless, the focus on sewage treatment works is very significant in that these point-sources are (relative to land runoff) particularly rich in bio-available P.

Mean Trophic Ranking – a system for comparing trophic status using water plants

Avoidance of further lowering of trophic status of water courses and assessment of the need to reduce nutrients, especially phosphate levels, of inputs, such as the effluents from large sewage treatment works (STW >10 k person equivalents), is essential to the UK's response to the EU Urban Waste Water Treatment Directive.

One system of assessment, using the phosphate tolerance of different species of water plants, has been developed and trialled by the Environment Agency (EA) in England and Wales.

Plant species were each given a ranking based upon their relative tolerance to phosphate ('Species Trophic Rank') and when comparing plant communities at different sites, particularly upstream and downstream of a discharge, the cover-related value for each species ('Species Cover Value') was averaged to create a rank for the site ('Mean Trophic Rank' or MTR).

This MTR system was recently assessed by the IFE after assembling the majority of the plant and relevant environmental data into an easily interrogatable database (from 250 sites

Figure 24. A river with little nutrient enrichment and an MTR score of about forty five; many aquatic plant species and no excessive algal growth.

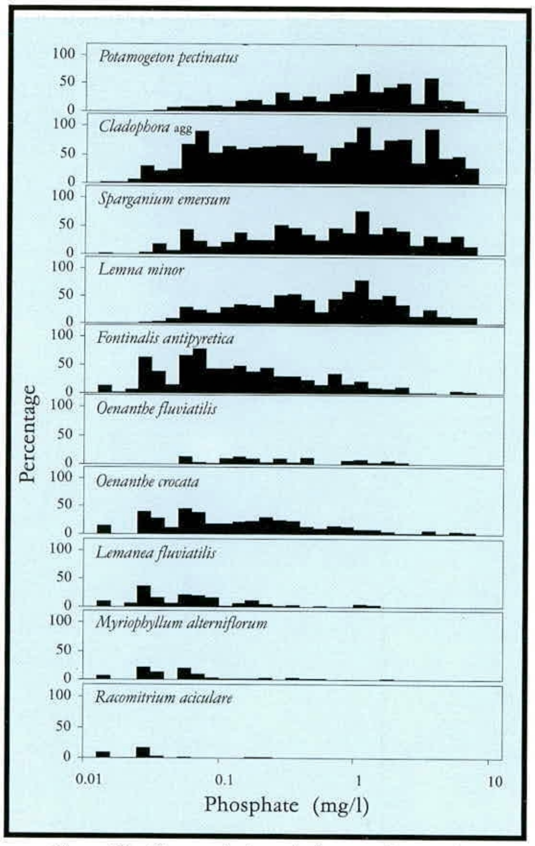


Figure 25. Cover of selected plant species, against phosphate concentration, on a logarithmic scale.

above and below STWs) of the three years of trial data from the EA together with data from Northern Ireland (SNIFFER funded).

The MTR methodology was found to be robust, with the majority of the plant species correctly ranked according to their tolerance to phosphates; this was made possible by access to 1700 surveys in the Scottish National Heritage – Countryside Council for Wales – English Nature database on rivers assessed for conservation value, i.e. plants from sites of high quality or high trophic status.

Further surveys at sites with unexpected or variable MTR site-ranking, were used to refine the system, as a basis on which to give guidance and to improve the procedural manual. Comparisons were made at some sites with another system based on river diatoms developed for the EA at Durham University and which was useful in clarifying the combination of effects such as organic pollution and toxic compounds.

River Habitat Survey – a system for assessing the physical habitat of rivers for conservation

Classification of the quality and modification of the habitats of differing types of river is required for the UK's response to the EU Habitats Directive and for the statutory duties of the Environment Agency (EA). A system encapsulating the physical and morphological aspects of the structure of rivers and their immediate environment in a computer-compatible form to ease analysis, interrogation and planning, has been developed for the EA in collaboration with the IFE and other specialists.

The four years of this study has incorporated stratified random

Mean Trophic Ranking provides a system to compare the trophic status of rivers receiving effluents.

Figure 26. A eutrophic river with an MTR score of about twenty; abundant green algae and only a few other aquatic species.

River Habitat Survey provides a system to classify the quality and modification of rivers.

sampling of field sites in each 10 km by 10 km square three times in England and Wales, twice in Northern Ireland and once in Scotland. Additional orientated projects have used the River Habitat Survey (now totalling over 7 000 surveys) as a framework for assessing the actual or potential effect on riverine habitat and include run-of-river hydro-electric schemes, crayfish habitat, marginal plant assessment, selection of indicator species or isolation of special habitats.

Rivers are currently grouped together into eleven types of greater similarity based upon a combination of map-derived factors which may create, drive and/or modify them. Thus, for sites on British rivers, the height of source, distance from source, height of site and slope at site (or their surrogates) are important factors.

Analysis of field data on the number and type of modifications to river channels, has enabled a preliminary Habitat Modification Index to be produced and rivers to be grouped into five classes from unmodified semi-natural rivers through to highly modified resectioned and/or reinforced sections of rivers.

Analysis of features of semi-natural rivers and streams enables a typical description of good quality sites of each type to be generated and for the probability of features typical of that type of river such as cascades, vegetated or unvegetated side or mid-channel bars, to be derived. Such data are used in a Habitat Quality Score or Assessment against which partly or grossly degraded sites can be judged and classed.

These RHS data have been assembled together with other relevant environmental data into an easily-interrogatable data-presentation of ~7 000 sites for the years from 1994 with some interesting overseas sites included to expand the usefulness of the database and rigour of the classification of its river types.

Using angler opinion to set minimum flows

Much of the research associated with reduced flows, abstraction and stream support in rivers has concentrated on the biological requirements of the flora and fauna inhabiting them. This work has resulted, for example, in the developoment of models such as PHABSIM used for setting minimum prescribed flows. However, the determination of flows at which abstraction must cease or stream support starts, needs to take account of all parts of the user communities.

Recently the IFE has been involved with the Environment Agency in developing a protocol for incorporating angler opinion into the decision-making process. Initial trials using panels of independent experts and local anglers in assessing the quality of fishing on the River Avon at varying flows have been encouraging, with perceived declines in angling quality coinciding with declines in flow (Figure 27).

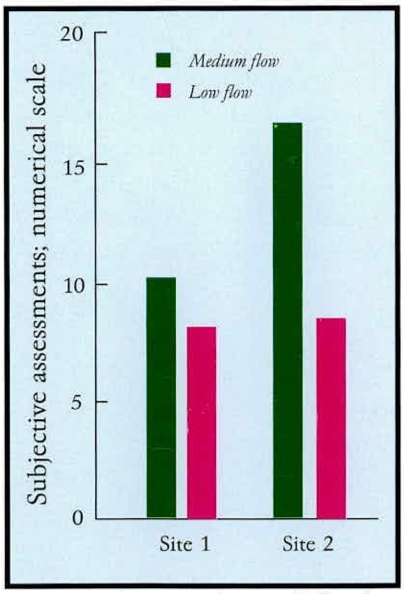


Figure 27. Assessment, by a panel of anglers, of the angling quality of dry fly fishing at two sites of the River Avon at two different flows (15 represents 'good' quality fishing).

Figure 28. Lower Malmesbury.

Permanent records of the conditions in fixed locations are now being collected by using high quality video footage. These can be presented to independent panels at any stage of the decision making process to corroborate the evidence collected from site visits. If the relationship between flow and angling quality can be described in terms of a proportion of a benchmark flow, such as average daily flow, then that relationship could be transferred directly to similar rivers.

Modelling growth of salmon parr

As part of a larger project funded by the European Commission, a functional model has been developed for the maximum growth of Atlantic salmon parr, *Salmo salar*. Salmon used in the growth experiments were bred from parents from two populations in northwest England. Individual growth rates were obtained for 81 salmon feeding on natural invertebrate food, and the experiments were performed at nine constant temperatures in the range 3.8–21.7°C.

The growth model was an excellent fit with no significant differences between parr from the two rivers. The model also described approximately the growth of three year-classes of Atlantic salmon parr in the River Eden in northwest England (Figure 29). All the five parameters in the model can be interpreted in biological terms. These are the minimum, optimum and maximum temperatures for growth, a weight exponent and the growth rate of a 1 g fish at the optimum temperature. As the same model has also been used for brown trout and stone-loach, estimates of the five parameters can be compared between the three species (Figure 30). The weight exponent did not vary greatly between the three species but the other parameter estimates were clearly very different. The optimum temperature for growth was highest for stone-loach which also had the widest limits for growth. However, the values for salmon parr were higher than those for trout. Immature stone-loach would therefore grow best in warmer waters but the thermal requirements for growth in salmon are higher than those for trout. Perhaps the most surprising result of these comparisons is that the growth rate of a 1 g fish at the optimum temperature is highest for salmon parr.

Model development is an iterative process and the growth model for freshwater fish will continue to be developed and improved in the future, as in the past.

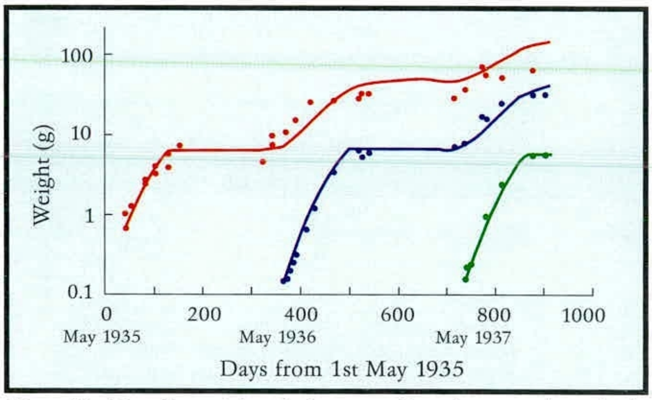


Figure 29. Mean live weights of salmon parr from three year-classes in the River Eden. The lines are the expected weights predicted from the model with cessation of growth of first-year fish from mid-September to mid-March (note that weight is on a log scale).

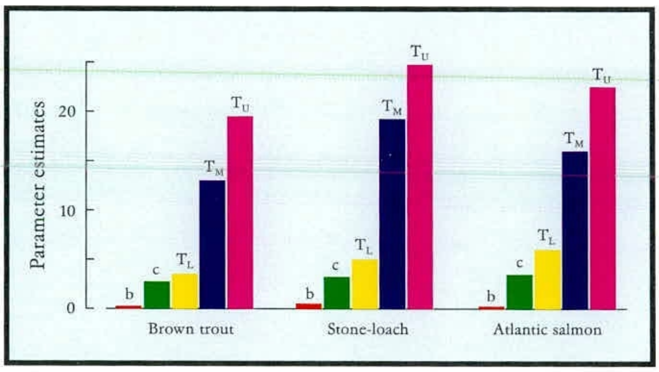


Figure 30. Comparison of estimates of the five parameters in the model for parr of brown trout, immature stone-loach, and parr of Atlantic salmon; parameters are the weight exponent (b), the growth of a 1 g fish at the optimum temperature (c), and the optimum (T_M), minimum (T_L) and maximum (T_U) temperatures for growth.

The growth model can therefore be used to investigate both inter- and intra-specific differences. Model development is an iterative process and the growth model will continue to be developed and improved in the future, as in the past.

The schooling dynamics of river fish

A clear understanding of the genetic and social relationships which exist between schooling fish is vital to enable the application of effective management processes to wild stocks.

Many species of fish form schools which improve foraging efficiency, increase the probability of survival and may have other benefits for individual fish. However, despite this the relationships between fish, both within and between schools, are poorly understood yet may be fundamental to our understanding of evolutionary processes and behaviour.

In collaboration with St Andrews University and by field and laboratory studies on European minnows and guppies from the West Indies, some of the key questions are being addressed. Are schools simply random assemblages of fish or is school membership and movement predictable over space and time? Does familiarity influence the choice of schooling partner? Are schooling decisions made on the basis of kinship or familiarity or both? These are among the critical issues.

A range of experiments have been conducted both in the laboratory and under near-natural conditions. Minnows were found to prefer schooling with familiar schoolmates and female guppies from the Lower Tacarigua River, in Trinidad, to preferentially associate with their nearest school neighbours. Contrary to expectations, the presence of a model predator had no effect on nearest neighbour preference in minnows.

In the case of guppies the preference for associating with familiar individuals (in females) gradually develops over a period of 12 days and once established is maintained. This contrasts sharply with 'condition-dependent recognition' in which fish quickly learn to discriminate between individuals of their own species on the basis of obvious morphological characteristics such as body size.

The ability of fish to recognise familiar associates is already well known but most of the work has been laboratory based. In tests with guppies in the Tunapuna River, Trinidad, it was confirmed that wild female guppies prefer to school with familiar individuals and that their recognition abilities are constrained by the number of fish with which they interact. Guppies do not seem to have

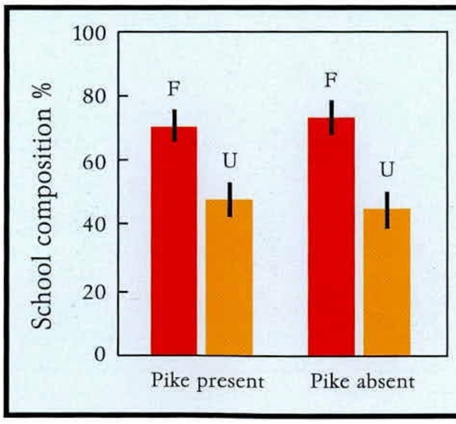


Figure 31. Composition of minnow schools in the presence or absence of pike predator. Mean % ± s.e. is given (n=20).

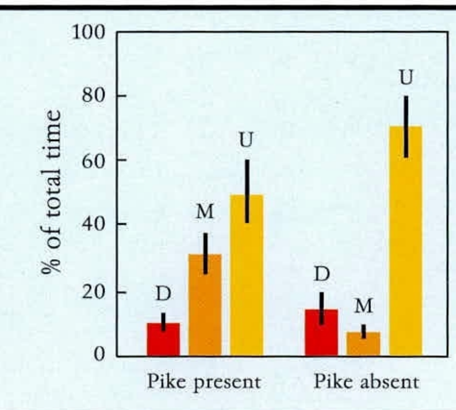


Figure 32. Distribution of minnows between three sections of the fluvarium in the presence or absence of pike predator. Mean % time ± s.e. is given (n=20).

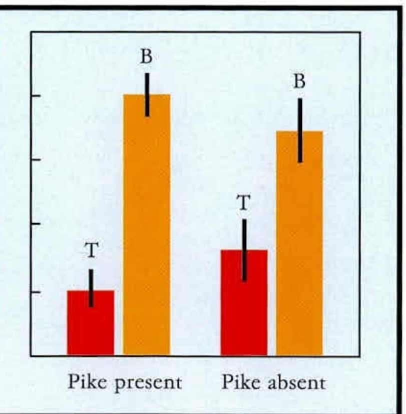


Figure 33. Distribution of minnows between top and bottom half of fluvarium water column, in presence of pike. Mean % time (of 15 min available) given ± s.e. (n=20).

any preference for schooling with either kin or with non-kin but more work will be needed to fully assess this aspect.

Further experiments with minnows, in the effectively natural conditions of a 'fluvarium' on the River Frome in Dorset, revealed a tendency for leader and follower fish to choose the same partners. It was shown that minnows have an overall preference for swimming with familiar schoolmates.

In the near future additional studies using mark-recapture techniques, laboratory experiments with related and unrelated guppies and investigations of the visual and olfactory clues used by fish to recognise their neighbours should help to fill some of the existing gaps in understanding of the dynamics of schooling fish.

Selective breeding for stress tolerance in aquacultured fish

Stress is an unavoidable component of the finfish aquaculture environment, primarily because ideal husbandry practices are unavoidably compromised by the economic constraints of large-scale fish production. Repeated exposure to acute stressors, or to continued challenge, causes substantial deleterious effects on growth, flesh quality, reproductive function and immunocompetence.

In a project part-funded by the EC, the IFE, together with groups at the University of Tromsø, the Norwegian College of Veterinary Medicine, and the Universities of Las Palmas, Barcelona and Granada, is investigating whether the responsiveness of fish to stress is a feature which has a distinct genetic component and may therefore be modified by selective breeding. By increasing the tolerance of fish to stress, thereby ameliorating some of the effects of unavoidable stress, it may be feasible to generate strains of fish which display improved performance within the aquaculture environment, across a number of traits, and indirectly improve the welfare of farmed fish.

During the first year of this four-year project, work at the IFE has focused on identifying fish with a consistently high or consistently low physiological responsiveness to disturbance. These fish have formed the basis of breeding stock with which the heritability of stress responsiveness will be assessed. Surprisingly, fish showing the most pronounced physiological response to standardised stressors are larger and better conditioned than low-responding fish; the converse of what was expected (Figure 34). The offspring of nearly forty separate crosses are currently being reared and tested in a rigorous programme of evaluation. Further work is now needed on the response of these fish to both acute and chronic stresses but it is conceivable that the received wisdom regarding the desirability of a low responsiveness to aquacultural stressors may be misplaced.

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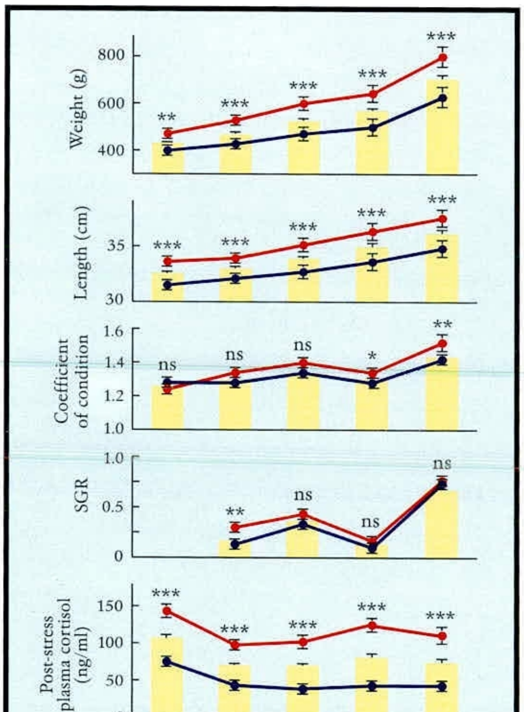

*Figure 34. Weight, length, coefficient of condition, specific growth rate (SGR) and post-stress blood cortisol levels in fish selected for high (red line) and low (blue line) responsiveness to a standardised stressor, sampled in successive months (n = 46). The histograms represent the mean population values (n = 223-166). Significant differences between the high- and low-responding groups are denoted by * P<0.05, ** P<0.01, *** P<0.001.*

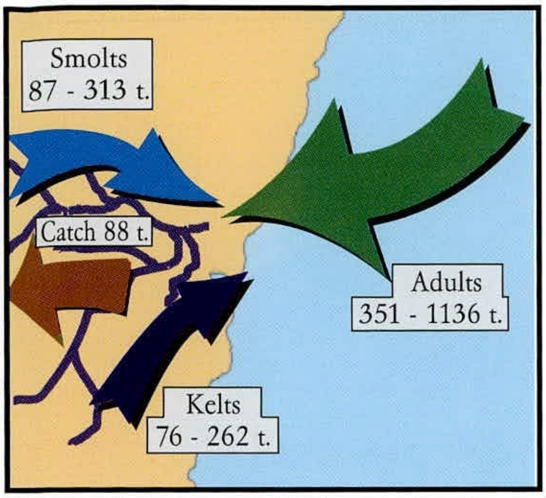

Figure 35. The components of the biomass exchange between rivers and the sea by Atlantic salmon and sea trout. The values given are the combined totals for the Rivers Tweed, Aln, Coquet, Tyne, Wear, Tees and Esk in north-east England.

Migratory salmonids as vectors of C, N and P between freshwater and marine environments

Migratory salmonids introduce marine-derived elements into freshwater ecosystems.

The role of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta* in transferring carbon (C), nitrogen (N) and phosphorus (P) between freshwater and marine environments was studied for seven rivers in north-east England for the period 1989-95.

Exchange processes

The spring exodus of two-year-old fish (smolts) exports freshwater-derived material from rivers to the sea. Adults returning to spawn after one to three years at sea import marine elements through excretion, reproduction and carcass decomposition. Most die but some fish (kelts) survive spawning and return to sea.

Fish numbers and biomass

Fish numbers and biomass at each stage are assessed from fishing statistics, angling exploitation ranges, and sea-survival-rates. Of the 2–6.5 million smolts produced, 140 000–475 000 survive to become adult spawners, of which 31 000–115 000 return to sea as kelts. The component values of the biomass exchanges are shown in Figure 35 and constitute a net flux of 190 to 560 t into the rivers.

C, N and P fluxes

The percentage body content of C, N and P is similar for both species (Figure 36). The annual import by adults ranged between 49–157 t C, 11–34 t N and 2–5 t P. Total annual export by smolts and kelts ranged between 20–72t C, 5–16 t N and 1–3 t P. However, the net fluxes of C, N and P by these fish represented only 0.09–0.24% of the total annual river loads.

Significantly, the import by adults is almost entirely composed of marine-derived elements and migratory fish are the only direct source of such materials to freshwater ecosystems.

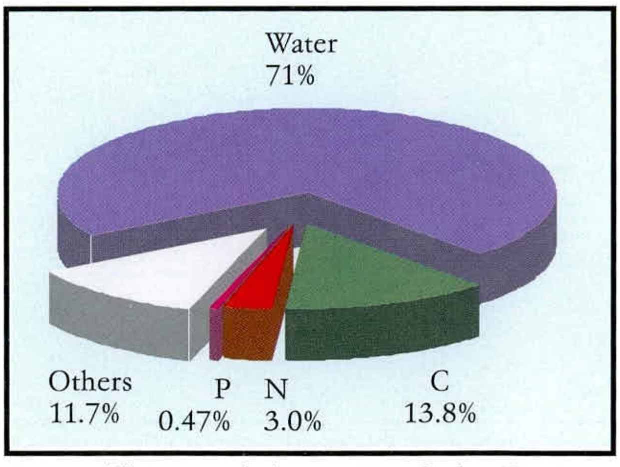

Figure 36. The percentage body compositions of carbon (C), nitrogen (N) and phosphorus (P) for adult Atlantic salmon and sea trout.