

Conservation ecology of the vendace (*Coregonus albula*) in Bassenthwaite Lake and Derwent Water, U.K.

Ian J. Winfield*, Janice M. Fletcher & J. Ben James

CEH Windermere, The Ferry House, Far Sawrey, Ambleside, Cumbria LA22 0LP, U.K. (*e-mail: ijw@ceh.ac.uk)

Received 3 Oct. 2003, revised version received 8 Apr. 2003, accepted 16 May 2003

Winfield, I. J., Fletcher, J. M. & James, J. B. 2004: Conservation ecology of the vendace (*Coregonus albula*) in Bassenthwaite Lake and Derwent Water, U.K. — *Ann. Zool. Fennici* 41: 155–164.

Following extinction of two populations in Scotland, the vendace (*Coregonus albula*) is now found in only two U.K. lakes, i.e. Bassenthwaite Lake and Derwent Water in north-west England. Although the latter remains mesotrophic, the former has undergone significant eutrophication with associated dissolved oxygen problems and vendace monitoring has shown a declining population status. Additional threats originate from land erosion with subsequent in-lake siltation, and the unconsented introduction of non-native fish species including roach (*Rutilus rutilus*), ruffe (*Gymnocephalus cernuus*) and dace (*Leuciscus leuciscus*). The impact of ruffe as a predator of vendace eggs is considered through diet studies during the spawning period. Climate change may also significantly impact local environmental conditions and these threats to the continued local survival of the vendace are assessed and descriptions given of resulting management measures. The latter include phosphorus-stripping, artificial spawning substratum, egg incubation in captivity, control of further introductions, and establishment of refuge populations.

Introduction

The vendace (*Coregonus albula*) is a medium-sized and typically lacustrine coregonid occurring principally in northern areas of Europe, although it has also been introduced to lakes further south for fisheries purposes (Lelek 1987). Like other members of the genus *Coregonus*, it prefers relatively high concentrations of dissolved oxygen (Dembinski 1971), low water temperatures (Hamrin 1986), and spawning areas with no or limited fine sediments (Wilkońska & Zuromska 1982). More specifically, the vendace feeds extensively on zooplankton such as *Daphnia* spp. throughout its life cycle and reduced

availability of such prey may lead to marked population declines (Auvinen 1988).

Within the U.K., vendace populations have historically been recorded from four lakes (Maitland 1966a), although the two populations of Castle Loch (54°50'N, 4°40'W) and Mill Loch (55°8'N, 3°27'W) near Lochmaben in south-west Scotland (Fig. 1) are now believed to be extinct (Maitland & Lyle 1990). The two remaining populations occur in Bassenthwaite Lake and Derwent Water of the English Lake District in north-west England (Fig. 1), which are connected by the River Derwent flowing from the latter to the former over a distance of 5.5 km. Although Bassenthwaite Lake (54°39'N, 3°13'W, altitude

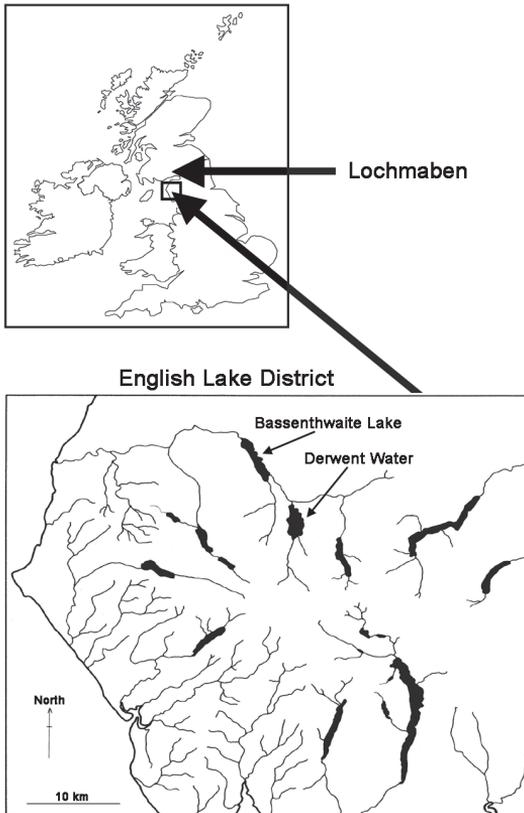


Fig. 1. Locations of Lochmaben and the English Lake District, including Bassenthwaite Lake and Derwent Water, in the U.K. Partly redrawn with permission from Ramsbottom (1976).

69 m, surface area 528 ha, maximum depth 19 m, mean depth 5 m) and Derwent Water (54°34'N, 3°8'W, altitude 74 m, surface area 535 ha, maximum depth 22 m, mean depth 5 m) are physically similar and lie near to each other in the same catchment, they differ significantly with respect to trophic status (considered further below) and fishery activities. In addition to vendace, fish species native to both lakes include Atlantic salmon (*Salmo salar*), brown and sea trout (*Salmo trutta*), eel (*Anguilla anguilla*), minnow (*Phoxinus phoxinus*), perch (*Perca fluviatilis*) and pike (*Esox lucius*) (Winfield *et al.* 1996). At Bassenthwaite Lake, fishing is largely limited to non-game, particularly pike, species but at Derwent Water most activity is focussed on game angling for brown trout. Genetic investigations have revealed that the vendace populations of these two lakes are not significantly differenti-

ated, possibly as a result of gene flow from occasional accidental migrants or the relative youth of the lakes (Beaumont *et al.* 1995).

Due to the limited distribution and loss of two populations described above, the vendace is the U.K.'s rarest freshwater fish species and is consequently protected under nature conservation legislation. It is also a U.K. Biodiversity Action Plan species. There are thus no current commercial or recreational fisheries for this species, and indeed the only record of this fish being exploited in the U.K. was for the now extinct populations of Lochmaben (Maitland 1966b). The objectives of this paper are to report the historical and current status of the vendace in Bassenthwaite Lake and Derwent Water, to identify and assess threats to these populations, and to describe conservation measures recently or currently undertaken for this species in the U.K.

Historical and current status

Information sources

In the absence of current or historical fisheries, this source of information is unavailable for the vendace populations of Bassenthwaite Lake and Derwent Water. No information at all is available for the pre-1960s period and only three brief studies were subsequently made prior to the 1990s. In the mid 1960s, Maitland (1966a) obtained samples from both lakes, as did Mubamba (1989) in the mid 1980s, while in the early 1970s Broughton (1972) obtained a sample of vendace from Bassenthwaite Lake only. Since the early 1990s, the present authors have investigated the vendace populations of both lakes extensively (Winfield *et al.* 1996) and currently monitor them by a combination of echo sounding and gill netting (Winfield *et al.* 2002a, Winfield *et al.* 2002b).

Bassenthwaite Lake

Based on samples collected in 1965, Maitland (1966a) described the vendace population of Bassenthwaite Lake as 'thriving', i.e. of good status. Limited data presented in Broughton (1972)

from sampling in 1972 also indicated a good population status, but by 1987 the samplings and examinations carried out by Mubamba (1989) showed that the status had declined to poor as a result of inconsistent recruitment. This situation persisted into the early 1990s (Winfield *et al.* 1996), after which it declined even further with continued inconsistent recruitment and consequently reduced population abundance (Winfield *et al.* 2002a).

Derwent Water

Maitland (1966a) described the vendace population of Derwent Water as 'thriving' based on samples taken in 1965. This good status persisted through the 1987 samples of Mubamba (1989) and the early 1990s samples of Winfield *et al.* (1996), and has continued to the present (Winfield *et al.* 2002a).

Identification and assessment of threats

Approach

Reviews of generic threats facing the conservation of fish communities in the U.K. and European studies on the vendace by Winfield (1992) and Winfield *et al.* (1994), respectively, were used to frame the approach of the present work, augmented by other studies of local environmental conditions and unpublished data held by CEH Windermere. This resulted in the initial identification of four broad threats, i.e. eutrophication, siltation, species introductions and climate change, which have subsequently been assessed by a combination of field and laboratory studies.

Eutrophication

The adverse effects of advanced eutrophication on coregonids are now well known from many case histories throughout Europe, e.g. Wilkońska and Żuromska (1982), with the two primary impacting mechanisms being low hypolimnetic

dissolved oxygen levels and the siltation of spawning grounds. For Bassenthwaite Lake, examination of fossil diatoms to reconstruct trophic history over the last 250 years revealed the onset of eutrophication during the 1960s (Bennion *et al.* 2000), and water chemistry and algal data from recent decades have confirmed this trend (May *et al.* 2001). Derwent Water, in contrast, has retained its natural mesotrophic conditions (CEH Windermere unpubl. data).

Although historical measurements of dissolved oxygen levels are unavailable, profiles from the 1990s (CEH Windermere unpubl. data) show that summer levels may fall to ca. 3 mg l⁻¹ in the hypolimnion of both lakes (*see* Fig. 2), which is the level about which vendace distribution begins to be impacted (Dembinski 1971). Clearly, any further reductions in dissolved oxygen levels could have significant adverse impacts on the vendace populations. The issue of siltation, which may also have origins unassociated with eutrophication, is considered below. In addition to impacts through oxygen availability and deterioration of spawning grounds, the observed eutrophication of Bassenthwaite Lake may also impact its vendace population indirectly by shifting potential competitive conditions from those favouring coregonids and salmonids, to those favouring cyprinids (*see* Persson 1991).

Stimulated in part by concern for the vendace, a nutrient budget constructed for Bassenthwaite Lake in the early 1990s showed that the Keswick sewage treatment works upstream of the lake was a major source of phosphorus and that the introduction of phosphorus-stripping would reduce algal populations (May *et al.* 2001). Derwent Water is unaffected by this sewage treatment works because it lies upstream of its discharge.

Siltation

The presence of large amounts of fine sediments was observed in the late 1990s by underwater video inspections of all known vendace spawning grounds in Bassenthwaite Lake but not Derwent Water (Winfield *et al.* 1998a), although subsequent chemical analysis has shown that

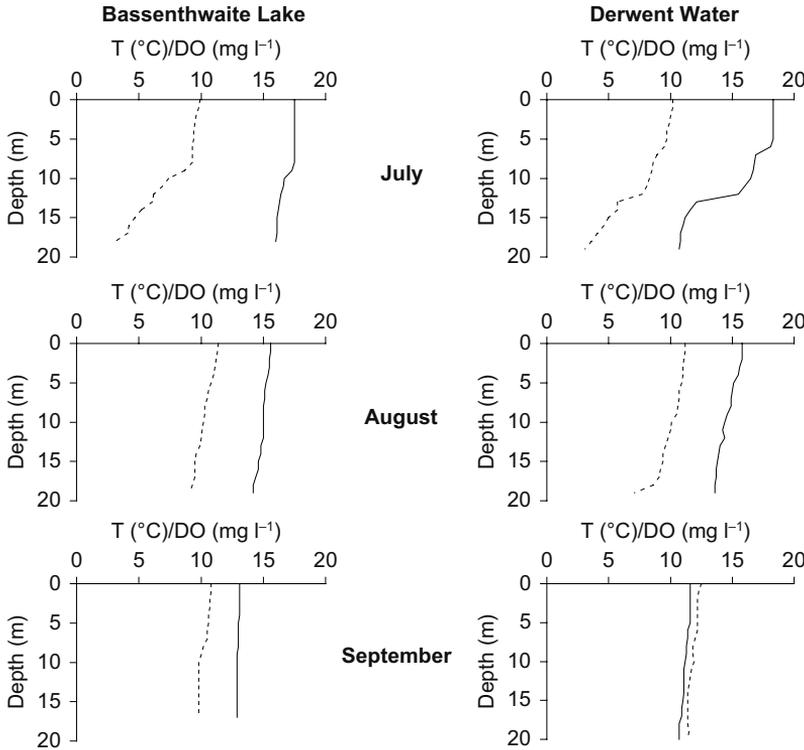


Fig. 2. Summer temperature (T) and dissolved oxygen (DO) profiles of Bassenthwaite Lake and Derwent Water from 1992 which are illustrative of those of the 1990s as a whole (CEH Windermere unpubl. data). Profiles at the former lake were taken on 13 Jul. 1992, 24 Aug. 1992 and 21 Sep. 1992, while those at Derwent Water were taken on 9 Jul. 1992, 20 Aug. 1992 and 14 Sep. 1992.

this material is largely inorganic and appears to be the result of erosion in the lake's catchment (CEH Windermere unpubl. data). Similar investigations at Blelham Tarn in another catchment of the English Lake District have shown increased sedimentation to be attributable to surface soil erosion, largely as a direct response to increased pressure from sheep (*Ovis aries*) grazing (van der Post *et al.* 1997). Whatever its origins, the presence of this material in Bassenthwaite Lake makes successful vendace egg incubation extremely unlikely.

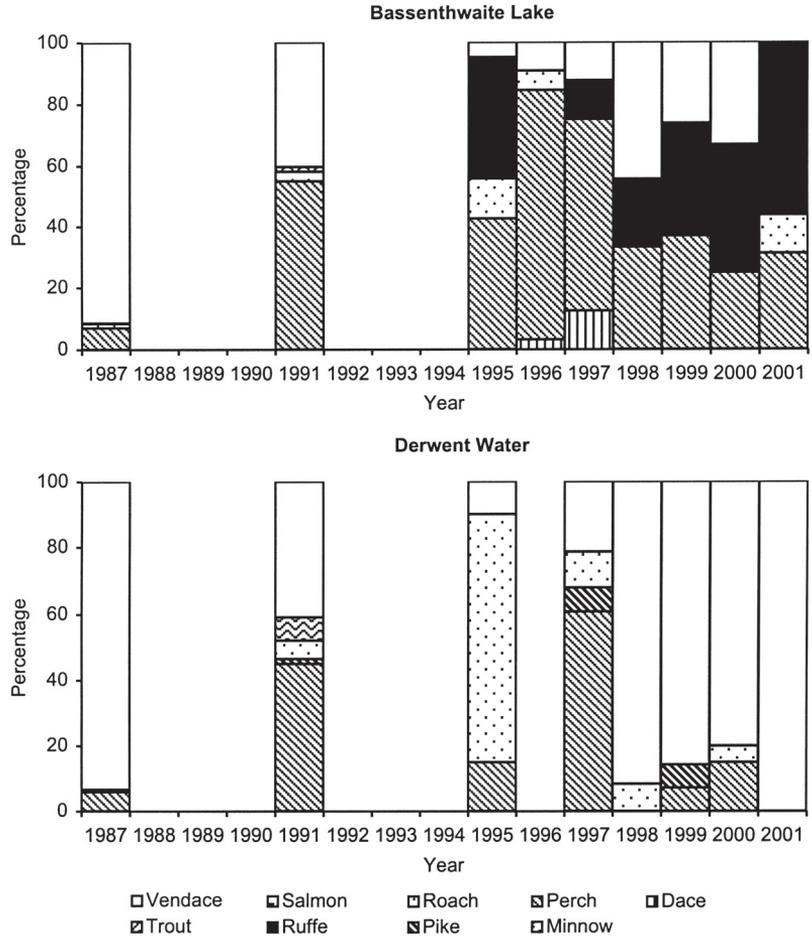
Species introductions

The introduction of new fish species is widely considered to be one of the greatest threats to aquatic biodiversity conservation on a global basis, with introduced species potentially acting as predators, competitors or environmental degraders (Winfield 1992). U.K. lakes are particularly susceptible to this threat because their fish communities are naturally species-poor as a result of the last glaciation ca. 10 000 years B.P.

This particular threat to the vendace populations was raised in 1986 for Bassenthwaite Lake by the lake's first record of roach (*Rutilus rutilus*) discovered during sampling of its deep-water area (Mubamba 1989), to which vendace are restricted outside the spawning period. Equivalent sampling of Derwent Water did not record this species (Mubamba 1989). The competitive abilities of roach for zooplanktonic prey (Persson 1991) gave rise to concern over its possible impact on the vendace of Bassenthwaite Lake. Furthermore, the existence of the connecting River Derwent between this lake and Derwent Water, with no significant obstacles to fish migration, also meant that this and other fish species could colonise the latter lake by a short riverine migration.

Initial full assessments of the fish communities of both lakes, including both deep water and shallow water sampling locations, were undertaken in the early 1990s as described by Winfield *et al.* (1996). From the mid 1990s, more extensive sampling involving echo sounding and gill netting has been continued to monitor the fish communities as described by Winfield *et al.*

Fig. 3. Species compositions by numbers of the deep-water fish communities at Bassenthwaite Lake (total sample size 927 individuals) and Derwent Water (total sample size 1354 individuals) between 1987 and 2001. Regular monitoring by survey gill net has only been undertaken at Bassenthwaite Lake since 1995 and at Derwent Water since 1997, but results from earlier gill net surveys in 1987 (data from Mubamba (1989)) and 1991 at both lakes and at Derwent Water in 1995 are also shown. For consistency, species lists have been retained from those of the entire lake communities given in Winfield *et al.* (2002b).



(2002b), where combined data from the deep and shallow areas of each lake are presented. In addition to confirming the increase of the Bassenthwaite Lake roach population discovered by Mubamba (1989), this work also produced the first records of ruffe (*Gymnocephalus cernuus*) in Bassenthwaite Lake and roach in Derwent Water in 1991 (Winfield *et al.* 1996), and dace (*Leuciscus leuciscus*) in the former lake in 1996 and in the latter lake in 1999 (Winfield *et al.* 2002b). Subsequently, ruffe have also been recorded in Derwent Water in 2001 (Winfield *et al.* 2002a). Species compositions by numbers of the deep-water fish communities of both lakes during this period began with a strong domination by vendace, but finished with Bassenthwaite Lake dominated by introduced ruffe and roach (Fig. 3). Dace have remained a minor component of the deep-water fish communities in both lakes.

Assessments of the likely impacts of the above introductions on the vendace populations have been made by a combination of diet and distribution studies of young and adult life stages, in the context of roach as a potential competitor and ruffe as a potential predator of vendace eggs (Winfield & Durie 2004). While it was concluded that there was no evidence that roach posed a threat in either lake, a conclusion subsequently supported by an independent study of roach and vendace in Sweden (Beier 2001), there remains concern over the impact of ruffe. Vendace eggs were absent from the diet of this percid in the vendace spawning period of 1995 (Winfield *et al.* 1998b), but were subsequently found in varying amounts in the corresponding periods of 1996 and 2001 (Fig. 4). The diet of ruffe in Derwent Water has not yet been examined. Finally, the introduced dace have remained

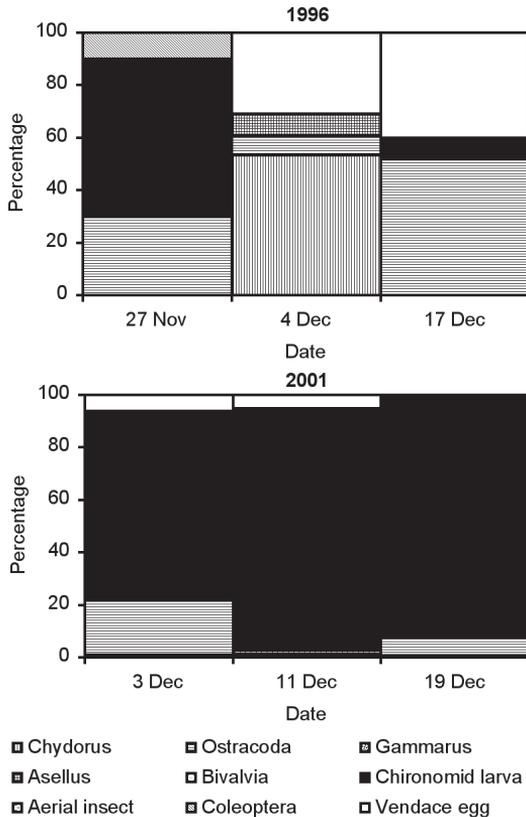


Fig. 4. Diet composition (by numbers of prey) of ruffe on a vendace spawning ground on three dates in the spawning periods of 1996 (total sample size 10 individuals, size range 45 to 124 mm) and 2001 (total sample size 46 individuals, size range 68 to 104 mm) at Bassenthwaite Lake. Note that although the three prey types Aerial insect, Bivalvia and Gammarus were present in the diet on some occasions, they never comprised more than 1% of the diet composition.

at relatively low abundance in both lakes, so it is unlikely that they pose a serious threat to vendace even though they have been shown to predate coregonid larvae in the laboratory (Shirobokov 1992).

Climate change

The biology of aquatic poikilothermic animals is greatly affected by variations in water temperature, and so changes associated with climate change have a great potential to influence the ecology of many lacustrine fish species. Such effects are not simply directly attributable to

temperature itself and, for example, a study of growth in non-coregonid species in North America has shown the importance of associated changes in the timing of lake stratification (King *et al.* 1999). For coregonids, which generically share a requirement for relatively low temperatures and high dissolved oxygen levels, global warming may present the additional complication of causing mortalities through suffocation as predicted for the whitefish (*Coregonus lavaretus*) in Lake Constance, Europe (Trippel *et al.* 1991). In both Bassenthwaite Lake and Derwent Water, temperature and dissolved oxygen conditions (Fig. 2) are already periodically near the tolerance limits of vendace and so any further deterioration could have catastrophic consequences.

Assessment of the threat posed by climate change to the conservation of vendace in the English Lake District is currently being undertaken by modelling temperature and dissolved oxygen profiles in relation to local weather conditions, including wind speed and its effects on stratification, and thus calculating the lake volume inhabitable by vendace (V. A. Bell pers. comm.). This approach will ultimately allow hindcasting of temperature and oxygen profiles prior to the 1990s when their routine monitoring began, and by coupling the model to climate change models the approach will also allow the forecasting of future impacts under various scenarios of environmental change.

Conservation measures

Approach

Identifying, recommending and applying appropriate and feasible conservation measures for the vendace of Bassenthwaite Lake and Derwent Water are inherently complex tasks and involve a wide range of stakeholders. Much of the science underpinning this management has been performed and reported by the authors under contract to various local and national regulatory bodies, with the aim of conserving the two vendace populations in their natural habitats. However, the precarious status of the vendace in Bassenthwaite Lake has also forced additional and less preferred measures.

Conservation measures addressing the threat of climate change are obviously a general environmental issue and have aspects far beyond the management of the U.K. vendace populations. Consequently, they are not considered further here.

Eutrophication

Following the identification of Keswick sewage treatment works as a major contributor to the phosphorus budget of Bassenthwaite Lake, phosphorus-stripping was introduced during 1994 and 1995 (May *et al.* 2001). Improvement towards mesotrophic conditions has subsequently been limited, with little impact on dissolved oxygen conditions (CEH Windermere unpubl. data). This slow progress is partly the result of the phosphorus-stripping process being overwhelmed by high water volumes during periods of high rainfall, and partly due to internal loading in the lake sediments (Reynolds & Winfield 2002). Eutrophication is thus being actively addressed, but is unlikely to show significant improvement in the immediate future with respect to vendace habitat requirements.

Siltation

The problem of siltation on vendace spawning grounds in Bassenthwaite Lake undoubtedly has a eutrophication-induced component, but it is apparently dominated by processes beginning elsewhere in the catchment. As a result, its management is both complex and difficult. Moreover, even if the source or sources in the catchment were to be identified and rectified, it would probably take a considerable time period before natural flushing removed those problem sediments already in the lake.

In view of the severity of the siltation problem with respect to incubating vendace eggs, an assessment of the feasibility of introducing clean artificial spawning substratum was made during the vendace spawning season of 1998 (Winfield 1999). Mats of a type of plastic grass that had previously been successfully used as an incubation substratum for whitefish eggs (Winfield *et al.* 2002c) were introduced on a spawning ground on

5 December 1998, but on their subsequent inspection only 15 days later they had become heavily silt-laden and thus inhospitable to vendace eggs. The frequent resuspension of exogenous fine sediments currently presents an insurmountable problem for the successful incubation of vendace eggs in Bassenthwaite Lake. Moreover, like eutrophication, this is likely to remain a problem for at least a considerable number of years.

Egg incubation in captivity

If vendace eggs cannot currently be incubated successfully in Bassenthwaite Lake over at least the next few years due to siltation on all known spawning grounds, then a potential emergency measure is to bypass these conditions by stripping fish and incubating their eggs in captivity before returning the resulting young to the lake. Although such capture and husbandry presented no technical problems in the late 1990s (*see* Lyle *et al.* 1999), attempts to catch appropriate broodstock in 2000 and 2001 were unsuccessful due to very low population abundance of vendace (Winfield & Fletcher 2002).

Species introductions

In contrast to the above threats, species introductions are an issue in both Bassenthwaite Lake and Derwent Water. In addition to now being present in both lakes, it is highly probable that populations of roach, ruffe and dace have also established in the connecting River Derwent. However, with respect to the vendace, only the ruffe has been concluded to pose a significant threat under current circumstances.

Although similar introductions of ruffe elsewhere in the U.K., mainland Europe and North America have been recognised as a threat to coregonid populations for many years (Winfield *et al.* 1998c), intensive attempts to find appropriate biological, chemical or molecular control measures have been unsuccessful (Gunderson *et al.* 1998). Moreover, for the specific case of Bassenthwaite Lake the observed spatial overlap between ruffe and vendace in the deep-water areas (Fig. 3) means that any physical removal

method such as trawling or gill netting would produce a significant and counter-productive lethal bycatch of vendace.

Control of the introduced ruffe populations in Bassenthwaite Lake and Derwent Water is thus impractical, but the threat of species introductions still needs to be addressed on a more generic level by preventing the introduction of further potentially problematical species. There is strong evidence that such introductions, along with some to other water bodies of the English Lake District, are attributable to discarded or escaped live-bait used by anglers during recreational angling for pike (Winfield & Durie 2004). Consequently, the Environment Agency, the relevant regulatory body, proposed a change to local fisheries byelaws to ban the use or possession with intended use of any dead or alive freshwater fish, salmonids or eel as bait in 14 named lakes of the English Lake District, including Bassenthwaite Lake and Derwent Water (Winfield & Durie 2004). This proposal successfully passed through an extensive public consultation phase and has subsequently been approved by the Department of the Environment, Food and Rural Affairs with effect from 26 July 2002.

Refuge populations

All of the above measures share the aim of conserving the last two U.K. vendace populations in their natural habitats of Bassenthwaite Lake and Derwent Water. However, given the poor status of vendace in the former lake and the low probability of an improvement in local environmental conditions in the near future, the establishment of refuge populations has also been given attention.

In order to avoid the generation of new conservation problems at the recipient site, introductions to establish refuge populations are rightly subject to the same conditions and safeguards as those required for fisheries purposes. A feasibility study was consequently undertaken on 87 potential recipient sites in or near the English Lake District (Lyle & Winfield 1999). During a desk study, 34 sites were eliminated on the above grounds as they or their catchments contained other rare fish species, while another 49 sites were concluded not to meet the habitat require-

ments of vendace. The remaining four sites were evaluated by field visits including the sampling of their fish communities, but none was found to be ideal. Consequently, refuge populations of vendace have not yet been established in England.

However, attempts have been made to reintroduce vendace to Scotland using donor material from Bassenthwaite Lake and Derwent Water by stripping adults during three spawning seasons from 1996 to 1998 and incubating the resulting eggs in captivity. As the original vendace localities of Castle Loch and Mill Loch remain environmentally unsuitable, after appropriate evaluation and consultation newly-hatched larvae from Bassenthwaite Lake have been introduced to Loch Skeen (55°26'N, 3°18'W) and those from Derwent Water to Daer Reservoir (55°21'N, 3°37'W) (Lyle *et al.* 1999). The outcomes of these introductions have yet to be determined.

Closing remarks

The degrees of threats to the conservation of vendace in Bassenthwaite Lake and Derwent Water diverged dramatically in the latter years of the previous century following the development of eutrophication and sedimentation issues at the former lake, and its more developed history of introduced species. Prospects for the local survival of vendace in Bassenthwaite Lake may now be poor, although they may be marginally enhanced by the possible occasional natural input of individuals from the more robust and less threatened population of Derwent Water by passage along the connecting River Derwent. Under these circumstances, there is now an even greater reason to ensure that the vendace population of the latter lake, which is now the last consistently recruiting such population in the U.K., is not itself placed under additional threats.

In a country that draws extensively on its natural resources, and not always in a sustainable way, mapping such ideals from theory to practice is not an easy task. The successful conservation of the vendace in the U.K., and indeed equivalent actions with other species elsewhere, must ensure that scientific understanding is firmly con-

nected to environmental policy and management. In order to achieve this, the onus is on fish ecologists to devote effort to make the move towards their managerial colleagues, even if achievement metrics currently commonly used in science do not recognise such activities (Meffe 2002). Even when such objective information has been successfully inoculated into the managerial domain, fish ecologists still have a vital role to play in securing appropriate decisions by harnessing public opinion through increased awareness and understanding (Cambray & Pister 2002).

Acknowledgements

We thank all of our colleagues, too numerous to mention individually, for their help with field work during this project. Components of this work were funded by the Natural Environment Research Council, the Environment Agency, English Nature and United Utilities.

References

- Auvinen, H. 1988: Factors affecting the year class strength of vendace (*Coregonus albula* (L.)) larvae in Lake Pyhäjärvi (Karelia, SE Finland). — *Finn. Fish. Res.* 9: 235–243.
- Beaumont, A. R., Bray, J., Murphy, J. M & Winfield, I. J. 1995: Genetics of whitefish and vendace in England and Wales. — *J. Fish Biol.* 46: 880–890.
- Beier, U. 2001: Habitat distribution and size structure in freshwater fish communities: effects of vendace on interactions between perch and roach. — *J. Fish Biol.* 59: 1437–1454.
- Bennion, H., Monteith, D. & Appelby, P. 2000: Temporal and geographical variation in lake trophic status in the English Lake District: evidence from (sub)fossil diatoms and aquatic macrophytes. — *Freshw. Biol.* 45: 394–412.
- Broughton, N. M. 1972: *Taxonomy of some British coregonids*. — Dissertation, Queen's University, Belfast.
- Cambray, J. A. & Pister, E. P. 2002: The role of scientists in creating public awareness for the conservation of fish species: African and American case studies. — In: Collares-Pereira, M. J., Coelho, M. M. & Cowx, I. G. (eds.), *Conservation of freshwater fishes: options for the future*. 414–423. Fishing News Books, Blackwell Scientific Publications, Oxford.
- Dembinski, W. 1971: Vertical distribution of vendace *Coregonus albula* L. and other pelagic fish species in some Polish lakes. — *J. Fish Biol.* 3: 341–357.
- Gunderson, J. L., Klepinger, M. R., Bronte, C. R. & Marsden, J. E. 1998: Overview of the International Symposium on Eurasian Ruffe (*Gymnocephalus cernuus*) Biology, Impacts and Control. — *J. Great Lakes Res.* 24: 165–169.
- Hamrin, S. F. 1986: Vertical distribution and habitat partitioning between different size classes of vendace, *Coregonus albula* in thermally stratified lakes. — *Can. J. Fish. Aquat. Sci.* 43: 1617–1625.
- King, J. R., Shuter, B. J. & Zimmerman, A. P. 1999: Empirical links between thermal habitat, fish growth, and climate change. — *Trans. Am. Fish. Soc.* 128: 656–665.
- Lelek, A. 1987: *The freshwater fishes of Europe. Volume 9. Threatened fishes of Europe*. — AULA-Verlag, Wiesbaden.
- Lyle, A. A., Maitland, P. S. & Winfield, I. J. 1999: *Re-introduction of vendace: Phase II extension. Final report*. — Report to Scottish Natural Heritage. ED/T11063y7/4.
- Lyle, A. A. & Winfield, I. J. 1999: *Cumbria vendace translocation feasibility study*. — Institute of Freshwater Ecology Report to Environment Agency, North West Region. ED/T11068q7/1.
- Maitland, P. S. 1966a: The present status of known populations of the Vendace, *Coregonus vandesius* Richardson in Great Britain. — *Nature* 210: 216–217.
- Maitland, P. S. 1966b: The fish fauna of the Castle Loch and the Mill Loch, Lochmaben, Dumfriesshire, with special reference to the Lochmaben Vendace, *Coregonus vandesius* Richardson. — *Trans. Dumfr. Gall. Nat. Hist. Soc.* 43: 31–48.
- Maitland, P. S. & Lyle, A. A. 1990: Practical conservation of British fishes: current action on six declining species. — *J. Fish Biol.* 37 (Suppl. A): 255–256.
- May, L., Bailey-Watts, A. E. & Hilton, J. 2001: An assessment of the likely effects of phosphorus load reduction on phytoplankton biomass in Bassenthwaite Lake, Cumbria, England. — *Verh. Internat. Verein. Limnol.* 27: 4009–4012.
- Meffe, G. K. 2002: Connecting science to management and policy in freshwater fish conservation. — In: Collares-Pereira, M. J., Coelho, M. M. & Cowx, I. G. (eds.), *Conservation of freshwater fishes: options for the future*. 363–372. Fishing News Books, Blackwell Scientific Publications, Oxford.
- Mubamba, R. 1989: *The ecology of the coregonid fishes in the English Lake District*. — Ph.D. thesis, University of Wales, Cardiff.
- Persson, L. 1991: Interspecific interactions. — In: Winfield, I. J. & Nelson, J. S. (eds.), *Cyprinid fishes: systematics, biology and exploitation*: 530–551. Chapman & Hall, London.
- Ramsbottom, A. E. 1976: *Depth charts of the Cumbrian lakes*. — Freshwater Biological Association Scientific Publication No. 33.
- Reynolds, C. S. & Winfield, I. J. 2002: *The urban waste water treatment directive: the state of Windermere and Bassenthwaite Lake, 2002*. — CEH Windermere Report to Environment Agency, North West Region. WI/C01752/4.
- Shirobokov, I. I. 1992: Estimation of numbers and identification of larval whitefish (*Coregonidae*) in the diet of some predators. — *J. Ichthyol.* 32: 77–84.

- Trippel, E. A., Eckmann, R. & Hartmann, J. 1991: Potential effects of global warming on whitefish in Lake Constance, Germany. — *Ambio* 20: 226–231.
- van der Post, K. D., Oldfield, F., Haworth, E. Y., Crooks, P. R. J. & Appelby, P. G. 1997: A record of accelerated erosion in the recent sediments of Blelham Tarn in the English Lake District. — *J. Paleolimnol.* 18: 103–120.
- Wilkońska, H. & Żuromska, H. 1982: Effect of environmental factors and egg quality on the mortality of spawn in *Coregonus albula* (L.) and *Coregonus lavaretus* (L.). — *Pol. Arch. Hydrobiol.* 29: 123–157.
- Winfield, I. J. 1992: Threats to the lake fish communities of the U.K. arising from eutrophication and species introductions. — *Neth. J. Zool.* 42: 233–242.
- Winfield, I. J. 1999: *A preliminary investigation of the feasibility of improving the spawning grounds of vendace in Bassenthwaite Lake. Final report.* — Institute of Freshwater Ecology Report to English Nature, Environment Agency, Lake District National Park Authority and North West Water Ltd. WI/T11050d2/5.
- Winfield, I. J. & Durie, N. C. 2004: Fish introductions and their management in the English Lake District. — *Fish. Mgmt Ecol.* [In press].
- Winfield, I. J. & Fletcher, J. M. 2002: *Captive rearing of the vendace of Bassenthwaite Lake, with an analysis of the winter diet of ruffe.* — CEH Windermere Report to Environment Agency, North West Region. WI/C01644/1.
- Winfield, I. J., Fletcher, J. M. & Cragg-Hine, D. 1994: *Status of rare fish — a literature review of freshwater fish in the U.K.* — National Rivers Authority, R&D Report 18.
- Winfield, I. J., Cragg-Hine, D., Fletcher, J. M. & Cubby, P. R. 1996: The conservation ecology of *Coregonus albula* and *C. lavaretus* in England and Wales, U.K. — In: Kirchhofer, A. & Hefti, D. (eds.), *Conservation of endangered freshwater fish in Europe*: 213–223. Birkhäuser Verlag, Basel.
- Winfield, I. J., Fletcher, J. M. & Cubby, P. R. 1998a: *Spawning beds of vendace in Bassenthwaite Lake and Derwentwater. Final report.* — Institute of Freshwater Ecology Report to English Nature. WI/T11063f1/2.
- Winfield, I. J., Fletcher, J. M. & Cubby, P. R. 1998b: The threat to vendace (*Coregonus albula*) eggs from introduced ruffe (*Gymnocephalus cernuus*) in Bassenthwaite Lake, U.K. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 50: 171–177.
- Winfield, I. J., Dodge, D. P. & Rösch, R. 1998c: Introductions of the ruffe, *Gymnocephalus cernuus*, to new areas of Europe and to North America: history, the present situation and management implications. — In: Cowx, I. G. (ed.), *Stocking and introduction of fish*. 191–200. Fishing News Books, Blackwell Scientific Publications, Oxford.
- Winfield, I. J., Fletcher, J. M. & James, J. B. 2002a: *The urban waste water treatment directive — Monitoring the vendace populations of Bassenthwaite Lake and Derwentwater, 2001.* — CEH Windermere Report to Environment Agency, North West Region. WI/C01752/3.
- Winfield, I. J., Fletcher, J. M. & James, B. J. 2002b: Species introductions to two English lake fish communities of high conservation value: a 10-year study. — In: Collares-Pereira, M. J., Coelho, M. M. & Cowx, I. G. (eds.), *Conservation of freshwater fishes: options for the future*. 271–281. Fishing News Books, Blackwell Scientific Publications, Oxford.
- Winfield, I. J., Fletcher, J. M. & Winfield, D. K. 2002c: Conservation of the endangered whitefish (*Coregonus lavaretus*) population of Haweswater, UK. — In: Cowx, I. G. (ed.), *Management and ecology of lake and reservoir fisheries*. 232–241. Fishing News Books, Blackwell Scientific Publications, Oxford.