# Life history and ecological correlates of extinction risk in European freshwater fishes[1]

John D. Reynolds, Thomas J. Webb, and Lorraine A. Hawkins

**Abstract:** We used phylogenetically based comparative analyses to test for associations between extinction risk in European freshwater fishes and a variety of life history, ecological, and biogeographical traits. Based on the World Conservation Union classification scheme, a total of 47% of Europe's 287 native species are classified as threatened with extinction. Threatened species are significantly smaller than less-threatened species in the same genera when analyses are restricted to fully freshwater species. This trend is reversed when anadromous genera are included. These comprise many large-bodied species in which fishing has often played a greater role in declines than in other taxa. Threatened species did not differ significantly in their habitats, although they tended to occupy a narrower variety of habitats biased toward streams and rivers. Threatened species occupy much narrower latitudinal ranges than close relatives that are less threatened, and they also have more southerly distributions where pressures on habitats are intense. This study suggests that links between life histories and threat status of freshwater fishes are not as clearcut as for marine species. For fish restricted entirely to freshwater, small-bodied species are most at risk owing to their naturally small ranges, which may put them in a more precarious position when their habitats are impacted by humans.

**Résumé :** Nous avons utilisé des analyses comparatives de nature phylogénitique pour évaluer chez les poissons d'eau douce d'Europe les associations entre le risque d'extinction et une variété de caractéristiques démographiques, écologiques et biogéographiques. D'après le schéma de classification de l'Union mondiale pour la nature, 47 % des 287 espèces indigènes de poissons d'Europe sont menacées d'extinction. Dans un même genre, les espèces menacées ont une taille significativement inférieure à celle des espèces moins menacées, lorsque l'analyse ne considère que les espèces franchement dulcicoles. La tendance est inversée si on inclut les genres anadromes; ceux-ci comprennent plusieurs espèces de grande taille corporelle, chez lesquelles la pêche a joué un rôle plus important dans le déclin que chez les autres taxons. Les espèces menacées ne diffèrent pas significativement par leurs habitats, bien qu'elles aient tendance à occuper une gamme plus étroite d'habitats, surtout concentrée dans les ruisseaux et les rivières. Les espèces menacées occupent des aires de répartition en latitude plus étroites que les espèces proches moins menacées et elles ont aussi des répartitions plus australes dans lesquelles les pressions sur les habitats sont intenses. Notre étude indique que les liens entre le cycle biologique et le statut de vulnérabilité de l'espèce ne sont pas aussi clairs que chez les espèces marines. Chez les poissons entièrement restreints aux eaux douces, les espèces de petite taille corporelle sont plus à risque à cause de leurs répartitions naturellement plus restreintes, ce qui peut les placer dans une situation plus précaire lorsque leurs habitats subissent l'impact des activités humaines.

[Traduit par la Rédaction]

## Introduction

Freshwater fish species face severe threats in many parts of the world. The main problems include physical alteration of habitats, introduction of alien species, pollution, and fishing (Miller et al. 1989; Leidy and Moyle 1998; Harrison and Stiassny 1999). It is not yet possible to say with any confidence what percentage of the world's fish species are threatened with extinction because the global assessments by the World Conservation Union (IUCN 2003) have considered only approximately 5% of the 28 000 fish species that have been described. When analyses are restricted to the 20 countries for which assessments are most complete, 17% of freshwater fish species are considered threatened (IUCN 2003). This new estimate matches the suggestion by Leidy and Moyle (1998) that more than 20% of species may be at risk

Received 5 February 2004. Accepted 13 October 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 10 May 2005.
J17993

**J.D. Reynolds.**[2] Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK.
**T.J. Webb.** Environment Department, University of York, Heslington, York YO10 5DD, UK.
**L.A. Hawkins.** Gatty Marine Laboratory School of Biology, University of St Andrews, Fyfe, KY16 8BL, Scotland.

[1]This article was part of a special symposium entitled Building on Beverton's legacy: life history variation and fisheries management, which took place on 11–14 August 2003 in Québec, Quebec, during the 133rd annual meeting of the American Fisheries Society.

[2]Corresponding author (e-mail: reynolds@uea.ac.uk).

 doi: 10.1139/F05-066 

of extinction. The comparable figures for birds and mammals are 12% and 24%, respectively (IUCN 2003). These assessments confirm the consensus that freshwater fishes are facing severe threats globally (Bruton 1995; Harrison and Stiassny 1999; Duncan and Lockwood 2001).

The paucity of information about the status and ecology of fishes, compared, for example, with information from the world's birds and mammals, has seriously hampered efforts to assess conservation status and manage populations accordingly. Distributions and ecological requirements are often poorly known, and population trends are rarely available (except for commercially important species).

It may be possible to predict the conservation status of fishes by examining life history and ecological correlates of extinction risk (Reynolds et al. 2001*a*). There have been several attempts to do this for marine species that are subject to fisheries (Jennings et al. 1998; Rochet 2000; Dulvy and Reynolds 2002). Most of these studies have found correlations between the extent of population decline under fishing pressure and one or more life history traits such as body size and age at maturity. These findings support theoretical predictions that “fast” life histories, including associated traits such as rapid growth and maturity, should be related to the ability of populations to withstand fisheries (Rochet 2000; Reynolds et al. 2001*b*; Reynolds 2003).

It is more difficult to make predictions about links between life histories and conservation status of freshwater fishes. This is because unlike most commercially important marine fishes where there is a single overriding threat (direct mortality by fisheries), freshwater fishes often face a greater range of threats. The effects of this variety of threats on species with various types of life history cannot be predicted easily (Duncan and Lockwood 2001). For example, if small-bodied species tend to occur in heavily impacted habitats, small size and associated fast life history traits would be correlated with extinction risk. This would reverse the predicted relationships between life histories and population status compared with those found in marine species. Indeed, a study of freshwater fishes in Virginia found no overall association between body size and vulnerability to extinction and a tendency of small-bodied minnows (Cyprinidae) to be more extinction prone (Angermeier 1995). Parent and Schriml (1995) also found no overall association between body size and risk status of fishes in the Great Lakes – St. Lawrence drainage of North America, although species with late ages at maturity tended to be under greater threat. This study found relationships between risk of extinction and characteristics of habitats. In contrast with the two studies above, Froese and Torres (1999) reported a weak association between large body size and threat status of freshwater species based on the IUCN's Red List (IUCN 1996).

The conflicting results of studies of freshwater fishes may stem from regional differences in the nature of threats as well as differences in methodology. Ambitious analyses such as the study by Froese and Torres (1999) provide wide spatial coverage at the expense of highly uneven taxonomic and geographical sampling. An important issue in taxonomic sampling and analyses involves the treatment of individual species as separate data points (Harvey and Pagel 1991; Reynolds et al. 2001*a*). Related species share many aspects of life histories and ecology as a result of inheritance from common ancestors rather than as the result of independent evolutionary events. Caution is therefore required in any analysis that attempts to treat them as independent data points.

In this study, we provide the first analyses of relationships between threat status, life histories, and ecology of native European fishes. The conservation status of nearly all of the native species has been assessed in this region (Lelek 1980; Maitland 2000; IUCN 2003), and a reasonable amount of information is available concerning key life history traits and habitat characteristics. Most of our analyses use methods that make explicit use of evolutionary relationships among taxa. This method thereby yields comparisons that are more robust statistically than traditional cross-species comparisons. Furthermore, by comparing differences among species within lineages, we control for many potentially spurious differences that can arise when distantly related taxa are combined in cross-species analyses.

## Materials and methods

### Taxonomic and geographic scope

We compiled a database of life histories, ecology, and conservation status of native European freshwater fishes. The region corresponds to that used by Maitland (2000) bordered by the Arctic and Atlantic oceans and the Mediterranean and Black seas and extending east to the Caucasus Mountains, the Caspian Sea, and the Ural Mountains. We considered all native fish species that spend a significant part of their life cycle in fresh water based on descriptions by Maitland (2000). We include anadromous species but analyse the data both with and without them. We exclude 29 nonnative species as well as borderline cases involving fish that primarily occupy marine habitats but also occasionally enter brackish waters or the lower reaches of waters that enter the sea. These criteria yield a total of 316 species for an overall assessment of threat status. We then focus on 138 species that could be paired between close relatives that differed in threat status (see below).

Our taxonomy follows Maitland (2000), which in turn follows Kottelat (1997), with a few exceptions such as salmonids, where Maitland (2000) is much more conservative regarding species status. This taxonomy is still in a considerable state of flux (Kottelat 1998).

### Assessment of threatened status

We used Maitland (2000) as the main source of information on threat status and compared summary statistics of percentages of species under various levels of threat with the IUCN's 2003 Red List (IUCN 2003). Both sources of information used the IUCN's 1994 criteria for assessing status (IUCN 1994). However, Maitland's (2000) treatment is more comprehensive and up to date because the threat status of species appearing on the 2003 Red List had actually first been reported in 1996. In general, there was strong congruence between the two assessments, and based on further consideration of species where the assessments disagreed, we felt that Maitland's (2000) designations were better supported. For the sake of consistency, we have resisted the temptation to make ad hoc updates to the statuses of some species, pending a new assessment vetted by the IUCN. For example, we understand that *Coregonus oxyrhinchus* may now be extinct, *Alosa macedonica* may be endangered, and most sturgeon species are probably critically endangered. Such changes in the status of these species do not change the significance of our results.

### Life history and ecological data

Life history and ecological data were derived from a variety of sources starting with Lelek (1980), Wheeler (1983), Pivnicka et al. (1992), Cihar (1998), Kirchhofer and Hefti (1996), Miller and Loates (1997), and Maitland (2000). We also made use of volumes in the Freshwater Fishes of Europe series (Holcik 1986; Hoelstlandt 1991; Banarescu and Paepke 2002; Banarescu and Bogutskaya 2003). This information was cross-checked and supplemented with journal publications and FishBase (Froese and Pauly 2003). We were able to collect data on the following variables on life histories, which were not distinguished between the sexes owing to lack of information for most of the species. Maximum size was the maximum total length (centimetres) recorded based primarily on Maitland (2000) and FishBase (Froese and Pauly 2003). Size at maturity was the minimum total length at maturity (centimetres). Age at maturity was the lower end of any range given for mature individuals in years. Maximum clutch size was the largest number of eggs recorded. This was the most widely available measure, but it was crude and ultimately unsatisfying (see Discussion). The mean trophic level was taken from FishBase (Froese and Pauly 2003), with each level denoting the number of energy transfer steps to its position in the food chain. The mid-latitudinal range and total extent of latitudinal range of each species' distribution were taken from FishBase where available or else calculated from range maps or descriptions of ranges in the references cited above.

We analysed a number of habitat characteristics as follows: typical spawning substrate size (1, sand; 2, gravel; 3, stones), inclusion of vegetation as a spawning substrate (yes or no), water flow of typical habitat (1, stagnant and (or) slow; 2, wide range; 3, fast), and habitat size (1, marsh; 2, ponds and creeks; 3, springs and streams; 4, rivers; 5, lakes). We also counted the number of habitats typically occupied based on the habitats listed in "habitat size", and we assessed whether there was a general tendency toward living in running water. Although it was not always possible to score these variables precisely, our system enabled us to meet our objective, which was to ask whether threatened species were equal to, less than, or greater than closely related less threatened species in their ranks for each variable within each taxonomic paired comparison (see below).

### Analyses

Most of the analyses were based on "matched pairs comparisons" between closely related species (Harvey and Pagel 1991). This involved making comparisons between related sister taxa in which one member of the pair is more threatened than the other. In nearly all cases, this entailed a comparison of taxa that were classified as least concern (i.e., nonthreatened) with taxa that were listed as threatened (e.g., vulnerable, endangered, or critically endangered). In addition to the advantage of providing statistically independent comparisons, this method also helps reduce "apples and oranges comparisons" whereby species would be pooled together that differ greatly in many biological and ecological characteristics that can create a great deal of "noise" when making comparisons (Harvey and Pagel 1991; Reynolds et al. 2001*a*). This was borne out by initial cross-species analyses, indicating that while all of the trends reported here were apparent, they were in most cases less significant.

Most of the pairings were based on taxonomy rather than strict phylogenies owing to lack of phylogenetic information, with all but one pairing occurring between species within genera (Table 1). We obtained 33 independent taxon pairs for the analyses, with a mean of 2.0 ± 1.8 SD species in the threatened side of each comparison and 2.3 ± 1.7 SD species contributing to each less-threatened category. Mean values of traits for species on each side of the comparison were used for the analyses. Although some within-genus phylogenies were available, we were unable to use them owing to lack of adequate biological information. An exception involved Acipenseridae, where phylogenetic analyses (Birstein and DeSalle 1998; Birstein et al. 2002) allowed us to use *Acipenser ruthenus* as a sister taxon to the species *Huso huso*, while other members of the genus *Acipenser* were compared with each other.

We log-transformed all continuous variables for the analyses and accepted statistical significance at $p < 0.05$.

## Results

### Overview of status

The European freshwater fish fauna consists of a (very) provisional total of 316 species, of which 287 are considered native, including anadromous species. These figures are subject to the caveats discussed in the Materials and methods section concerning taxonomic uncertainties, use of a conservative species concept, and an attempt to limit the scope to include species that typically spend a significant part of their life cycle in fresh water. The status of all but seven of the native species has been determined (Fig. 1). Of the native species, 47% are considered threatened (Maitland 2000). These include 88 species considered vulnerable, 38 endangered, and five critically endangered. The assessment by the IUCN (2003) is limited to 191 native species (excluding two nonnative species on their list). Of these, 29% were considered threatened and 34% were considered data deficient. The Red List considers one species to be extinct, the Turskyi dace (*Leuciscus turskyi*), which Maitland (2000) considered data deficient. The skadar nase (*Chondrostoma scodrense*) is the only species listed as extinct in the wild by Maitland (2000). The Red List categorizes it as critically endangered.

### Life histories

There was no significant difference in body size between threatened and less-threatened native species, with a trend toward threatened taxa being slightly larger (paired $t_{31} = 1.233$, $p = 0.227$) (Fig. 2). However, when six pairs of anadromous species were excluded, the trend was reversed and threatened species proved to be 26% smaller than less-threatened ones (paired $t_{25} = 2.747$, $p = 0.001$) (Fig. 2). The anadromous pairs removed for this analysis were in the following genera: *Lethenteron*, *Acipenser*, *Huso*, *Alosa*, *Clupeonella*, and *Salmo*. While not all members of these genera are anadromous, removal of the individual anadromous spe-

**Table 1.** Pairings of species used for the analyses.

| Pair | Threatened species | Status | Less-threatened species | Status |
|---|---|---|---|---|
| 1 | *Eudontomyzon hellenicus* | CR | *Eudontomyzon danfordi* | VU |
| | | | *Eudontomyzon mariae* | VU |
| | | | *Eudontomyzon vladykovi* | VU |
| 2 | *Lethenteron zanandreai* | CR | *Lethenteron camtschaticum* | VU |
| 3 | *Acipenser baeri* | EN | *Acipenser nudiventris* | VU |
| | *Acipenser gueldenstaedtii* | EN | | |
| | *Acipenser naccarii* | EN | | |
| | *Acipenser stellatus* | EN | | |
| | *Acipenser sturio* | EN | | |
| 4 | *Huso huso* | EN | *Acipenser ruthenus* | VU |
| 5 | *Alosa alosa* | EN | *Alosa macedonica* | LR |
| | *Alosa fallax* | EN | | |
| 6 | *Clupeonella abrau* | VU | *Clupeonella cultriventris* | LR |
| 7 | *Alburnus albidus* | EN | *Alburnus alburnus* | LR |
| | | | *Alburnus charusini* | LR |
| 8 | *Barbus cyclolepis* | VU | *Barbus barbus* | LR |
| | *Barbus prespensis* | VU | *Barbus meridionalis* | LR |
| | | | *Barbus plebejus* | LR |
| 9 | *Barbus macedonicus* | VU | *Barbus peleponnesius* | LR |
| 10 | *Chalcalburnus chalcoides* | VU | *Chalcalburnus belvica* | LR |
| 11 | *Chondrostoma genei* | VU | *Chondrostoma nasus* | LR |
| | *Chondrostoma knerii* | EN | *Chondrostoma oxyrhynchum* | LR |
| | *Chondrostoma phoxinus* | VU | *Chondrostoma polylepis* | LR |
| | *Chondrostoma toxostoma* | VU | *Chondrostoma prespense* | LR |
| | | | *Chondrostoma soetta* | LR |
| | | | *Chondrostoma willkommii* | LR |
| 12 | *Gobio albipinnatus* | VU | *Gobio benacensis* | LR |
| | *Gobio banarescui* | VU | *Gobio ciscaucasicus* | LR |
| | *Gobio uranoscopus* | EN | *Gobio gobio* | LR |
| | | | *Gobio kessleri* | LR |
| 13 | *Leuciscus aphipsi* | VU | *Leuciscus borysthenicus* | LR |
| | *Leuciscus carolitertii* | VU | *Leuciscus cephalus* | LR |
| | *Leuciscus danilewskii* | VU | *Leuciscus idus* | LR |
| | *Leuciscus illyricus* | VU | *Leuciscus keadicus* | LR |
| | *Leuciscus microlepis* | VU | *Leuciscus leuciscus* | LR |
| | *Leuciscus polylepis* | EN | *Leuciscus pyrenaicus* | LR |
| | *Leuciscus souffia* | VU | | |
| | *Leuciscus svallize* | VU | | |
| | *Leuciscus ukliva* | EN | | |
| | *Leuciscus turskyi* | EX?* | | |
| 14 | *Phoxinellus pstrossi* | EN | *Phoxinellus alepidotus* | VU |
| | | | *Phoxinellus croaticus* | VU |
| | | | *Phoxinellus epiroticus* | VU |
| | | | *Phoxinellus ghetaldii* | VU |
| 15 | *Pseudophoxinus beoticus* | VU | *Pseudophoxinus stymphalicus* | LR |
| 16 | *Rutilus lemmingii* | VU | *Rutilus alburnoides* | LR |
| | *Rutilus macedonicus* | VU | *Rutilus frisii* | LR |
| | *Rutilus macrolepidotus* | EN | *Rutilus rubilio* | LR |
| | *Rutilus meidingeri* | EN | *Rutilus rutilus* | LR |
| | *Rutilus pigus* | EN | | |
| 17 | *Scardinius racovitzai* | VU | *Scardinius graecus* | LR |
| | | | *Scardinius erythrophthalmus* | LR |
| 18 | *Tropidophoxinellus spartiaticus* | VU | *Tropidophoxinellus hellenicus* | LR |
| 19 | *Vimba melanops* | VU | *Vimba vimba* | LR |
| 20 | *Cobitis calderoni* | VU | *Cobitis bilineata* | LR |
| | *Cobitis elongata* | VU | *Cobitis caspia* | LR |
| | *Cobitis meridionalis* | VU | *Cobitis caucasica* | LR |

**Table 1** (*concluded*).

| Pair | Threatened species | Status | Less-threatened species | Status |
|---|---|---|---|---|
| | *Cobitis paludica* | VU | *Cobitis conspersa* | LR |
| | | | *Cobitis maroccana* | LR |
| | | | *Cobitis taenia* | LR |
| 21 | *Sabanjewia larvata* | VU | *Sabanjewia balcanica* | LR |
| | *Sabanjewia romanica* | VU | | |
| 22 | *Barbatula angorae* | VU | *Barbatula barbatula* | LR |
| | | | *Barbatula bureschi* | LR |
| | | | *Barbatula merga* | LR |
| 23 | *Coregonus autumnalis* | EN | *Coregonus albula* | LR |
| | *Coregonus oxyrhinchus* | EN | *Coregonus lavaretus* | LR |
| | | | *Coregonus nasus* | LR |
| | | | *Coregonus peled* | LR |
| | | | *Coregonus pidschian* | LR |
| 24 | *Salmo marmoratus* | EN | *Salmo trutta* | LR |
| | *Salmo salar* | VU | | |
| 25 | *Aphanius iberus* | VU | *Aphanius fasciatus* | LR |
| 26 | *Pungitius hellenicus* | EN | *Pungitius platygaster* | LR |
| | | | *Pungitius pungitius* | LR |
| 27 | *Gymnocephalus baloni* | VU | *Gymnocephalus acerina* | LR |
| | *Gymnocephalus schraetser* | EN | *Gymnocephalus cernuus* | LR |
| 28 | *Sander marina* | VU | *Sander lucioperca* | LR |
| | *Sander volgensis* | VU | | |
| 29 | *Zingel asper* | EN | *Zingel zingel* | VU |
| | *Zingel streber* | EN | | |
| 30 | *Economidichthys pygmaeus* | VU | *Economidichthys trichonis* | LR |
| 31 | *Knipowitschia goerneri* | EN | *Knipowitschia panizzae* | VU |
| | | | *Knipowitschia punctatissima* | VU |
| 32 | *Neogobius fluviatilis* | VU | *Neogobius cephalarges* | LR |
| | | | *Neogobius gymnotrachelus* | LR |
| | | | *Neogobius kessleri* | LR |
| | | | *Neogobius melanostomus* | LR |
| | | | *Neogobius syrman* | LR |
| 33 | *Padogobius nigricans* | VU | *Padogobius martensii* | LR |

**Note:** Each pair consists of one or more threatened species matched with closely related species that are less threatened. LR, lower risk; VU, vulnerable; EN, endangered; CR, critically endangered; EX, extinct.

*Considered data deficient by Maitland (2000).

**Fig. 1.** Threat status of the 280 native species of European freshwater fishes that have been assessed by Maitland (2000) and IUCN (2003).

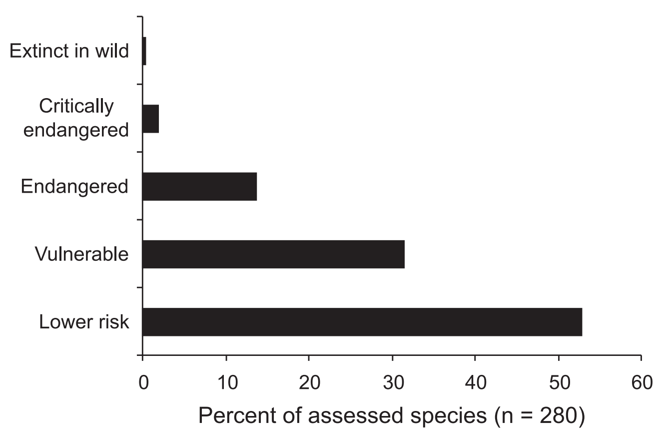
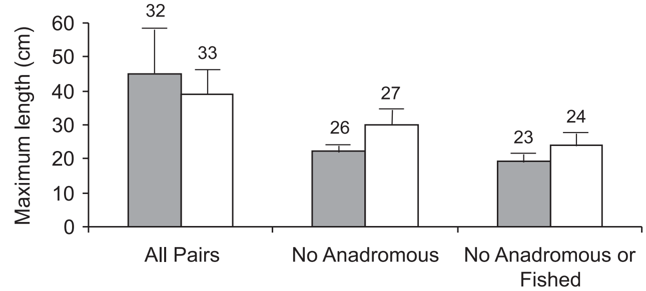



**Fig. 2.** Body sizes of native European freshwater fishes comparing threatened species (shaded bars) with closely related species that are less threatened (open bars). Means + 1 SE are depicted. Numbers above bars are the number of genera containing species in each category. "No anadromous" excludes pairs from six anadromous genera, and "no anadromous or fished" excludes three additional genera that include nearly all of the heavily fished species.



cies within these genera resulted in a loss of the paired comparisons owing to lack of data for species in either the threatened or less-threatened category. The 13 anadromous species in the data set were much larger than non-anadromous ones (cross-species analysis: anadromous mean = 166.2 cm ± 33.7 SE, $n$ = 13; nonanadromous mean = 29.2 cm ± 2.1 SE, $n$ = 121; $t_{132}$ = 7.572, $p$ < 0.001).

It was difficult to distinguish between the effects of fishing and anadromy because most anadromous species are (or were) fished heavily, and they have all suffered from damming of waterways. Most of the other species that are fished heavily are in three genera, *Coregonus*, *Vimba*, and *Sander*, although fishing has not been implicated as the main problem faced by these species (Lelek 1980). Removal of these genera did not affect the results, with threatened species still being smaller than less-threatened ones (paired $t_{22}$ = 2.230, $p$ = 0.036) (Fig. 2).

Minimum size at maturity did not differ between threatened and less-threatened species, regardless of whether anadromous species were included (including anadromous, paired $t_{29}$ = 0.281, $p$ = 0.781; excluding anadromous, paired $t_{23}$ = 1.276, $p$ = 0.215) (Fig. 3*a*). Age at maturity showed similar trends and a tendency toward later age at maturity in threatened species when anadromous species were included (paired $t_{12}$ = 1.843, $p$ = 0.092) (Fig. 3*b*). When anadromous species were excluded, the sample size was reduced to seven pairs for which data were available, and there was no difference between threatened and less-threatened species in age at maturity (paired $t_6$ = 0.778, $p$ = 0.466) (Fig. 3*b*). Removal of heavily fished species reduced the sample size to five pairs and the findings were similar (not shown).

We found no significant relationship between threat status and maximum fecundity, with a mean value of 802 975 ± 636 795 SE eggs for threatened species and a mean of 191 096 ± 79 640 SE for less-threatened species (paired $t_8$ = 0.124, $p$ = 0.904). Note the enormous variation in fecundity within each threat category and the small number of pairs for which data were available.

## Biogeography and ecology

The mean trophic level did not differ between threatened and less-threatened species (mean threatened = 3.27 ± 0.48, mean less threatened = 3.27 ± 0.46; paired $t_{24}$ = 0.242, $p$ = 0.811). This result was unaffected by exclusion of anadromous species (not shown).

Threatened species have latitudinal ranges that are only 56% as large as those of related taxa that are less threatened (all species, paired $t_{27}$ = 3.003, $p$ = 0.006) (Fig. 4*a*). Exclusion of the anadromous pairs accentuated this difference (paired $t_{21}$ = 4.748, $p$ < 0.001) (Fig. 4*a*). Threatened species also occur farther south than their less-threatened relatives (all species, paired $t_{27}$ = 2.292, $p$ = 0.030; excluding anadromous species, paired $t_{21}$ = 3.186, $p$ = 0.004) (Fig. 4*b*). These results for latitudinal range size and location remain unchanged when the three heavily fished genera are excluded (not shown).

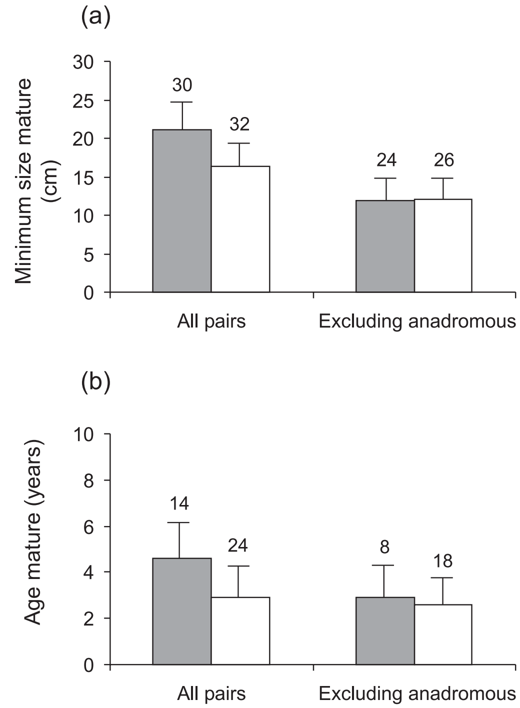



**Fig. 3.** (*a*) Minimum size at maturity and (*b*) age at maturity of threatened species (shaded bars) in comparison with their nearest relatives that were less threatened (open bars) (mean + 1 SE).

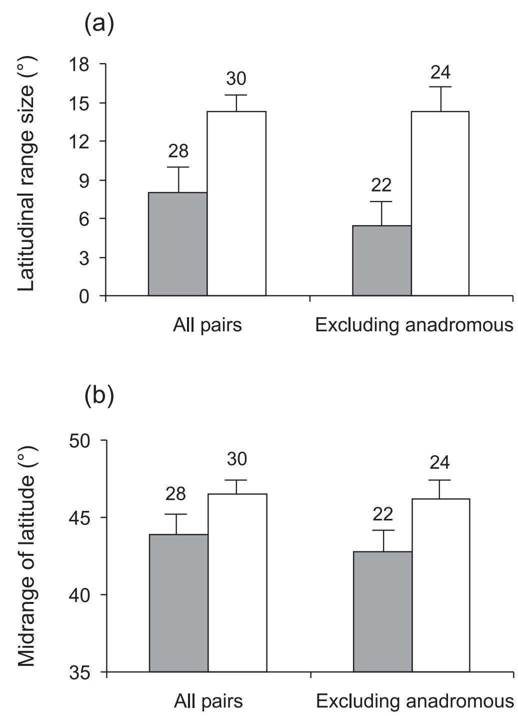



**Fig. 4.** (*a*) Latitudinal range size and (*b*) midrange of latitude of threatened species (shaded bars) in comparison with their nearest relatives that were less threatened (open bars) (mean + 1 SE).

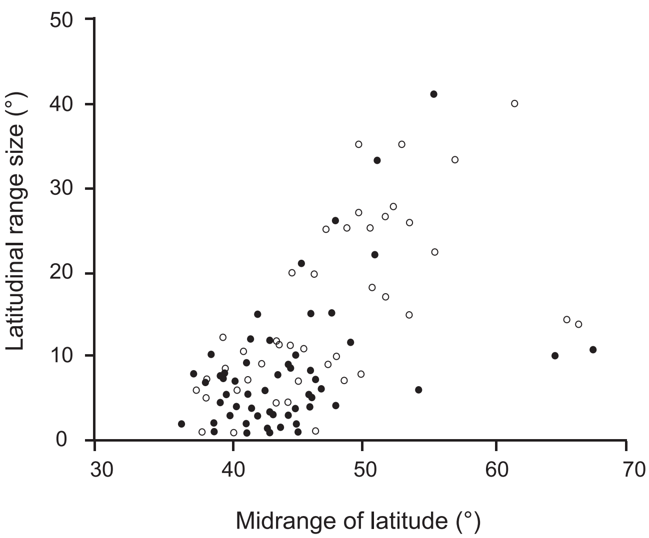
The links described above between threat status, small body size, small range size, and southerly distribution were also tested more generally by examining correlations among these traits using cross-species comparisons. As expected from the matched pairs results, there was a strong positive correlation among all species between their latitudinal position and the extent of their latitudinal range ($r$ = 0.54, $p$ <

**Table 2.** Habitat characteristics of threatened and less-threatened species of native European freshwater fishes including anadromous species.

| Variable | Threatened = less-threatened | Threatened < less-threatened | Threatened > less-threatened |
|---|---|---|---|
| Substrate size | 14 | 3 | 1 |
| Vegetation for spawning | 21 | 3 | 2 |
| Water flow | 18 | 6 | 7 |
| Habitat size | 14 | 9 | 5 |
| Number of habitats used | 15 | 11 | 5 |
| Riverine | 19 | 4 | 8 |

**Note:** Data are the number of pairs in which the value for the threatened taxa is either equal to, less than, or greater than that for their less-threatened relatives for each habitat characteristic. The variables are as follows: Typical spawning substrate size: 1, sand; 2, gravel; 3, stones; inclusion of vegetation as a spawning substrate: yes or no; water flow of typical habitat: 1, stagnant and (or) slow; 2, wide range; 3, fast; habitat size: 1, marsh; 2, ponds and creeks; 3, springs and streams; 4, rivers; 5, lakes. Number of habitats used is based on the habitats listed in habitat size. Riverine denotes tendency to occupy running water.

**Fig. 5.** Size of latitudinal distribution versus location of the middle of each species' range. Solid circles, threatened species; open circles, species at lower risk.




0.001, $n$ = 94) (Fig. 5). Visual inspection of the individual species in Fig. 5 also supports the matched pairs statistics for smaller range sizes of threatened species as well as their predominance at southerly latitudes (Fig. 4). Furthermore, with threat statuses combined, larger-bodied species had larger ranges ($r$ = 0.48, $p$ < 0.001, $n$ = 92), which were farther north ($r$ = 0.34, $p$ < 0.001, $n$ = 96). These correlations remained significant if anadromous and (or) the three additional heavily fished genera were excluded (not shown). The relationship between body size and midrange of latitude did not differ significantly between threatened and nonthreatened species (analysis of covariance, $F_{[1,47]}$ = 2.028, $p$ = 0.161). A logistic regression was used to attempt to predict whether nonanadromous species are threatened based on their body size and the midrange of their latitude. The overall predictive power was 66% correct, with 68% of nonthreatened species classified correctly and 65% of threatened species classified correctly. The relationship between threatened status and midrange of latitude is significant (logistic regression $p$ = 0.034), whereas the relationship with body size is weaker ($p$ = 0.103).

The search for habitat differences among threatened species and less-threatened close relatives did not reveal strong patterns in the paired comparisons (Table 2). There were nonsignificant trends for threatened species to live in smaller habitats (9/14 taxon pairs in which we could discern differences in habitat size) and threatened species tended to live in fewer habitats (11/16 pairs in which habitat number differed) ($g$ tests, $p$ > 0.05). They also tended to be more "riverine" (9/14 pairs). Exclusion of six anadromous genera and (or) three additional heavily fished genera did not alter these results (not shown). These results were largely unchanged in cross-species analyses, which ignore phylogenetic pairings, with the tendency for threatened species to occupy fewer habitats becoming significant (threatened mean = 1.6 ± 0.7 SD, nonthreatened mean = 1.9 ± 0.8; $t_{117}$ = 2.110, $p$ = 0.037).

## Discussion

The phylogenetically based comparisons in this study reveal that for European fish species whose life cycles are entirely restricted to fresh waters, threatened species are smaller bodied than species that are at lower risk. Inclusion of anadromous species reverses this trend. We found no differences in minimum size at maturity or in age at maturity. Threatened species have narrower latitudinal distributions, which are more southerly than those of lower-risk species. Threatened species do not have different trophic positions, and there were nonsignificant tendencies toward occupation of fewer habitats, which are more riverine. Most of these findings are contrary to the patterns that have been found in studies of marine fishes. Furthermore, they contradict some previous studies of freshwater fishes. Below, we try to resolve these discrepancies in light of theories concerning links between life histories, population ecology, and conservation.

The traditional prediction has been that species of animals with fast life histories, i.e., short generation times and associated traits such as small body size, should be able to persist better and recover more quickly from threats caused by humans (reviewed by Reynolds 2003). This prediction has been confirmed by studies of marine fishes that are exploited commercially (Jennings et al. 1998; Denney et al. 2002; Hutchings and Reynolds 2004). Furthermore, when species are exploited directly by humans, large-bodied species are usually preferred and more susceptible to capture. These generalizations are true not only for commercially exploited fishes but for most other exploited taxa as well, including mammals (Peres 2000; Purvis et al. 2000) and birds (Owens and Bennett 2000). However, this result depends critically on direct mortality being the main threat (Reynolds 2003). If habitats are destroyed, life histories may be much less relevant to susceptibility of populations. For most freshwater fishes, habitat degradation has been the primary cause of extinction, through physical alterations such as damming, canalization, and water abstraction and pollution, with additional problems from the introduction of alien species and overfishing (Harrison and Stiassny 1999). These problems may affect small-bodied species as much as they impact upon large-bodied ones. Indeed, it has been suggested that in many regions, the impacts on freshwater habitats may be so severe that life histories may simply be irrelevant (Duncan and Lockwood 2001).

Our finding that relationships between body size and threat status depend on whether or not anadromous species are included in the analyses supports the arguments above concerning the importance of distinguishing among threats. Most anadromous species suffer acutely from physical blockage of waterways, are large bodied, and are (or were) fished heavily (e.g., Elvira 1996; Keith and Allardi 1996). When we exclude anadromous species, as well as additional species that are fished heavily, we are left with species in which fishing plays little if any role in their threat status (Lelek 1980). This breaks the predicted link between large body size and susceptibility. Indeed, we find that smaller-bodied species are under greater threat than their larger-bodied relatives.

Why should smaller-bodied species face a greater risk of extinction than larger-bodied ones? We did not find compelling links between threat status and habitat specialization, although there was a trend for threatened species to occupy fewer habitats. Arguably, there may be an element of circularity in the latter trend, since some species are confined to single watersheds or water bodies. At this extreme, threat status based on range size will be correlated with “narrowness” of habitat usage. More important is the fact that many small-range endemics will have been listed as threatened on the basis of their range size, which accounts for many of the narrow latitudes illustrated here. This result by itself cannot explain the body size patterns. We believe the main reason for small-bodied species being under greater threat lies in our finding that they tend to occur farther south. Regions such as the Iberian Peninsula and Greece support many small-range endemics that are naturally “rare” in terms of range size but also suffer additional threats from humans. For example, 12 of the 19 Iberian endemics are considered endangered, with the key problems being habitat destruction, pollution, and exotic predators (Economidis 1995; Elvira 1996; Bernardo et al. 2003). Overfishing has not been implicated in the endangerment of any of these species, whereas the combination of overfishing and the presence of about 11 000 large dams has led to all anadromous species being classified as threatened.

This study was limited by availability of fundamental life history and ecological data for many species, although the situation is far better in Europe than in most other parts of the world (Lundberg et al. 2000). The fecundity data were sparse and highly imprecise and ultimately probably meaningless for the comparisons. Similarly, it is difficult at present to produce objective descriptions of ecological requirements of most species, so the nonsignificant trends reported here should also be regarded as preliminary. As noted in the Materials and methods section, our knowledge of threat status of many species is improving rapidly, with the potential for a full revision in the future. We tried various permutations of the analyses to account for a number of upgrades and downgrades of the status as currently published and found that our overall findings were robust. Finally, Kottelat (1997) has pointed out that we still have much to learn about the systematics and nomenclature of European fish species. As we learn more about species boundaries and relationships, it will become possible to go beyond the conservative use of matched pairs comparisons within genera that we have explored here, taking advantage of the full range of phylogenetic relationships among taxa.

In conclusion, this study has found that threatened species of European freshwater fishes are smaller bodied, have smaller latitudinal range sizes, and occur farther south than close relatives that are less threatened. The body size relationship disappears when anadromous species are included, suggesting that links between life history traits and risk of extinction depend on relationships between migratory behaviour and threats such as blockage of waterways and fishing. Future progress in studies of the biology of vulnerability in fishes and other taxa may come from further analyses that distinguish explicitly between various threatening processes, overlaid onto finer-scale mapping of specific threats onto distributions.

## Acknowledgements

We thank Brian Shuter, Peter Abrams, and Erin Dunlop for inviting us to a stimulating symposium on life histories and fisheries at the American Fisheries Symposium in Québec in August 2003. Jörg Freyhof warned us about a number of anomalies in the statuses of fishes as currently published, leading to various permutations of the analyses to verify the overall robustness of our results.

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