Trophic flexibility by roach *Rutilus rutilus* in novel habitats facilitates rapid growth and invasion success

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Stable isotope and gut content analyses, in conjunction with backcalculated length-at-age estimates of growth, were employed to examine the relationship between trophic ecology and growth rate of a successful invader, *Rutilus rutilus*, in eight lakes in Ireland. The data revealed that *R. rutilus* was a trophic generalist in Irish lakes. It utilized a greater proportion of pelagic resources in mesotrophic lakes than in eutrophic lakes, potentially due to a greater density of benthic macroinvertebrates in eutrophic systems. The species was characterized by a large dietary and isotopic niche width and high temporal and spatial variations in diet. Growth rates were typical of those found in the native range of the species and were unrelated to either lake productivity or fish's diet. A generalist trophic ecology confers significant advantages on an invasive species, allowing it to exploit a variety of novel resources and fluctuations in prey availability.

INTRODUCTION

Invasive species are a major threat to global biodiversity (Mack *et al.*, 2000), leading to dramatic changes in species composition and ecosystem function (Gozlan *et al.*, 2010). Of the many fish species introduced into new habitats, however, only a small proportion becomes invasive (Copp *et al.*, 2007). As such, a reliable understanding of the ecological characteristics that distinguish potentially invasive species from non-risk species is crucial in predicting the likelihood of a species becoming invasive (Levine & D'Antonio, 1999; García-Berthou, 2007). Successful invasive species often display early maturation and high fecundity (Lockwood *et al.*, 2007). In fishes, female size is

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a well-established factor governing fecundity (Winemiller & Rose, 1992; Lappalainen *et al.*, 2008), while age of maturation, particularly in males, is closely related to growth rate (Paull *et al.*, 2008). As such, a species that can utilize the resources available in a novel environment to maintain a high growth rate may be well suited to becoming invasive (Sax *et al.*, 2007).

An objective was to examine how trophic ecology is related to growth in an invasive cyprinid, roach *Rutilus rutilus* (L. 1758), which has a ubiquitous distribution across western Eurasia and is found in a wide variety of freshwater habitats (Kottelat & Freyhof, 2007). Numerous facets of their reproductive ecology, *e.g.* high fecundity and early maturation, highlight *R. rutilus* as a potentially successful invasive species (Persson, 1983*a*; Hjelm *et al.*, 2003; Lappalainen *et al.*, 2008). *Rutilus rutilus* are trophic generalists, employing a broad trophic niche, and utilize prey resources ranging from detritus (Persson, 1983*a*) and cyanobacteria (Kamjunke *et al.*, 2002) to zooplankton (Haertel & Eckmann, 2002), macrophytes and benthic macroinvertebrates (Persson & Hansson, 1999). Within their native range, they are considered a competitor of lentic species such as perch, *Perca fluviatilis* L. 1758, ruffe *Gymnocephalus cernua* L. (1758) and bream *Abramis brama* (L. 1758), typically shifting to pelagic prey in the presence of specialist benthivores (Persson, 1983*b*; Bergman & Greenberg, 1994).

In order to understand the response of invasive taxa to novel environments, there is much to be gained from studying evolutionarily young populations (Vander Zanden *et al.*, 1999; Sax *et al.*, 2007). The island of Ireland, located on the western edge of Europe, has a depauperate native fish fauna (Griffiths, 1997) and represents an ideal location to examine the ecology and effects of invasive species. *Rutilus rutilus* was originally introduced to Ireland in 1889 and, following an extended period during which they were restricted to a single river catchment, colonized the island between 1960 and 1980 (Fitzmaurice, 1981). *Rutilus rutilus* is currently among the most abundant fish on the island and dominates the fish communities of many lakes and rivers, including systems containing species with threatened conservation status (Harrod *et al.*, 2001). Resource competition with *R. rutilus* has been proposed as a cause of local extinction of Arctic charr, *Salvelinus alpinus* (L. 1758), populations in Irish lakes (Igoe & Hammar, 2004). In addition, dietary niche overlap observed between invasive *R. rutilus* and resident *A. brama* has been associated with a reduction in population size of *A. brama* (Hayden *et al.*, 2010, 2011).

To assess the role played by trophic ecology in the success of *R. rutilus* as an invasive species, four hypotheses were tested. First, *R. rutilus* would dominate the most productive resource in each system. Thus, in mesotrophic lakes, *R. rutilus* would be closely aligned to the littoral food web, while in eutrophic lakes, which are dominated by pelagic primary production, *R. rutilus* would utilize a greater proportion of pelagic-derived prey. Secondly, it was predicted that seasonal variation would be evident in the diet of *R. rutilus*, as this generalist species modified its trophic behaviour to take advantage of temporal variations in prey availability. Thirdly, it was suggested that the growth rates of *R. rutilus* would not be related to resource use, indicating that *R. rutilus* are equally successful when feeding on different resources. Finally, it was hypothesized that, as a successful invader encountering conditions within its evolutionary scope, the growth rate of *R. rutilus* populations in Ireland would not differ significantly from those in the native range of the species.

MATERIALS AND METHODS

FIELD SAMPLING

Populations of *R. rutilus* were sampled from eight Irish lakes (Table I), consisting of four culturally eutrophic and four mesotrophic systems (Clabby *et al.*, 2008). *Rutilus rutilus* was introduced to each watercourse during a similar period (1970–1980) and, at the time of sampling, it dominated the fish community in each lake. Sampling was conducted at the majority of sites during early spring and late summer of 2006. Ross Lake was sampled in spring and summer of 2007. Stable isotope values of fish muscle tissue reveal an individual's trophic position over the preceding 3–6 months (Post, 2002); obtaining samples in early spring and late summer allowed the identification of seasonal variation in resource use between the summer and winter periods exhibiting greatest variation in resource availability. The survey data were supplemented with data from Lough Neagh (summer 2009); as this site was not included in the original field surveys, spring data were not available.

On each sampling occasion, three replicate water samples were collected from the midpoint of each lake to determine concentrations (mg l^{-1}) of total phosphorus (TP), total organic nitrogen (TON) and chlorophyll-*a*. Fish were sampled using benthic-set Nordic gillnets (length 30 m, height 1.5 m) comprising twelve 2.5 m panels with stretched mesh sizes ranging from 5 to 55 mm (Appelberg, 2000). Netting was conducted over two consecutive nights. On both nights, two nets were set in the littoral zone (< 5 m) in each lake and retrieved after a period of 12 h. Gillnetting is a destructive sampling technique (Huntingford *et al.*, 2006), but it provides the most effective method of sampling fishes in lakes and is the current European standard for assessing lake fish communities (CEN, 2005). When fishes were removed from nets, live fishes were euthanized by percussion stunning (Metcalfe & Craig, 2011). Mass (± 1 g) and fork length (L_F; ± 1 mm) of *R. rutilus* were recorded on site. A sample of scales was removed from the anterior end of the dorsal flank for growth analysis.

Rutilus rutilus diet was assessed using a combination of analyses of gut contents and δ^{13}C and δ^{15}N stable isotope analysis (SIA). Gut content analysis (GCA) describes a fish's diet during the preceding 12–24 h and may be subject to bias regarding prey identification, often difficult in cyprinid species that masticate their prey, and diurnal variation in diet (Haertel & Eckmann, 2002). In contrast, stable isotope values of muscle tissue indicate a consumer's predominant resource use over a period of months, but lack the resolution of GCA (Post, 2002). As such, an accurate, time-integrated assessment of diet may be achieved using both methods in tandem (Vinson & Budy, 2010).

As *R. rutilus* lack a defined stomach, the anterior third of the gut was removed and stored in 70% ethanol for later dissection. A sample of dorsal muscle tissue was dissected from a sub-sample of fish ($n = 30$) and frozen (−20° C) for SIA. Filter feeding bivalves and grazing gastropods were used as isotopic baseline values for the pelagic and littoral food webs (Post, 2002). A minimum of five individuals of each group were collected from littoral habitat (< 5 m) using an Eckman grab and frozen.

Semi-quantitative estimates of benthic macroinvertebrate (BMI) community structure, conducted by the Irish Environmental Protection Agency (EPA), were obtained for six of the eight study lakes (neither Lough Neagh nor Leixlip Reservoir are sampled by the EPA) to obtain a measure of prey availability. Estimates of BMI abundance used by the EPA are based on total number of individuals recorded from 2 min kick samples, conducted at a single littoral location (Table I).

LABORATORY ANALYSIS

Due to the macerating effect of pharyngeal teeth, it was impossible to identify prey items consumed by *R. rutilus* to a fine taxonomic resolution. Hence, items were subdivided into 10 readily discernible prey categories: molluscs, detritus, chironomid larvae, Trichoptera larvae, Oligochaeta, crustaceans, Insecta, chironomid pupae, Hydracarina and macrophytes (Hayden *et al.*, 2011). The relative proportion of each group in the gut was calculated using the points method (Swynnerton & Worthington, 1940).

TABLE I. Location and abiotic characteristics of eight study lakes. Water quality data refer to annual mean ± S.E. values. The year of colonization by *Rutilus rutilus* and survey year are also provided

	Lough Neagh	Leixlip Reservoir	Lough Ramor	Lough Conn	Lough Ennell	Lough Cullin	Ross Lake	Lough Corrib
Latitude (N)	54° 36′	53° 21′	53° 49′	54° 1′	53° 27′	53° 58′	53° 22′	53° 28′
Longitude (W)	6° 24′	6° 30′	7° 05′	9° 14′	7° 24′	9° 10	9° 12′	9° 17′
Altitude (m.a.s.l.)	10	25	80	6	77	6	6	5
Surface area (km²)	392	4	8	57	14	10	2	178
Mean TP (mg l⁻¹)	0.090 ± 0.005	0.102 ± 0.017	0.115 ± 0.040	0.0130 ± 0.001	0.033 ± 0.005	0.012 ± 0.001	0.014 ± 0.003	0.014 ± 0.002
Mean TON (mg l⁻¹)	0.370 ± 0.090	1.527 ± 0.250	0.048 ± 0.246	0.499 ± 0.207	0.615 ± 0.175	$<0.049 (0)$	0.313 ± 0.013	0.175 ± 0.054
Mean chlorophyll-*a* (mg l⁻¹)	29.800 ± 1.100	8.937 ± 1.918	74.180 ± 17.290	7.701 ± 0.591	5.951 ± 0.660	2.907 ± 0.287	3.638 ± 0.807	3.642 ± 0.394
Trophic status	Eutrophic	Eutrophic	Eutrophic	Eutrophic	Mesotrophic	Mesotrophic	Mesotrophic	Mesotrophic
Year invaded	1980	1978	1978	1980	1979	1980	1980	1980
Survey year	2010	2006	2006	2006	2006	2006	2007	2006
BMI abundance (*n* min⁻¹)*								
Crustacea	–	–	262	898	281	118	393	262
Diptera	–	–	160	37	5	44	8	19
Mollusca	–	–	96	2	2	4	1	5
Trichoptera	–	–	146	26	13	40	17	31
Other	–	–	31	222	53	155	116	112

TP, total phosphorous; TON, total organic nitrogen; *Benthic macroinvertebrate (BMI) values were obtained from 2 min shoreline kick samples conducted by the Irish Environmental Protection Agency.

Invertebrate and fish tissue samples were dried at 60° C for 48 h, ground to a fine powder and weighed (1 ± 0.01 mg) into tin capsules for analysis of δ^{13}C and δ^{15}N stable isotope ratios. Isotope analysis was conducted using a Europe Scientific 20–20 isotope ratio mass spectrometer with a Europa Scientific Roboprep-CN preparation module at Iso-Analytical Ltd (www.iso-analytical.co.uk). Analytical error (S.D.) for δ^{13}C and δ^{15}N was estimated at 0·01‰. As lipid stores are ^{13}C depleted (DeNiro & Epstein, 1977), δ^{13}C values of fish muscle tissue were lipid corrected to remove the influence of variable lipid concentrations prior to analysis (Kiljunen *et al.*, 2006).

Scales were cleaned with a saline solution to remove any residual epithelial tissue and dried mucus and viewed under a Bell & Howell MT633 microfiche reader (www.bellhowell.com/). Annual checks were recorded as the point where circuli became closely spaced followed by areas of widely spaced circuli. Annual checks were only confirmed when associated structures could be viewed around the circumference of the check (Cragg-Hine & Jones, 1969). At least three scales were read for each fish to confirm the age and 20% of scales were cross-checked by a second analyst to avoid bias; in cases of irresolvable difference between the measurements of both analysts, samples were removed from the study.

DATA ANALYSIS

Stable isotope analysis

Due to variation in isotopic baseline values, direct comparisons of stable isotope ratios between lakes or seasons are of limited usefulness. Consequently, to test the hypotheses relating to resource use of *R. rutilus*, the Bayesian mixing model stable isotope analysis in R (SIAR) was used to assess the relative contribution of pelagic and littoral prey to the diet of *R. rutilus* in each lake (Parnell *et al.*, 2010). Standard trophic fractionation values for muscle tissue (Δ^{13}C $= 1·03 \pm 0·3$, Δ^{15}N $= 2·9 \pm 0·3$) were used in all cases (McCutchan *et al.*, 2003). Where resource use of one population was outside the 95% credibility limits of another population, both populations were deemed to be using significantly different levels of the particular resource. Isotopic niche width, calculated as a small sample size corrected standard ellipse of fish isotope values (E_C), was calculated for each population using stable isotope Bayesian ellipses in R (SIBER) analysis, performed in the SIAR package (Jackson *et al.*, 2011).

Pair-wise comparisons of resource use (95% credibility limits) and isotopic niche width (paired Welch *t*-test) between spring and summer samples were carried out to test the second hypothesis that *R. rutilus* would display seasonal variation in trophic ecology. Regression was used to examine ontogenetic variation by regressing individual δ^{13}C or δ^{15}N values on L_F.

Gut content analysis

In the majority of cases, GCA data collected were not normally distributed; consequently, non-parametric statistics were used throughout the analysis. The first two hypotheses, concerning spatial and temporal variation in the diet of *R. rutilus*, were tested using PERMANOVA, a non-parametric, permutation-based analogue of ANOVA between multiple groups based on a distance measure; in this case, the Bray-Curtis similarity matrix (Anderson, 2001). A similarity matrix was created from non-transformed GCA data. A three-factor PERMANOVA, performed in PRIMER 6 (PRIMER-E; www.primer-e.com), was employed to test the effect of trophic status (eutrophic : mesotrophic; fixed), lake (eight levels; random; nested within trophic status) and season (spring: summer; fixed) on variation within the dataset. Interactions between factors were derived to determine seasonal variation in diet within lakes and lake types.

Niche width and levels of individual specialization were established to determine the feeding strategy of *R. rutilus* in each location. Dietary niche width of each population was estimated using the standardized Levins' index (Levins, 1968). Total niche width (TNW) was subdivided into a within-individual component (WIC), representing the dietary niche of each fish, and a between-individual component (BIC), *i.e.* the niche width between individual fish. The level of individual specialization of fish within the population was calculated as WIC per TNW (Bolnick *et al.*, 2003). Dietary niche metrics were calculated using IndSpec (Bolnick *et al.*, 2003). Variation in mean niche width and level of individual specialization between lake classes and seasons was tested using a Welch *t*-test.

Growth

Growth rates were calculated to test the final two hypotheses. Growth rate of each fish was estimated by backcalculating L_F-at-age (Bagenal & Tesch, 1978) using the body proportion hypothesis (Horppila, 2000). Mean ($\pm$ 95% C.I.) values of both the theoretical asymptotic L_F (L_∞) and the rate at which this length is attained (k) were derived from the von Bertalanffy non-linear growth equation, calculated using the software package SIMPLY GROWTH (Pisces Conservation Ltd; www.pisces-conservation.com). Due to variation in the sample sizes of large fish between lakes, analysis of growth was based on backcalculated L_F-at-age of fish aged $1-6$ years; however, 7-year-old fish were included in the sample form Lough Conn as growth in the first 6 years did not approach an asymptote and consequently yielded erroneous results. To address the third hypothesis, that growth rate of *R. rutilus* would not be determined by resource use, k and L_∞ of each population were compared with proportion of pelagic resource used, as derived from the SIAR mixing model, using Spearman rank correlation. To test the final hypothesis (that growth rates would not vary between invasive and native populations), von Bertalanffy growth characteristics of *R. rutilus* from 35 European populations were obtained from a literature review. Where von Bertalanffy growth values were not provided, they were derived from mean length-at-age data supplied in the literature. Mean von Bertalanffy characteristics (k and L_∞) were compared from native (European) and invasive (Irish) populations using the Welch t-test. Welch t-tests were performed in the R statistical computing package (R Development Core Team; www.r-project.org/).

RESULTS

WATER QUALITY

Variation in water quality was evident between lakes and supported the original classifications (Table I). Welch t-tests indicated that several measures of trophic status were lower in those lakes classified as mesotrophic, *e.g.* TP (spring: $t = -2\cdot25$, d.f. $= 9\cdot6$, $P < 0\cdot05$; summer: $t = -8\cdot3$, d.f. $= 25\cdot08$, $P < 0\cdot001$) and chlorophyll-α (spring: $t = -3\cdot5$, d.f. $= 8$, $P < 0\cdot01$; summer: $t = -4\cdot8$, d.f. $= 24\cdot7$, $P < 0\cdot01$. Variation in TON was evident in spring ($t = -3\cdot5$, d.f. $= 7\cdot9$, $P < 0\cdot01$) but not in summer ($t = -0\cdot8$, d.f. $= 30\cdot8$, $P > 0\cdot05$).

Hypothesis 1: Rutilus rutuilus would draw most energy from benthic resource in mesotrophic lakes and from pelagic resources in eutrophic lakes.

Stable isotope data revealed a general trend of elevated pelagic resource use in mesotrophic relative to eutrophic lakes, in direct contrast to the hypothesis [Fig. 1(a)]. Significant levels of variation in resource use were, however, evident between lakes within both eutrophic and mesotrophic categories (Table II): Within the eutrophic lakes, *R. rutilus* in Lough Conn displayed consistently high levels of littoral resource (mean value in spring $= 75\%$, summer $= 74\%$), while the population in Lough Ramor utilized the greatest recorded proportion of pelagic resources (mean value in spring $= 92\%$, summer $= 80\%$). Lower variation was evident between the mesotrophic lakes [Fig. 1(a)]. Levels of pelagic resource use in each lake generally fell within the 95% credibility intervals of all other lakes, although variation was evident between populations in Lough Cullin and Ross Lake [Fig. 1(a)]. Gut content of *R. rutilus* did not reveal any variation associated with the trophic status of the study system (PERMANOVA: pseudo $F_{1,421} = 0\cdot64$, $P > 0\cdot05$). Variation was observed between lakes within each trophic status group (PERMANOVA: *Pseudo* $F_{6,421} = 23\cdot9$, $P < 0\cdot01$). The consumption of zooplankton was highest in the spring sample of Lough Ramor but no
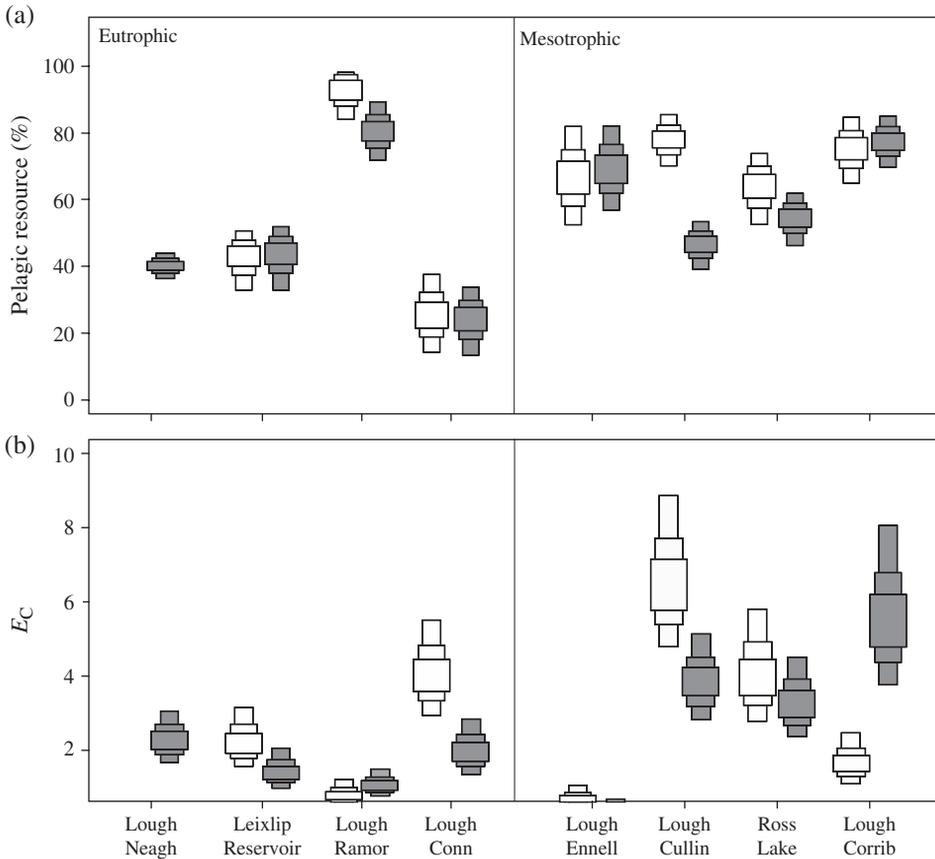
FIG. 1. (a) Percentage of pelagic resources assimilated and (b) isotopic niche width (E_C) of *Rutilus rutilus*. Spring (□) and summer (■) samples are presented; gradations represent 50, 75 and 95% credibility intervals.

evidence of increased zooplanktivory, indicative of pelagic feeding, was observed in eutrophic lakes relative to mesotrophic lakes. Rather, the most commonly encountered prey items in eutrophic lakes were molluscs, crustaceans, chironomid and trichopteran larvae (Fig. 2 and Table SI, Supporting Information).

Isotopic niche width (E_C) did not vary between eutrophic and mesotrophic lakes (Welch *t*-test: $t = -1.07$, d.f. $= 8.96$, $P > 0.05$). E_C was not related to dietary niche width (Spearman correlation coefficient: $r_s = 0.19$, $n = 15$, $P > 0.05$) or levels of individual specialization (Spearman correlation coefficient: $r_s = -0.34$, $n = 15$, $P > 0.05$). Estimates of dietary niche width (standardized Levins' index) ranged from 0.17, indicative of a small specialized niche, in Loughs Cullin and Neagh to 0.47 in Lough Conn. Levins' index of dietary niche width was not correlated with sample size (Spearman correlation coefficient: $r_s = 0.05$, $n = 16$, $P > 0.05$). On an average, Levins' index values did not vary between mesotrophic and eutrophic systems (Table II; Welch *t*-test: $t = 0.76$, d.f. $= 10.9$, $P > 0.05$). Levels of individual specialization did not vary between mesotrophic and eutrophic lakes (Table II; Welch *t*-test: $t = -0.75$, d.f. $= 11.2$, $P > 0.05$).

TABLE II. Seasonal variation in mean ± s.d. δ^{13}C and δ^{15}N stable isotope ratios and gut content of *Rutilus rutilus* in eight study lakes. Mean fork length (L_F), minimum and maximum values in parentheses and the number of individuals analysed are provided, in addition to ontogenetic variation in stable isotope values (r^2), isotopic (EC) and dietary (Levins' index, α) niche width, pair-wise PERMANOVA of gut content and a measure of individual dietary specialization (Ind)

| Status	Lake	Season	L_F (mm)	Stable isotope analysis						Gut content analysis			
				n	δ^{13}C	r^2	δ^{15}N	r^2	EC	n	PERMANOVA	α	Ind
Eutrophic	Lough Neagh	Spring	–	–	–		–		–	–	–	–	–
		Summer	130 (62–227)	60	−27.9 (1)	0.38*	18.9 (0.7)	0.59**	2.27	53	–	0.17	0.54
	Leixlip Reservoir	Spring	189 (95–290)	31	−28.5 ± 1.0	0.06	15.5 ± 0.8	0.09	1.4	33	$P < 0.01$	0.41	0.52
		Summer	184 (75–305)	29	−28.8 ± 0.8	0.01	15.0 ± 0.5	0.02	1.3	28		0.35	0.42
	Lough Ramor	Spring	175 (58–300)	20	−28.8 ± 0.3	0.03	14.6 ± 0.5	0.04	0.49	20	$P < 0.01$	0.18	0.41
		Summer	187 (100–290)	31	−28.1 ± 0.6	0.14*	14.1 ± 0.6	0.38**	0.84	30		0.35	0.55
	Lough Conn	Spring	181 (105–310)	42	−27.8 ± 1.8	0.02	14.0 ± 0.9	0.04	4.13	27	$P < 0.01$	0.47	0.40
		Summer	200 (93–280)	28	−27.3 ± 1.2	0.02	13.3 ± 0.5	0.04	1.87	15		0.33	0.57
Mesotrophic	Lough Ennell	Spring	300 (238–358)	21	−28.9 ± 0.3	0.07	17.6 ± 0.5	0.08	0.34	16	$P < 0.01$	0.25	0.82
		Summer	284 (226–365)	29	−29.0 ± 0.2	0.19*	17.3 ± 0.3	0.09	0.23	24		0.25	0.54
	Lough. Cullin	Spring	186 (80–305)	36	−27.7 ± 1.9	0.03	13.8 ± 1.2	0.15*	6.80	25	$P > 0.05$	0.22	0.53
		Summer	170 (65–295)	44	−25.6 ± 2.0	0.01	13.4 ± 0.9	0.01	3.80	37		0.17	0.41
	Ross Lake	Spring	170 (102–310)	28	−32.1 ± 1.6	0.49**	12.6 ± 0.8	0.31**	4.20	29	$P < 0.01$	0.39	0.54
		Summer	164 (75–260)	37	−31.5 ± 1.4	0.33*	12.2 ± 0.8	0.19**	3.30	43		0.35	0.49
	Lough Corrib	Spring	139 (58–339)	28	−28.0 ± 1.2	0.01	13.0 ± 0.4	0.09	1.50	22	$P < 0.01$	0.39	0.51
		Summer	158 (59–314)	33	−27.8 ± 1.4	0.01	12.1 ± 1.3	0.09	3.40	20		0.25	0.38

$*P < 0.05$; $**P < 0.01$.
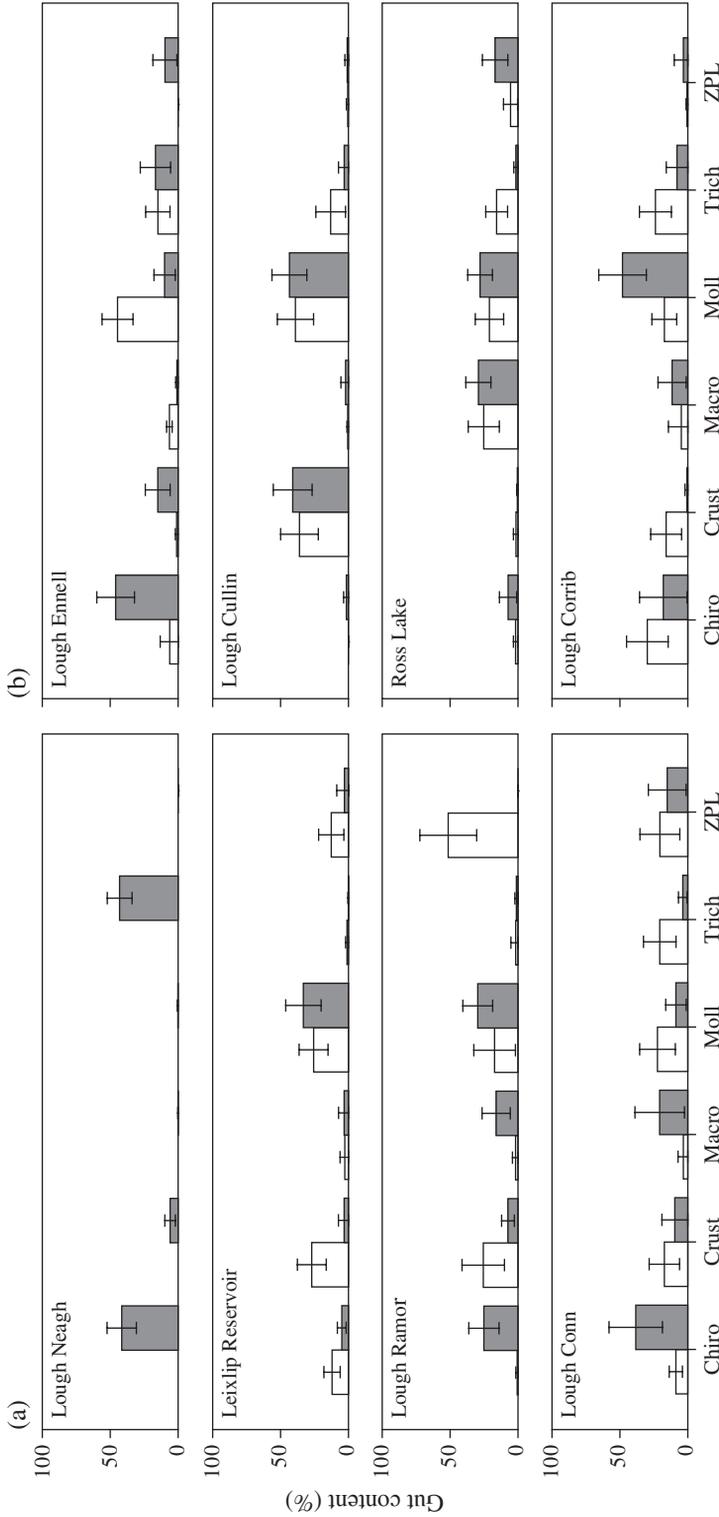
FIG. 2. Mean ± 95% c.i. percentage of chironomid larvae (Chiro), crustaceans (Crust), macrophytes (Macro), trichopteran larvae (Trich) and zooplankton (ZPL) in the gut content of *Rutilus rutilus* in (a) eutrophic and (b) mesotrophic lakes. Spring (□) and summer (■) samples are presented.

TABLE III. Growth characteristics, limited to the first 6 years of life, of studied populations of *Rutilus rutilus*. Number of individuals (n) and fork length range (L_F) of analysed sub-samples are presented along with von Bertalanffy growth rate (k), theoretical asymptotic L_F (95% C.I. given in parentheses) and theoretical age at length 0

Status	Lake	n	L_F (mm)	k	L_∞	t_0
Eutrophic	Lough Neagh	74	62–227	0·35 (0·01)	196 (2)	0·52
	Leixlip Reservoir	80	65–300	0·21 (<0·01)	317 (2)	0·22
	Lough Ramor	61	65–290	0·22 (<0·01)	305 (2)	0·45
	Lough Conn*	87	93–310	0·22 (<0·01)	370 (5)	0·53
Mesotrophic	Lough Ennell	33	238–358	0·37 (0·01)	328 (1)	0·54
	Lough Cullin	57	65–280	0·22 (<0·01)	341 (2)	0·60
	Ross Lake	38	102–227	0·24 (0·01)	224 (2)	0·12
	Lough Corrib	58	59–320	0·16 (0·01)	339 (7)	0·20

*Values for Lough Conn include fish aged 7+ years.

Ontogenetic variation in δ^{13}C values was evident in five samples (Table II). In the majority of these, it indicated a shift from consumption of pelagic (^{13}C depleted) to littoral (^{13}C enriched) resources: only in Lough Ramor, where pelagic resource use was highest, was the opposite trend observed. Ontogenetic enrichment of ^{15}N was observed in the summer sample in Lough Ramor and both samples in Ross Lake (Table II). An ontogenetic depletion in δ^{15}N was observed in the summer sample in Lough Neagh and the spring sample in Lough Cullin.

Hypothesis 2: seasonal variation would be evident in the diet and resource use of R. rutilus.

Seasonal variation in resource use was not evident in the majority of lakes [Table II and Fig. 1(a)]. Variation was uniquely evident in Lough Cullin, where fish sampled during the summer assimilated an increased proportion of littoral resources [Fig. 1(a)]. Isotopic niche width (E_C) was not significantly larger in either season when assessed across all sites (paired Welch *t*-test: $t = 0·95$, d.f. = 6, $P > 0·05$). Some seasonal variation in isotopic niche width, however, was evident [Fig. 1(b)]: E_C was larger in the spring samples from Loughs Conn and Cullin, while the opposite was true in Lough Corrib [Table II and Fig. 1(b)].

Seasonal variation in gut content was evident in most lakes (PERMANOVA lake × season: *Pseudo* $F_{5,421} = 6·91$, $P < 0·01$; Table II and Fig. 2). Dietary niche width was generally consistent between seasons (paired Welch *t*-test: $t = 0·93$, d.f. = 6, $P > 0·05$) but in Lough Ramor niche width in summer was twice as broad as that recorded during the spring. Overall, levels of individual dietary specialization did not vary between seasons (paired Welch *t*-test: $t = 0·88$, d.f. = 6, $P > 0·05$).

Hypothesis 3: growth rate of R. rutilus is not related to resource use of the population.

Rutilus rutilus in eutrophic lakes had greater L_F-at-age values than those in mesotrophic lakes during the first 6 years of life (paired Welch *t*-test: $t = 6·62$, d.f. = 5, $P < 0·01$). This variation was largely driven by exceptionally fast growth in Lough Conn and exceptionally slow growth in Ross Lough (Table III, Table SII and Fig. 3.)

To test the third hypothesis, that growth rate would be related to resource use, correlations between proportion of pelagic resources assimilated by *R. rutilus*, as derived
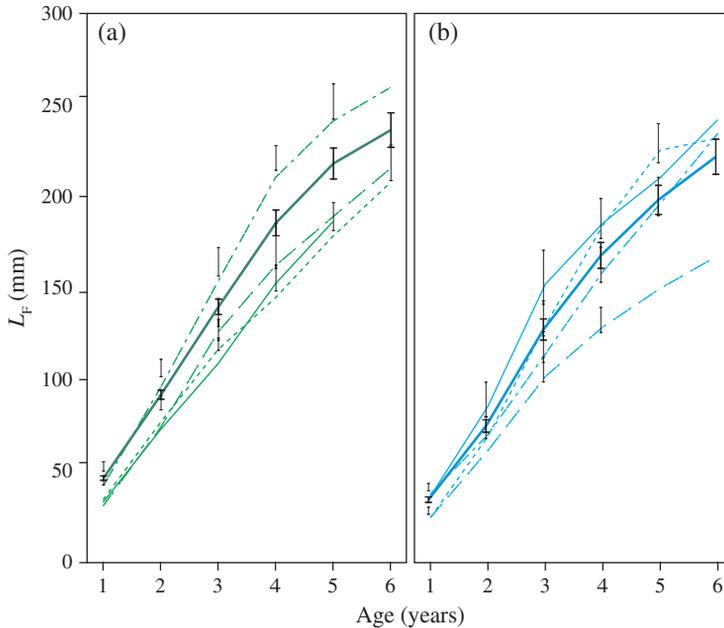
FIG. 3. Mean ± 95% C.I. backcalculated fork length (L_F)-at-age growth rates (solid bold lines) of *Rutilus rutilus* in (a) eutrophic and (b) mesotrophic lakes. Population growth rates: ___, Lough Neagh; ___. Lough Ennell; _ _ _, Leixlip Reservoir; _ _ _ _. Lough Cullin; _ _, Lough Ramor; _ _, Ross Lough; . _ _, Lough Conn; . _ _, Lough Corrib.

from the SIAR mixing model, and the von Bertalanffy growth parameters were examined. In both cases, there was no statistical support for relationships between growth performance and trophic ecology in invaded lakes (k, Spearman correlation coefficient: $r_s = 0.21$, $n = 16$, $P > 0.05$; L_∞, Spearman correlation coefficient: $r_s = -0.18$, $n = 16$, $P > 0.05$).

Hypothesis 4: growth rate of invasive populations of R. rutilus is comparable to that observed within their native range.

Published von Bertalanffy k values ranged from 0·04 to 0·32 (Table IV), exceeding the range evident in Irish lakes. Mean values, however, did not differ significantly from the values recorded from Irish populations (Welch *t*-test: $t = 161·5$, d.f. $= 10·34$, $P > 0.05$). Similarly, L_∞ in Irish populations was statistically indistinguishable from native populations (Welch *t*-test: $t = -0·41$, d.f. $= 9·72$, $P > 0·05$).

DISCUSSION

Four independent hypotheses were set out to test interrelationship of trophic ecology and invasion success by *R. rutilus*. The first hypothesis that *R. rutilus* would utilize a greater proportion of pelagic resources in eutrophic lakes was rejected. Although significant variation in resource use between lake types was observed, *R. rutilus* in eutrophic lakes showed a greater reliance on benthic resources. The second hypothesis that seasonal variation would be evident in the diet of *R. rutilus* was supported by both

TABLE IV. Location, latitude, longitude, von Bertalanffy growth rate (k), theoretical asymptotic fork length (L_∞) and theoretical fork length (L_F) at time zero (t_0) of 35 *Rutilus rutilus* population encompassing the European distribution of the species

Country	°N	°E	k	L_∞	t_0	Source
Finland	59·83	22·97	0·05	624	−0·44	Lappalainen *et al.*, 2001
Finland	59·83	22·97	0·04	579	−1·27	Lappalainen *et al.*, 2001
Finland	61·08	25·54	0·29	203	−0·24	Horppila & Nyberg, 1999
Finland	61·08	25·53	0·32	190	−0·02	Horppila, 2000
Finland	61·08	25·53	0·32	181	0·05	Horppila, 2000
France	43·73	6·13	0·29	284	0·18	Chappaz *et al.*, 1990
France	45·66	2·98	0·16	256	−0·63	Jamet & Desmolles, 1994
France	46·43	6·55	0·21	344	−0·26	Ponton & Gerdeaux, 1987
Greece	40·68	23·47	0·08	349	−1·27	Papageorgiou, 1979
Holland	52·89	5·79	0·23	207	−0·23	Goldspink, 1979
Italy	45·95	8·63	0·29	358	−0·40	Volta & Jepsen, 2008
Norway	60·34	9·37	0·29	229	0·76	Vøllestad & L'Abée-Lund, 1990
Norway	59·29	11·12	0·17	301	1·21	Vøllestad & L'Abée-Lund, 1990
Norway	59·34	11·05	0·19	274	0·64	Vøllestad & L'Abée-Lund, 1990
Norway	60·25	7·81	0·26	203	−0·37	Vøllestad & L'Abée-Lund, 1990
Norway	59·43	10·98	0·15	262	0·99	Vøllestad & L'Abée-Lund, 1990
Norway	59·73	9·02	0·18	260	0·52	Vøllestad & L'Abée-Lund, 1990
Poland	53·67	14·52	0·13	321	−0·39	Wieski & Zalachowski, 2000
Sweden	59·32	18·05	0·16	256	−0·63	Kempe, 1962
Switzerland	45·98	8·96	0·30	368	–	Guthruf, 2002
Turkey	40·72	30·25	0·16	390	−0·18	Okgerman *et al.*, 2009
U.K.	50·28	−3·65	0·20	229	0·20	Burrough & Kennedy, 1979
U.K.	52·55	−0·56	0·16	257	−0·10	Cragg-Hine & Jones, 1969
U.K.	50·89	−3·49	0·17	285	−0·19	Cowx, 1988
U.K.	50·92	−2·28	0·12	343	−0·17	Mann, 1973
U.K.	52·72	1·48	0·08	443	−0·71	Cryer *et al.*, 1986
U.K.	52·93	0·05	0·12	357	−0·12	Coles, 1979
U.K.	52·56	1·61	0·10	289	−0·50	Hartley, 1947
U.K.	55·96	−3·46	0·27	195	0·54	Mills, 1969
U.K.	52·88	−3·63	0·16	306	0·19	Jones, 1953
U.K.	56·11	−4·62	0·18	319	0·49	Mills, 1969
U.K.	53·35	−2·39	0·13	447	−0·22	Goldspink, 1978
U.K.	52·91	−2·88	0·31	317	0·51	Goldspink, 1978
U.K.	53·32	−2·37	0·29	372	0·82	Goldspink, 1978
U.K.	51·46	−0·96	0·20	198	−0·33	Williams, 1967

stable isotope and gut content data. The final two hypotheses that trophic ecology of *R. rutilus* is not related to growth rate and that the growth rates of invasive Irish *R. rutilus* populations would not differ from those in the native range of the species were also supported by the data.

Contrary to the original hypothesis, *R. rutilus* in eutrophic systems were, on the whole, more closely associated with littoral than pelagic food webs, potentially due to the higher density of BMIs in these lakes. Lough Ramor was the single exception to this and also exhibited the highest chlorophyll-*a* levels recorded in the study. While the

gut content of *R. rutilus* revealed a high degree of seasonal variation, the results of the isotope mixing model, indicative of long-term assimilated diet, detailed greater variation between lakes than seasons. Thus, while *R. rutilus* are more closely aligned with a particular trophic resource (*i.e.* benthic or pelagic), the prey species they consume within this resource may vary over time. In addition, levels of ontogenetic variation in diet varied between localities. While no clear trend relating to ontogenetic dietary shift was evident, variation in δ^{13}C and δ^{15}N was typically observed in unison, indicating that the shift in isotopic position related to a dietary shift.

Temporal and spatial variation in isotopic and dietary niche width was also evident, indicating that *R. rutilus* varied its feeding strategy in different lakes, *i.e.* it was a generalist. Levins' index of dietary niche width may be affected by sample size (Levins, 1968). Consequently, best practice dictates that sample sizes are standardized before between-population analyses are conducted. Due to small sample sizes in certain populations, Levins' niche width calculations were not standardized to the smallest sample in the present analysis, but the absence of a significant correlation between sample size and niche width suggests that the estimates provided here are robust. The only aspect of feeding ecology of *R. rutilus* that did not exhibit variation between systems was the level of individual specialization within the population. In all cases, *R. rutilus* acted as a generalist rather than a population of individual specialists, highlighting the ability of individual fish to utilize a wide range of resources (Bolnick *et al.*, 2003).

The present data reveal that *R. rutilus* populations in Ireland exhibit growth rates typical of those within its native range. The similarity in growth of *R. rutilus*, both between lake categories, and between invaded and native populations is of key interest in determining the success of the species as an invader. The interaction, or lack thereof, between resource use and growth reveals that, for a generalist, a distinct variation in resource availability may not prove a barrier to invasion. *Rutilus rutilus* can vary their diet over a short or longer period without affecting their growth, allowing fish to achieve the earliest possible maturation regardless of their diet. It is worth noting, however, that prey resources are unlikely to be limiting in the study lakes (Hayden *et al.*, 2011). Consequently, growth may not be directly related to diet in these lakes, as prey were readily available in all systems. The addition of oligotrophic lakes in future investigations may be necessary to better define the relationship between diet and growth (Goldspink, 1978).

Variation in growth rate, not explained by resource use, was evident between populations and requires further attention. Growth rate of fishes is typically regulated by water temperature (Fry, 1971), prey availability or other density-dependent factors, *e.g.* resource competition (Byström & García-Berthou, 1999). Due to the small geographical range of the study sites, variation in water temperature is unlikely to be a factor influencing the variation in growth recorded between populations (Lappalainen *et al.*, 2008). In the absence of other evident causes, it appears likely that growth rate of *R. rutilus* in the studied populations is mediated by some form of inter or intraspecific density dependence. As fish density was not estimated for the study lakes, few conclusions can be drawn in this regard.

An absence of significant variation in the diet of *R. rutilus* between eutrophic and mesotrophic systems indicates that diet is affected to a greater degree by lake-specific factors than by the trophic status of the water body. Although all study lakes contain predominantly the same fish species, variation in consumer density may affect the diet of the *R. rutilus* population. *Abrama brama* and *R. rutilus* × *A. abrama* hybrids,

which feed predominantly on BMIs, are common in Lough Ramor, Leixlip Reservoir, Ross Lough, Lough Corrib and Lough Neagh (Hayden *et al.*, 2011). Conversely, brown trout *Salmo trutta* L. 1758 are found in greatest densities in Lough Ennell, Lough Corrib, Lough Conn and Lough Cullin (Kelly *et al.*, 2008, 2009), predominantly alkaline systems that contain large charaphyte beds and dense macroinvertebrate populations. Interestingly, *R. rutilus* exhibited elevated growth rates in these lakes. Resource competition between *R. rutilus* and *S. trutta* has been proposed as a factor contributing to declining *S. trutta* populations in many Irish lakes; however, both species appear to thrive in sympatry here. A comparison of diet of *R. rutilus* and *S. trutta* in these particular lakes revealed that both species maintained distinct isotopic niches (Massa-Gallucci, 2009). This suggests that in productive mesotrophic conditions, both *R. rutilus* and *S. trutta* can utilize distinct resources and maintain effective growth rates.

In addition to influencing its likely success as an invasive species, it is suggested that a species' trophic ecology will ultimately determine the effect of an invader on putative competitors resident in the invaded habitat. Specialist invaders may be able to dominate their preferred trophic resource, out-competing native species (Bøhn & Amundsen, 2001). Although a resident taxon may be able to use an alternative niche, in extreme cases, such competition may lead to extirpation (Olden *et al.*, 2006, 2008). Conversely, a generalist species is less likely to out-compete a resident for its preferred resource. Rather, both species will utilize the same resources, to the likely detriment, but not extirpation of resident taxa (Hayden *et al.*, 2011, 2013). It is suggested that further investigation around this hypothesis is merited and would be of potentially great interest to the field.

Invasion success is typically characterized by three stages, *i.e.* introduction, establishment and expansion (Jeschke & Strayer, 2005). While an organism's trophic ecology has no discernible influence over its likelihood of introduction, it is proposed that a generalist ecology is of fundamental benefit to an organism moving from an established stage to a full invasion (Sax *et al.*, 2007). When becoming established in a new location, an invasive specialist may utilize morphological adaptations to occupy its preferring niche, potentially relegating resident taxa to alternate niches (Bøhn *et al.*, 2008). To expand from this limited local distribution, invasive species, particularly freshwater fishes, must overcome habitats to which they may not be well adapted. Data presented here displays how a generalist trophic ecology may confer a significant advantage to an invasive species in this regard it is highlighted. An ability to achieve rapid growth, while using a wide variety of novel prey types, contributed to the invasion success of *R. rutilus*. Thus, while an absence of dietary specializations may be a disadvantage when competing with an ecological specialist, present findings suggest that a generalist trophic ecology confers advantages to establishing and expanding invasive populations.

Supporting Information

Supporting Information may be found in the online version of this paper:
Table SI. Mean (±S.D.) proportion of molluscs (Moll), detritus (Det), chironomid larvae (Chiro), trichoptera larvae (Tric), plant material (Plant), crustaceans (Crust),

zooplankton (ZPL), insect nymphs (Insecta), terrestrial adult insects (Ter), hydracarina (Hydra) and oligochaeta worms (Oligo) recorded in the gut content of *Rutilus rutilus*

Table SII. Mean ($\pm$s.d.) backcalculated fork length (L_F)-at-age values of studied populations of *Rutilus rutilus*

References

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26,** 32–46.

Appelberg, M. (2000). Swedish standard methods for sampling freshwater fish with multi-mesh gillnets. *Fiskeriverket Information* **1,** 3–32.

Bagenal, T. B. & Tesch, F. W. (1978). Age and growth. In *Methods for Assessment of Fish Production in Fresh Waters* (Bagenal, T. B., ed), pp. 101–136. London: Blackwell Scientific Publications Ltd.

Bergman, E. & Greenberg, L. A. (1994). Competition between a planktivore, a benthivore, and a species with ontogenetic diet shifts. *Ecology* **75,** 1233–1245.

Bøhn, T. & Amundsen, P.-A. (2001). The competitive edge of an invading specialist. *Ecology* **82,** 2150–2163.

Bøhn, T., Amundsen, P.-A. & Sparrow, A. (2008). Competitive exclusion after invasion? *Biological Invasions* **10,** 359–368.

Bolnick, D. I., Svanback, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* **161,** 1–28.

Burrough, R. J. & Kennedy, C. R. (1979). The occurrence and natural alleviation of stunting in a population of roach, *Rutilus rutilus* (L.). *Journal of Fish Biology* **15,** 93–109.

Byström, P. & García-Berthou, E. (1999). Density dependent growth and size specific competitive interactions in young fish. *Oikos* **86,** 217–232.

CEN (2005). *EN 14757 - Water Quality Sampling of Fish with Multi-mesh Gillnets*. Brussels: European Committee for Standardization.

Chappaz, R., Brun, G. & Olivari, G. (1990). The factors of development of roach (*Rutilus rutilus*) L. introduced in a recent oligotrophic reservoir - analysis of mesological (temperatures) and biological parameters. *Comptes Rendus De L Academie Des Sciences Serie Iii* **310,** 27–33.

Clabby, K. J., Bradley, C., Craig, M., Daly, D., Lucey, J., McGarrigle, M., O'Boyle, S., Tierney, D. & Bowman, J. (2008). *Water Quality in Ireland 2004–2006*. Wexford: The Environmental Protection Agency.

Coles, T. F. (1979). Investigations into fish populations in Lincolnshire Rivers. In *The First British Freshwater Fisheries Conference* (O'Hara, K. & Dickson, B. C. eds), pp. 345–363. Liverpool: University of Liverpool.

Copp, G. H., Templeton, M. & Gozlan, R. E. (2007). Propagule pressure and the invasion risks of non-native freshwater fishes: a case study in England. *Journal of Fish Biology* **71,** 148–159.

Cowx, I. G. (1988). Distribution and variation in the growth of roach, *Rutilus rutilus* (L) and dace *Leuciscus leuciscus* (L), in a river catchment in Southwest England. *Journal of Fish Biology* **33,** 59–72.

Cragg-Hine, D. & Jones, J. W. (1969). Growth of dace *Leuciscus leuciscus* (L) roach *Rutilus rutilus* (L) and chub *Squalius cephalus* (L) in Willow Brook, Northamptonshire. *Journal of Fish Biology* **1,** 59–82.

Cryer, M., Peirson, G. & Townsend, C. R. (1986). Reciprocal interactions between roach, *Rutilus rutilus*, and zooplankton in a small lake: prey dynamics and fish growth and recruitment. *Limnology and Oceanography* **31,** 1022–1038.

DeNiro, M. J. & Epstein, S. (1977). Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* **197,** 261–263.

Fitzmaurice, P. (1981). The spread of roach *Rutilus rutilus* (L) in Irish waters. In *Proceedings of the 2nd British Freshwaters Fisheries Conference* (O'Hara, K. & Dickson, B. C. eds) pp. 154–161. Liverpool: Liverpool University Press.

Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. In *Fish Physiology* (Hoar, W. S. & Randall, D. J., eds), pp. 1–87. New York, NY: Academic Press.

García-Berthou, E. (2007). The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology* **71,** 33–55.

Goldspink, C. R. (1978). Comparative observations on growth-rate and year class strength of roach *Rutilus rutilus* L. in two Cheshire lakes, England. *Journal of Fish Biology* **12,** 421–433.

Goldspink, C. R. (1979). The population density, growth rate and reproduction of roach *Rutilus rutilus* (L.) in Tjeukemeer, The Netherlands. *Journal of Fish Biology* **15,** 473–498.

Gozlan, R. E., Britton, J. R., Cowx, I. & Copp, G. H. (2010). Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* **76,** 751–786.

Griffiths, D. (1997). The status of the Irish freshwater fish fauna: a review. *Journal of Applied Ichthyology* **13,** 9–13.

Guthruf, J. (2002). Die biologie des Rotauges im Luganer-see (Kanton TI). *BUWAL, Mitteilungen zur Fischerei* **74,** 89.

Haertel, S. S. & Eckmann, R. (2002). Diel diet shift of roach and its implications for the estimation of daily rations. *Journal of Fish Biology* **60,** 876–892.

Harrod, C., Griffiths, D., McCarthy, T. K. & Rosell, R. (2001). The Irish pollan, *Coregonus autumnalis*: options for its conservation. *Journal of Fish Biology* **59,** 339–355.

Hartley, P. H. T. (1947). The natural history of some British freshwater fishes. *Proceedings of the Zoological Society of London* **117,** 129–206.

Hayden, B., Pulcini, D., Kelly-Quinn, M., O' Grady, M., Caffrey, J., McGrath, A. & Mariani, S. (2010). Hybridisation between two cyprinid fishes in a novel habitat: genetics, morphology and life-history traits. *BMC Evolutionary Biology* **10,** 169.

Hayden, B., Massa-Gallucci, A., Caffrey, J., Harrod, C., Mariani, S., O'Grady, M. & Kelly-Quinn, M. (2011). Trophic dynamics within a hybrid zone – interactions between an abundant cyprinid hybrid and sympatric parental species. *Freshwater Biology* **56,** 1723–1735.

Hayden, B., Holopainen, T., Amundsen, P.-A., Eloranta, A. P., Knudsen, R., Præbel, K. & Kahilainen, K. K. (2013). Interactions between invading benthivorous fish and native whitefish in subarctic lakes. *Freshwater Biology* **58,** 1234–1250.

Hjelm, J., van de Weerd, G. H. & Sibbing, F. A. (2003). Functional link between foraging performance, functional morphology, and diet shift in roach (*Rutilus rutilus*). *Canadian Journal of Fisheries and Aquatic Sciences* **60,** 700–709.

Horppila, J. (2000). The effect of length frequency ranges on the back-calculated lengths of roach, *Rutilus rutilus* (L.). *Fisheries Research* **45,** 21–29.

Horppila, J. & Nyberg, K. (1999). The validity of different methods in the backcalculation of the lengths of roach - a comparison between scales and cleithra. *Journal of Fish Biology* **54,** 489–498.

Huntingford, F. A., Adams, C., Braithwaite, V. A., Kadri, S., Pottinger, T. G., Sandøe, P. & Turnbull, J. F. (2006). Current issues in fish welfare. *Journal of Fish Biology* **68,** 332–372.

Igoe, F. & Hammar, J. (2004). The arctic charr *Salvelinus alpinus* (L.) species complex in Ireland: a secretive and threatened ice age relict. *Biology and Environment* **104B,** 73–92.

Jackson, A. L., Inger, R., Parnell, A. C. & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* **80,** 595–602.

Jamet, J. L. & Desmolles, F. (1994). Growth, reproduction and condition of roach (*Rutilus rutilus*, L.), perch (*Perca fluviatilis*, L.) and ruffe (*Gymnocephalus cernuus*, L.) in eutrophic Lake Aydat. *International Review of Hydrobiology* **79,** 305–322.

Jeschke, J. M. & Strayer, D. L. (2005). Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences of the United States of America* **102,** 7198–7202.

Jones, J. W. (1953). Part I-Scales of Roach, Part 11-Age and growth of trout, grayling, perch and roach of Llyn Tegid (Bala) and the roach from the River Birket. *Fisheries Investigations London Series* **1,** 1–18. London: H.M. Stationery Office.

Kamjunke, N., Schmidt, K., Pflugmacher, S. & Mehner, T. (2002). Consumption of cyanobacteria by roach (*Rutilus rutilus*): useful or harmful to the fish? *Freshwater Biology* **47,** 243–250.

Kelly, F., Connor, L. & Champ, T. (2008). *WFD surveillance Monitoring - Fish in Lakes 2007*. Dublin: Central Fisheries Board.

Kelly, F., Connor, L., Wightman, G., Matson, R., Morrissey, E., O'Callaghan, R., Feeney, R., Hanna, G. & Rocks, K. (2009). *Sampling Fish For the Water Framework Directive - Summary Report 2008*. Dublin: Inland Fisheries Ireland.

Kempe, O. (1962). The growth of roach (*Rutilus rutilus* L.) in some Swedish lakes. *Report of the Institute of Freshwater Research*, *Drottningholm* **44**, 42–104.

Kiljunen, M., Grey, J., Sinisalo, T., Harrod, C., Immonen, H. & Jones, R. I. (2006). A revised model for lipid-normalizing δ^{13}C values from aquatic organisms, with implications for isotope mixing models. *Journal of Applied Ecology* **43,** 1213–1222.

Kottelat, M. & Freyhof, J. (2007). *Handbook of European Freshwater Fishes*. Cornol: Publications Kottelat.

Lappalainen, A., Rask, M., Koponen, H. & Vesala, S. (2001). Relative abundance, diet and growth of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) at Tvärminne, northern Baltic Sea, in 1975 and 1997: responses to eutrophication. *Boreal Environment Research* **6,** 107–118.

Lappalainen, J., Tarkan, A. S. & Harrod, C. (2008). A meta-analysis of latitudinal variations in life-history traits of roach, *Rutilus rutilus*, over its geographical range: linear or non-linear relationships? *Freshwater Biology* **53,** 1491–1501.

Levine, J. M. & D'Antonio, C. M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87,** 15–26.

Levins, R. (1968). *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton, NJ: Princeton University Press.

Lockwood, J. L., Hoopes, M. F. & Marchetti, M. P. (2007). *Invasion Ecology*. Oxford: Blackwell Publishing.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M. & Bazzaz, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10,** 689–710.

Mann, R. H. K. (1973). Observations on age, growth, reproduction and food of roach *Rutilus-rutilus* (L) in 2 rivers in Southern England. *Journal of Fish Biology* **5,** 707–736.

Massa-Gallucci, A. (2009). Trophic interactions, population structure and admixture analysis of key fish species in selected Irish waters. PhD Thesis, University College Dublin, Ireland. https://library.ucd.ie/iii/encore/record/C__Rb1870814__Salexia__Orightresult__X4?lang=eng&suite=cobalt

McCutchan, J. H., Lewis, W. M., Kendall, C. & McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* **102,** 378–390.

Metcalfe, J. D. & Craig, J. F. (2011). Ethical justification for the use and treatment of fishes in research: an update. *Journal of Fish Biology* **78,** 393–394.

Mills, D. H. (1969). The growth and population densities of roach in some Scottish waters. In *Proceedings of the Fourth British Coarse Fish Conference* (O'Hara, K. & Aprahamian, C. eds), pp. 50–57. Liverpool: Liverpool University Press.

Okgerman, H., Oral, M. & Yigit, S. (2009). Biological aspects of *Rutilus rutilus* (Roach) in Sapanca Lake (Turkey). *Journal of Animal and Veterinary Advances* **8,** 441–446.

Olden, J. D., Poff, N. L. & Bestgen, K. R. (2006). Life-history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs* **76,** 25–40.

Olden, J. D., Poff, N. L. & Bestgen, K. R. (2008). Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology* **89,** 847–856.

Papageorgiou, N. K. (1979). Length weight relationship, age, growth and reproduction of the roach (*Rutilus rutilus*) in Lake Volvi. *Journal of Fish Biology* **14,** 529–538.

Parnell, A. C., Inger, R., Bearhop, S. & Jackson, A. L. (2010). Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* **5,** e9672.

Paull, G. C., Lange, A., Henshaw, A. C. & Tyler, C. R. (2008). Ontogeny of sexual development in the roach (*Rutilus rutilus*) and its interrelationships with growth and age. *Journal of Morphology* **269,** 884–895.

Persson, L. (1983*a*). Food-consumption and the significance of detritus and algae to intraspecific competition in roach *Rutilus-rutilus* in a shallow eutrophic lake. *Oikos* **41,** 118–125.

Persson, L. (1983*b*). Effects of intraspecific and interspecific competition on dynamics and size structure of a perch *Perca fluviatilis* and a roach *Rutilus rutilus* population. *Oikos* **41,** 126–132.

Persson, A. & Hansson, L. A. (1999). Diet shift in fish following competitive release. *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 70–78.

Ponton, D. & Gerdeaux, D. (1987). Roach (*Rutilus rutilus* (L)) in Lake Geneva in 1983–85 - Age structure, recruitment and growth. *Bulletin Francais de la Peche et de la Pisciculture* **305,** 43–53.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83,** 703–718.

Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D., Grosberg, R. K., HastingS, A., Holt, R. D., Mayfield, M. M., O'Connor, M. I. & Rice, W. R. (2007). Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* **22,** 465–471.

Swynnerton, G. H. & Worthington, E. B. (1940). Note on the food of fish in Haweswater (Westmorland). *Journal of Animal Ecology* **9,** 183–187.

Vander Zanden, M. J., Casselman, J. M. & Rasmussen, J. B. (1999). Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* **401,** 464–467.

Vinson, M. R. & Budy, P. (2010). Sources of variability and comparability between salmonid stomach contents and isotopic analyses: study design lessons and recommendations. *Canadian Journal of Fisheries and Aquatic Sciences* **68,** 137–151.

Vøllestad, L. A. & L'Abée-Lund, J. H. (1990). Geographic-variation in life-history strategy of female roach, *Rutilus rutilus* (L). *Journal of Fish Biology* **37,** 853–864.

Volta, P. & Jepsen, N. (2008). The recent invasion of *Rutilus rutilus* (L.) (Pisces: Cyprinidae) in a large South-Alpine lake: Lago Maggiore. *Journal of Limnology* **67,** 163–170.

Wieski, K. & Zalachowski, W. (2000). Growth of roach, *Rutilus rutilus* (L.), in the River Odra estuary. *Acta Ichthyologica et Piscatoria* **30,** 3–17.

Williams, W. P. (1967). The growth and mortality of four species of fish in the River Thames at Reading. *Journal of Animal Ecology* **36,** 695–720.

Winemiller, K. O. & Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 2196–2218.