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The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere

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The ideal free distribution (IFD) theory is one of the most influential theories in evolutionary ecology. It predicts how animals ought to distribute themselves within a heterogeneous habitat in order to maximize lifetime fitness. We test the population level consequence of the IFD theory using 40-year worth data on pike (*Esox lucius*) living in a natural lake divided into two basins. We do so by employing empirically derived density-dependent survival, dispersal and fecundity functions in the estimation of basin-specific density-dependent fitness surfaces. The intersection of the fitness surfaces for the two basins is used for deriving expected spatial distributions of pike. Comparing the derived expected spatial distributions with 50 years data of the actual spatial distribution demonstrated that pike is ideal free distributed within the lake. In general, there was a net migration from the less productive north basin to the more productive south basin. However, a pike density-manipulation experiment imposing shifting pike density gradients between the two basins managed to switch the net migration direction and hence clearly demonstrated that the Windermere pike choose their habitat in an ideal free manner. Demonstration of ideal free habitat selection on an operational field scale like this has never been undertaken before.

Keywords: density dependence; predator–prey interaction; habitat use; dispersal; *Esox lucius*

1. INTRODUCTION

The ideal free distribution (IFD) theory, as proposed by Fretwell and Lucas (Fretwell & Lucas 1970; Fretwell 1972), predicts that individuals within a habitat complex consisting of areas differing in quality will, if costs are negligible, distribute themselves in a way that results in equalized mean individual fitness among habitats as a result of individuals seeking to maximize their own fitness by making optimal habitat choices (Holt & Barfield 2001). This process can be considered an evolutionary game and when the population settles down at equilibrium, fitness should be equal across habitats. It has recently been demonstrated that the IFD is an evolutionary stable strategy in single-species systems (Cressman *et al.* 2004). Although such a large-scale prediction was the original motivation of the IFD theory, most of its tests relate to small-scale habitat use of foraging individuals over fairly short time periods (see, e.g. Tregenza 1995; Sutherland 1996; Lampert *et al.* 2003). Recently, some large-scale population-level IFD-motivated studies have been published (Bautista *et al.* 1995; Brown *et al.* 1995; Marshall & Frank 1995; Swain & Wade 1993 reviewed in Diffendorfer 1998; Morris *et al.* 2004; Shepherd & Litvak 2004), predominantly covering only a short time span. Only a few studies have compared IFD-predicted distributions with observed distributions (Swain & Wade 1993; Marshall & Frank 1995; Doncaster *et al.* 1997). However, studies having compared observed with IFD-predicted distributions all base their predictions on theory alone (e.g. Morris 1997; Morris & Davidson 2000). To our knowledge, no large-scaled study utilizing data-based *a priori* knowledge of how fitness varies with density for a given habitat complex has been reported.

In this paper, we test the population level consequence of the IFD theory using 40-year worth capture–mark–recapture (CMR) data on pike (*Esox lucius*) from Windermere in northwest England. This lake comprises two basins that differ in productivity. We estimate empirically derived density- and basin-specific fitness functions, incorporating survival- and dispersal probability as well as fecundity, to produce predictions of expected spatial distributions of the Windermere pike. These model-based predictions are compared with the observed historical spatial distributions. During the study period, a 6-year density-manipulation experiment was performed. The result of this manipulation provides a basis for experimentally testing our statistically derived conclusion regarding the presence of an IFD-motivated habitat selection in Windermere pike.

2. THE WINDERMERE PIKE AND THE IDEAL FREE DISTRIBUTION MODEL SYSTEM

(a) *Long-term data series*

Pike is the top predator in Windermere, primarily preying upon perch, *Perca fluviatilis* (Le Cren 1987). The lake

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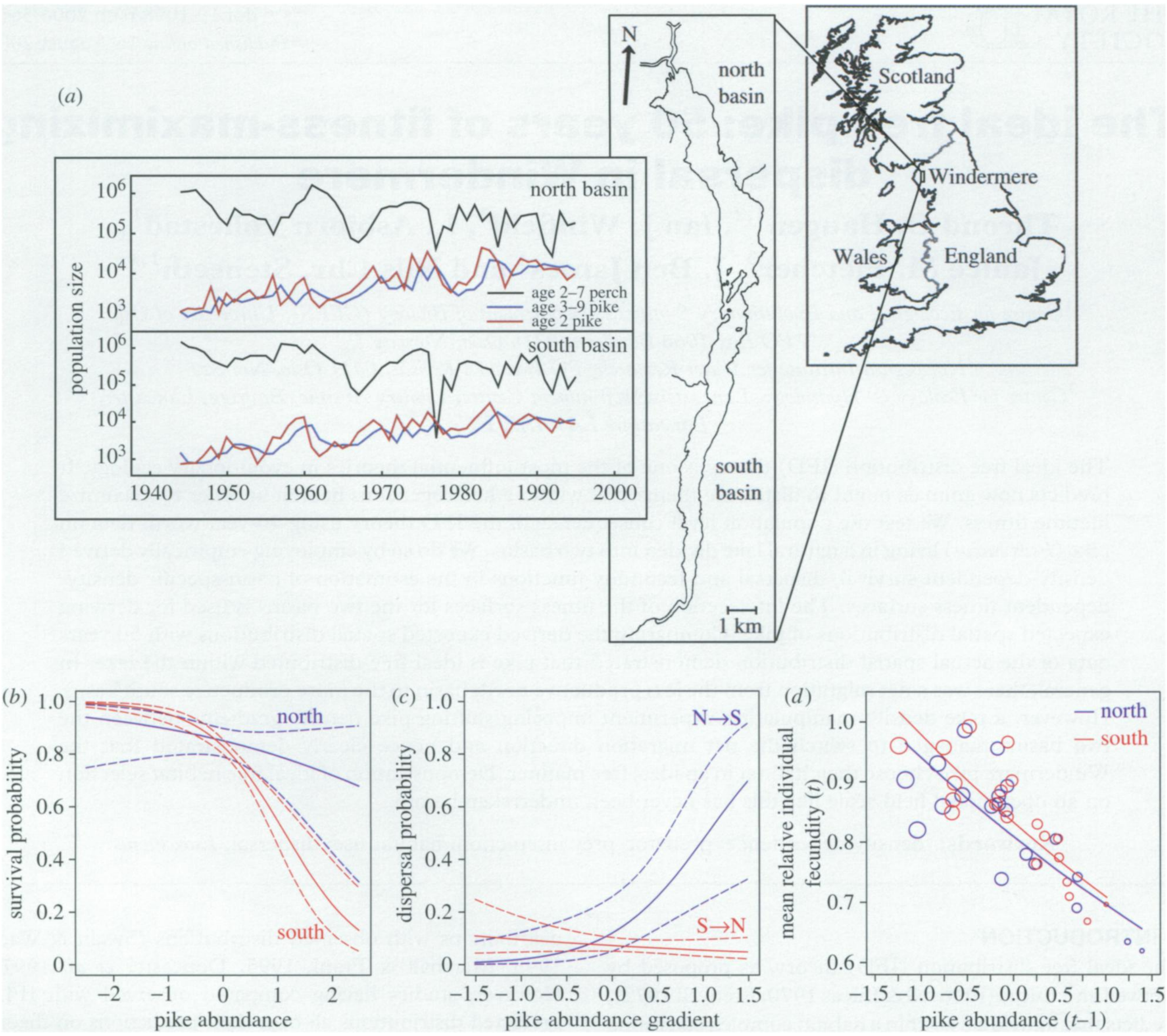

Figure 1. The study lake, abundance time-series and density-dependence of demographic components. (*a*) The study lake and time-series of annual pike and perch abundance estimates. (*b*) Estimated survival response with corresponding 95% confidence boundaries (dashed lines) as a function of age 3–9 pike abundance for males in the two study basins. (*c*) Estimated dispersal probability with corresponding 95% confidence bounds (dashed lines) as function of age 3–9 pike abundance gradient between the north and south basins. (*d*) The relationship between mean individual fecundity and pike abundance. The bubble sizes are proportional to the mean body weight of mature females during the spawning season. (*b*) and (*c*) have been estimated under a mean abundance of age 2 pike and mean abundance of perch.

consists of two basins (figure 1*a*) differing in morphology and productivity (Le Cren 1987). Both pike and perch have been subjected to extensive investigations since 1940, and during this time period, data on the total catch in standardized gears have been recorded (Kipling 1983, see electronic supplementary material). Based on these catch data, the abundance of pike and perch have been estimated annually for each basin (des Clers *et al.* 1994). The estimates of population abundance clearly demonstrate that both species have experienced profound annual fluctuations over the 50-year period for which such data are available (figure 1*a*).

An extensive CMR sampling programme on pike covering most of the same 50-year period as described (Kipling & Le Cren 1984) enabled us to derive estimates of age- and size-specific survival and dispersal probabilities, all as functions of perch- and pike abundances (Haugen *et al.* submitted). The resulting model fitted to the CMR data demonstrated that survival was much more sensitive to variation in pike density in the south basin compared with the north basin (figure 1*b*). On the other hand, between-basin dispersal probability was much more sensitive to the between-basin pike abundance gradient for the north-basin pike compared with the south-basin pike (figure 1*c*). Samples of more than 20 years of individual fecundity data facilitated the estimation of abundance-related fecundities (figure 1*d*). The mean relative (to maximum) fecundity was estimated as a decreasing exponential function of pike density and varied slightly between basins (table 1). Having these basin- and density-dependent fitness and dispersal components at hand enabled us to generate estimates of expected fitness under a variety of basin-specific pike density settings, and hence predict how the Windermere pike ought to distribute themselves according to the IFD theory.

Table 1. Parameters used for fitness estimation. (Survival and dispersal parameters are taken from Haugen *et al.* submitted) and have been estimated on a logit scale, and all covariates have been standardized to mean = 0 and s.d. = 1. The model explained 81 and 94% total and process variance in survival, respectively. For dispersal, the model explained 66 and 87%, respectively. The model structure for the fecundity models is: fecundity$(t)=\beta_0^*\exp(\beta_1^*$age 3–9 pike abundance$(t-1))$, where the pike abundance is on a standardized scale. The fitted models explained 66 and 71% variation for the south and north basins, respectively.)

response	term	estimate	s.e.m.
survival	intercept	1.35	0.10
	basin	0.14	0.24
	sex	0.25	0.10
	perch abundance	−0.02	0.08
	age 2 pike abundance	0.41	0.13
	age 3–9 pike abundance	−1.40	0.23
	basin × age 3–9 pike abundance	1.00	0.27
	age 2 pike abundance × perch abundance	−0.22	0.12
dispersal	intercept	−3.62	0.47
	basin	0.07	0.49
	sex	0.99	0.43
	age 3–9 pike abundance gradient	−0.54	0.29
	basin × age 3–9 pike abundance gradient	2.74	0.66
	perch abundance gradient	0.35	0.32
	basin × perch abundance gradient	−1.45	0.62
fecundity	intercept (north basin)	0.814	0.015
	age 3–9 pike abundance (north basin)	−0.136	0.027
	intercept (south basin)	0.836	0.012
	age 3–9 pike abundance (south basin)	−0.150	0.024

(b) *Density-manipulation experiments*

As mentioned earlier, the Windermere system experienced profound density variations both in the prey and the predator species from 1943–1995, an important prerequisite for performing field-based tests of the IFD theory. In addition, the between-basin pike density structure has been manipulated over a period of 6 years. From 1956–1962, the staff at the Freshwater Biological Association performed an experiment where they manipulated the pike densities in the two basins such that high densities were created in the north basin during the 3 years, 1956–1958 (i.e. low fishing effort in the northern basin relative to the southern basin, figure 2*a*). During the 3 subsequent years, the densities in the two basins were manipulated in the opposite direction. The high-fishing intensity treatment resulted in 15–28% removal of the pike population in the basin involved, whereas only 0.8–2.1% were removed during the low-effort treatment. This produced tremendous density gradients between the two basins. On average, the first treatment period resulted in an abundance difference of 1800 individuals in favour of the north basin, whereas the second produced a gradient of 4100 individuals in favour of the south basin. For comparison, the average population sizes in the two basins were 5400 and 6300 individuals in the period 1944–1995

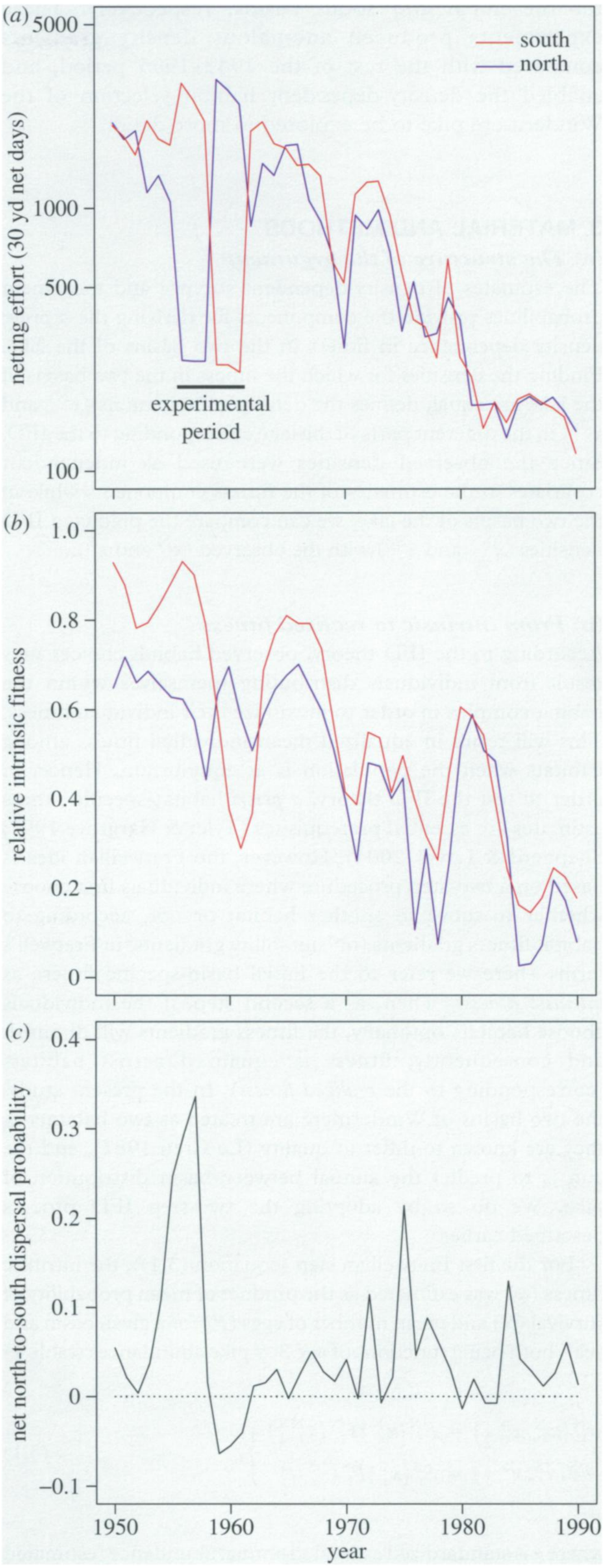

Figure 2. Basin-specific annual values of fishing effort, dispersal and intrinsic fitness. (*a*) The total basin-wise fishing effort during the winter fisheries in Windermere, 1950–1990. Pay attention to the 1956–1962 period when the pike density manipulation experiments were carried out. (*b*) Relative (to lake maximum) basin-wise annual intrinsic fitness (w_t). These values illustrate what would be the expected fitness consequences if there were, on average, no net dispersals between the basins. (*c*) Annual net north-to-south dispersal rates ($\psi_t^{NS}-\psi_t^{SN}$) estimated from mark-recapture data.

for the north and south basins, respectively. These experiments produced anomalous density gradients compared with the rest of the 1943–1995 period, and enabled the density-dependent habitat selection of the Windermere pike to be explored in more detail.

3. MATERIAL AND METHODS

(a) *The structure of the argument*

The estimates of density-dependent survival and movement probabilities provide the components for deriving the *a priori* density dependence in fitness in the two basins of the lake. Finding the densities for which the fitness in the two basins of the lake are equal, defines the density combinations (x^{N*} and x^{S*}) in the different parts of the lake corresponding to the IFD. Since the observed densities were used as independent covariates in the estimates of the fitness components while in the two basins of the lake, we can compare the predicted IFD densities (x^{N*} and x^{S*}) with the observed (x^N and x^S).

(b) *From intrinsic to realized fitness*

According to the IFD theory, observed habitat choices may result from individuals distributing themselves within the habitat complex in order to maximize their individual fitness. This will result in equalized mean individual fitness among habitats when the population is at equilibrium. Hence, in order to test the IFD theory, *a priori* habitat-specific fitness estimates are essential prerequisites (Tyler & Hargrove 1997; Shepherd & Litvak 2004). However, the Fretwellian idea is based on a two-step procedure where individuals first choose whether to move to another habitat or not, according to habitat fitness gradients (or 'suitability gradients' in Fretwell's terms—here we refer to the initial basin-specific fitness as *intrinsic fitness*). Then, as a second step, if the individuals choose habitats optimally, the fitness gradients will diminish and consequently, fitness is equalized across habitats (corresponding to the *realized fitness*). In the present study, the two basins of Windermere are treated as two habitats as they are known to differ in quality (Le Cren 1987), and the aim is to predict the annual between-basin distribution of pike. We do so by adopting the two-step IFD process described earlier.

For the first Fretwellian step (equation (3.1)), the intrinsic fitness (w) was estimated as the product of mean probability of survival (S) and mean number of eggs (F) for a given basin and year, both being functions of age 3–9 pike abundances (table 1)

$$\left.\begin{aligned} w_t^N(x_t^N, x_{t-1}^N) &= S_t^N(x_t^N)F_t^N(x_{t-1}^N) \\ w_t^S(x_t^S, x_{t-1}^S) &= S_t^S(x_t^S)F_t^S(x_{t-1}^S) \end{aligned}\right\}, \tag{3.1}$$

where x is standardized estimated annual abundance (estimated for May) of age 3–9 pike, S is the annual survival rate and superscripts of N and S indicate the basin.

By differentiating these basin-specific density-dependent fitness functions, we were able to predict the expected net dispersal direction and probability. The predictions of between-basin dispersal rates were compared with annual observed migration rates assessed from the CMR data. In particular, we explored the between-basin dispersal pattern observed during a pike density manipulation experiment (see §2*b*).

When modelling the second Fretwellian step (equation (3.2)), we estimated the expected realized fitness (λ) as:

$$\begin{aligned} \lambda_t^N(x_t^N, x_{t-1}^N, x_t^S, x_{t-1}^S) &= S_t^N(x_t^N)\psi_t^{NN}(x_t^N, x_t^S)F_t^N(x_{t-1}^N) \\ &\quad + S_t^N(x_t^N)\psi_t^{SN}(x_t^N, x_t^S)F_t^N(x_{t-1}^S) \\ \lambda_t^S(x_t^N, x_{t-1}^N, x_t^S, x_{t-1}^S) &= S_t^S(x_t^S)\psi_t^{SS}(x_t^N, x_t^S)F_t^S(x_{t-1}^S) \\ &\quad + S_t^S(x_t^N)\psi_t^{NS}(x_t^N, x_t^S)F_t^S(x_{t-1}^N), \end{aligned} \tag{3.2}$$

where ψ is the annual dispersal probability and superscripts of SN and NS indicate dispersal from south to north basin and from north to south basin, respectively. In order to explore the unique contribution from pike abundance on survival, dispersal and fecundity variation, we fixed perch and age 2 pike abundance at their mean values (i.e. mean $=0$). The age 2 pike constitute both potential prey and competitors for the age 3–9 pike. This did not produce a perch abundance gradient between the two basins, a factor known to affect Windermere pike dispersal (table 1; Haugen *et al.* submitted).

It might be said that the λ function is a highly simplistic fitness function for an age-structured species living in a temporary variable environment like the pike in Windermere. Choosing the appropriate fitness measure is not an easy task, especially with varying population size. However, a modelling study performed by Benton & Grant (2000) demonstrated that measures of reproductive performance, like the λ used in our study, produce reliable results when compared with more advanced, but less tractable methods (methods like 'evolutionarily unbeatable strategies'). Furthermore, as stated by Holt & Barfield (2001), even crude fitness measures can quite reasonably capture the IFD outcome. Having said this, we are well aware that the λ fitness function used in this study relies on the strong assumption that survival from egg to age 3 does not depend on female quality. It is well known in fishes that large females produce larger eggs than small females (also the case in pike; Kipling & Frost 1969) resulting in larger offspring (not necessarily the case in pike; Wright & Shoesmith 1988) with better prospects of survival. We tested the sensitivity of the predicted isodar to variation in effective fecundity, where effective fecundity was estimated as the predicted fecundity (see §3*d*) multiplied with a survival coefficient β_{surv} that affected the slope of the density-dependent fecundity function. The sensitivity of the predicted isodar to β_{surv} was tested first, under similar β_{surv} between basins and second, under conditions with basin-specific β_{surv} values. The first analyses covered up to a doubling of the fecundity slopes resulting in predicted isodars varying between 0.85 and 0.91 (elasticities varied between 0.10 and 0.14). The second analyses covered up to a twofold difference between basins in fecundity slopes producing isodars varying between 0.84 and 0.87 (elasticities varied between 0.02 and 0.07). We therefore find the predicted isodar results to be very robust regarding the assumption of egg-to-age 3 survival among females without variation.

With these estimates of the fitness components, we could explore the fitness consequences of the deduced density-dependent dispersal probabilities. The resulting λ values could be presented as surfaces in the x_t^N versus x_t^S space. In accordance with the IFD theory prediction of equal fitness across habitats, we wanted to estimate the between-basin pike distributions over which mean fitness is equal between basins. The intersection between the two fitness surfaces ($\lambda_t^N(x_t^N, x_t^S) = \lambda_t^S(x_t^N, x_t^S)$), also called the isodar

(Morris 1988), represents the combination of densities in the two basins corresponding to ideal free basin distribution of pike in Windermere. We refer to this realized-fitness-surface-derived isodar as the *predicted* isodar. The confidence bounds of the predicted isodar were estimated by a parametric bootstrapping method (Schweder in press). First, a total of 3000 sets of parameter values were re-sampled from the variance–covariance matrix of the survival, dispersal and fecundity parameter estimates, assuming that all parameters were normally distributed on their estimation scales (logit scale for survival and dispersal and linear scale for fecundity). Second, isodars were estimated for all 3000 of the re-sampled sets of parameters. Finally, percentile statistics were assessed at every 0.05 unit of x^{N} (i.e. standardized abundance of north basin pike). The confidence bounds were then fitted by a spline function (d.f.$=3$) to the assessed 97.5 and 2.5 percentile data, respectively.

By applying the dispersal probabilities to a matrix of all possible basin-specific pike abundances, we could predict the expected distribution of pike under which dispersal will equalize fitness across the two basins. In order to evaluate the predictive power of the predicted basin distributions of pike, we compared them with the 50 years of historical abundance estimates available from Windermere.

(c) *Estimation of survival and dispersal probabilities*

Survival- and dispersal probabilities were estimated as functions of annual pike- and perch abundances in May, incorporating sex and basin effects, by fitting 37 years of CMR data (Haugen *et al.* submitted). Using the software MARK (White & Burnham 1999), we fitted the CMR data to a multistate model structure (Brownie *et al.* 1993; Nichols & Kendall 1995), which provided estimates of basin-specific survival and dispersal probabilities under the influence of both density-dependent and -independent factors (table 1, Haugen *et al.* submitted). Because suitable pike area is similar between the two basins, standardized (i.e. (ln(abundance) − mean(ln(abundance))/std(ln(abundance)) abundance estimates were used as density in all models. The optimal model structure was chosen using quasi-corrected Akaike's information criterion (Burnham & Anderson 1998) that corrected for a slight over-dispersion ($\hat{c}=1.2$). There was no indication of lack of fit to the chosen conditional Arnason–Schwarz model structure ($\chi^2_{39}=49.3$, $p=0.13$, see electronic supplementary material for a brief introduction to the CAS parameterization). The best model explained 81 and 94% of the total and process (adjusted for sampling error) variance in survival, respectively. For dispersal, the best model explained 66 and 87%, respectively. All estimates provided in this paper relate to individuals that are larger than 55 cm ('large pike' in Haugen *et al.* submitted), and survival and dispersal probabilities have been estimated at a half-year scale (however, note that in the fitness estimation, we use annual values). Since all pike caught in the gill-net sampling of the scientific sampling programme were retained and reported, and as this gill netting is the only removal sampling occurring in Windermere for this species, the survival estimates could be interpreted as natural survival estimates. In addition, owing to the closed nature of the Windermere system, survival and dispersal were estimated under no influence of immigration from or emigration to external systems.

(d) *Estimation of density-dependence in fecundity*

Gonad investments in pike are constrained by conditions prevailing 1 year prior to spawning (Billard 1996). We therefore fitted basin-specific mean-scaled fecundity ($F_t=\text{fecundity}_t/\max(\text{fecundity})$) at year t to standardized pike abundance at time $t-1$ (figure 1*d*; Craig & Kipling 1983). In total, 20 years of fecundity data were available based on 1847 individuals. The mean-scaled fecundity was predicted from a decreasing exponential function and varied slightly between basins (table 1). A total of 71 and 66% of the variance was explained by the fitted models for the north and the south basins, respectively.

4. RESULTS

Comparisons between annual basin-specific intrinsic fitness demonstrate that between-basin gradients in intrinsic fitness have existed throughout the study period and the south basin, on average, has the highest intrinsic fitness (figure 2*b*). From 1949–1990, the annual dispersal was in favour of north-to-south migration for all but 7 years (figure 2*c*). In particular, during 1956–1958, migration in the north-to-south direction had the highest estimated probabilities over the entire data series. During the next 3 years, the highest habitat-specific dispersal rate was, for the only period in the entire data series, in favour of the south-to-north direction.

The predicted density-dependent realized fitness surfaces differ between the two basins (figure 3*a*,*b*), the main difference being that the north-basin fitness is more sensitive to variation in the north-basin pike abundance than the south-basin pike fitness. As can be seen, north-basin pike, on an average, have lower expected realized fitness than the south-basin pike when north-basin abundance is high. However, the expected realized fitness is highest for north-basin pike when both south-basin and north-basin pike abundances are low.

The predicted isodar (figure 3*c*, solid black line) explains 69.7% inter-annual variations in the historical abundance estimates and 74% abundance estimates were confined by its 95% confidence envelope. The fitted linear isodar (figure 3*c*, solid red line) explains 70.1% inter-annual variations in the historical abundance estimates.

5. DISCUSSION

The results found in this study support predictions derived from the IFD theory and clearly indicate that: (i) pike in Windermere choose habitat according to intrinsic fitness gradients and consequently (ii) distribute themselves in a way that equalizes fitness across habitats.

Under conditions with intrinsic habitat fitness gradients, the IFD theory predicts that dispersal ought to occur to equalize fitness between the two basins. On application of this theory to the estimated basin-specific intrinsic fitness values, the IFD theory predicts habitat-specific dispersal probability to be highest for the north-to-south direction as intrinsic fitness, in general, is higher in the latter. This prediction is clearly supported by the between-basin dispersal estimates revealed in this study (figure 2*c*). The pike density-manipulation experiments provide further support for an IFD-driven habitat choice in Windermere pike: (i) during the first period (1956–1958), migration in the north-to-south direction increased to 'historical' levels (the highest estimated for the entire data series) and (ii) when the fishing effort regime was changed so as to lead to high densities in the south basin and low in the north basin, the net dispersal probability was, for the only period in the

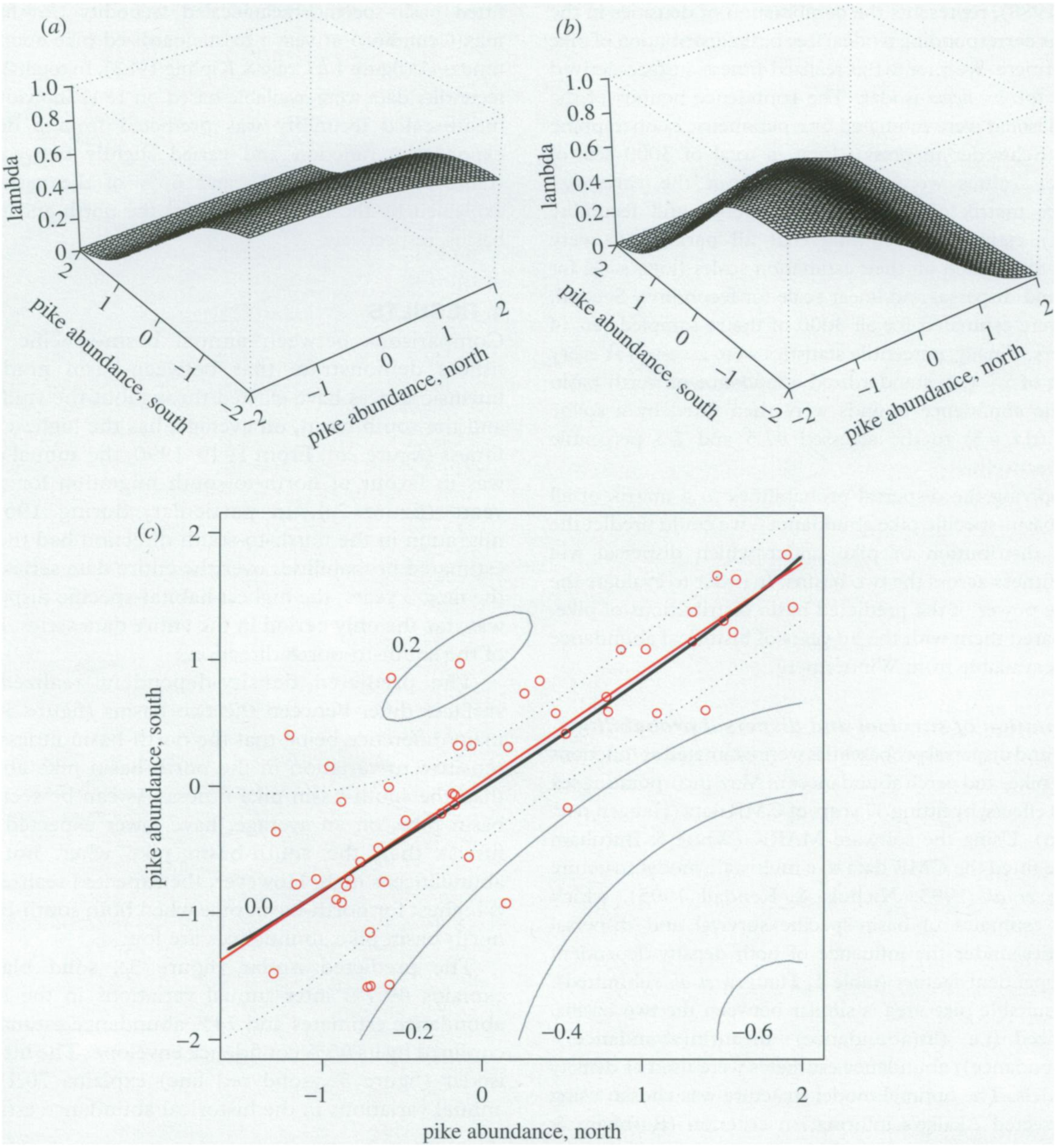

Figure 3. Estimated realized fitness surfaces and the predicted and linear isodars. The estimated realized fitness (λ in: (*a*) the south basin and (*b*) the north basin as functions of basin-specific pike abundances. (*c*) The predicted isodar (i.e. the intersection line between the two fitness surfaces, thick black line) and the corresponding 95% confidence boundary lines (dotted lines). Numbers attached to grey lines represent isocline values for the difference $\lambda^{\text{north basin}} - \lambda^{\text{south basin}}$, where the zero isocline constitutes the predicted isodar. The red open dots constitute the historical pike abundance estimates and the red line is the estimated linear isodar for these abundances (*sensu* Morris 1988). This linear isodar ($x_t^{\mathrm{S}} = 0.04 + 0.86x_t^{\mathrm{N}}$) explained 70.1% variation and the intercept is not significantly different from 0 ($p = 0.17$), whereas the slope is significantly different from both 0 ($p < 0.0001$) and 1 ($p = 0.013$).

entire data series, in favour of the south-to-north direction. That is, when intrinsic fitness gradients were manipulated to increase, the pike responded directly by increasing their dispersal rate accordingly.

The IFD theory assumes that the cost of movement between habitats should be negligible and that all individuals are able to assess the required habitat quality information to make optimal habitat choices (Fretwell 1972; Fretwell & Lucas 1970). Pike may move considerable distances (more than 2 km; Lucas 1992) during a day and are known to be able to respond to density (Grimm & Klinge 1996). Windemere is not very large (7 km between basin midpoints) compared to the daily dispersal distances observed, and pike can be expected to have no difficulty in obtaining sufficient information with relatively few costs, so as to be able to choose optimally between the two basins within the course of a year. Indeed, estimates from the CMR data clearly demonstrate that individual dispersal probability is asymmetrically density-dependent between the two basins in favour of net north-to-south dispersal (figure 2*c*), and that habitat choice hence seems likely to occur (figure 1*c*).

The IFD-expected spatial distribution of pike in Windermere (i.e. the predicted isodar) corresponded closely to the observed basin-specific distribution of pike and explained almost as much of the inter-annual variation in abundance estimates as did the fitted linear isodar (figure 3*c*). This strongly suggests that pike in Windermere distribute themselves according to the IFD theory. In fact, the slope of the linear isodar could be qualitatively predicted to be less than 1 from the density-related fecundity and survival functions (figure 1*b*,*d*). As survival in the southern basin drops off precipitously at high pike abundance, whereas relative fecundities are almost similar between basins, these relationships imply strongly converging fitness functions that yield an isodar with slope less than 1. This prediction is in accordance with the fitted slope (equals 0.86, figure 3*c*). Jonzén *et al.* (2004) demonstrate that the isodar method is sensitive to assumptions about temporal variation in habitat quality. In fact, the predicted isodar estimated in this study is based on fixed prey abundances (i.e. mean abundance of age 2–7 perch and age 2 pike). Obviously, the prey abundances fluctuate with time (figure 1*a*) in both Windermere basins. When fitting a generalized additive model (GAM) with perch abundance as a predictor of the residuals from the predicted isocline model, a significant effect with estimated d.f. = 2.8 (decided by generalized cross-validation) was found for north basin perch abundance and this variable explained 20.1% of the residual variation. This GAM showed that perch abundance had a significant contribution to the residual variation for large residual values, usually found when densities of pike were low in both basins (figure 3*c*). Even though perch abundance variation can explain some of the deviation from the predicted IFD, a lack-of-fit test ($F_{1,48} = 0.023$, $p = 0.88$) indicated no systematic deviation from the predicted central tendency. This result was further supported by fitting a GAM between historical north and south pike abundances, allowing the optimal number of knots in the spine function to be decided by a generalized cross-validation procedure. The outcome of this analysis showed that this relationship was best explained by a straight line. In conclusion, the isodar will not change, on inclusion of the perch abundance during estimation of the between-basin distribution of pike, but will be predicted with a higher precision. Hence, both the predicted and the fitted linear isodars relevantly describe the ultimate result of this study, the Windermere pike distribute themselves according to the IFD theory.

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