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DENSITY DEPENDENCE AND DENSITY INDEPENDENCE IN THE DEMOGRAPHY AND DISPERSAL OF PIKE OVER FOUR DECADES

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Abstract. Quantifying the effects of density-dependent and density-independent factors in demographic and dispersal processes remains a major challenge in population ecology. Based on unique long-term capture–mark–recapture (CMR) data (1949–2000) on pike (*Esox lucius*) from Windermere, United Kingdom, we provide estimates of density-dependent and density-independent effects, under the influence of individual size and sex, on natural survival, fishing mortality, and dispersal. Because survival is expected to be related to the individual growth process, we also explore the degree of parallelism between the two processes by applying the best-supported survival model structure to individual growth data. The CMR data were analyzed using sex- and age-structured multistate models (two lake basins: north and south) assuming no seasonal variation in survival and dispersal. Total survival and dispersal probabilities were insensitive to this assumption, and capture probability was shown to be robust to assumptions about intra-annual variation in survival and dispersal. The analyses revealed that large pike (>55 cm) displayed marked basin-specific differences in survival and dispersal responses to the abundance of conspecifics in which pike from the south basin show high density dependence in survival and a low degree of density dependence in dispersal, whereas the opposite was found for those of the north basin. Both large- and small-pike dispersals were found to be dependent upon the between-basin gradient in perch (*Perca fluviatilis*, the main prey) abundance, but most so for north-to-south dispersal. The strength and pattern of density-dependent mortality in small pike was influenced by temperature in a peculiar way: at low summer temperatures survival was lowest at high small-pike abundances and low perch abundances; at low temperatures, survival was lowest at high small-pike abundances and high perch abundances. Analyses of individual small-pike growth trajectories showed a similar modulation of the positive perch abundance effect on growth rate when temperature increases. The growth analysis also indicated that cannibalism may be biased in favor of rapidly growing individuals or at least increased growth rate for the surviving individuals. Altogether, this study provides evidence of a complex interplay between density-dependent and density-independent factors affecting survival, dispersal, and individual growth of an aquatic top predator.

Key words: cannibalism; capture–mark–recapture; demography; density dependence; Esox lucius; *growth; harvesting;* Perca fluviatilis; *predator–prey interaction; temperature; Windermere, United Kingdom.*

INTRODUCTION

Survival and dispersal are key elements in the determination of the overall dynamics of animal and plant populations. The rates of both survival and dispersal are typically affected by density-dependent (endogenous) and density-independent (exogenous) factors (Turchin 1995), and the effects of these ecological processes are commonly mediated by the size and state of the individuals involved (Lomnicki 1988). However, statistical modeling of such vital rates only rarely simultaneously consider both density-dependent and density-independent factors under the influence of individual status (but see Clobert et al. 1988, Leirs et al. 1997, Milner et al. 1999, Catchpole et al. 2000). Capture–mark–recapture (CMR) data retrieved from systems consisting of multiple sites offer a rare opportunity to study survival and dispersal processes (Altwegg et al. 2003, Schaub and Pradel 2004). Since most CMR data typically cover a short time span, the possibility for drawing general inferences regarding the role of exogenous and endogenous effects on survival and dispersal is usually very limited. However, in situations in which long-term CMR data exist, the inclusion of individual in addition to period-specific covariates allows the explicit testing of simultaneous

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effects from these variables on survival and dispersal (e.g., Franklin et al. 2000, Zabel and Achord 2004).

Using unique long-term (1949–2000) CMR data on pike (*Esox lucius*) from Windermere, United Kingdom (Kipling and Le Cren 1984), we here estimate both survival and dispersal probabilities under the influence of density-dependent and density-independent factors as well as the sex and size of the individual. The study lake consists of two basins that differ in morphology and productivity (Fig. 1), within which pike is the top predator and perch (*Perca fluviatilis*) is its main prey (Frost 1954). Over the duration of the data set, both species experienced marked fluctuations in annual abundances (Fig. 1), and in 1976 the adult perch population was almost extirpated by an epizooic infection that reduced its biomass by ~98% (Bucke et al. 1979). Owing to the close predator–prey relationship that exists between perch and pike in Windermere (Kipling and Frost 1970), it is likely that the fluctuations in abundance of these populations are related to density-dependent interaction processes between this prey and predator. However, in addition to the population density fluctuations, there have been annual variations in the local water temperature (Fig. 1) as well as in harvesting intensity (Kipling and Frost 1970). Previous work, based on catch data, has been aimed at separating the effects of density-dependent and density-independent factors on population abundance in Windermere (Kipling 1983*b*, Le Cren 1987, Mills and Hurley 1990), but none of these studies has been able to separate mortality from dispersal responses, nor have they been able to handle the effects of variation in individual size. These earlier studies, however, have generated specific hypotheses on which we base many of our model assumptions (see *Hypotheses emerging from earlier studies of the Windermere pike*).

The amount of data available and the fact that the system is a closed one facilitate a robust separation of dispersal and mortality over all capture occasions without having to take into account the influence of transient individuals (Pradel et al. 1997). Hence, the prime objective of this study is to estimate the simultaneous effects from specific density-dependent and density-independent factors on sex- and size-specific natural survival, fishing mortality, dispersal, and growth of the pike population of Windermere.

HYPOTHESES EMERGING FROM EARLIER STUDIES OF THE WINDERMERE PIKE

The Windermere pike has been studied since the early 1940s (Kipling 1984). Based on experiences and suggestions from these studies and also from the general pike literature (Craig 1996*a*), we have generated a set of specific hypotheses that will be our main focus.

Males are far more active than females during the spawning period because they stay at the spawning grounds for a longer period and they are involved in extensive territorial fights in which small males are prone to suffer from biting by the larger males (Fabricius and Gustafson 1958, Billard 1996). From this we should expect differential size-related survival between sexes. We therefore test the following hypothesis.

1) Small males experience a lower size-related survival than small females. Earlier studies on Windermere pike (and also elsewhere) suggest that pike survival is largely determined by individual size (see references in Craig 1996*a*). From this, one may deduce that growth and survival processes are determined by the same environmental factors. Kipling (1983*a*) suggested that growth in Windermere pike is highly dependent upon the interaction between temperature and perch abundance (i.e., food). We therefore test the following hypothesis.

2) Survival (and growth) in small pike (i.e., <55 cm) is affected by the interaction between perch abundance and temperature. The separation of small and large pike is related to observations of differential growth rates between these groups (Kipling 1983*a*), their differential susceptibility to cannibalism (Craig 1996*b*, Nilsson and Brönmark 2000, Persson et al. 2004), their differential risk of being caught in gill nets (Frost and Kipling 1967), and finally that small males are at high risk of being seriously wounded in fights with larger males during the spawning period (Fabricius and Gustafson 1958, Billard 1996). All of these processes behave differently for individuals that are larger or smaller than 50–55 cm. We therefore define small individuals as being smaller than 55 cm and large individuals as those larger than 55 cm. From this, we expect that abundance of small pike should have a negative influence on small-pike survival (competition) and a positive influence on large-pike survival (cannibalism). However, as both size groups of pike eat perch, the degree of between- and within-size group interactions has been suggested to depend upon perch abundance (Le Cren 1987). We therefore test the following hypothesis.

3) Survival in small and large pike is differentially affected by the interaction between small-pike abundance and perch abundance. Despite the fact that pike individuals may move over several kilometers in a few hours (Diana et al. 1977, Chapman and Mackay 1984), many studies demonstrate that most individuals do not, over extensive periods, move far from their home range (Grimm and Klinge 1996, references in Craig 1996*b*). From the Windermere data we know that ~20% of the tagged pike are recaptured in the basin opposite to the one in which they were tagged (Craig 1996*b*). Very little is known about the dynamics determining home range size in pike, but it is reasonable to expect from the general theory that prey abundance and abundance of competitors should influence this process (Krebs and Davies 1997). From this one should expect dispersal (i.e., search for unoccupied area) to increase with decreasing food abundance and increased abundance of conspecifics. As we know that annual abundances of

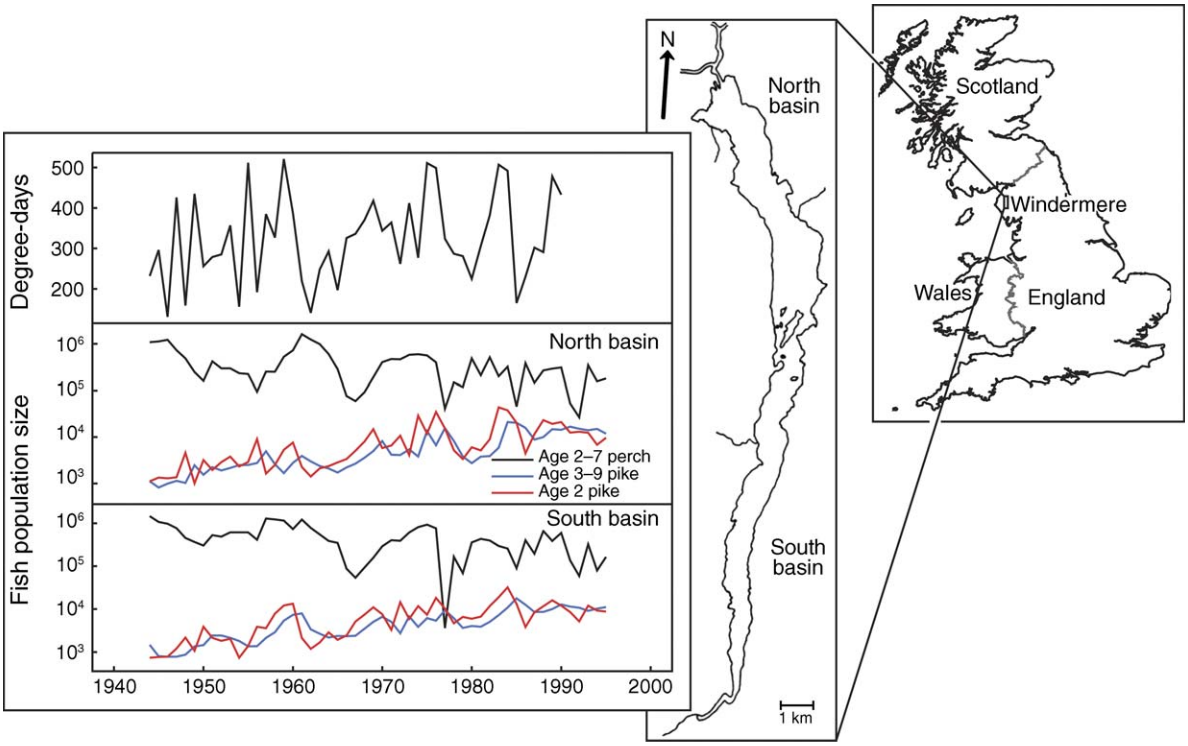

FIG. 1. Location of the study system, Windermere in northwest England, United Kingdom, and some characteristics of data used in this study. The left-most panel shows (from the top) time-series plots of temperature (number of degree-days above 14°C during May–October) and estimated abundances of perch (*Perca fluviatilis*, ages 2–7), small pike (*Esox lucius*, age 2), and large pike (ages 3–9) in the north and south basins from the 1940s to the 1990s.

both pike and perch vary between the two basins of Windermere (Fig. 1), we test the following hypothesis.

4) The probability of dispersing from one basin to the other increases when there is relatively low density of perch and high density of pike in the basin the individual currently inhabits. From catch data, we know that the 64-mm mesh size pike nets used in scientific studies on Windermere since the 1940s in general catch individuals larger than 55 cm (Frost and Kipling 1967). The recruitment of small pike into this scientific sampling (and, hence, the fishing mortality) is therefore expected to be determined by the same growth processes that are expected to influence small-pike survival. We therefore test the following hypothesis.

5) Recruitment of small pike to the gill net sampling is affected by the interaction between perch abundance and temperature. In addition to these specific hypotheses, we also explore some more generic ecological processes, including density dependence in survival (i.e., small-pike abundance will have a negative influence on small-pike survival; large-pike abundance will have a negative influence on large-pike survival). Finally, results from previous Windermere pike (and perch) population dynamics studies have demonstrated basin effects (e.g., Kipling and Frost 1970). Hence, all hypotheses have been tested taking this spatial aspect into account.

MATERIAL AND METHODS

The data

Since the 1940s, the pike, perch, and Arctic charr (*Salvelinus alpinus*) populations of Windermere have been studied in a parallel series of sampling programs (Mills and Hurley 1990), all of which have contributed components of CMR data pertinent to the present study (Fig. 2A). A spring (March–June) sampling program conducted primarily for perch monitoring purposes has also produced significant numbers of pike for tagging, for which all individuals were sexually mature (Kipling and Frost 1970, Kipling and Le Cren 1984) and has also facilitated recaptures of previously tagged pike. All such pike were sexed and weighed, and their total lengths were measured. The tags used were made of monel metal with punched individual numbers. Since 1953, all tags have been attached to the maxilla bone (upper jaw), whereas pre-1953 tags were attached to the opercular bone (Kipling and Le Cren 1984). The jaw tags have been tested and found to have very low loss rates (Kipling and Le Cren 1984), but it should be noted that, due to the existence of some tag losses, survival estimates might be biased low, although dispersal probabilities (as they are conditional on survival) should be approximately unbiased. The tagged fish were caught using four different methods: perch traps, seine nets, gill

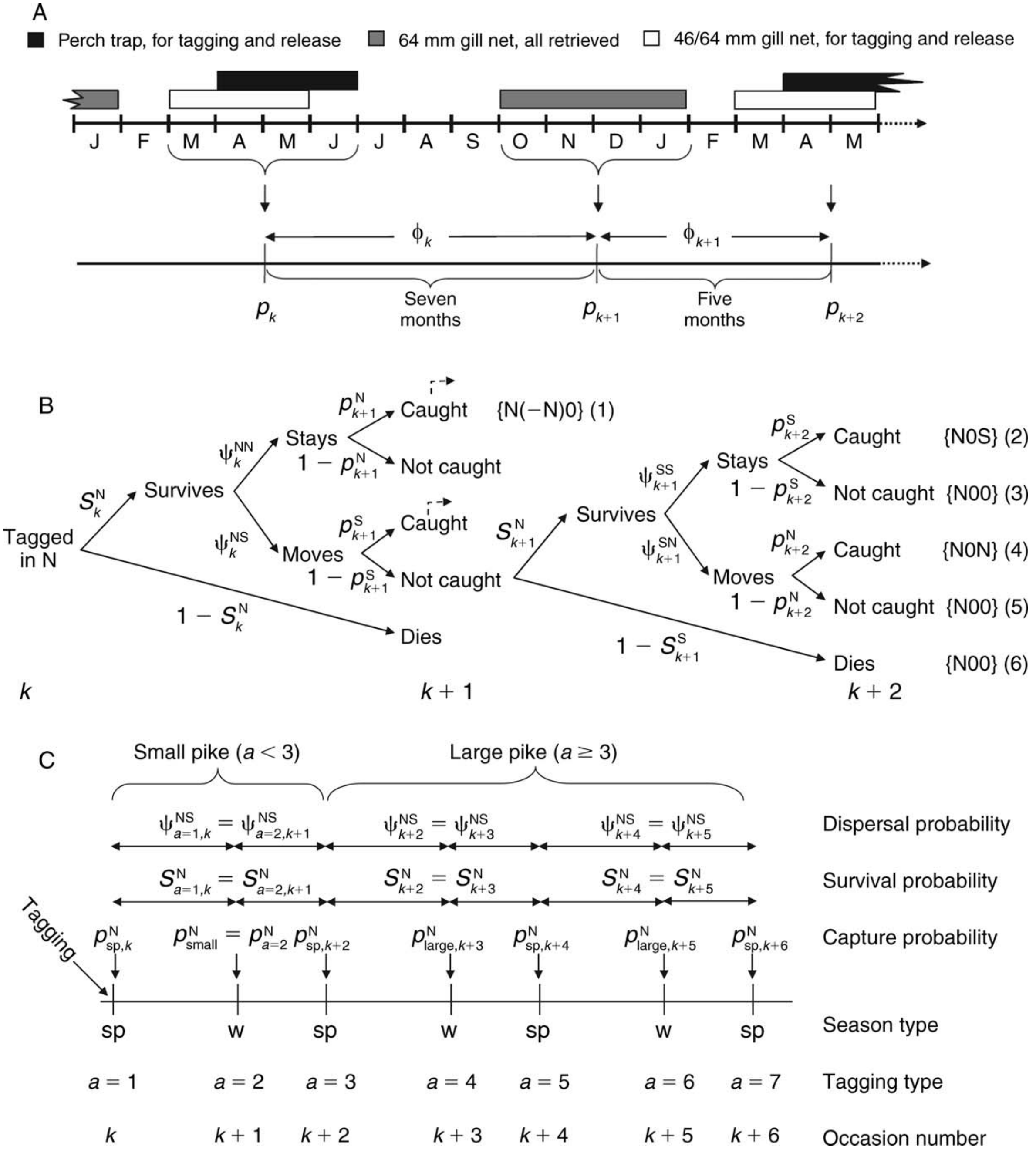

FIG. 2. (A) The sampling design and definition of capture occasions. Capture probabilities (p) were estimated for capture occasion midpoints separated by a survival period over which the survival probability (ϕ) could be estimated. (B) Multistate fate diagram of pike marked in the north basin at occasion k, separated into the Markovian steps describing survival and dispersal processes involved over two capture occasions. Following the conditional Arnason-Schwarz parameterization (Arnason 1973), S_k^N is the survival probability over the k to $k+1$ period for individuals that stayed in basin N at occasion k, ψ_k^{NS} is the probability of dispersing from N to S basin during the k to $k+1$ period (ψ_k^{NN} is the probability of staying), and p_k^N is the probability of being captured at occasion k. Capture histories for some example fates are provided in brackets to the right; 0, not caught; N, caught in the north basin; S, caught in the south basin; –N, caught in north basin and right censored. (C) The tagging age and seasonal structure of the parameters fitted to the Windermere pike capture–mark–recapture (CMR) data. An example of pike marked in the north basin at occasion k is shown. Over tagging ages less than 3 (i.e., $a < 3$) the "small-pike" parameterization was used; "large-pike" parameterization was used for $a \geq 3$. Typically, the individual size covariate was applied for small-pike parameters because size-related processes were hypothesized to be most pronounced for these individuals. There was no tagging during winter occasions, and all winter occasion recaptures were censored (all were killed); therefore, survival and dispersal parameters were constrained to be similar across spring-to-winter and winter-to-spring occasions (i.e., no seasonal variation). Capture probability parameters were possible to model for all occasions, and here we modeled with tagging age structure on winter (w) capture probabilities, but not for spring (sp) capture probabilities because the individuals were assumed to have grown into the "large-pike" group at one year following tagging.

nets, and by recreational anglers. The anglers' reports of tagging sightings were not included in this analysis because of a need to discretize the data into distinct sampling occasions (see *CMR modeling*; Fig. 2A). As recreational fishing goes on throughout the year this part of the data did not fit into the discretization criteria. The seine netting ceased in 1953, but the other capture methods have been continued to the present with varying degrees of sampling effort as described most recently by Paxton et al. (1999) for gill nets and Paxton et al. (2004) for perch traps. The gill nets were of two mesh sizes: 46 mm and 64 mm (Kipling and Le Cren 1984). There are no indications of reduced performance or survival that can be traced back to the sampling method used for accessing tagging individuals. In fact, for some batches 87% of the tagged individuals were subsequently recaptured (Kipling and Le Cren 1984), which is a very high recapture rate in fish. Gillnetting is generally considered a rough and so potentially damaging method for sampling of fish, especially for tagging and release, and small individuals are more likely than large individuals to be injured by the sampling process (gill damage). In contrast, the individuals retrieved by perch trapping and seining are unaffected by such factors. We therefore tested whether sampling method influenced length-specific survival over the first year following tagging by grouping the tagged individuals according to the sampling method from which they were retrieved. By fitting a general Cormack-Jolly-Seber model to a particularly data-rich subset of the CMR data series (1949–1965), we found a general tendency that seine- and perch-trap-caught pike had slight, but nonsignificant higher length-specific survival probabilities than gill net caught individuals (T. O. Haugen, I. J. Winfield, L. A. Vøllestad, J. M. Fletcher, J. B. James, and N. C. Stenseth, *unpublished data*). In addition to the spring (perch traps, seine nets, and gill nets), annual winter (October–February) sampling using 64-mm mesh size gill nets has also been performed throughout the time series. All pike caught during this winter sampling, including recaptured tagged pike, were killed, sexed, measured, and aged by examination of their opercular bones. Thus, no tagging was performed during the winter. Owing to reduced sampling effort in recent years, the number of pike tagged and recaptured after 1990 has been very low. Consequently, in order to standardize the data maximally (same tags and high sampling effort) only data for the 1953–1990 period have been used here, a restriction that also avoids potential complications related to a 1990s increase in lake temperature (Winfield et al. 2004) and expansion in the local roach (*Rutilus rutilus*) population (Winfield and Durie 2004). The utilized data thus relate to a total of 4543 tagged pike individuals, of which 57.9% have been recaptured at least once.

Annual age-specific abundances of both perch and pike (Fig. 1) have been estimated using a set of standard coupled fisheries population dynamics and catch models (des Clers et al. 1994) and unpublished estimates (see Appendix A for details on the estimations). The annual abundances refer to the population size in May, which corresponds to the month of recruitment of new cohorts. These abundance estimates were used as covariates, along with measurements of water temperature and fishing effort, in the CMR modeling.

In order to allow for estimation of interactions between and within size groups, the pike abundance estimates were split into age-2 and older-than-age-2 abundances. This splitting into age groups of pike is related to the growth pattern of Windermere pike, which grow rapidly up to sizes larger than 50–55 cm at ages of 3–4 yr, after which the growth ceases rapidly in males and slowly in females (Kipling 1983*a*). The importance of various sources of mortality changes dramatically as the pike become larger than 50–55 cm, being exposed to cannibalism and aggressive interactions (e.g., biting) if below this size and to the winter gill net sampling if above it. Daily surface water temperatures were measured in the junction area between the two basins and are given as degree-days (i.e., the sum of daily temperatures) of temperatures above 14°C for the April–October period (Kipling and Roscoe 1977).

CMR MODELING

Data were analyzed using a multistate capture–mark–recapture modeling approach (Brownie et al. 1993, Nichols and Kendall 1995; Fig. 2B). As sampling occasions lasted for three months, we pooled all captures into a midpoint date within each period, which is equivalent to saying that two individuals captured less than three months apart were defined to be captured at the same date (Fig. 2A). Julliard et al. (2001) used a similar approach in a study of cod (*Gadus morhua*) survival. Based on previously acquired information (see *Hypotheses emerging from earlier studies of the Windermere pike*), we have always included basin and sex effects in the models. Size-related processes were assumed to be most prominent over the period immediately following tagging (i.e., for the interval $a = 1$ to $a = 2$: Fig. 2C). There was large heterogeneity in size at tagging, and 82% of the tagged individuals were in the 30–50 cm interval (mean = 43.7 cm). According to hypotheses 1 and 4, we expect this size variation at time of tagging to impose large variability in survival, dispersal, and capture probability and, therefore, that this should be modeled explicitly. Consequently, all models fitted were structured according to tagging age in which parameters for the first two time intervals following tagging ($a = 1$ and $a = 2$) were constrained to be size dependent. Virtually all individuals attain sizes vulnerable to gill net sampling one year following tagging (i.e., $a \geq 3$, mean size at $a = 3$ was 62.6 cm), and at this time most pike have grown out of size ranges vulnerable to cannibalism (Grimm 1981). We therefore assumed that size-related effects were most prominent during this rapid-growth stage (i.e., during $a = 1$ to $a = 2$)

and that survival, catch probability, and dispersal were not related to size during later periods (i.e., $a \geq 3$). Hereafter we will refer to the "$a = 1$ to $a = 2$ models" as small-pike models and "$a \geq 3$ models" as large-pike models (Fig. 2C).

In order to test the density dependence hypotheses (i.e., hypotheses 2–5), we included age-2 and older-than-age-2 pike abundances along with perch abundance as covariates in the CMR models. Here, age-2 pike abundance was considered the appropriate covariate for modeling intra-size group interactions for small-pike parameterization and, likewise, older-than-age-2 pike abundances were used for modeling intra-large-pike interaction parameters.

In order to check for goodness of fit (GOF) of the models, multistate GOF tests were performed for spring captures only (Pradel et al. 2003). Owing to censoring of winter captures (Fig. 2B), these individuals could not be included in the GOF tests as no test has yet been developed for data including censored individuals. All GOF tests were performed using the software U-CARE 2.0 (Choquet et al. 2003). Tests of whether all individuals present at any given time on the same site behave similarly whatever their past capture history (test 3G) and whether they are currently captured or not (test M) indicated no deviations from these assumptions (test 3G, $\chi^2_{53} = 23.47$, $P = 0.99$; test M, $\chi^2_{27} = 29.89$, $P = 0.32$; see Pradel et al. 2003 for detailed descriptions of the tests). We tested the general model fit for two different multistate parameterization approaches, i.e., the Jolly MoVe (JMV) model (Brownie et al. 1993) and the conditional Arnason-Schwarz (CAS) model (Arnason 1972, 1973, Schwarz et al. 1993). The JMV model differs from the CAS model in that it permits the capture probability for the current capture occasion to depend on the state at both the current and the previous occasions. Hence, the CAS model constitutes a special case of the JMV model as it permits the recapture probability to depend only upon the current state and time. Even though the JMV structure seemed to fit the data slightly better than the CAS structure (goodness-of-fit statistics, JMV, $\chi^2_{72} = 72.3$, $P = 0.47$; CAS, $\chi^2_{39} = 49.3$, $P = 0.13$), a likelihood ratio (LR) test indicated no difference in fit between the two (LR test, $\chi^2_{34} = 23.0$, $P = 0.92$). We therefore decided to use the CAS structure. However, this decision was also motivated by the fact that (1) this structure requires fewer parameters to be estimated and (2) we have no a priori reason for expecting capture probability to be dependent upon previous captures (other than what is explicitly modeled as size-dependent recruitment to winter occasion catches). There was some degree of over-dispersion in the general time-dependent CAS model ($\hat{c} = 49.3/39 = 1.26$). However, this degree of over-dispersion is estimated under a situation without influence from covariates. The $\hat{c}$ estimate drops slightly to 1.20 ± 0.09 (mean ± SE) when using the "median c-hat" approach available in program MARK (White and Burnham 1999: Supplement S) under additive influence of external covariates. We used this $\hat{c}$ value when ranking the models. Unfortunately, there is no procedure available for estimation of $\hat{c}$ under influence of individual covariates. Hence, the $\hat{c}$ value used in this study may be biased upward.

Colinearity among predictor variables involved in the same analysis may cause correlation between parameter estimates and hence affect their inferences (Legendre and Legendre 1998). The correlation between abundance estimates and temperatures ranged between 0.05 and 0.59 and might cause colinearity artifacts. However, we have no reason to believe that the results obtained represent any artifact, as the parameter estimates were generally robust to inclusion/exclusion of correlated predictor variables in the models fitted. Moreover, in most cases we made inferences on covariate effects in an integrated fashion among covariates.

Parameterization, model selection, and model inferences

For each individual, a capture history was constructed based on information on (re)captures at each capture occasion. A capture history consists of zeroes for non-captures and N or S letters for captures in the north or south basin, respectively. Following Brownie et al. (1993), the probability of a given capture history, under a multistate setting, may be estimated as a function of (1) the probability of survival (S) from occasion k to $k + 1$, given alive at k and staying in or coming from basin j (S^j_k), (2) the probability of being (re)captured (p) when staying or entering basin i at occasion k (p^i_k), and (3) the probability of dispersing (ψ) from basin j at occasion $k - 1$ to basin i at occasion k (ψ^{ji}_k). As an example, imagine that we have two individuals, (a) and (b), that have the following capture histories: (a) NSN… and (b) N0S…. Individual (a) has been tagged in the north basin at occasion $k = 1$, recaptured in the south basin at occasion $k = 2$, and recaptured in the north basin at occasion $k = 3$. Individual (b) was tagged in the north basin, not seen at occasion $k = 2$, and recaptured in the south basin at occasion $k = 3$. The probability of having these capture histories can be estimated from: $\Pr(\mathrm{a}) = S^{\mathrm{N}}_1 \psi^{\mathrm{NS}}_1 p^{\mathrm{S}}_2 S^{\mathrm{S}}_2 \psi^{\mathrm{SN}}_2 p^{\mathrm{N}}_3 \ldots$ and $\Pr(\mathrm{b}) = S^{\mathrm{N}}_1 (\psi^{\mathrm{NS}}_1 q^{\mathrm{S}}_2 S^{\mathrm{S}}_2 \psi^{\mathrm{SS}}_2 + \psi^{\mathrm{NN}}_1 q^{\mathrm{N}}_2 S^{\mathrm{N}}_2 \psi^{\mathrm{NS}}_2) p^{\mathrm{S}}_3 \ldots$, respectively (where $q^i_k = 1 - p^i_k$).

Each of these parameters may be estimated as functions of external and/or internal covariates. In order to constrain the probabilities between 0 and 1, we used the logit link function to incorporate such predictor variables into the models. For example, the response of survival to a basin (B) effect, a sex (G, gender) effect, and a continuous covariate x is

$$S(\mathrm{B}, \mathrm{G}, x_k) = \frac{e^{(\beta_0 + \beta_{\mathrm{B}} + \beta_{\mathrm{G}} + \beta_1 x_k)}}{1 + e^{(\beta_0 + \beta_{\mathrm{B}} + \beta_{\mathrm{G}} + \beta_1 x_k)}}$$

where the βs are estimated coefficients. All covariates were standardized to mean = 0 and SD = 1 (see Table 1 for standardization parameters). Parameters were estimated by numerically maximizing the log-likelihood function

TABLE 1. Abbreviations, together with mean and variance metrics for the north and south basins used for standardization of variables in the capture–mark–recapture (CMR) analyses for pike (*Esox lucius*) and perch (*Perca fluviatilis*).

		Standardization parameters, mean (SD)	
Abbreviation	Meaning	North	South
B	basin, north (N) or south (S)		
x	estimated population size for age-2 pike, ln-transformed	8.65 (0.99)	8.47 (0.98)
y	estimated population size for age-3–9 pike, ln-transformed	8.39 (0.90)	8.31 (0.83)
z	estimated population size for age-2–7 perch, ln-transformed	12.61 (0.94)	12.80 (1.07)
a	tagging age; differs from biological age: $a = 1$ at tagging occasion		
l	individual length at tagging (cm)	50.7 (10.6)	
e	gill-net effort during winter sampling (net-days/yr)	796 (759)	945 (826)
G	sex (gender), male or female		
d	between-basin gradient in relative abundance of pike older than age 2; $y_N - y_S$		
g	between-basin gradient in relative abundance of age-2 pike; $y_N - y_S$		
f	between-basin gradient in relative abundance of perch, $z_N - z_S$		
T	degree-days (i.e., sum of daily temperatures) for water temperatures above 14°C during May–October	325 (109)	
t	time		
k	capture occasion		
j	the "from state," i.e., the basin the individual occupied at occasion $k - 1$		
i	the "to state," i.e., the basin the individual occupied at occasion k		
sp	summer occasions		
w	winter occasions		

with respect to the parameters using the software MARK (White and Burnham 1999). To examine the contribution of the covariates to model fit, we compared alternative models comprising various combinations of variables using QAIC$_c$ (the corrected quasi Akaike's Information Criterion [Burnham and Anderson 1998], $\mathrm{QAIC_c} = -2\ \text{log-likelihood}/\hat{c} + 2K + 2K(K+1)/(n_{\mathrm{eff}} - K - 1)$, where K is the number of parameters, n_{eff} is the effective number of observations, and $\hat{c}$ is the variance inflation factor). When interpreting the relevance of the various models fitted we used the Akaike model weight (w): $w_i = \exp(-0.5\Delta\mathrm{QAIC}_{ci})/\Sigma \exp(-0.5\Delta\mathrm{QAIC}_{ci})$, where $\Delta\mathrm{QAIC_c} = \mathrm{QAIC}_{ci} - \mathrm{QAIC}_{c\mathrm{min}}$.

Following Lebreton et al. (1992), we adopted a model-fitting strategy in which capture probability was modeled under full temporal variation of survival and dispersal probability and also including basin × sex effects (fully basin × sex × time models did not converge due to sparseness of data, hence the full model was basin × sex + time). After finding the most supported capture probability model, we continued by fitting dispersal probability models under the most supported capture probability model and with temporal variation in survival. Similarly, the most supported survival probability models were found under the most supported capture and dispersal probability model structures. In the end, to test for model robustness, we once more fitted capture probability models under the most supported survival and dispersal models (J. Clobert, *personal communication*). Prior to fitting models testing for support of specific a priori hypotheses (see *Hypotheses emerging from earlier studies of the Windermere pike*), we checked for evidence of temporal variation compared with constant models. The model selection procedure was based on fitting related and alternative hypotheses to the a priori hypotheses (e.g., test of additivity or interaction effect of covariates). The proportion of variation in survival and dispersal explained by the covariates included to test the specific hypotheses was estimated using two methods. First, using estimates of variance components (available in MARK [White et al. 2001]), we could estimate the proportion of survival variation explained by the covariates from: $r^2 = 1 - \sigma^2_{\mathrm{cov}}/\sigma^2_t$, where σ^2_{cov} and σ^2_t constitute the process variances (i.e., variances adjusted for sampling variance) in survival in the presence and in the absence of covariate influence, respectively (see Loison et al. 2002). Second, we used analysis of deviance to estimate the fraction of the total variance in survival and dispersal explained by the covariates, being defined as [deviance(constant model) − deviance(covariate model)]/[deviance(constant model) − deviance(time-dependent model)] (Skalski et al. 1993). We did not perform statistical tests when exploring the specific hypotheses presented in *Hypotheses emerging from earlier studies of the Windermere pike*. We rather explore and discuss their degree of support by comparing the AIC$_c$ values of the relevant model fitted with alternative models. We also use information from the relevant parameter estimates and their confidence intervals when discussing the strength of the effect of interest.

The occasions $k = 2, 4, 6$, etc., constitute winter occasions (Fig. 2C). All individuals caught during winter occasions were killed and therefore right censored. The right censoring of all winter catches obstructed estimation of seasonal survival and dispersal rates and also necessitated some constraints on the estimation of seasonal capture probabilities. All estimates of survival and dispersal rates were therefore constrained to be equal over both seasons from spring to spring (Fig. 2C), even though the between-season time spans were slightly different. There are no biological reasons for making such strong assumptions. However, due to the sampling scheme being employed, we are forced to make such assumptions. It should therefore be made clear that all CAS results presented in this paper are conditional on these assumptions. We have, however, explored the consequences for using the current parameterization by comparing it with an annual model structure (see Appendix B for details) and found that the two approaches produce essentially similar results. Hence, the parameter estimates of the seasonal model structure used in this paper do indeed seem to provide adequate annual values of the vital rates under study. In addition to this, we have also explored to what degree winter recapture rates are sensitive to variation in intra-annual survival and dispersal (see details in Appendix B). The results from this sensitivity analysis showed that p_w-related parameters are surprisingly robust towards variation in intra-annual survival and dispersal constraints as just 5.5% (4 out of 72) of the parameter estimates had values not confined by the corresponding parameter estimate confidence interval for the original model.

Since the spring capture process involved three gear types, in which effort varied both among gears and years, capture probabilities during spring could not successfully be constrained by gear-specific external covariates such as fishing effort (even though the efforts are known). These capture probability models were therefore fitted under maximum temporal variation, which necessarily required a high number of parameters to be estimated (basin × sex + time models involved 36 parameters; parameters for 1986–1990 were constrained to be similar because the number of observations was low in this period and the same effort and combination of sampling gear was used). As capture probability during winter represents the probability of being caught in gill nets during the winter program, we were specifically interested in the recruitment process to this sampling. This special feature of our data was used for the exploration of hypothesis 3, namely that recruitment of small pike to the gill net sampling is affected by the growth conditions prevailing under the growth season preceding each winter sampling occasion. For the second winter sampling occasion (i.e., $a = 4$) and thereafter, we have assumed that all surviving individuals have grown to harvestable sizes. Hence, for $a > 2$ the same winter capture parameterization was applied over all tagging ages (Fig. 2C).

Since all pike caught during the winter gill net sampling were retained and reported and because this gillnetting is the only removal fishery occurring in Windermere for this species, the estimated winter capture probabilities correspond to the fishing mortality (F). The survival estimates could be interpreted therefore as natural survival estimates, although unreported accidental mortalities due to anglers' activities (which in general is based on catch-and-release) may introduce a minor bias towards underestimation. We could therefore estimate components of total annual mortality (Z) from the sum between fishing mortality ($F = S_{\text{sp-w}} p_w S_{\text{w-sp}}$) and natural mortality ($M = 1 - S_{\text{sp-w}} S_{\text{w-sp}}$).

Factors affecting growth-related processes

Many of the models for the small pike were fitted to test for effect of size and growth on survival and/or winter capture probability. Owing to the fact that individual growth patterns could only be estimated for live and recaptured individuals, the effect of growth per se on these parameters could not be tested directly. Based on suggestions from numerous previous studies (e.g., Kipling 1983*a*, Diana 1996), we therefore included relevant environmental variables and their interactions as external covariates aiming at estimating the average effect of growth conditions on survival and winter capture probability. In order to test hypothesis 2, we fitted models including (temperature) × (perch abundance) and (perch abundance) × (age-2 pike abundance) interactions both when analyzing the CMR data and when analyzing individual back-calculated length-at-age data. The back-calculated lengths were estimated from the relationship between fish length and the opercular bone radius, using year–zone (so-called annuli) radii to assess estimates of an individual's length at the end of each winter (Kipling 1983*a*). Hence, these data constitute estimates of each individual's growth trajectory for the period up to capture. Parts of these back-calculated size-at-age data have previously been analyzed (Kipling 1983*a*), but not to the same extent as the current analyses covering the entire 1944 to 1990 period, which in total includes 14 543 individuals. We performed two separate growth analyses that covered most of the small-pike growth intervals, namely, growth between ages 2 and 3 and between ages 3 and 4. The analyses were done by ordinary multiple linear regressions (least sum of squares fitting, using the "lm" function in S-plus; S-PLUS version 6.1 2002; Insightful Corporation, Seattle, Washington, USA).

RESULTS

Constant vs. temporal vs. covariate models

Even though there was evidence for temporal variation in (re)capture, dispersal, and survival probability (temporal models had QAIC_c values that were more than 200 units lower than models with constant basin and sex effects; see Appendix C) this temporal variation was more efficiently explained by the combined effects of external and individual covariates (covariate models had QAIC_c values that were 200 units lower than temporal models). The individual size covariate was extremely important. When fitting the best model (model 1 in Table 2) without including the individual size covariate in the small-pike parameters,

TABLE 2. Model ranking and fit parameters for conditional Arnason-Schwarz (CAS) models with the change in corrected quasi Akaike's Information Criterion ($\Delta\mathrm{QAIC_c}$) ≤ 5.

Model structure for $S_{a=1}$	$\Delta\mathrm{QAIC_c}$	w_i	np	Deviance
1) $\mathrm{B} + \mathrm{G} + z + x + y + l + T + \mathrm{G} \times l + x \times z + T \times z$	0.00	0.84	74	6954.70
2) $\mathrm{B} + \mathrm{G} + z + x + y + l + T + \mathrm{G} \times l + x \times z$	2.24	0.10	73	6959.01
3) $\mathrm{B} + \mathrm{G} + z + l + T + \mathrm{G} \times l + T \times z$	2.53	0.05	71	6963.44
4) $\mathrm{B} + \mathrm{G} + z + x + y + l + \mathrm{G} \times l + x \times z$	4.41	0.01	72	6963.25
5) $\mathrm{B} + \mathrm{G} + t$	17.55	0.00	87	6945.23
6) $\mathrm{B} + \mathrm{G}$	52.76	0.00	57	7042.54

Notes: All provided models are for small-pike survival modeled under the following remainder model structure: $\{S_{a>1}(\mathrm{B}+\mathrm{G}+z+x+y+\mathrm{B}\times y+x\times z)p_{a=1,\mathrm{w}}(\mathrm{B}+e+z+l+T+T\times z)p_{a>1,\mathrm{w}}(\mathrm{B}+\mathrm{G}+e+\mathrm{B}\times\mathrm{G})p_{\mathrm{a}>1,\mathrm{sp}}(\mathrm{B}\times\mathrm{G}+t)\psi_{a=1}(\mathrm{B}+\mathrm{G}+\mathrm{B}\times f)\psi_{a>1}(\mathrm{B}+\mathrm{G}+d+f+\mathrm{B}\times d+\mathrm{B}\times f)\}$. Models 5 and 6 constitute fully temporal and constant models, respectively. A more detailed model-ranking table is provided in Appendix C. Abbreviation symbols are available in Table 1. Key to abbreviations: np, number of parameters; w_i, the Akaike weight of model i [$= \exp(-0.5\Delta\mathrm{QAIC}_{ci})/\Sigma \exp(-0.5\Delta\mathrm{QAIC}_{ci})$]; deviances and $\Delta\mathrm{QAIC_c}$ ($= \mathrm{QAIC}_{ci} - \mathrm{QAIC_{cmin}}$) have been estimated under an inflation factor of $\hat{c} = 1.20$. The number of individuals used in the analyses is 4543, and the number of occasions is 74.

$\mathrm{QAIC_c}$ increased by 197.2 units. The best model explained 81% and 94% of the total and process variance in survival, respectively. For dispersal, the best model explained 66% and 87%, respectively. The dynamics resulting from model 1 are visualized in Fig. 3.

Survival, dispersal, and fishing mortality in small pike individuals

For small pike, length at tagging was important for all three parameter types (p, ψ, S) in both basins. A pronounced sex × length effect (hypothesis 1) estimated survival probability in females smaller than 55 cm at time of tagging to be more than 0.9, whereas males in the same size range (30–55 cm) were estimated to have survival probabilities of 0.3–0.8 at average levels of perch and pike abundances and temperature (i.e., 0; Fig. 4A, Tables 2 and 3). Models including interaction effects between temperature and perch abundance (hypothesis 2) and between perch abundance and age-2 pike abundance (hypothesis 3) also obtained high support. According to these models, small-pike survival was more sensitive to variation in perch and age-2 pike abundance under cold conditions than under warm conditions, and generally the survival probability increased with increasing temperature (Fig. 5A–E). In general, all models estimated small pike in the north basin to have slightly lower survival probabilities than small pike in the south basin. For small pike individuals, dispersal probability (ψ) was sensitive to the between-basin difference in perch abundance, and the highest ranked model estimated dispersal probability to increase when perch abundance was lower in the departure basin compared to the destination basin (hypothesis 4). However, dispersal in the north-to-south direction was more sensitive to this gradient than dispersal in the south-to-north direction. Capture probability during the winter sampling was estimated to increase with increasing size at tagging and was generally highest in the north basin (Fig. 4B). Interestingly, there was no evidence of a sex effect on small-pike winter sampling capture probability, but models with a temperature × perch abundance effect received high support ($\Delta\mathrm{AIC_c} = 3.9$ compared to a model without the interaction, but otherwise similar), predicting that the positive effect of perch abundance is more profound under warm conditions than cold conditions (hypothesis 5; Table 3).

Growth analysis

The growth analysis revealed very similar basin and sex-specific effects from the covariates on both age 2–3 and age 3–4 growth (Table 4). Temperature, perch abundance, and older-than-age-2 pike abundance all had a significant positive effect on growth increment, whereas age-2 pike abundance had a negative effect on growth increment. Interaction effects between temperature and perch abundance and between perch abundance and age-2 pike abundance were significant and had the same signs as in the small-pike survival model (hypothesis 2; Table 3). The data did not support any interaction effect between sex and length at age 3 on length at age 4 ($P = 0.18$), and there was no evidence for a basin effect on length at age 3 ($P = 0.90$).

Survival, dispersal, and fishing mortality in large pike individuals

For large pike, the best survival models (Tables 2 and 3) estimated survival to be higher in the north basin and highest for males within that basin. Also, models including an interaction effect between basin and abundance of older-than-age-2 pike obtained high rankings and estimated survival to be more density dependent in the south basin compared to the north basin (Fig. 6A). Large-pike survival probability was estimated to be almost unaffected by perch abundance and to increase with age-2 pike (rapid) abundance in both basins (hence, supportive of hypothesis 3 when combining with the results for small pike). North-to-south dispersal for large-pike individuals was estimated to be driven much more by between-basin relative

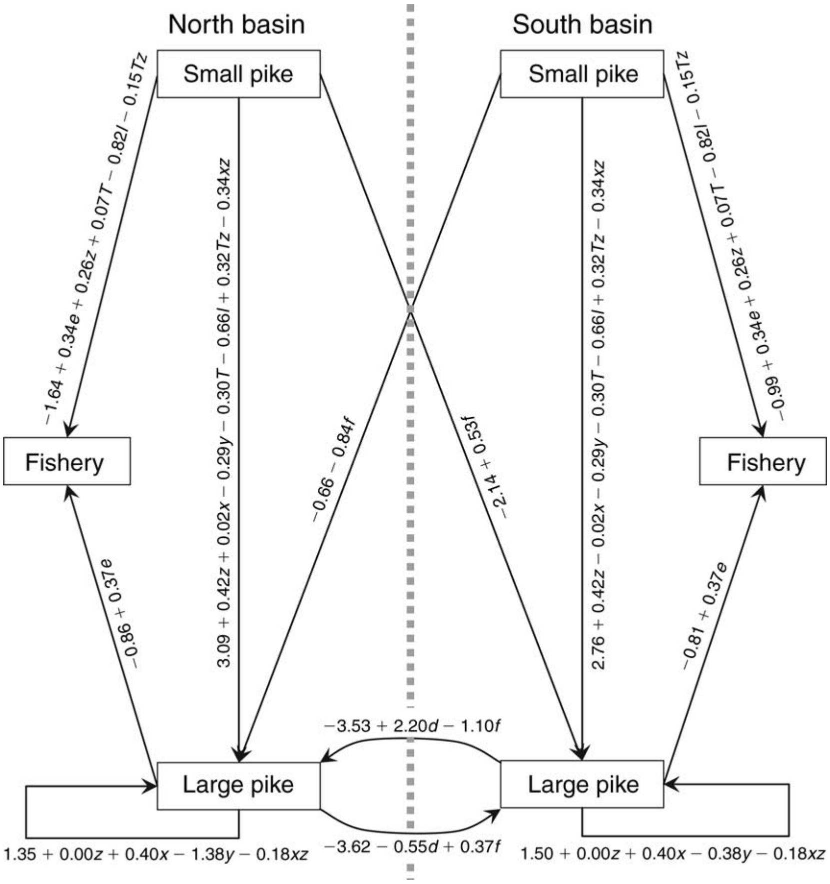

FIG. 3. Flow diagram of the population dynamics in the conditional Arnason-Schwarz (CAS) model described in Table 3. Arrows illustrate processes between spring sampling occasions and winter sampling occasions. Functions attached to each process arrow show the direction and magnitude (i.e., the coefficients) of the factors affecting these processes. Arrows that cross the dashed vertical line illustrate dispersal. Abbreviations of factors are identified in Table 1. Note that there is no dispersal between north and south basins for small pike because the small pike become large pike during the dispersal period (from spring to winter).

abundance differences of both older-than-age-2 pike and perch than was south-to-north dispersal (hypothesis 4; Fig. 6B). Hence, for situations with similar perch abundances (i.e., perch abundance gradient = 0) in both basins a difference in older-than-age-2 pike relative density of 1 SD unit in favor of the north basin would produce a north-to-south dispersal probability at 0.47 ± 0.12. Similarly, for a situation in which the older-than-age-2 pike density gradient is 1 SD unit in favor of the south basin, south-to-north dispersal probability is estimated to be 0.09 ± 0.03. Dispersal probability in large pike individuals was generally estimated to be higher in males than females. Winter capture probabilities in large pike individuals were, for a given fishing effort level, estimated to be significantly higher for north basin males than for all other sex and basin combinations (north males, $p_{wi} = 0.42 \pm 0.12$; remainder, $p_{wi} = 0.30 \pm 0.07$, for effort fixed at 0, i.e., the mean; see Fig. 7A). However, because north basin males have higher natural survival, the total mortality rate is only slightly higher for these individuals compared to the other individuals (Fig. 7A). In small pike individuals, males from both basins had much higher total mortality rates than the females when smaller than 55 cm at tagging, whereas the two sexes had very similar total mortalities at tagging sizes above 55 cm (Fig. 7B, C). The relative contribution to total mortality from fishing differed profoundly between sexes, always increasing with tagging length in males and remaining fairly stable in females.

DISCUSSION

Over the last few decades there has been considerable progress in the quantification of the effects of density-dependent and density-independent processes on population dynamics and demographic processes (see, e.g., Turchin 1995, Leirs et al. 1997, Julliard et al. 2001, Yoccoz et al. 2001). More recently, there has also been some interest in the quantification of the interaction between such density-dependent and density-independent factors (see, e.g., Coulson et al. 2001, Stenseth et al. 2004). Our study falls directly within these traditions and, by taking advantage of a long-term data series of CMR data, we have provided evidence of a complex interplay between density-dependent factors (prey and competitors) and density-independent factors (temperature) in determining the survival and dispersal probability of pike in this large natural lake system.

Long-term CMR data do provide important information about ecological processes

Long-term capture–mark–recapture data series are not numerous, but when available they have a tremendous potential for providing information about detailed ecological and evolutionary processes. Because most of them, at least for fish data series, have not been commenced with the purpose of enlightening such processes the data most likely violate various assumptions that are vital for performing CMR statistical analyses. In the current study, this was the case as there was no (re)release of tagged individuals during the winter sampling occasions, a prerequisite for most CMR models (Lebreton et al. 1992). Even though the sensitivity analyses undertaken in this study generally showed that most of our assumptions had little effect on the parameters under estimation, this was not an obvious result. For instance, Schaub et al. (2004) shows that multistate models perform well even in situations with temporary emigration from the sampling area. However, this was only true if not all parameters (survival, capture probability, and dispersal) varied over time and provided that capture and survival probability are relatively high. Hence, we want to emphasize that most of the CAS results presented in this paper are conditional on the rather strong assumption of no seasonal variation in survival and dispersal. Even though the parameter estimates produce estimates on annual scales that are consistent with similar estimates from models fitting annual rates directly (Appendix B) and even though capture probability proved to be robust for forced intra-annual variation in survival and dispersal (Appendix B), one must keep this condition in mind when interpreting the results. These sensitivity analyses, which we believe to be a fairly unique exercise in CMR studies, have only shown that some of the estimates are fairly robust, but we still do not know whether there is seasonal variation in any of the parameter types estimated. In the future, we strongly encourage researchers to construct CMR studies that enable testing for the presence of seasonal variation in these vital rates.

The specific hypotheses and relevance for pike ecology

In this study, we formulated a set of hypotheses of particular interest in pike ecology. Clearly, these hypotheses are also relevant for other top-predator species with indeterminate growth, but these general ecological aspects of our results will be discussed after having dealt with the more pike-specific features. The hypotheses were not tested by means of strict statistical testing, but by exploring the significance of the coefficients involved in the various hypotheses we will here discuss to what degree they received support in the data.

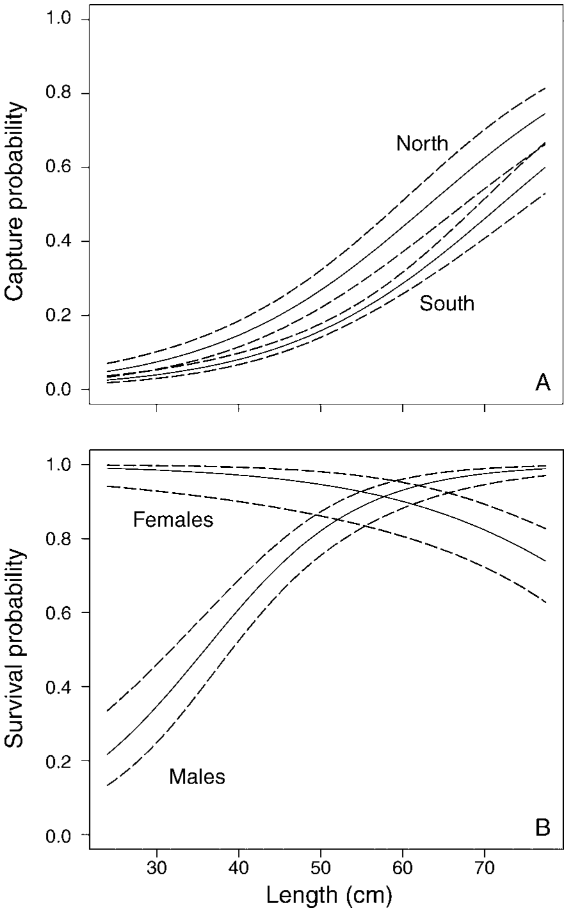

FIG. 4. Length effects on capture and survival probability immediately following the tagging occasion ($a = 1$). Solid lines are model predictions, and dashed lines correspond to 95% CI. (A) Estimated small-pike capture probability for pike from north and south basins as a function of size at tagging. This plot can also be considered as the size-dependent recruitment curve to the winter fisheries. (B) The interaction effect of sex and size on half-year natural survival probability for the period following tagging. Predictions apply to pike from the north basin where age-2 pike, pike older than age 2, and perch abundances all are fixed at 0, i.e., mean ln(abundance).

Hypothesis 1 tested whether small males experience a lower size-related survival than small females. Sex differences in survival of pike have been documented (see references in Craig 1996*b*), and some studies indicate size-related survival (e.g., Raat 1988). However, this study provides the first quantification of size-specific mortality in pike. The higher mortality rate of mature male pike smaller than 55 cm (Fig. 4A) compared to similarly sized females is supportive of hypothesis 1 and is in agreement with earlier studies (reviewed in Craig 1996*a*) and in particular with previous findings from Windermere (Kipling and Frost 1970). However, males

Table 3. Parameter estimates over the best conditional Arnason-Schwarz (CAS) model (model 1 in Table 2) fitted to Windermere pike capture–mark–recapture data.

Survival probability, S			Winter capture probability, p			Dispersal probability, ψ		
Parameter (interpretation)	Estimate	SE	Parameter (interpretation)	Estimate	SE	Parameter (interpretation)	Estimate	SE
Small pike								
β_0 (intercept)	3.09	0.53	β_0 (intercept)	−1.64	0.08	β_0 (intercept)	−2.14	0.14
β_B (basin)	−0.33	0.21	β_B (basin)	0.65	0.16	β_B (basin)	1.48	0.21
β_G (sex)	−1.11	0.52	β_e (effort)	0.34	0.06	β_G (sex)	−0.15	0.08
β_z (perch)	0.42	0.13	β_z (perch)	0.26	0.06	β_f (perch gradient)	0.53	0.17
β_x (small pike)	−0.02	0.21	β_T (temperature)	0.07	0.06	$\beta_{B\times f}$ (basin × perch gradient)	−1.37	0.32
β_y (large pike)	−0.29	0.13	β_l (length)	0.82	0.06			
β_T (temperature)	−0.30	0.14	$\beta_{T\times z}$ (temperature × perch)	−0.15	0.08			
β_l (length)	−0.66	0.18						
$\beta_{G\times l}$ (sex × length)	1.82	0.28						
$\beta_{T\times z}$ (temperature × perch)	0.32	0.14						
$\beta_{x\times z}$ (small pike × perch)	−0.34	0.14						
Large pike								
β_0 (intercept)	1.35	0.10	β_0 (intercept)	−0.86	0.12	β_0 (intercept)	−3.62	0.48
β_B (basin)	0.15	0.22	β_B (basin)	0.05	0.27	β_B (basin)	0.09	0.53
β_G (sex)	0.26	0.10	β_G (sex)	−0.03	0.15	β_G (sex)	1.01	0.42
β_z (perch)	0.00	0.09	$\beta_{B\times G}$ (basin × sex)	0.57	0.20	β_d (age >2 pike gradient)	−0.55	0.27
β_x (small pike)	0.40	0.14	β_e (effort)	0.37	0.05	$\beta_{B\times d}$ (basin × age >2 pike gradient)	2.75	0.62
β_y (large pike)	−1.38	0.24				β_f (perch gradient)	0.37	0.32
$\beta_{B\times y}$ (basin × large pike)	1.00	0.28				$\beta_{B\times f}$ (basin × perch gradient)	−1.47	0.65
$\beta_{x\times z}$ (small pike × perch)	−0.18	0.09						

Notes: The parameters are shown as β values indexed by their respective predictor variables. Spring capture probability estimates are not provided as they have been estimated under full temporal variation. The default basin (B) is north, and default sex (G) is male. All estimates are provided on a logit scale.

surviving beyond 55 cm experience higher survival prospects than do females. It is interesting to note that individuals that were tagged at lengths larger than 55 cm (but that were modeled as small pike) were estimated to have the same sex-specific level of survival as individuals modeled under the large-pike model (i.e., male survival is higher than female survival; Figs. 4A and 7A). Most of the sex differentiation in size effects on survival may be explained by the reproductive biology of pike (Lucas 1992). During the spawning period, males are far more active than females, they stay at the spawning grounds for a longer period, and they are involved in extensive territorial fights in which small males are prone to suffer from biting by the larger males (Fabricius and Gustafson 1958, Billard 1996). However, after reaching sizes beyond about 50 cm, the gape size of other males is too small to inflict serious bites.

The strong support for size-related variation in natural survival and fishing mortality found within this group of mature fish has important population ecology consequences. Simply distinguishing between mature and immature survival as such, which is a common practice in fish population ecology studies, is inadequate when performing population analyses for pike. As the length effect was very different between sexes, both length distribution and sex ratio should be included in any population analysis of this species.

Hypothesis 2 tested whether survival (and growth) in small pike is affected by the interaction between perch abundance and temperature. Indeed the perch × temperature interaction coefficients were shown to be statistically different from zero for both the survival and growth response (Tables 3 and 4), which is supportive of the hypothesis. By fitting both a growth and a survival model, using the same predictor model structure, we were able to explore the growth- and size-related processes involved in survival in greater detail than would have been the case if we had included only the survival analysis. In the hypothesis 2 context, the interaction effect between temperature and perch abundance in both the survival model and the growth model entails a modulation of the positive effect of increased perch abundance such that it is less pronounced under cold than warm conditions. However, the finding that temperature has an overall positive effect on growth, but not on survival, suggests that surviving individuals (being involved in our growth analysis) exhibit a different temperature-related behavior than those dying (being included in the survival analyses). One possibility would be that the dying individuals exhibit a more risk-prone behavior than the surviving individuals under warm conditions than under cold conditions. This is a testable hypothesis that should be explored in the future under controlled conditions. The predicted rise in temperature over all

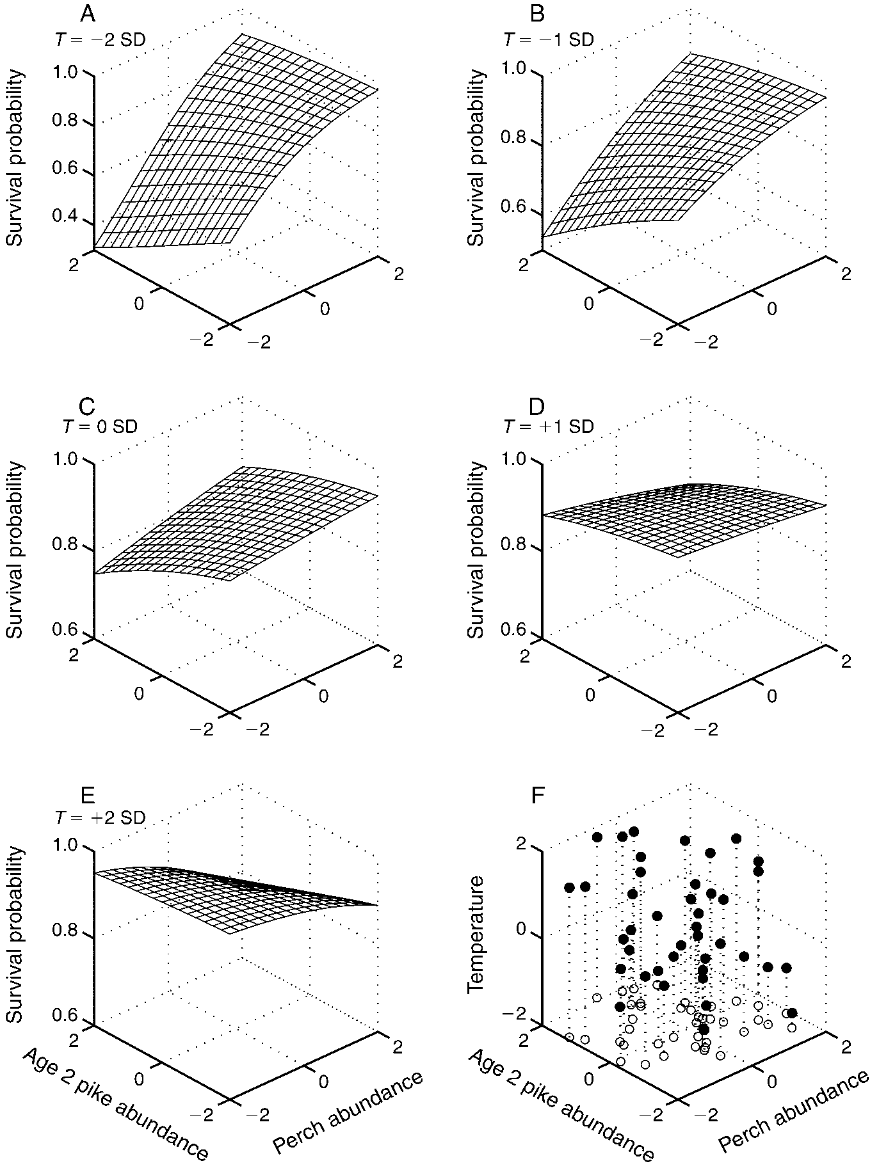

FIG. 5. The estimated interaction effect between mean standardized perch abundance and age-2 pike abundance in half-year survival of north-basin male pike for the period following tagging ($a = 1$) at a temperature of: (A) +2 SD units (543 degree-days), (B) +1 SD units (434 degree-days), (C) 0 SD units, i.e., at mean (325 degree-days), (D) −1 SD units (216 degree-days), (E) −2 SD units (117 degree-days). (F) Drop-line plot of the distribution of annual perch and age-2 pike abundances and temperatures. T values are standardized values of water temperature sums for water temperatures above 14°C during May–October. The values are provided in SD units.

of the northern pike distribution area in the northern hemisphere (Johns et al. 2003) makes this test particularly pertinent. Similarly, when comparing the effect from abundance of pike older than two years and temperature on survival and growth we also exposed an interesting feature as both effects were positive on pike growth, but negative on small-pike survival. Although this appears to be contradictory, owing to the negative influence of large pike on small-male pike survival, the surviving individuals, on whom we could perform the growth analysis, seem to experience better growth conditions due to the resulting reduction in competition. Alternatively, or in addition to this, pike older than two years may have a more negative impact on slow-growing individuals (which is very likely under size-biased cannibalism) than on rapidly growing individuals (Grimm 1981). The first alternative constitutes a phenotypic plastic response to increased food availability, whereas the second one constitutes natural selection that may, given that genetic variation is available, result in local adaptation to a cannibalistic regime. Our data do not allow for further exploration of these alterna-

TABLE 4. Parameter estimates and model fit statistics for linear models fitted to age-specific back-calculated length data.

	Response					
	ln(age-3 length)			ln(age-4 length)		
Effect	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	1.6462	0.0104	<0.0001	1.3233	0.0114	<0.0001
Basin	0.0000	0.0004	0.9009	−0.0008	0.0003	0.0044
Sex	0.0562	0.0101	<0.0001	0.0440	0.0108	0.0001
ln(age-2 [or age-3] length)	0.6354	0.0028	<0.0001	0.7081	0.0029	<0.0001
Perch	0.0043	0.0005	<0.0001	0.0043	0.0004	<0.0001
Age-2 pike	−0.0034	0.0004	<0.0001	−0.0024	0.0004	<0.0001
Older-than-age-2 pike	0.0022	0.0005	<0.0001	0.0014	0.0004	<0.0001
Temperature	0.0106	0.0005	<0.0001	0.0058	0.0004	<0.0001
Age-2 pike × perch	−0.0037	0.0006	<0.0001	−0.0004	0.0003	0.0813
Temperature × perch	0.0039	0.0005	<0.0001	0.0006	0.0003	0.0277
Sex × ln(age-2 [or age-3] length)	−0.0058	0.0027	0.0338	−0.0037	0.0027	0.1752

Notes: The model structure fitted corresponds to the best small-pike survival model (Table 3). For ln(age 3 length) and ln(age 4 length), respectively, summary model statistics are: multiple $R^2 = 0.86$ and 0.92; $F = 7738$ and 11 570; df = 10, 13 764 and 10, 11 277; $P < 0.0001$ for both ages.

tives. Further studies should focus on this, as revealing the relative role of the two processes will improve our ability to understand the process of self-structuring in this species and other top-predator fish species as well.

Before leaving the perch and temperature effects on survival of small pike, we want to look at the combined effect from these predictor variables with the effect of small pike, i.e., how did temperature modify the density-dependent effects of food availability (perch abundance) and competition (small-pike abundance) on survival? We did not formulate any a priori hypothesis for testing this highly relevant ecological formulation, but the combined effect of the perch × temperature and small pike × perch interactions (Fig. 5) demonstrated that the combined effect of competition and prey abundance is highly modulated by temperature. In particular, we find that if temperatures are high, an increase in perch abundance will actually decrease small-pike survival and particularly so if the abundance of competitors is high. Why should an increase in prey abundance be negative for small pike? When temperatures get high, metabolic costs from both swimming and digestion increase rapidly in a cold-water-adapted species such as northern pike (Diana 1996). Further, Jones et al. (1974) have documented that pike are very poor sustained swimmers, with critical swimming velocities at 0.5 body length units per second that can only be maintained over some two minutes. Such physiological constraints can become critical at high temperatures as the perch, a more warm-water-adapted species (Bergman 1987), may have higher escape success under warmer conditions and hence impose starvation and decreased survival in the small pike. This situation will of course become particularly critical if the number of competitors is high, as energy expended on agonistic behavior, such as territory defense, will impose further deficit to the energy budget and lead to reduced prospect of survival.

Survival of large pike responded differently to the interaction between perch and age-2 pike abundance than did survival in small pike. This is in accordance with hypothesis 3. For large pike, survival increased with increasing age-2 pike, but not with increasing perch density (Table 3). As both age-2 pike and perch are potential prey for large pike the lack of positive perch effect may seem counterintuitive. However, because age-2 pike also eat perch and thus may compete with larger pike, the outcome of the perch vs. age-2 pike abundance interaction effects on large-pike survival is not a straightforward prediction. One interpretation of the results is that intra-size group interactions among small-pike individuals impose more serious effects on small-pike survival than inter-size group interactions between small- and large-pike individuals impose on large-pike survival. There is indication of an inter-size group effect on large-pike survival as the increase in survival probability with increased perch abundance is estimated to be lower at high age-2 pike abundances than at low abundances.

Our study demonstrates that between-basin dispersal is driven by prey abundance gradients (both small and large pike) and density of conspecifics (large pike only), which is largely supportive of hypothesis 4. Models including pike (both age-2 and older-than-age-2) abundance gradient effects in small-pike dispersal consistently received less support ($QAIC_c$ was consistently more than 2.3 units larger; see Appendix C) than those not including such effects. This finding is not in accordance with hypothesis 4. Pike has previously been shown to respond to density gradients by dispersing (Grimm and Klinge 1996). Hence, we should therefore expect even small pike to respond to such gradients. One possible explanation for this result is that small pike disperse over larger distances in response to decreased prey density compared to the response to increased pike density. Consequently, our spatial scale of dispersal (i.e., between-basin) would be too coarse to detect conspecific density dependence of small-pike dispersal. There was a net migration rate from the north to the south basin,

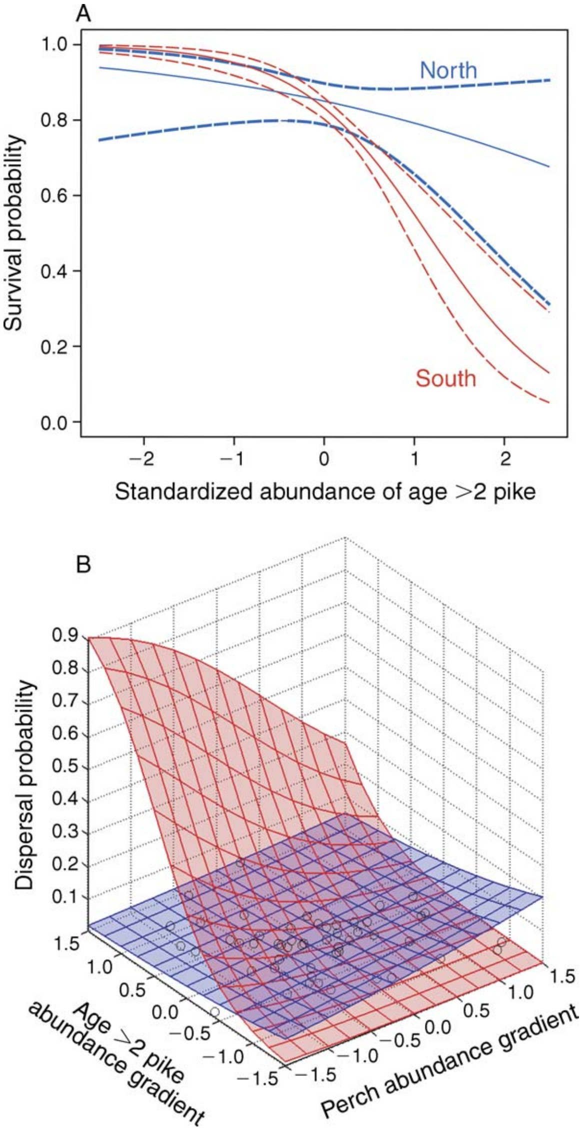

FIG. 6. Density-dependent effects on survival and dispersal in pike larger than 55 cm ($a > 1$). (A) Estimated natural survival probability in $a > 1$ pike as a function of standardized older-than-2-years pike abundance and basin. Values are adjusted to mean standardized ln(abundances) of perch and age-2 pike abundances (i.e., 0). Solid lines are model predictions, and dashed lines correspond to 95% CI. (B) Estimated simultaneous effects of between-basin abundance gradients of perch and pike older than age 2 on dispersal of large male pike. The abundance gradients have been estimated as the difference in standardized abundance between north and south basins (hence, high values indicate high relative abundance in the north basin compared to the south basin). Only male predictions are provided because the sex effect was additive in favor of higher male dispersal probability (Table 3). Red and blue surfaces are for north-to-south and south-to-north dispersals, respectively.

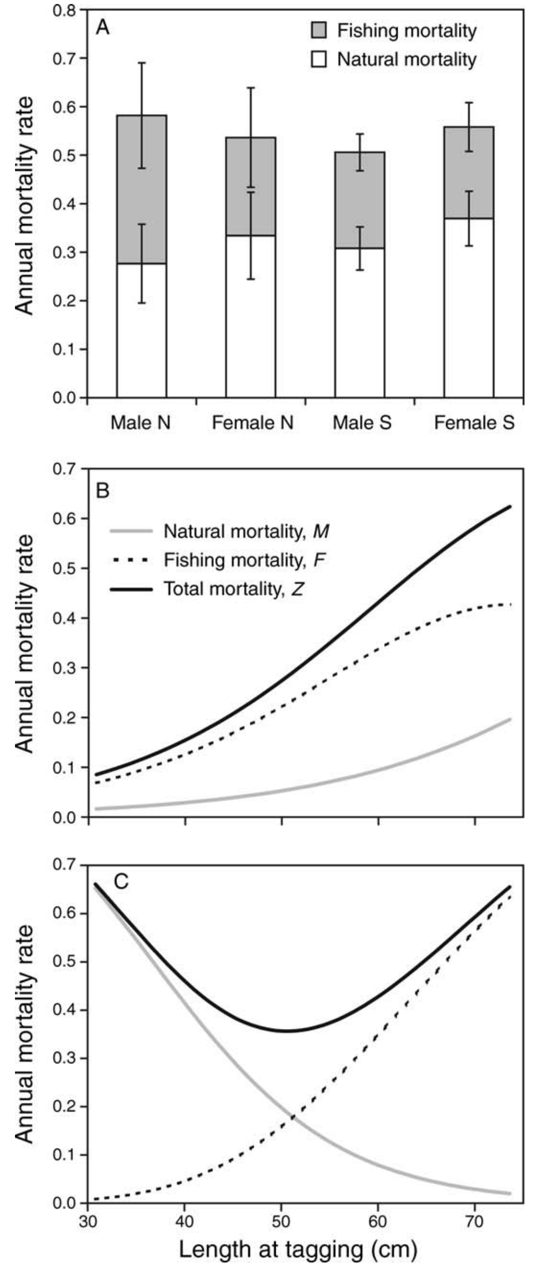

FIG. 7. Natural, fishing, and total mortality by pike sex and basin (N, north; S, south). The relative contributions from natural mortality (M) and fishing mortality (F) to the total mortality (Z) are shown for (A) large pike (mean and 95% CI), (B) female small pike, and (C) male small pike. In (B) and (C) the mortality rates are given as functions of size at tagging. All rates have been estimated from the best model (Table 3) and constrained to mean abundance of pike and perch and mean fishing effort.

which is as expected as the south basin is the most productive basin. The dispersal probability in the north-to-south direction may be substantial (>0.5 per season) under conditions with steep perch and pike abundance gradients. It is important to keep in mind the temporal resolution of the current dispersal results as they demonstrate that Windermere pike have quite high levels of between-basin dispersal from one spring to the next spring (i.e., annual scale). Knowing that pike individuals may move over several kilometers in a few hours (Diana et al. 1977, Chapman and Mackay 1984) they may indeed move between basins essentially instantaneously (the spatial extent of Windermere being 7 km between basin midpoints).

In hypothesis 5, recruitment of small pike to the gill net sampling was estimated to be significantly affected by the interaction between perch abundance and temperature. We expected this to be case because the fishing gear used during the winter fisheries is highly size selective (gill nets with mesh size 64 mm) and hence should capture fish that grow rapidly into sizes at risk for the gill net captures. Hence, the fishery recruitment process is hypothesized to be highly related to the individual growth process. Indeed, that is the case for the Windermere pike as temperature and prey abundance (perch) have a pronounced positive effect on both processes. However, the sign of the perch × temperature interaction effect differs between the two processes. As a consequence, high temperatures reduce the positive effect from high perch abundances for the fishery recruitment process, whereas the opposite is the case for individual growth. This discrepancy seems most likely linked to temperature-related changes in behavior. As mentioned above, perch is favored under warm conditions as pike experience higher metabolic costs from both swimming and digestion and have low critical swimming velocities that can be sustained for just a few minutes (Jones et al. 1974, Bergman 1987, Diana 1996). Consequently, perch may have higher escape success under warm than under cold conditions. The optimal feeding behavior for pike under warm conditions is therefore to reduce swimming activity and wait for the prey. In particular, this should be the case under high perch abundances as the frequency of prey encounters will then be higher due to a higher prey density. Such reduced swimming activity at high temperatures and perch abundances will make the pike less susceptible to gill net captures and thus constitute a candidate mechanism for explaining the discrepancy in the temperature × perch abundance interaction effect between the growth and fishery recruitment processes.

The generality of this study

Due to the unique and detailed long-term data available for the Windermere system, we have been able to study ecological process in more detail than has been feasible using other natural systems with other kinds of data. We believe that many of the results achieved are also applicable to other aquatic top predators, at least for aquatic top predators with indeterminate growth and cannibalistic propensities. We also believe that the results shed light on important ecological and evolutionary processes.

Survival, growth, and harvest rate for small pike were all shown to be density-dependent processes that were modulated by temperature. Since climate change models now predict that global temperatures will rise by the order of 0.1°–0.6°C per decade (IPCC 2001), any temperature-sensitive demographic process has the potential to affect future population dynamics and also evolution. An increasing number of review papers demonstrate that climate forcing has an important impact on the dynamics of both terrestrial and aquatic populations (Stenseth et al. 2002, Crick 2004, Lehodey et al. 2006, Sutherland 2006). Climate impact on individuals and populations may operate either directly through physiology (metabolic and reproductive processes) or indirectly through the ecosystem, including prey, predators, and competitors. According to Stenseth et al. (2002) there are at least five effects to consider:

(1) Delayed effects of climate may result as climate conditions experienced during the first year of life may impose effects that remain throughout life. For cohorts growing up under harsh conditions individual size may remain small throughout life, and the cohort that remains small will produce few recruits. In pike, this effect may be particularly pertinent due to the influence of cannibalism. Individuals growing up under cold conditions with low food availability will, due to their reduced growth (Table 4), result in a cohort with prolonged exposure to cannibalism, and hence, impose additional reduction of this cohort. This is an example of interaction effects between two density-dependent factors (food availability and cannibalism) and the density-independent factor of climate (temperature) that imposes delayed effects on the population (reduced abundance for older individuals and reduced recruitment).

(2) Climate factors often have differential effects on groups within the population such as sex and age groups. As a consequence, the effect of climate factors on population dynamics will depend on the age and sex structure (Coulson et al. 2001). For the pike in Windermere, we found that survival in large (adult) individuals was insensitive to temperature, but small (subadult) pike were highly sensitive to temperature. Hence, owing to this differential response a change in temperature may impose age structure changes in this population in the future.

(3) Climate change may lead to a higher frequency of extreme events, which often are ecologically more relevant than are fluctuations in the mean climate (Seastedt and Knapp 1993, Chan et al. 2005). For the Windermere pike, both extremely low-temperature summers and extremely warm summers had a negative impact on small-pike survival, but this effect is highly dependent upon the food and competition situation. Hence, in pike extreme events may impose changes in the population dynamics, depending upon the manner in which the perch population responds to the same events.

(4) Direct effects of climate may affect the entire organism as such or other organisms upon which the focal organism is directly dependent. For instance, direct negative climatic effect on just one out of two competing species will encourage expansion of the non-affected species (e.g., Sætre et al. 1999). In the Windermere pike

and perch system, differential direct effects of climate may significantly affect the predator–prey relationship as perch may be favored by an increase in water temperature.

(5) The fifth climate effect mechanism described in Stenseth et al. (2002) notes that the population response to climate variation may ultimately depend upon levels of density-related factors, measured as an interaction effect. The existence of interaction effects between climate factors and density-dependent factors is little considered in classical age-structured fisheries assessment models. In fact, until very recently most such models assumed that the stock recruitment process was the only population process under the influence of density-dependent mechanisms (Rothschild 1986, Hilborn and Walters 1992). More recent studies (e.g., Jenkins et al. 1999, Lobon-Cervia 2006) demonstrate that other demographic processes also are under density-dependent regulation, even in marine species (Helser and Almeida 1997, Stenseth et al. 1999). In fact, density-dependent growth has been proposed to be the key mechanism in the regulation of fish populations (Lorenzen and Enberg 2002). In the current study, we do not show only that both demographic processes and growth are influenced by density-dependent factors, but also that the degree of density dependence is modulated by temperature. Such interactions have received little attention in fish population biology studies. Examples from terrestrial systems demonstrate that failing to detect such interactions may lead to spurious relations between climate and the process studied (Forchhammer et al. 1998, Post et al. 1999). We therefore encourage fish population biologists to address this issue in future work in order to explore the manner in which such common interaction effects exist in fish populations and to what extent they affect population dynamics.

The basin specificity of dispersal (and survival) is an interesting result that may illuminate both general evolutionary as well as ecological hypotheses. For instance, our results support predictions made by the balanced dispersal hypothesis of McPeek and Holt (1992). Their analysis showed that when carrying capacities vary both spatially and temporally, as is likely to be the case for the two basins comprising Windermere, natural selection will favor only two genotypes (a high-dispersal and a no-dispersal genotype). They further show that this dimorphism can be invaded by one genotype with a particular combination of habitat-specific dispersal propensities in a ratio inversely proportional to the ratio of the population sizes. Our results cannot be used for evaluating which one of the two alternatives is the case in Windermere as we do not have information on any possible correlation between spatial variation in dispersal "willingness" and genetic variation. In order to explore this further, experiments with pike from the two basins will have to be performed under common garden conditions (i.e., varying density).

The basin-specific dispersal differentiation found in Windermere pike may also shed light on population dynamic theories. According to many recent dispersal studies (reviewed in Hanski 2001), dispersal may not only impose effects on population growth rate and density, it might even change the type of population dynamics, most often by simplifying what would be complex dynamics if the populations lived in isolation (Dieckmann et al. 2000). Pascual (1993) demonstrates that low dispersal values drive otherwise periodic predator–prey systems into aperiodic behavior (chaos).

The asymmetries found in basin-specific survival and dispersal may also be related to theories dealing with distributional processes. For instance, the well-studied ideal free distribution theory of Fretwell and Lucas (1970) may be explored in light of our results. By including information on density-dependent fecundity for pike in Windermere we were able to estimate basin-specific density dependence of fitness. This enabled us to test the real-scale relevance of the ideal free distribution (IFD) theory by using the Windermere pike results (Haugen et al. 2006). Indeed, the results indicated the Windermere pike to be ideally free distributed. This demonstration of the full-scale relevance of the IFD theory provides fisheries management with a convenient and simple tool for predicting distributional responses to harvesting, and it also highlights the point that population studies should include the potential for habitat selection (Morris 2006).

Many predator species are so-called self-regulating, a phenomenon that is characterized by a constant size/age structure over time. This phenomenon most often arises in cannibalistic systems in which the victim : cannibal size ratios are small. Typically, as in pike (Persson et al. 2006), recruitment of juveniles is controlled by cannibalism from older/larger individuals (see e.g., Tonn et al. 1994, Frankiewicz et al. 1999, Moksnes 2004, Wise 2006). In the current study of adults only, we found evidence that males seem more susceptible to lethal interactions with conspecifics than females. Even though the mortality rate is high for small males, this is probably not as important as a population-regulating force as the cannibalism on juveniles has proven to be in other pike and top-predator studies. The reason for this is that recruiting, juvenile pike are vulnerable to cannibalism from a far larger proportion of the pike population than adult males simply because they are smaller than the critical size limited by the gape width of potential cannibals (Nilsson and Brönmark 2000). Furthermore, because juvenile and small pike eat the same prey, smaller and younger individuals will suffer from both inter-cohort competition for food and inter-cohort cannibalism. This was evident at the small-pike and large-pike level in this study in which the observed negative effect from large pike on small-pike survival was larger than the influence from abundance of small pike, as would be expected in any system in which cannibals and their prey share common resources

(Claessen et al. 2000, Persson et al. 2004). We want to highlight the finding that even adult, male pike experience substantial size- and density-dependent mortality that most likely can be attributed to cannibalism, but it still remains to be explored whether this source of mortality is as important a self-regulating mechanism as is juvenile cannibalism.

Altogether, our study provides explicit estimates of the influences of and interactions between key environmental variables with respect to a number of vital rates involved in population dynamic processes. To the best of our knowledge, this is the first study to have disentangled the simultaneous influences of density-dependent and density-independent processes on survival, dispersal, and fishing rates under the influence of individual size. Thus, incorporating density dependence and density independence in these vital rates will certainly add to the literature of density dependence vs. density independence, which to a large extent refers to total populations sizes only (see, e.g., Turchin 1995). Improved understanding of the manner in which the density-dependent and density-independent processes are mediated through the vital rates will certainly improve our ability to manage pike and perch systems in a sustainable manner. Here we demonstrated that information encompassed in time-series data for studying ecological and evolutionary processes is invaluable. We encourage research institutions to continue such time series as these time-series studies may hold the information needed for understanding and predicting effects from climate change and hence the tools for construction of the proper mitigation actions.

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LITERATURE CITED

Altwegg, R., A. Roulin, M. Kestenholz, and L. Jenni. 2003. Variation and covariation in survival, dispersal, and population size in barn owls *Tyto alba*. Journal of Animal Ecology 72:391–399.

Arnason, A. N. 1972. Parameter estimates from mark-recapture experiments on two populations subjected to migration and death. Researches on Population Ecology 13:97–113.

Arnason, A. N. 1973. The estimation of population size, migration rates and survival in a stratified population. Researches on Population Ecology 15:1–8.

Bergman, E. 1987. Temperature-dependent differences in foraging ability of 2 percids, *Perca fluviatilis* and *Gymnocephalus cernuus*. Environmental Biology of Fishes 19:45–53.

Billard, R. 1996. Reproduction of pike: gametogenesis, gamete biology and early development. Pages 13–44 *in* J. F. Craig, editor. Pike: biology and exploitation. Chapman and Hall, London, UK.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–1187.

Bucke, D., G. D. Cawley, J. F. Craig, A. D. Pickering, and L. G. Willoughby. 1979. Further studies of an epizooic of perch, *Perca fluviatilis* L., of uncertain aetiology. Journal of Fish Diseases 2:297–311.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inferences. Springer Verlag, New York, New York, USA.

Catchpole, E. A., B. J. T. Morgan, T. N. Coulson, S. N. Freeman, and S. D. Albon. 2000. Factors influencing Soay sheep survival. Applied Statistics 49:453–472.

Chan, K. S., A. Mysterud, N. A. Oritsland, T. Severinsen, and N. C. Stenseth. 2005. Continuous and discrete extreme climatic events affecting the dynamics of a high-arctic reindeer population. Oecologia 145:556–563.

Chapman, C. A., and W. C. Mackay. 1984. Versatility in habitat use by a top aquatic predator, *Esox lucius* L. Journal of Fish Biology 25:109–115.

Choquet, R., A. M. Reboulet, R. Pradel, O. Gimenez, and J. D. Lebreton. 2003. U-Care user's guide. Version 2.0. Centre d'Ecologie Fonctionnelle et Evolutive/Centre National de la Recherche Scientifique, Montpellier, France.

Claessen, D., A. M. de Roos, and L. Persson. 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. American Naturalist 155:219–237.

Clobert, J., C. M. Perrins, R. H. McCleery, and A. G. Gosler. 1988. Survival rate in the great tit *Parus major* in relation to sex, age, and immigration status. Journal of Animal Ecology 57:287–306.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Craig, J. F., editor. 1996*a*. Pike: biology and exploitation. Chapman and Hall, London, UK.

Craig, J. F. 1996*b*. Population dynamics, predation and role in the community. Pages 201–217 *in* J. F. Craig, editor. Pike: biology and exploitation. Chapman and Hall, London, UK.

Crick, H. Q. P. 2004. The impact of climate change on birds. Ibis 146:48–56.

des Clers, S., J. M. Fletcher, I. J. Winfield, G. P. Kirkwood, P. R. Cubby, and J. R. Beddington. 1994. Long-term changes in Windermere perch and pike populations at the basin level. IFE Report WI/T11050d5/4, Institute of Freshwater Ecology, Lancaster, UK.

Diana, J. S. 1996. Energetics. Pages 103–124 *in* J. F. Craig, editor. Pike: biology and exploitation. Chapman and Hall, London, UK.

Diana, J. S., W. C. Mackay, and M. Ehrman. 1977. Movements and habitat preference of northern pike (*Esox lucius*) in Lac Ste Anne, Alberta. Transactions of the American Fisheries Society 106:560–565.

Dieckmann, U., R. Law, and J. A. J. Metz. 2000. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge, UK.

Fabricius, E., and K. J. Gustafson. 1958. Some new observations on the spawning behaviour of the pike (*Esox lucius* L.).

Report of the Institute of Freshwater Research, Drottningholm 39:23–54.

Forchhammer, M. C., N. C. Stenseth, E. Post, and R. Langvatn. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. Proceedings of the Royal Society B 265:341–350.

Frankiewicz, P., K. Dabrowski, A. Martyniak, and M. Zalewski. 1999. Cannibalism as a regulatory force of pikeperch, *Stizostedion lucioperca* (L.), population dynamics in the lowland Sulejow reservoir (Central Poland). Hydrobiologia 409:47–55.

Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs 70:539–590.

Fretwell, S. D., and H. J. Lucas. 1970. On territorial behavior and other factors influencing habitat distributions in birds. Acta Biotheoretica 19:16–36.

Frost, W. E. 1954. The food of pike, *Esox lucius* L, in Windermere. Journal of Animal Ecology 23:339–360.

Frost, W. E., and C. Kipling. 1967. A study of reproduction, early life weight–length relationship and growth of pike *Esox lucius* L in Windermere. Journal of Animal Ecology 36:651–693.

Grimm, M. P. 1981. Intraspecific predation as a principal factor controlling the biomass of northern pike (*Esox lucius* L). Fisheries Management 12:77–79.

Grimm, M. P., and M. Klinge. 1996. Pike and some aspects of its dependence on vegetation. Pages 125–156 *in* J. F. Craig, editor. Pike: biology and exploitation. Chapman and Hall, London, UK.

Hanski, I. 2001. Population dynamic consequences of dispersal in local populations and in metapopulations. Pages 283–298 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, New York, New York, USA.

Haugen, T. O., I. J. Winfield, L. A. Vøllestad, J. M. Fletcher, J. B. James, and N. C. Stenseth. 2006. The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. Proceedings of the Royal Society B 273:2917–2924.

Helser, T. E., and F. P. Almeida. 1997. Density-dependent growth and sexual maturity of silver hake in the north-west Atlantic. Journal of Fish Biology 51:607–623.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York, New York, USA.

IPCC [Intergovernmental Panel on Climate Change]. 2001. Climate change 2001. Page 398 *in* R. T. Watson and T. C. W. Team, editors. Synthesis Report. A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.

Jenkins, T. M., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80:941–956.

Johns, T. C., et al. 2003. Anthropogenic climate change for 1860 to 2100 simulated with the HadCM3 model under updated emissions scenarios. Climate Dynamics 20:583–612.

Jones, D. R., J. W. Kiceniuk, and O. S. Bamford. 1974. Evaluation of swimming performance of several fish species from Mackenzie River. Journal of the Fisheries Research Board of Canada 31:1641–1647.

Julliard, R., N. C. Stenseth, J. Gjosaeter, K. Lekve, J. M. Fromentin, and D. S. Danielssen. 2001. Natural mortality and fishing mortality in a coastal cod population: a release–recapture experiment. Ecological Applications 11:540–558.

Kipling, C. 1983*a*. Changes in the growth of pike (*Esox lucius*) in Windermere. Journal of Animal Ecology 52:647–657.

Kipling, C. 1983*b*. Changes in the population of pike (*Esox lucius*) in Windermere from 1944 to 1981. Journal of Animal Ecology 52:989–999.

Kipling, C. 1984. A study of perch (*Perca fluviatilis* L) and pike (*Esox lucius* L) in Windermere from 1941 to 1982. Journal du Conseil 41:259–267.

Kipling, C., and W. E. Frost. 1970. A study of mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L, in Windermere from 1944 to 1962. Journal of Animal Ecology 39:115–157.

Kipling, C., and E. D. Le Cren. 1984. Mark–recapture experiments on fish in Windermere, 1943–1982. Journal of Fish Biology 24:395–414.

Kipling, C., and M. E. Roscoe. 1977. Surface water temperature of Windermere. Occasional Publication Number 2. Freshwater Biological Association, Cumbria, UK.

Krebs, J. R., and N. B. Davies. 1997. Behavioural ecology: an evolutionary approach. Blackwell Science, Oxford, UK.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Le Cren, E. D. 1987. Perch (*Perca fluviatilis*) and pike (*Esox lucius*) in Windermere from 1940 to 1985—studies in population dynamics. Canadian Journal of Fisheries and Aquatic Sciences 44:216–228.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Elsevier, Amsterdam, The Netherlands.

Lehodey, P., et al. 2006. Climate variability, fish, and fisheries. Journal of Climate 19:5009–5030.

Leirs, H., N. C. Stenseth, J. D. Nichols, J. E. Hines, R. Verhagen, and W. Verheyen. 1997. Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. Nature 389:176–180.

Lobon-Cervia, J. 2006. Density-dependent growth in stream-living brown trout Salmo trutta L. Functional Ecology [doi:10.1111/j.1365-2435.2006.01204.x].

Loison, A., B. E. Saether, K. Jerstad, and O. W. Rostad. 2002. Disentangling the sources of variation in the survival of the European dipper. Journal of Applied Statistics 29:289–304.

Lomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton, New Jersey, USA.

Lorenzen, K., and K. Enberg. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society B 269:49–54.

Lucas, M. C. 1992. Spawning activity of male and female pike, *Esox lucius* L., determined by acoustic tracking. Canadian Journal of Zoology 70:191–196.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140:1010–1027.

Mills, C. A., and M. A. Hurley. 1990. Long-term studies on the Windermere populations of perch (*Perca fluviatilis*), pike (*Esox lucius*) and Arctic charr (*Salvelinus alpinus*). Freshwater Biology 23:119–136.

Milner, J. M., D. A. Elston, and S. D. Albon. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. Journal of Animal Ecology 68:1235–1247.

Moksnes, P. O. 2004. Self-regulating mechanisms in cannibalistic populations of juvenile shore crabs *Carcinus maenas*. Ecology 85:1343–1354.

Morris, D. W. 2006. Ecology—moving to the ideal free home. Nature 443:645–646.

Nichols, J. D., and W. L. Kendall. 1995. The use of multi-state capture–recapture models to address questions in evolutionary ecology. Journal of Applied Statistics 22:835–846.

Nilsson, P. A., and C. Brönmark. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. Oikos 88:539–546.

Pascual, M. 1993. Diffusion-induced chaos in a spatial predator–prey system. Proceedings of the Royal Society B 251:1–7.

Paxton, C. G. M., J. M. Fletcher, D. P. Hewitt, and I. J. Winfield. 1999. Sex ratio changes in the long-term Windermere pike and perch sampling program. Ecology of Freshwater Fish 8:78–84.

Paxton, C. G. M., I. J. Winfield, J. M. Fletcher, D. G. George, and D. P. Hewitt. 2004. Biotic and abiotic influences on the recruitment of perch (*Perca fluviatilis*) in Windermere, U.K. Journal of Fish Biology 65:1622–1642.

Persson, L., A. Bertolo, and A. M. De Roos. 2006. Temporal stability in size distributions and growth rates of three *Esox lucius* L. populations: A result of cannibalism? Journal of Fish Biology 69:461–472.

Persson, L., A. M. de Roos, and A. Bertolo. 2004. Predicting shifts in dynamics of cannibalistic field populations using individual-based models. Proceedings of the Royal Society B 271:2489–2493.

Post, E., M. C. Forchhammer, N. C. Stenseth, and R. Langvatn. 1999. Extrinsic modification of vertebrate sex ratios by climatic variation. American Naturalist 154:194–204.

Pradel, R., J. E. Hines, J. D. Lebreton, and J. D. Nichols. 1997. Capture–recapture survival models taking account of transients. Biometrics 53:60–72.

Pradel, R., C. M. A. Wintrebert, and O. Gimenez. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture–recapture model. Biometrics 59:43–53.

Raat, A. J. P. 1988. Synopsis of biological data on the northern pike *Esox lucius* Linnaeus, 1758. Report number 30. Revision 2. Food and Agricultural Organization of the United Nations, Rome, Italy.

Rothschild, B. J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, Massachusetts, USA.

Sætre, G. P., E. Post, and M. Kral. 1999. Can environmental fluctuation prevent competitive exclusion in sympatric flycatchers? Proceedings of the Royal Society B 266:1247–1251.

Schaub, M., O. Gimenez, B. R. Schmidt, and R. Pradel. 2004. Estimating survival and temporary emigration in the multistate capture–recapture framework. Ecology 85:2107–2113.

Schaub, M., and R. Pradel. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. Ecology 85:930–938.

Schwarz, C. J., J. F. Schweigert, and A. N. Arnason. 1993. Estimating migration rates using tag-recovery data. Biometrics 49:177–193.

Seastedt, T. R., and A. K. Knapp. 1993. Consequences of nonequilibrium resource availability across multiple time scales—the transient maxima hypothesis. American Naturalist 141:621–633.

Skalski, J. R., A. Hoffmann, and T. W. Sherry. 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies. Pages 9–28 *in* J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird populations. Birkhäuser Verlag, Basel, Switzerland.

Stenseth, N. C., O. N. Bjornstad, W. Falck, J. M. Fromentin, J. Gjosaeter, and J. S. Gray. 1999. Dynamics of coastal cod populations: intra- and intercohort density dependence and stochastic processes. Proceedings of the Royal Society B 266:1645–1654.

Stenseth, N. C., K.-S. Chan, G. Tavecchia, T. Coulson, A. Mysterud, T. Clutton-Brock, and B. Grenfell. 2004. Modelling non-additive and nonlinear signals from climatic noise in ecological time series: Soay sheep as an example. Proceedings of the Royal Society B 271:1985–1993.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292–1296.

Sutherland, W. J. 2006. Predicting the ecological consequences of environmental change: a review of the methods. Journal of Applied Ecology 43:599–616.

Tonn, W. M., I. J. Holopainen, and C. A. Paszkowski. 1994. Density-dependent effects and the regulation of crucian carp populations in single-species ponds. Ecology 75:824–834.

Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19–40 *in* N. Cappuccino and P. W. Price, editors. Population dynamics: new approaches and synthesis. Academic Press, San Diego, California, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

White, G. C., K. P. Burnham, and D. R. Anderson. 2001. Advanced features of Program Mark. Pages 368–377 *in* Wildlife, land, and people: priorities for the 21st century. Wildlife Society, Bethesda, Maryland, USA.

Winfield, I. J., and N. C. Durie. 2004. Fish introductions and their management in the English Lake District. Fisheries Management and Ecology 11:195–201.

Winfield, I. J., J. M. Fletcher, D. P. Hewitt, and J. B. James. 2004. Long-term trends in the timing of the spawning season of Eurasian perch (*Perca fluviatilis*) in the north basin of Windermere, U.K. Pages 95–96 *in* Percids III: The Third International Percid Fish Symposium. University of Wisconsin Sea Grant Institute, Madison, Wisconsin, USA.

Wise, D. H. 2006. Cannibalism, food limitation, intraspecific competition and the regulation of spider populations. Annual Review of Entomology 51:441–465.

Yoccoz, N. G., N. C. Stenseth, H. Henttonen, and A. C. Prevot-Julliard. 2001. Effects of food addition on the seasonal density-dependent structure of bank vole *Clethrionomys glareolus* populations. Journal of Animal Ecology 70:713–720.

Zabel, R. W., and S. Achord. 2004. Relating size of juveniles to survival within and among populations of chinook salmon. Ecology 85:795–806.

APPENDIX A

Estimation of pike abundances from catch data (*Ecological Archives* M077-014-A1).

APPENDIX B

Evaluation of the seasonal conditional Arnason-Schwarz model structure (*Ecological Archives* M077-014-A2).

APPENDIX C

Model ranking tables (*Ecological Archives* M077-014-A3).