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THE ECOLOGICAL NICHE OF *DAPHNIA MAGNA* CHARACTERIZED USING POPULATION GROWTH RATE

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Abstract. The concept of an organism's niche is central to ecological theory, but an operational definition is needed that allows both its experimental delineation and interpretation of field distributions of the species. Here we use population growth rate (hereafter, pgr) to define the niche as the set of points in niche space where pgr > 0. If there are just two axes to the niche space, their relationship to pgr can be pictured as a contour map in which pgr varies along the axes in the same way that the height of land above sea level varies with latitude and longitude. In laboratory experiments we measured the pgr of *Daphnia magna* over a grid of values of pH and Ca^{2+}, and so defined its "laboratory niche" in pH–Ca^{2+} space. The position of the laboratory niche boundary suggests that population persistence is only possible above 0.5 mg Ca^{2+}/L and between pH 5.75 and pH 9, though more Ca^{2+} is needed at lower pH values. To see how well the measured niche predicts the field distribution of *D. magna*, we examined relevant field data from 422 sites in England and Wales. Of the 58 colonized water bodies, 56 lay within the laboratory niche. Very few of the sites near the niche boundary were colonized, probably because pgr there is so low that populations are vulnerable to extinction by other factors. Our study shows how the niche can be quantified and used to predict field distributions successfully.

Key words: *calcium;* Daphnia magna; *ecological niche; fundamental niche; pH; population growth rate.*

Introduction

The concept of an organism's niche is fundamental to ecological theory and brings together two core ideas: (1) that environmental factors affect an organism's performance and thereby limit its geographical distribution, and (2) that organisms are adapted genetically to a limited range of environmental conditions. Although textbooks often treat the concept of an organism's ecological niche historically (emphasizing, among others, Hutchinson's [1957] rectilinear definition of the niche), early characterizations of the niche have generally been difficult to implement in practice. What is needed is an operational definition of the niche that allows both its experimental delineation, and interpretation of the field distributions of the species. A candidate approach, developed here, is a definition in terms of population growth rate (hereafter, pgr) measured in a "niche space" whose axes are physical or chemical variables such as temperature, size of food items, pH, and so forth. Specifically, here we define the niche as the set of points in niche space where pgr > 0, following Maguire (1973), Hutchinson (1978), Tilman (1982), Pulliam (2000), Sibly and Hone (2002), and Chase and Leibold (2003). If there were just two axes to niche space, their relationship to pgr could be pictured as a contour map in which pgr varies along the axes in the same way that the height of land above sea level varies with latitude and longitude.

When the niche is characterized at low population density and in the absence of predators, parasites, and interspecific competitors, it is referred to as the "fundamental niche." In the presence of such biological constraints, the set of points for which pgr > 0 is reduced and defined as the "realized niche" (Maguire 1973). Birch (1953) presents an important early example of the pgr approach in which grain beetle pgr was plotted as a function of both temperature and humidity. Knowing how temperature and humidity varied geographically, he was able to predict the field distributions of the beetles and to compare these predictions with what was observed. A similar interpretation of species distribution in terms of pgr was described by Caughley et al. (1988), in which the limit of species distribution was defined by a maximum pgr of 0. However, despite the clear utility of being able to predict species

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distributions on the basis of a quantified niche, this approach has not been widely adopted.

Here we first quantify the fundamental niche of an important aquatic indicator species, *Daphnia magna* Straus, under controlled laboratory conditions in relation to two important physicochemical variables known to affect its field distribution, pH and ionic Ca^{2+} concentration. In general, pH affects *Daphnia* by modifying their internal ionic regulation (Potts and Fryer 1979), whereas Ca^{2+} is required as an essential element (Wærvågen et al. 2002). Juveniles have a higher calcium demand than adults because the exoskeleton, and hence most of the total body calcium, is shed more frequently during the early life stages (Alstad et al. 1999). Any calcium lost in this process has to be replaced by uptake of calcium from the external media (Cowgill et al. 1986). Having quantified the "laboratory niche," we then investigate to what extent it can be used to predict the field distribution of *D. magna*. Finally we consider whether and how the pgr approach to niche definition can be implemented more widely.

Materials and Methods

Experimental animals and test design

We chose *D. magna* (see Plate 1) as our model organism because it has been widely studied and is easily cultured in the laboratory, and because we were able to assemble and report a large data set on its field distribution in relation to environmental variables. Ranta (1979) provided an important early characterization of its niche. Our laboratory study clone, IRCHA Type 5, came originally from the French National Institute for Applied Chemical Research. Prior to this experiment, the clone had been cultured in our laboratory for two years using reconstituted water (see *Materials and methods: Manipulation and measurement of chemical parameters*) in which hardness, pH, and conductivity ranged from 135 mg to 165 mg $CaCO_3$/L, pH of 7.8–8.2, and 369–470 μS/cm at 20°C, respectively. Further details of culturing methods are given in Hooper et al. (2006).

We determined the laboratory niche of *D. magna* in pH–Ca^{2+} space using the population growth rate (pgr) approach, taking advantage of a recent technical advance that uses image analysis for rapid measurement of pgr (Hooper et al. 2006). We measured pgr at 21 different combinations of pH and Ca^{2+} concentration, each replicated twice. Treatments were selected to cover the values measured in field studies and ranged from pH 5 to pH 9 and Ca^{2+} from 0.01 to 400 mg/L. Values of variables other than pH and calcium were kept constant. Two additional replicate populations were set up using culture water in which nominal Ca^{2+} concentration was equal to 53.39 mg/L and no adjustment of pH was made. These reference populations revealed the time course of unmanipulated water chemistry (see Fig. 1), but were not included in the statistical analyses.

Although suitable for comparison with field data (see Fig. 3), the experimental design was also influenced by several logistic constraints, including: only 44 test vessels could be accommodated within our experimental facility; 100% mortality occurred within 24 h with pH ≤ 4 regardless of Ca^{2+} concentrations up to 400 mg/L; populations became extinct within two weeks when no Ca^{2+} was added to the reconstituted media (pH ~7.5); and we were unable to maintain the test water at 400 mg Ca^{2+}/L and pH ≥ 9 in our experimental conditions because of calcium precipitation and substantial changes in other water chemistry parameters. Similarly logistic constraints prevented examination of more than two environmental gradients, even though it is recognized that *Daphnia* survivorship is under complex, multifactor control (Fryer 1985, Threlkeld 1987).

Test vessels consisted of 5-L glass aquaria, and the experiment was carried out at 20° ± 1°C (mean ± SD) with a 16-h light:8-h dark photoperiod. Populations were initiated with 10 third-brood neonates (<24 hours old) and exposed to the various pH × Ca^{2+} treatments for 14 days. Each population was fed the same daily amount of food, which consisted of dried baking yeast *Saccharomyces cerevisae* (Westmill Foods, Maidenhead, United Kingdom), and unicellular green algae, *Chlorella vulgaris* var. *viridis*. The yeast was dissolved in deionized water to give a concentration of 0.1 mg/mL. The algae were cultured in Bold's Basal Medium (BBM) and harvested by centrifuging at 3000 rpm. The supernatant was discarded leaving the algal cells in <2 mL of BBM. This was resuspended in deionized water to give a concentration of 0.5 mg carbon/mL, which was measured as the corresponding optical density at 440 nm. During the first week of the test, populations were provided with 0.2 mL (0.02 mg) of yeast and 0.5 mL (equivalent to 0.25 mg carbon) of algae per day. From the eighth day onward, when some populations produced their first offspring, both yeast and algal rations were increased so that food levels remained nonlimiting. The total volume of added food was 15.5 mL (i.e., 0.31% of the 5-L test water volume).

Manipulation and measurement of chemical parameters

The reconstituted aqueous solutions were prepared a week prior to the test by dissolving 82.20 mg $MgSO_4 \cdot 7H_2O$, 64.80 mg $NaHCO_3$, 5.80 mg KCl, and 0.002 mg Na_2SeO_3 per 1 L of reverse-osmosis water. Ca^{2+} concentrations were achieved by adding the appropriate amount of $CaCl_2 \cdot 2H_2O$ to each test vessel, either as a 0.5 mL solution prepared with deionized water (for nominal Ca^{2+} concentrations $\leq$1.0 mg/L), or by dissolving in ~50% of the test water. Ca^{2+} was measured over the course of the experiment (Fig. 1a) using an ELIT ion-selective electrode (ISE) and an ELIT silver chloride reference electrode (VWR International, Lutterworth, Leicestershire, United Kingdom). We used the most common method of analysis, direct potentiometry, in which water samples (10 mL) were deter-

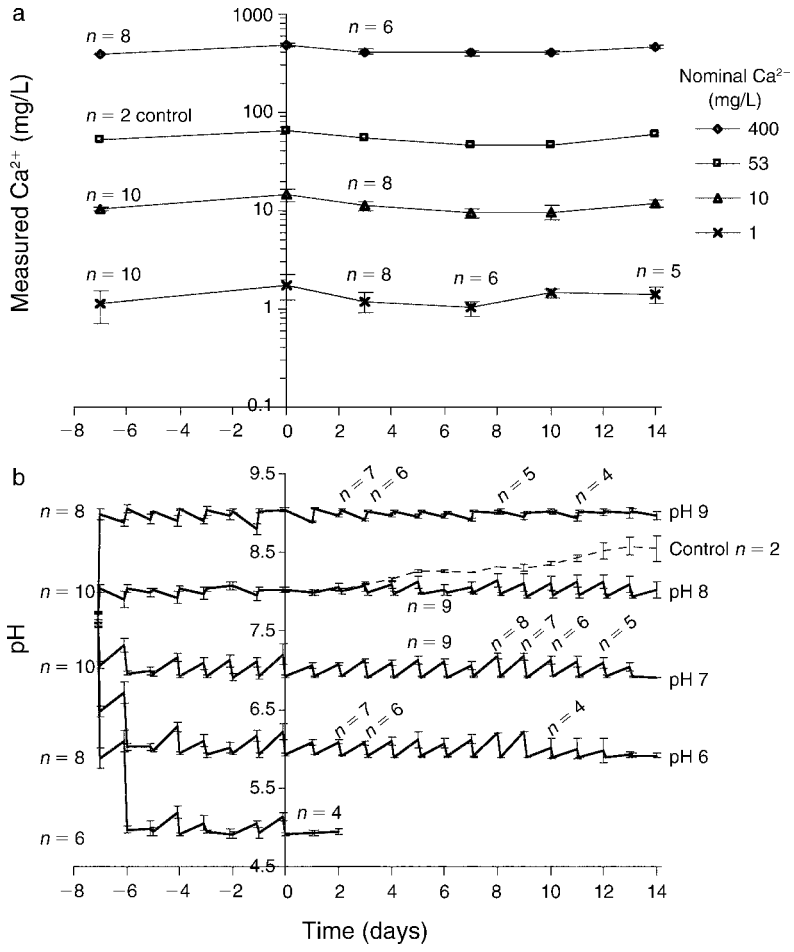

FIG. 1. (a) Measured Ca^{2+} concentrations (mean ± SD) over time. Note that concentrations ≤0.1 mg/L were below the limit of detection. Shown is the number (*n*) of extant populations of the same nominal Ca^{2+}, though varying in pH. Whatever the pH level, there was good control of Ca^{2+} levels. (b) Measured pH (mean ± SD) over time. Shown is the number (*n*) of extant populations of the same nominal pH, though varying in Ca^{2+}. Aqueous solutions were prepared a week (day −7) prior to the test, which began on day 0. From left to right, *n* remains the same until another value is given; *n* declines over time as some populations become extinct.

mined against known Ca^{2+} concentrations. A solution of 4 mol/L KCl was added to both the samples and Ca^{2+} standards (2% of volume) to maintain constant ionic strength among treatments. During our pilot studies we found that ISE estimates of Ca^{2+} correlated extremely well with atomic absorption spectrophotometry (AAS) measurements (regression analysis $R^2 = 0.948$, $n = 35$, $P < 0.001$).

The pH was measured at least once daily, usually between 12:00 and 14:00 h, using a Hanna HI8424 portable pH meter (Hanna Instruments, Leighton Buzzard, United Kingdom). The pH was adjusted using 0.2 mol/L HCl or 0.2 mol/L NaOH (Fisher Scientific, United Kingdom), and the total volume of these additions did not exceed 21.2 mL. Manipulations of pH were made a week prior to adding the *Daphnia* (see Fig. 1b), so that generally only small volumes of HCl or NaOH were required to maintain pH close to nominal throughout the two weeks of the test. In situ measurements of conductivity were made every two to three days using a Hanna HI8733 portable meter to measure changes in ionic activity. All analytical equipment was calibrated immediately before use and after every 5–10 measurements. Water chemistry analyses were carried out for all 44 populations but were discontinued if extinction occurred. Both Ca^{2+} and pH concentrations were maintained within narrow limits throughout the test, as shown in Fig. 1.

Biological parameters

Population growth rate was estimated from population surface area, measured using the automated digital imaging system described in Hooper et al. (2006). Population growth rate is better estimated from population surface area (i.e., the sum of individual surface areas) than from population abundance in *D. magna*, and indeed all organisms, provided that fecundity is well-correlated with body size in the study environment (Hooper et al. 2006). The advantages apply in particular when, as here, stressors are anticipated to

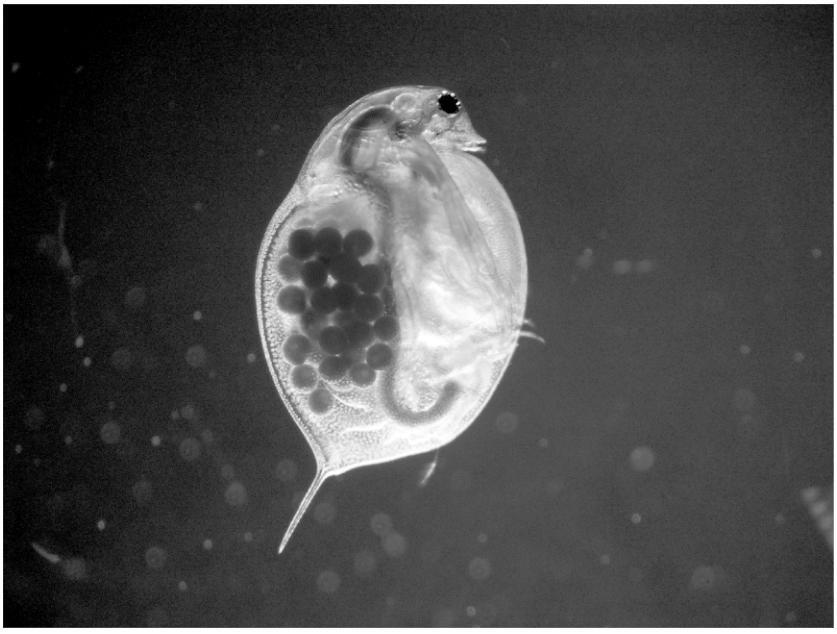

PLATE 1. *Daphnia magna* in the laboratory Reading, United Kingdom. Photo credit: R. E. Connon.

affect both the number and the reproductive value of individuals in the population. Population growth rate was calculated as $1/t \log_e(SA_t/SA_0)$, where SA_0 is the initial population surface area and SA_t is the population surface area at time t, the day the test ended or the day populations became extinct. In the latter case, SA_t was approximated as the surface area of the smallest extant population. This approximation has little effect on pgr due to the large influence of t.

Description of field data

D. magna is often described as a species of alkaline waters, but very few studies have actually documented its field distribution in relation to water chemistry. For this study we used the field data collected by Fryer (1985, 1993) and Yarwood-Buchanan (2005). With a much larger number of sites, Fryer (1985, 1993) surveyed 474 water bodies, ranging from peat bogs to calcareous lakes in Yorkshire, United Kingdom. Samples were taken over a 40-yr period at various times of the day mostly between the months of June and October. Crustaceans were collected from open water usually with a hand net from the shore but occasionally using a tow-net from a boat. Water samples were analyzed for pH and the concentrations of Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+}, by the UK Freshwater Biological Association. Yarwood-Buchanan (2005) sampled the cladoceran fauna of 70 minimally impaired ponds (8–13 270 m^2) in lowland (<400 m) England and Wales, once in the spring and once in the summer of 2002. Collections were made in open water and other defined mesohabitats using a hand net with an extendable handle. Chemical measurements were made on samples collected at various times of the day during an earlier national pond survey (Biggs et al. 2005). The numbers of sites that had both Ca^{2+} and pH measurements were 396 (Fryer) and 42 (Yarwood-Buchanan), respectively.

RESULTS

Effects of pH and calcium on population growth rate

Population growth rate (pgr) was significantly affected by both Ca^{2+} and pH concentration, (two-way ANOVA, $F_{4,33} = 12.4$, $P < 0.001$; $F_{4,33} = 48.9$, $P < 0.001$, respectively). Specifically, pgr was highest between pH 6 and 8, and increased with Ca^{2+} concentration (Fig. 2). Population growth rate declined markedly below pH 6 and when Ca^{2+} levels were low, and showed some decline above pH 8. Rank deficiency prevented analysis of the interaction between $\log_{10}Ca^{2+}$ and pH over the whole data set, but the interaction is significant when the analysis is restricted to the four highest Ca^{2+} values and pH 6–8 ($F_{6,12} = 14.7$, $P < 0.001$). In addition, analysis by quadratic regression was significant for $\log_{10}Ca^{2+}$ (linear term, $t_{36} = 3.30$, $P < 0.002$; quadratic term, $t_{36} = -2.67$, $P = 0.011$), pH (linear term, $t_{36} = 9.55$, $P < 0.001$; quadratic term, $t_{36} = -8.90$, $P < 0.001$), and their interactions (pH $\times$ $\log_{10}Ca^{2+}$, $t_{36} = -2.41$, $P = 0.021$). Together, these factors explain 84% of observed variance of pgr with a multiple regression of the form $pgr = -12.9 + 3.37\ pH + 0.637 \log_{10}Ca^{2+} - 0.218\ pH^2 - 0.0483 (\log_{10}Ca^{2+})^2 - 0.0613\ pH \times \log_{10}Ca^{2+}$.

The joint effects of Ca^{2+} and pH on *D. magna* can be seen more clearly by plotting contours of pgr (Fig. 3a). Populations performed best (i.e., highest pgr) in the Ca^{2+} range of 20–316 mg/L (1.3 to 2.5 log units) and around pH 8. As pH declined, increasing amounts of Ca^{2+} were

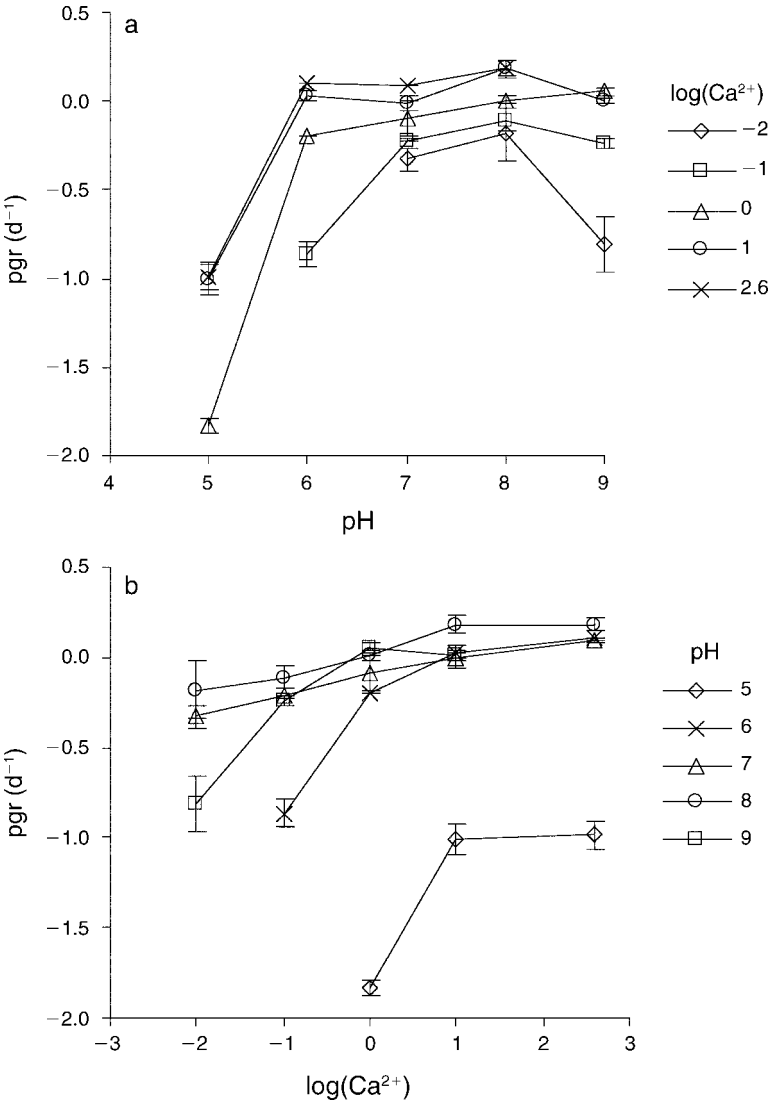

FIG. 2. The effects of Ca^{2+} and pH on the population growth rate (pgr) of laboratory populations of *Daphnia magna*, shown as line graphs (mean ± SE) in two forms. (a) Population growth rate plotted against pH ($n = 2$); lines refer to log-transformed Ca^{2+} concentrations (originally measured as mg/L). (b) Population growth rate plotted against Ca^{2+} concentrations; lines refer to pH levels.

necessary to maintain pgr at the same level (Fig. 3a). The pgr = 0 contour is of particular importance since it indicates the limits of the conditions under which populations can persist. Under laboratory conditions, population persistence (i.e., pgr $\geq$ 0) is possible above pH 5.75 provided Ca^{2+} is above 10 mg/L (1 log units). As Ca^{2+} declines, less acidity is tolerated and at 1 mg Ca^{2+}/L (0 log units) persistence is only possible above pH 8.

Field distribution of D. magna *in relation to pH and calcium*

In Fryer's surveys (1985, 1993) *D. magna* was found in waters exhibiting calcium concentrations ranging from 5.0 to 280 mg Ca^{2+}/L (0.7–2.4 log units) and from pH 6.9 to pH 10.2, but were most common in sites around 100 mg Ca^{2+}/L (2.0 log units) and from pH 7.4 to pH 7.8 (Fig. 3b). These sites included small fishless ponds (a habitat typically associated with *D. magna*), as well as larger water bodies where fish were present and where *D. magna* frequented littoral habitats. In contrast, analysis of Yarwood-Buchanan's (2005) data suggest that *D. magna* was able to tolerate more acidic conditions in southern regions of the United Kingdom as three of the six sites inhabited had a pH between 5.6 and 6.4. Measurement error is unlikely to account for the outlier pond in which *D. magna* occurred at the lowest pH (Fig. 3b). Instead this particular pond was located near heathland and had calcareous sandstone geology with a

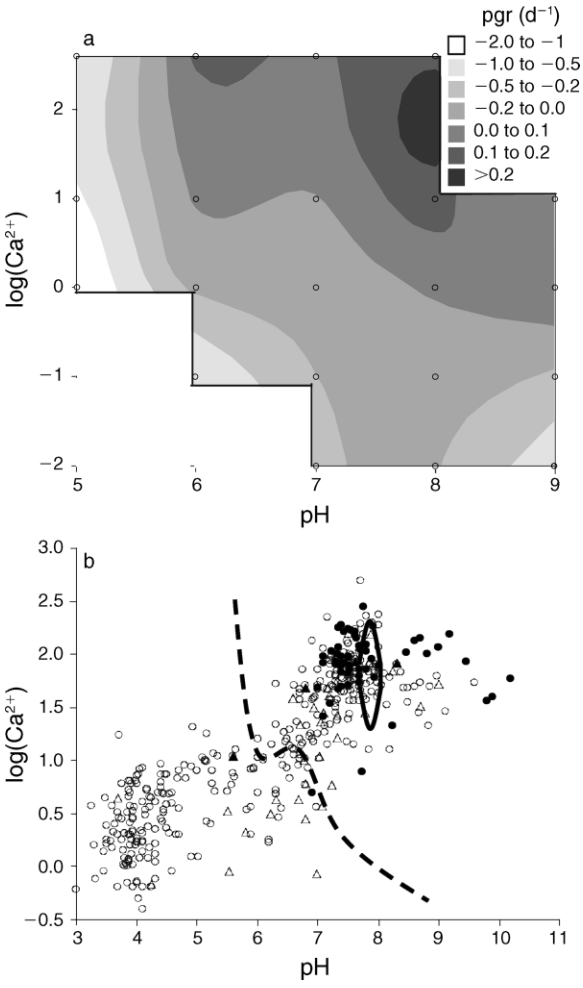

FIG. 3. (a) Population growth rate (pgr) contours plotted against nominal Ca^{2+} and pH concentrations. Open circles represent Ca^{2+} × pH treatments. Population growth rate contours were generated from the raw data ($n = 42$ *Daphnia* populations) on a 5 × 5 grid with seven contours at specified values of pgr using Minitab 14. The minimum and maximum contour levels reflect the measured pgr range of −1.87 to 0.23. Measurements were not made in the areas in the top right and bottom left corners. (b) The field data showing presence (solid symbols) and absence (open symbols) of *D. magna* in relation to Ca^{2+} and pH. Circles indicate the data of Fryer (1985; $n = 396$) while triangles denote the data of Yarwood-Buchanan (2005; $n = 42$). Dashed and solid lines represent the pgr = 0 and 0.2 contours, respectively, from Fig. 3a.

sand pond base (Biggs et al. 2005, Yarwood-Buchanan 2005).

As in the laboratory data, both pH and $\log_{10}$-transformed calcium concentrations contributed to predictions of where *D. magna* occurred. For example, using binary logistic regression, the probability (P) of occurrence of *D. magna* is given by $P/(1 - P) = -10.006 + 0.602\ \text{pH} + 2.36\ \log_{10}Ca^{2+}$, with significant coefficients for both pH ($P = 0.009$) and Ca^{2+} ($P < 0.0005$). Prediction was improved if $\log_{10}K^{+}$ was also used, and $P/(1 - P) = -9.760 + 0.555\ \text{pH} + 1.661\ \log_{10}Ca^{2+} + 1.552\ \log_{10}K^{+}$, but no further improvement was obtained by adding $\log_{10}Na^{+}$ or $\log_{10}Mg^{2+}$.

Comparison of laboratory niche with field distribution

Laboratory niche predictors were compared qualitatively with the field distribution of *D. magna* by superimposing the pgr = 0 and pgr = 0.2 contours onto plots of *Daphnia* in relation to pH and Ca^{2+} concentrations (Fig. 3b). Overall only two out of the 58 occurrences of *D. magna* were outside of the predicted laboratory niche (where pgr > 0); one with a lower pH, the other with lower Ca^{2+}. In addition, very few of the water bodies close to the boundary of the laboratory niche contained *D. magna*. Although six of the sites containing *D. magna* had values above pH 9, laboratory predictions in this region of Ca^{2+}–pH space were uncertain because it was not possible to maintain the test water above pH 9 in our laboratory experiments. In general, very few of the water bodies were occupied when laboratory pgr was below 0.05 d^{-1}, whereas occupancy increased by ~15% between pgr of 0.05 d^{-1} and 0.10 d^{-1}, and 35% when laboratory pgr exceeded 0.10 d^{-1} (Fig. 4).

DISCUSSION

In principle, species distribution should be a function of physiological constraints combined with biological interactions, yet to date there are few examples of the quantification and scientific evaluation of species niches (but see Birch 1953). Here we have measured change in pgr in crossed gradients of pH and calcium to quantify the ecological niche of *Daphnia* (Figs. 2 and 3), an aquatic invertebrate central to material and energy transfer within aquatic food webs. Overall, qualitative fit of predicted and observed distributions was good, with

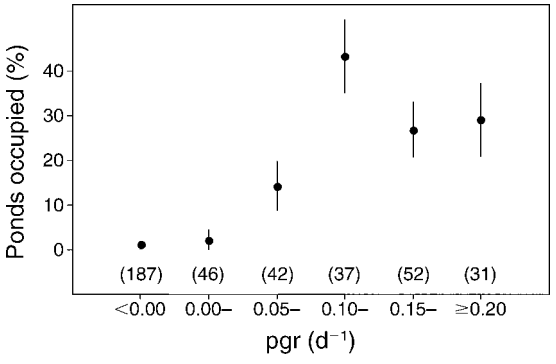

FIG. 4. Percentage of water bodies containing *D. magna* in the field in relation to population growth rate (pgr) values calculated from the laboratory niche. Regions of pH–Ca space with specified pgr values were identified using pgr contours as in Fig. 3a. These regions were then superimposed onto Fig. 3b to calculate, for each region, the percentage of water bodies that contained *D. magna*. Numbers of water bodies in each region are shown within parentheses. Data shown are meas ± SE.

56 out of 58 observed occurrences lying within the predicted laboratory niche (Fig. 3b). However very few of the sites near the niche boundary were colonized (0.00 $d^{-1} <$ pgr < 0.10 d^{-1}; Figs. 3 and 4), suggesting that populations at the edge of the niche may have reduced capacity to resist environmental perturbations because of low growth rates. Similarly, as only 35% of potentially suitable habitats were actually occupied by *D. magna*, our results both bound the potential importance of pH and Ca^{2+} as controls on *D. magna* distribution, and also point to the need to incorporate other biotic, chemical, and physical controls in forecasting species occurrence. Such prediction will be increasingly important in the future, as global warming and widespread disruptions of biogeochemical cycles continue.

Our laboratory results are consistent with previous studies showing that the Ca^{2+} threshold for *Daphnia* survival is 0.1–0.5 mg/L (Hessen and Rukke 2000), that reproduction is unlikely below pH 5.5 (Parent and Cheetham 1980), that death usually occurs within 24 h at pH ≤ 5 (Locke 1991), and that survival is temporarily prolonged by elevated levels of Ca^{2+} (Haves 1985). Calcium is known to mitigate the toxicity of acidic waters in many aquatic animals including *D. magna* (Haves 1985), although the mechanism is not completely understood. One explanation is that Ca^{2+} reduces membrane permeability to H^+ and Na^+ ions, so that H^+ uptake and Na^+ loss are reduced. However, a recent study suggests that sodium uptake rather than loss determines whole body sodium levels in *D. magna*, and that in the absence of Ca^{2+} in the external media, sodium influx is stimulated at low pH; conversely sodium uptake is inhibited at low pH when Ca^{2+} is high (Glover and Wood 2005).

Improvement of our characterization of the niche of *D. magna* will require better understanding of the discrepancies between predictions and observations. Despite our success in predicting the field distribution of *D. magna*, only 35% of apparently suitable sites contained *D. magna* even well inside the laboratory niche where pgr was >0.10 d^{-1} (Fig. 4). This is to be expected as other factors are also involved in determining occurrence. Apart from the vagaries of chance in the dispersal of inoculating propagules/ephippia and such ecologically important factors as the lack of suitable food (Walker and Martin-Creuzburg 2007), the presence of predators (Gliwicz and Stibor 1993), competitors (Hanski and Ranta 1983), parasites (Ebert et al. 2000), and unsuitable physical or chemical features may also limit colonization success. It is of interest that the highest laboratory pgr (>0.2 d^{-1}) did not correspond to the highest frequency in the field, but instead with the laboratory conditions under which our clone of *D. magna* has been cultured for 24 generations (pH $\sim$8, Ca^{2+} 53.39 mg/L or 1.73 log units), a pattern that suggests that discrepancies between pgr-predicted niche and observed distributions may arise because of local adaptation of populations (Potts and Fryer 1979). Further discrepancies between the laboratory niche and field distribution may also reflect temporal variation in the pH of individual water bodies. For example, the pH of circumneutral and alkaline water bodies are known to fluctuate seasonally and diurnally by up to three pH units, as a result of photosynthesis driven in part by light intensity (Philip 1927, Talling 1976). Similarly, multiple measurements of high pH sites (9.8–10.2) by Fryer (1985, 1993) demonstrate that pH varied by up to 2.75 pH units, consistent with transient effects of intense photosynthesis. In contrast, Ca^{2+} concentrations are generally relatively stable, although variation may occur depending on a number of factors such as the rate of weathering of the underlying rock, rainfall, runoff, desiccation, and the buffering capacity of the water body (see for example Muri and Brancelj 2003).

The pgr approach may be particularly useful for quantifying and comparing fundamental and realized niches of species whose distributions are well-documented, and for which pgr can be measured. Measurement of pgr requires the ability to maintain populations in relevant environmental conditions for at least a generation. Provided individuals are observable, pgr can be measured by direct counting or by rapid image analysis methods, as demonstrated here. The use of larger experimental environments should help alleviate technical constraints and allow multiple factor interactions to be assessed.

In an age of global climatic change and habitat shifts and consequent threats to endangered and conserved species, increased understanding is required of the factors that promote population viability and health. We hope the pgr approach to quantifying the ecological niche may prove of wide use in understanding and predicting field distributions, and in diagnosing the causes of population declines (e.g., Ricciardi and Rasmussen 1999). For example, the pgr approach may now show particular promise for defining the suitability of marine protected areas and other conservation regimes in which physical or chemical agents are important controls of species viability. Similarly, application of pgr to temperature regime changes should clearly forecast the conditions under which species may exhibit range expansion or loss. By providing new methods for the prediction of field distributions and the diagnosis of the causes of population declines, we hope to provide conservation biology with additional diagnostic instruments for the ecologist's tool kit.

Acknowledgments

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