

# Climate and body size influence nest survival in a fish with parental care

C. D. SUSKI and M. S. RIDGWAY

Harkness Laboratory of Fisheries Research, Aquatic Research and Development Section, Ontario Ministry of Natural Resources, Trent University, 2140 East Bank Drive, Peterborough, ON, K9J 7B8, Canada

## Summary

1. The current study examined the effect of broad-scale climate and individual-specific covariates on nest survival in smallmouth bass over a 20-year period.
2. Large-scale climate indices [winter North Atlantic Oscillation (NAO) and winter El Niño/Southern Oscillation (ENSO)] and body size of parental males were important covariates in nest survival along with nest age and a quadratic trend in survival.
3. We did not find an effect due to a habitat covariate (total effective fetch) or a phenology covariate (degree-days at start of nesting) on nest survival.
4. Male size in the second half of the nesting season was a more influential covariate on nest success than male size in the first half or throughout the nesting period.
5. We present evidence showing that winter NAO/ENSO indices establish limnological conditions the following spring that influence thermal stability of the lake during the nesting period.
6. The combined climate and body size covariates point to nest survival as a function of lagged climate-scale influences on limnology and the individual-scale influence of bioenergetics on the duration of parental care and nest success.

*Key-words:* limnology, North Atlantic Oscillation, recruitment, reproduction, smallmouth bass, temperature.

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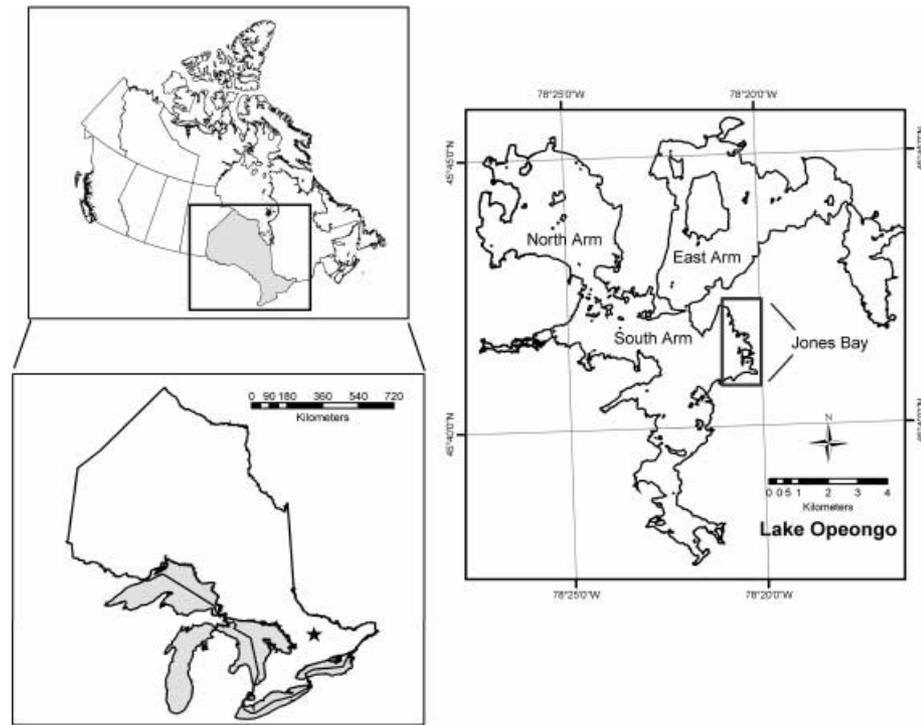
## Introduction

Large-scale climate indices, such as the North Atlantic Oscillation (NAO) and the El Niño/Southern Oscillation (ENSO) have been shown to capture weather patterns across the northern hemisphere (Hurrell 1995; Bonsal *et al.* 2001; Diaz, Hoerling & Eischeid 2001; Hurrell *et al.* 2003). Climate indices act as proxies for atmospheric behaviour taking complex weather parameters and distilling them to a single parameter (Ottersen *et al.* 2001) and can have a pronounced impact on biological systems, ecosystem function and animal populations (Ottersen *et al.* 2001; Stenseth *et al.* 2002). These large-scale predictors of climate often outperform small-scale weather variables at predicting ecological mechanisms (Hallett *et al.* 2004), likely due

to the temporal and spatial scales covered by these indices, as well as the fact that large-scale indices incorporate a host of climate variables such as temperature and precipitation (Stenseth & Mysterud 2005).

Large-scale climate factors have been shown to be one of two major mechanisms that can influence recruitment and cohort strength in smallmouth bass *Micropterus dolomieu* (Lacepède) across the northern tier of their range. Over 50 years ago, summer climate conditions were shown to dictate cohort formation in smallmouth bass through a positive relationship between summer warmth and growth in juveniles (Fry & Watt 1957; Watt 1959). Shuter *et al.* (1980) showed that winter severity and overwinter mortality of young-of-year smallmouth bass interact to define cohort size, body size distribution after the first winter, and the northern boundary of the species' range. The strength of the relationship between environment and recruitment for smallmouth bass has resulted in a level of mechanistic understanding that is relatively rare in fish recruitment research, and has led others to conclude that our understanding of recruitment processes in

Correspondence and present address: C. D. Suski, University of Illinois at Urbana-Champaign, Department of Natural Resources and Environment Sciences, 1102 S. Goodwin Ave., Urbana, IL, USA 61801. Tel.: (217)244-2237. Fax: (217)244-3219. E-mail: suski@uiuc.edu



**Fig. 1.** Map showing the location and size of Lake Opeongo and the Jones Bay study site within Canada (shaded province), and also within the province of Ontario (location of Lake Opeongo denoted by the star).

smallmouth bass is a ‘spectacular success’ in the broad area of environmental influences on fish recruitment (Myers 1998, p. 288). Rarely, however, have the effects of both individual and climatic parameters on nesting success been examined concurrently.

In the current study, we determine the effect of nest-specific parameters and large-scale climatic factors on the earliest stages of cohort formation in smallmouth bass, i.e. nest survival. Focusing on the nesting period provides an assessment of variables that may shape cohorts from the start, prior to first year growth and survival of juveniles where our best insight into cohort dynamics currently lies. In addition to the correlations between climate and recruitment of cohorts, a number of other factors influence smallmouth bass nesting ecology. The timing of nest initiation in this species is based on body size and cumulative degree-days (Ridgway, Shuter & Post 1991; Lukas & Orth 1995; Wiegmann & Baylis 1995). Fetch is important in large lake ecosystems in terms of nest disruption (Goff 1985; Steinhart *et al.* 2005) and nest distribution (Rejwan *et al.* 1997). Male size is important in terms of survival, maturation schedule, and reproductive success (Raffeto, Baylis & Serns 1990; Baylis, Wiegmann & Hoff 1993; Shuter & Ridgway 2002; Dunlop *et al.* 2005b; Dunlop, Shuter & Ridgway 2005a). We incorporated 20 years of nesting data for a northern population of smallmouth bass, and focused on the effects of five parameters on nest survival: nesting phenology, nest age, effective fetch, male size and large-scale climatic indices (NAO and ENSO).

## Methods

This study was conducted in Jones Bay, Lake Opeongo, Ontario (45°42′N, 78°22′W). Lake Opeongo is a large (area = 5780 ha) oligotrophic lake (secchi disk readings of up to 6 m) containing a self-sustaining smallmouth bass population that has been studied for decades (Fig. 1) (Shuter, Matuszek & Regier 1987).

### NESTING VARIABLES

Male smallmouth bass provide sole parental care of offspring from egg deposition in a nest constructed by the male through metamorphosis of the young until the male departs from the nest site; parental care can last for several weeks (Ridgway 1988). Surveys of nesting male smallmouth bass used in this study began in 1983 and continued unchanged and uninterrupted until 2005 (with the exception of the 1986 and 1987 seasons) providing a 20-year data set. Nesting bass were located by snorkel survey in the spring, and surveys were conducted approximately every third day to monitor the progress of brood development. Surveys began when water was 13–15 °C and not on a set calendar date because start times of nesting males vary with spring warming rate (Ridgway *et al.* 1991). The first survey of each year was designated as day 1 for our analyses, and each day of the nesting period was sequentially numbered thereafter for daily survival estimates. Each nesting male in the study was captured by hook-and-line angling, measured to the nearest millimetre (fork

length, FL), given an individually numbered tag, and then released back on to his nest (Ridgway & Friesen 1992). The location of each nest was recorded either using a Wide Area Augmentation System (WAAS) differentially corrected global positioning system (GPS) with an accuracy of < 5 m (eTrex Venture, Garmin International Inc., Olathe, KS, USA), or by transcribing the nest location to a map of the Jones Bay shoreline (scale approximately 1 : 2000) that allowed the placement of a nest within 5 m of its actual location. Our definition of nesting success was consistent with previous work involving smallmouth bass; a nest was considered successful if offspring reached the green fry (metamorphosis) stage, a period when males begin to range further in their daily movements around the nest (Scott, Ridgway & Noakes 1997).

#### LIMNOLOGICAL VARIABLES

Water temperature profile data in Lake Opeongo during July and August were collected over a 27-year period (1958–62, 1965, 1971–87, 1991 and 1994–96) at sites adjacent to the Jones Bay nesting area using either a bathythermograph (Spilhaus 1937) or hand-held thermistors (King, Shuter & Zimmerman 1999a). Profile data were used to calculate the summer thermocline depth, defined as the depth at which the rate of temperature change between the epilimnion and hypolimnion was the greatest (King *et al.* 1999a). In addition, the epilimnetic and hypolimnetic temperatures 1 m below the surface and 1 m from the bottom (respectively) and the maximum temperature difference between the hypolimnion and epilimnion were also recorded over a 39-year period (1958–96) from multiple sites in Lake Opeongo (King *et al.* 1999a). King *et al.* (1999a) used these water temperature data, along with additional weather variables such as air temperature and amount of sunshine, as part of a canonical correlation analysis to explain the relationship between limnological parameters and weather variables for Lake Opeongo. Positive canonical correlation scores as defined by King *et al.* (1999a) refer to shallow thermoclines, a warm epilimnion, and a large thermal gradient between the epilimnion and hypolimnion. The canonical correlation stratification scores generated by King *et al.* (1999a) over a 39-year period, as well as 27 years of thermocline depth data, were used as part of this study to define annual limnological conditions in Lake Opeongo.

Daily water temperature data during the spawning season were collected using automated digital recorders (Ryan Temp-Mentors, Ryan Instruments Inc., Kirkland, WA, USA, and StowAway TidbiT, Onset Computer Corp, Pocasset, MA, USA), continuous paper recorders (Ryan Thermistors, Ryan Instruments Inc.) or conventional thermometers at 1 m depth. Water temperatures were collected at the Jones Bay site for 15 of the 20 study years. For the remaining 5 years, water temperatures were collected from an adjacent site within Lake Opeongo. Highly significant relationships in mean

hourly water temperatures between the two sites from early May until early July across 4 years ( $r^2 = 0.86$ ,  $P < 0.0001$ ,  $n = 9052$  measurements) allowed for the calculation of water temperature at the Jones Bay site when water temperature data were collected only at the adjacent site. Mean daily water temperature data were used to calculate the accumulated degree days for each nest by summing the mean daily water temperatures above 10 °C in a particular year ending on the day a male spawned (Ridgway *et al.* 1991; Lucas & Orth 1995).

#### EFFECTIVE FETCH

The exposure of a smallmouth bass nest to prevailing winds can increase its susceptibility to wave actions from storms potentially inducing nest abandonment (Steinhart *et al.* 2005). As well, Rowan, Kalff & Rasmussen (1992) demonstrated a link between wave energy and sediment distribution in lakes such that the distribution of substrate within littoral areas is dependent upon fetch. Fetch (exposure) within littoral areas is therefore an excellent indicator of both the potential for a nest to receive disruptive wave forces, as well as being a proximate indicator of substrate size. We incorporated a measure of nest-specific effective fetch for all nests in our study based on the methods of Håkanson & Jansson (1983). For this, wind direction and velocity (recorded every 10 min) were collected from a weather station (Campbell Scientific, Edmonton, AB, Canada) on Lake Opeongo 3 m above the water surface approximately 3 km from the Jones Bay site from 2001 to 2005. These data were pooled and the cumulative wind velocity (in  $\text{m s}^{-1}$ ) was calculated for 48 compass directions (every 7.5° of a possible 360°) from 21 May to 7 July of each year (the approximate duration of nesting activity in Lake Opeongo). The cumulative wind velocity along each of the 48 compass directions was then divided by the total summed wind velocity for all directions across all 5 years of data collection to determine the proportion of wind blowing along each of the 48 compass directions. A geographical information system (GIS, ArcView V3.2, ESRI, Redlands CA, USA) was then used to divide the Lake Opeongo shoreline into 5 m × 5 m cells, and the distance to shore (m) along each of the 48 compass directions was calculated for each cell. All distances to shore were weighted by the proportion of wind blowing along each of the 48 compass directions, and the weighted distances to shore were summed to generate a measure of effective fetch for each 5 m × 5 m cell. Each smallmouth bass nest was then assigned to a single 5 m × 5 m cell using either the GPS location of the nest or the nesting maps, and an effective fetch value was then generated for each nest.

#### LARGE-SCALE CLIMATE VARIABLES

The NAO is defined as the difference in sea-level air pressure between Iceland and the Azores in the northern

Atlantic Ocean and is the main factor influencing weather across the North Atlantic throughout the year – particularly during winter (December–March) (Hurrell *et al.* 2003). The El Niño/Southern Oscillation (ENSO) is a sporadic, anomalous shift in sea surface temperatures in the equatorial and eastern Pacific (Huang, Higuchi & Shabbar 1998).

Monthly mean values of NAO and standardized ENSO values (Tahiti-Darwin Sea Level Pressure) were obtained from the National Oceanic and Atmospheric Administration (NOAA) website (<http://www.cpc.ncep.noaa.gov>). As suggested by previous work (Hurrell 1995), the winter period extended from December to March prior to the onset of spawning, and mean NAO and ENSO values during this time were generated and applied to all nests in a particular year. Similarly, the spring period in the current study extended from April to June, and mean NAO and ENSO values during this time were generated and applied to each nest within a particular year.

#### STATISTICAL ANALYSES

Both July–August thermocline depths and canonical correlation stratification scores for Lake Opeongo were compared with large-scale climate indices (NAO and ENSO) in winter and spring with linear regression analysis using JMPIN Version 4.0.4 (SAS Institute Inc., Cary, NC, USA).

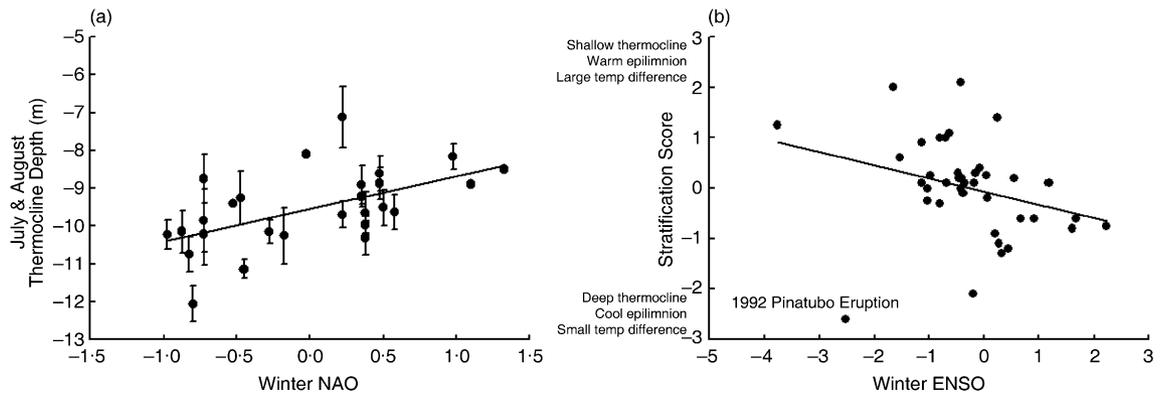
To determine the impacts of the various biotic and abiotic parameters on nesting success, the nest survival

module of Program MARK (Version 5.1) was used (White & Burnham 1999). The nest survival module in Program MARK uses maximum likelihood models to estimate nest survival probabilities across a specified time interval, and is intended to generate nest survival probabilities in studies where nests are visited periodically throughout the nesting cycle (Dinsmore, White & Knopf 2002). More importantly, the ability to include individual and group covariates in models allows for a more extensive examination of factors shaping nest survival in Program MARK in comparison with alternatives such as the Mayfield estimator and the Stanley method (Jehle *et al.* 2004).

To assess nesting success, we pooled all 20 years of nesting data and limited our analyses to 32 a priori models based on past literature describing the impacts of various biotic and abiotic factors on nesting success in smallmouth bass (Table 1). The simplest model was a single estimate of nest survival for the entire nesting period (labelled  $S_{(j)}$  in Table 1). We then created a model that examined the effect effective fetch (abbreviated F in Table 1) on daily nest survival. Four subsequent models examined the independent impacts of large-scale climate indices (abbreviated ENSO and NAO in Table 1) in winter prior to spawning (indicated by  $_{W}$  added to climate indices in Table 1) and spring during spawning (indicated by  $_{S}$  added to climate indices in Table 1). We then combined ENSO and NAO values into two models that examined the impacts of seasonal climate on nest survival (winter and spring). We then generated a model that examined the impact of male

**Table 1.** Model selection results. Model selection results for daily nest survival probabilities of 1187 smallmouth bass nests monitored over 20 years in Lake Opeongo, Ontario, Canada. Models are ranked by differences in AIC values ( $\Delta AIC_c$ ), and the model with the lowest  $\Delta AIC_c$  value is the best fit to the data. To simplify the table, 10 models each having a  $\Delta AIC_c > 100$  have not been shown

Model and abbreviation	AICc	$\Delta AIC_c$	AICc weight	Model likelihood	No. parameters	Deviance
$S_{(W\_NAO+W\_ENSO+FL2ndHalf+Q+A)}$	3604.66	0.00	0.577	1.000	6	3592.66
$S_{(W\_NAO+FL2ndHalf+Q+A)}$	3606.78	2.12	0.200	0.347	5	3596.78
$S_{(W\_NAO+W\_ENSO+FL(Entire)+Q+A)}$	3606.85	2.19	0.193	0.335	6	3594.85
$S_{(W\_NAO+W\_ENSO+FL1stHalf+Q+A)}$	3610.58	5.92	0.030	0.052	6	3598.58
$S_{(Q+A)}$	3631.88	27.22	0.000	0.000	3	3625.88
$S_{(W\_NAO+W\_ENSO+FL(2ndHalf)+Q)}$	3637.75	33.09	0.000	0.000	5	3627.75
$S_{(W\_NAO+FL2ndHalf+Q)}$	3640.41	35.75	0.000	0.000	4	3632.40
$S_{(A)}$	3642.44	37.78	0.000	0.000	2	3638.44
$S_{(S\_NAO+FL2ndHalf+Q)}$	3653.78	49.12	0.000	0.000	4	3645.78
$S_{(Q)}$	3661.33	56.67	0.000	0.000	2	3657.33
$S_{(W\_NAO+W\_ENSO+FL2ndHalf)}$	3689.41	84.75	0.000	0.000	4	3681.41
$S_{(W\_NAO+FL2ndHalf)}$	3690.01	85.35	0.000	0.000	3	3684.01
$S_{(S\_NAO+FL2ndHalf)}$	3701.27	96.61	0.000	0.000	3	3695.27
$S_{(S\_NAO+S\_ENSO+FL2ndHalf)}$	3703.21	98.55	0.000	0.000	4	3695.21
$S_{(FL)}$	3703.57	98.91	0.000	0.000	2	3699.57
$S_{(W\_ENSO+FL(2ndHalf))}$	3703.74	99.07	0.000	0.000	3	3697.73
$S_{(DD+FL2ndHalf)}$	3704.65	99.99	0.000	0.000	3	3698.65
$S_{(W\_NAO)}$	3726.68	122.02	0.000	0.000	2	3722.68
$S_{(DD)}$	3735.49	130.83	0.000	0.000	2	3731.49
$S_{(j)}$	3735.55	130.88	0.000	0.000	1	3733.55
$S_{(S\_NAO)}$	3735.81	131.15	0.000	0.000	2	3731.81
$S_{(F)}$	3737.32	132.65	0.000	0.000	2	3733.32



**Fig. 2.** (a) Relationship between the summer (July and August) thermocline in Lake Opeongo, Ontario Canada, and the value of the North Atlantic Oscillation (NAO) during the preceding winter (December–March) for 27 years, and (b) relationship between canonical stratification score as generated by King *et al.* (1999a) and the value of the El Niño/Southern Oscillation (ENSO) during the preceding winter (December–March) over a 38-year period. For the comparison of canonical stratification score and ENSO values, the 1992 year has been removed from analyses because the volcanic eruption of Mt Pinatubo resulted in an anomalous stratification score. If this point is included in the analysis,  $P = 0.07$ .

size on nest survival, but only applied the effect of male size in the second-half of the nesting period [abbreviated FL(2ndHalf) in Table 1] – a more detailed explanation for treating male size in this way is explained below. Fork length was then combined with effective fetch in a model that examined the impact of size and habitat/exposure on daily nest survival. We then combined the seasonal climate indices (alone and paired with spring and winter indices) with male fork length to examine the combined effects of these variables. Next, past research on the nesting bass population in Lake Opeongo has shown that accumulated degree-days at the time of spawning determines nesting phenology that in turn could affect nest survival (Ridgway *et al.* 1991). Six additional models were generated that incorporated our degree-day covariate as a test of nesting phenology (abbreviated DD in Table 1): alone, in combination with male size (in the second half of the spawning season), and in combination with all four climate indices. Based on the number of nests active each day in our data set we did not believe that an assumption of a linear trend in nest survival was reasonable; as such, we added a quadratic time trend (abbreviated as Q in Table 1; Dinsmore *et al.* 2002) to the three best-fit models generated so far and also to a model with the nest age parameter. We then added a nest age parameter (abbreviated as A in Table 1) to the two best-fit models following the addition of the quadratic time trend. The effects of nest age and the quadratic time trend were then each quantified alone. All models were generated with a common intercept, and covariates were not scaled or standardized in any model.

Allometric patterns of energy reserves and use can affect nest survival among smallmouth bass males of different size (Wiegmann & Baylis 1995; Mackereth, Noakes & Ridgway 1999), and this effect may be most apparent later in the nesting cycle when males have depleted stored energy reserves (Ridgway & Shuter 1994). To test the hypothesis that male size is indeed

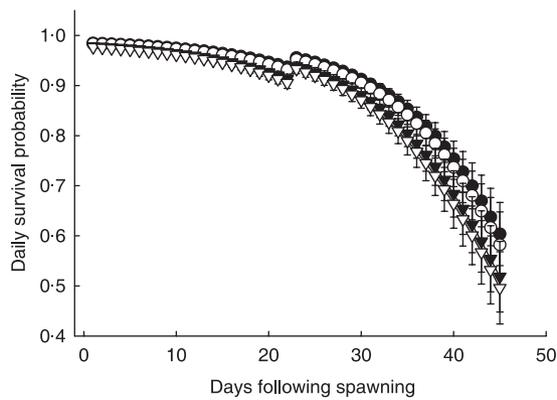
most important in the latter-stages of the nesting cycle, we first constructed all models in the model set described above with the male size parameter applied only to the second half of the nesting cycle. Then, the best-fitting model that contained the fork length parameter was re-run with the effects of male size applied to the first-half of the nesting cycle only [abbreviated FL(1stHalf) in Table 1], and across the entire nesting cycle [abbreviated FL(Entire) in Table 1].

To compare the fit of each model with the data set, Akaike's Information Criterion (AIC analysis) was used (Akaike 1973). AIC analysis is based on likelihood theory and considers the number of parameters and residual variances to rank candidate models and identify the most parsimonious fit to the data based on AIC differences ( $\Delta AICc$ ) (Burnham & Anderson 2002). In general,  $\Delta AICc$  values  $< 2$  suggest strong evidence that the model is the best fit to the data, with  $\Delta AICc > 10$  being strong evidence that a model is not the best fit to the data (Burnham & Anderson 2002).

## Results

### LIMNOLOGICAL PARAMETERS

The summer thermocline depth in the Lake Opeongo increased significantly with mean winter NAO values ( $r^2 = 0.30$ ,  $F_{1,25} = 10.9$ ,  $P = 0.003$ ,  $n = 27$ ; Thermocline Depth =  $-9.5 + 0.86$  Winter NAO; Fig. 2a). In contrast, the canonical standardized stratification score for the South Arm of Lake Opeongo (King *et al.* 1999a) decreased with higher winter ENSO values ( $r^2 = 0.28$ ,  $F_{1,36} = 13.9$ ,  $P = 0.007$ ,  $n = 38$ ; Stratification Score =  $-0.02 - 0.44$  ENSO; Fig. 2b). Thermocline depths were not significantly influenced by winter ENSO, spring ENSO, or spring NAO (all  $P > 0.05$ ). Similarly, canonical standardized stratification scores were not significantly influenced by spring ENSO, winter NAO, or spring NAO (all  $P > 0.05$ ).



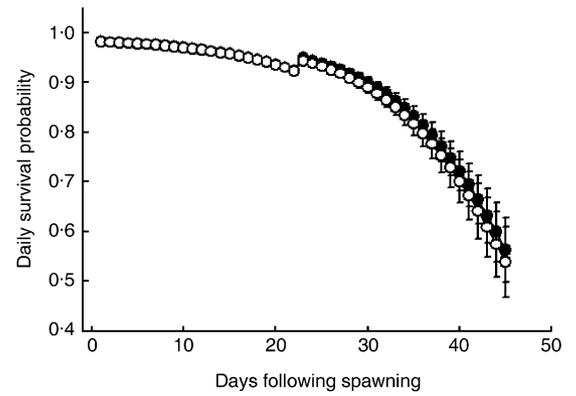
**Fig. 3.** Daily nest survival probabilities for smallmouth bass as influenced by large-scale climate indices during the winter preceding spawning. The figure was generated using the best-fitting model from Table 1. Circles represent survival probabilities in a year with a high value of the North Atlantic Oscillation (NAO) during winter (December–March), and triangles represent survival probabilities in a year with a low value of the NAO during winter. High and low values for NAO phase correspond to the 75th and 25th percentile (respectively) for all 55 years of NAO data available. Filled symbols represent survival probabilities for a year with a low value of the El Niño/Southern Oscillation (ENSO) during the winter (El Niño conditions) and open symbols represent survival probabilities during a winter with a high ENSO value (La Niña conditions). High and low values for El Niño/La Niña conditions correspond to the 75th and 25th percentile (respectively) for all 54 years of ENSO data available. When generating these different lines, male size was held constant at the population average (317 mm) and males were assumed to have spawned on day 1 of the nesting cycle. The inflection in the trendline observed at day 24 occurred because the effect of male size was not entered into the model until day 24 of the nesting cycle.

#### SURVIVAL MODELS

During the 20 years of this study, the survival of 1187 nests were monitored; 587 of the males surveyed (49.5%) successfully reared their young to the green fry stage. The best-approximating model from our candidate set indicated that daily nest survival was influenced by large-scale climate indices in the winter (particularly winter NAO) and the size of the attending male applied to the second half of the nesting cycle and the age of his brood (Table 1). This model also included a quadratic time effect. The logistic regression equation (including  $\hat{\beta}$ -values), with one standard error (SE) for each parameter shown in parentheses, for the best fit models is:

$$\begin{aligned} \text{logit}(\hat{S}_t) = & 3.93 (0.09) + 0.37\text{WinterNAO} (0.08) - \\ & 0.07\text{WinterENSO} (0.04) + \\ & 0.002\text{FL}(2\text{ndHalf}) (0.0005) - \\ & 0.001\text{QuadraticTrend} (0.0002) - \\ & 0.04\text{NestAge} (0.008) \end{aligned}$$

The  $\hat{\beta}$ -value for winter NAO was positive in the best-fit model indicating that the probability of nest survival



**Fig. 4.** Daily nest survival probabilities for large (filled circles) and small (open circles) nest-guarding smallmouth bass in relation to day of nesting cycle. The figure was generated using the best-fitting model from Table 1. Large males [Fork length (FL) = 349 mm] correspond to the 75th percentile for all 1187 nests in the 20-year study, while small males (FL = 280 mm) correspond to the 25th percentile for all males. The inflection in the trend-line observed at day 24 occurred because the effect of male size was not entered into the model until day 24 of the nesting cycle. When generating the two lines, climate indices were held constant at mean values for all available data and males were assumed to have spawned on day 1 of the nesting cycle.

increased with higher values of winter NAO. The  $\hat{\beta}$ -value for winter ENSO from the best-fit model was negative indicating that nest survival probabilities were higher with lower values of ENSO during the winter (El Niño conditions) (Fig. 3). The  $\hat{\beta}$ -value for male fork length in the second half of the nesting cycle was positive indicating the probability of nest survival increased for larger males relative to small males. The  $\hat{\beta}$ -value was negative for nest age pointing to a decrease in nest survival later in the season relative to early in the season (Fig. 4). In the top four models shown in Table 1, the  $\hat{\beta}$ -values for all parameters were similar in magnitude and were identical in sign. The one exception to this was the parameter FL1stHalf (fork length in the first half of the nesting season), where the  $\hat{\beta}$ -value was negative indicating that larger males are subject to somewhat lower nest survival under any limnological conditions given their early nesting starts each year.

Overall mean daily nest survival from the best-fit model was  $0.96 \pm 0.007$  SE (total variance), or  $\pm 0.004$  SE if only process variance is used, indicating that 41.5% of the overall SE resulted from sampling variance. In years with high winter NAO values (75th percentile for all 55 years of NAO data available) combined with low winter ENSO (El Niño) conditions (25th percentile for all 54 years of ENSO data available), the probability that the brood of an average-sized male (317 mm) spawned on day 1 of the nesting period would survive until day 25 of the nesting cycle was 44.4%. Following winters with low (25th percentile) NAO and high (75th percentile) ENSO (La Niña) conditions, the probability that the brood of an averaged-sized male

spawned on day 1 of the season would survive until day 25 of the nesting cycle was 28.9%.

Additions of a parameter for male size (FL) to the second-half of the nesting period improved the fit of our models to the data (Table 1). Models that considered the effect of male size only in the second-half of the nesting period were a better predictor of nest survival than identical models with male size applied only to the first-half of the nesting period, or across the entire nesting cycle (Table 1).

To simplify our results, 10 models were removed from Table 1; all deleted models had  $\Delta\text{AICc}$  values greater than 100 indicating they did little to explain the observed pattern of nest abandonment. Model-averaged parameter estimates were not determined because the  $\Delta\text{AICc}$  values between the best candidate model and the second best model was  $> 2.0$  and the AICc weight was 0.74 for the best model.

## Discussion

Daily nest survival probabilities for smallmouth bass were highest following winters with high NAO and El Niño (low ENSO) conditions, compared with winters with low NAO and La Niña conditions. When the NAO is in its positive phase, the central portion of North America experiences warmer winters and a modest decrease in winter storm activity relative to years with a negative phase (Hurrell *et al.* 2003). While the effects of ENSO events are most prominent in western North America, the cooling effects of La Niña winters can be observed in the central portions of North America, including the region where our study occurred (Shabbar & Khandekar 1996). As a result of relatively warm, storm-free conditions during high NAO and El Niño winters, smallmouth bass experience an increased probability of nest survival, likely due to limnological differences in lake characteristics. Our model selection analysis has identified the influence of both of these major climatic indices on smallmouth bass nest success – an outcome consistent with known continental boundaries of these indices (Shabbar & Khandekar 1996).

Warm, calm conditions around the time of ice-out for temperate lakes, such as those associated with positive NAO values and El Niño winters (Hurrell *et al.* 2003), result in increased thermocline temperatures (King *et al.* 1999a), shallow thermocline depths (King *et al.* 1999a), earlier onset of thermal stratification (Robertson & Ragotzkie 1990), and a larger temperature difference between the epilimnion and hypolimnion (King *et al.* 1999a) relative to cooler conditions. A large temperature difference between the epilimnion and hypolimnion represents a significant barrier to mixing between lake layers, preventing the upwelling of cold hypolimnetic water into the epilimnion that is often observed following storms or prolonged wind events (Wetzel 1983; Robertson & Ragotzkie 1990). Sudden reductions in water temperature have previously been

shown to induce nest abandonment for brood-guarding smallmouth bass (Neves 1975; Shuter *et al.* 1980; MacLean *et al.* 1981) likely due to adverse impacts on the attending male rather than on his brood (Webster 1948); once the brood of a smallmouth bass is left unattended, littoral predators will quickly consume developing offspring resulting in zero reproductive output for that spawning event (Philipp *et al.* 1997). Limnological conditions that prevent this upwelling of cold water into littoral areas result in stable thermal conditions for nest-guarding smallmouth bass, decreasing the probability of nest abandonment, and likely explaining the increased nest survival associated with positive NAO conditions observed in our best-fit model. Several studies have suggested that wave action associated with storm events can be responsible for nest abandonment in smallmouth bass due to physical forces that disrupt both nests and embryos (Goff 1985; Steinhart *et al.* 2005). Because fetch (nest site exposure) was not a covariate that improved the fit of any of our models, we believe that wave effects and substrate size were not primarily responsible for reductions in nest survival in Lake Opeongo. Rather, we believe that the upwelling of cold water following storm events is responsible for reductions in nest survival as such disturbances are likely to impact nesting bass across the study area regardless of site exposure. Thus, large-scale climatic factors dictate limnological conditions in Lake Opeongo that facilitate nest survival in smallmouth bass.

Examination of our best-fit model showed that daily nest survival in smallmouth bass was influenced by the age of a brood, as well as the size of the attending male, with size being particularly important in the latter stages of the nesting period. Models that applied the male size parameter across the entire nesting cycle, or only during the early stages of the nesting cycle, ranked lower than models that considered the effects of male size only in the latter half of the nesting cycle. The coefficient for male size in the first half of the nesting season was negative indicating that larger males nesting early in the season have reduced nest survival relative to smaller males nesting later. In our experience, even under favourable climatic conditions, some cold water intrusions do occur prior to full thermocline formation at a time when large males normally initiate nesting (Ridgway *et al.* 1991).

The  $\beta$ -value for male size in the best-fit model was positive, while the  $\beta$ -value for nest age was negative, indicating that survival was lower for smaller males and that the probability of survival decreased as the nesting period progressed. The inclusion of a quadratic parameter in the model also indicated that nest survival declined at an accelerating rate towards the end of the parental care period. These results can likely be explained by two possible mechanisms, both of which may be linked. First, male smallmouth bass only feed opportunistically during the prolonged nesting period (Hinch & Collins 1991). Nest-guarding male bass rely on stored lipids for energy at this time and males

experience a significant decrease in lipid reserves as the nesting period progresses (Mackereth *et al.* 1999). Indeed, the importance of lipid stores for nesting male bass is underscored in studies by Ridgway & Shuter (1994) who showed that supplemental feeding of brood-guarding smallmouth bass increased parental care duration and nesting success. Larger smallmouth bass contain a greater mass-specific quantity of lipids than smaller individuals (Shuter *et al.* 1980), the mass-specific metabolic rate of fish correlates negatively with size (Brett & Groves 1979), and larger fish have a smaller energetic cost of swimming than do smaller fish (Schmidt-Nielsen 1972). Thus, larger brood-guarding smallmouth bass contain more energy and use energy at a lower rate than smaller individuals, suggesting that brood abandonment may occur earlier in smaller individuals as they deplete energy reserves and abandon their nests in search of food.

A second reason for increased nest survival for larger smallmouth bass centres on brood size. Several studies have demonstrated that larger nesting smallmouth bass obtain a greater number of eggs in a mating attempt than smaller individuals (Ridgway 1989; Philipp *et al.* 1997), and that males guarding large broods invest more energy in defence than do males guarding small broods (Suski & Philipp 2004). Because a larger brood represents greater potential future reproductive returns, large (old) males that have fewer reproductive opportunities prior to the end of their life may choose to continue investing in their current brood following a disturbance such as temperature fluctuation rather than abandoning. Smaller male bass have a greater number of future reproductive opportunities left during their lives, and may choose to abandon their current brood and conserve energy for future reproductive bouts following a disturbance such as temperature change (Williams 1966). As a result of one (or both) of these potential mechanisms, large nest guarding male bass exhibit increased nest survival relative to smaller individuals.

Understanding mechanisms that control fluctuations in population size has been a common theme in animal ecology research for decades (Sibly & Hone 2002). Indeed, this area of research has been extensively pursued by fisheries biologists (Shepherd & Cushing 1990), including an abundance of work that has used bass from the genus *Micropterus* as study organisms (Parkos & Wahl 2002). While research has documented changes in the population size of various fish species, the causes of these fluctuations are often unclear and may result from stochastic events (Shepherd & Cushing 1990). For smallmouth bass, the mechanism controlling recruitment is water temperature expressed as young-of-year growth in summer and survival as a function of winter severity in the first year of life (Shuter *et al.* 1980). Recruitment is influenced to some degree by adult abundance (Shuter & Ridgway 2002) with density-dependent growth occurring from ages 1 to 4 prior to maturation (Ridgway *et al.* 2002; Shuter & Ridgway

2002). The current study does not support the idea of density-dependent nest survival for smallmouth bass. Our results show that population-level nesting success is driven by exogenous climate, independent of population size, with little indication of any compensatory dynamics; if climatological conditions are favourable, offspring production at the start of cohorts should increase, while unfavourable climate conditions will result in low nest survival and reduced cohort strength at the start. As a result, we recommend that fisheries managers provide protection to nest-guarding smallmouth bass because disturbances to nest-guarding bass through human disturbances (such as angling) can inadvertently reduce individual nest survival (Philipp *et al.* 1997; Suski & Philipp 2004); should human-induced abandonment occur in years with unfavourable climate, reduced offspring production would be inevitable.

Studies have suggested that global temperatures have been increasing over the past century and that this warming trend is likely to continue (DeStasio *et al.* 1996; Barnett *et al.* 2005). Part of the reason for this warming trend has been an increased persistence of the NAO in its positive phase, possibly due to accumulations of greenhouse gasses in the atmosphere (Hurrell 1995; Hoerling, Hurrell & Xu 2001). If the NAO remains in its positive phase and warming scenarios do indeed continue, northern populations of smallmouth bass may experience increased nest survival (this study), increased recruitment (cohort strength) (Shuter *et al.* 1980; Casselman *et al.* 2002), above-average adult growth (King, Shuter & Zimmerman 1999b) and northward range expansion (Shuter, Minns & Lester 2002). The presence of male body size in the second half of the parental care period as a covariate in the best-fitting model confirms more detailed work on the bioenergetics of male size and its influence on parental care is warranted (Ridgway & Shuter 1994; Mackereth *et al.* 1999). Population and recruitment ecology of smallmouth bass provides a model system for investigating how individuals, populations, and ecosystems respond to NAO phase so we can predict future population trends and better understand the factors that dictate recruitment in fishes.

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