

Effects of wind-induced spatial variation in water temperature and zooplankton concentration on the growth of young-of-the-year smallmouth bass, *Micropterus dolomieu*

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Synopsis

Young-of-the-year (YOY) smallmouth bass, *Micropterus dolomieu*, spend their first summer in littoral areas near their nests. Evidence indicates that nests of smallmouth bass in Lake Opeongo, Ontario, Canada are more abundant in downwind locations than in upwind areas. We hypothesize that wind-induced lower water temperatures and food availability in upwind nesting areas lead to lower growth rates of YOY bass in upwind than in downwind nesting areas. We show that water temperatures were 0.6–1.3 °C higher in downwind than upwind littoral areas during the period from mid-June to mid-July, when the YOY bass were on or near their nests. Although quite variable, zooplankton concentrations were also higher at downwind sites. In addition, bioenergetic simulations based on time series of field-measured temperatures predicted higher growth rates of YOY bass in the downwind sites. Growth rates based on sequential sampling of bass fry from their nests did not, however, differ statistically between upwind and downwind sites, although fry consistently weighed more downwind than upwind in the basin with the longer fetch possibly due to earlier spring warming. Our hypothesis is thus only partially supported and we call for further research on effects of spatial gradients on smallmouth bass life history.

Introduction

Smallmouth bass, *Micropterus dolomieu*, a native species in eastern and central North America, nests in shallow littoral zones of lakes and in rivers. The parental male builds a nest in early spring, spawning follows shortly after and hatched larvae swim up into the water column but remain closely associated with the nest which the male guards for several weeks (Ridgway 1987). Following this period, the larvae leave the immediate vicinity of the nest but remain in the littoral zone near the nesting area until the end of the growing season

(Gross & Kapuscinski 1997). Habitat conditions in the nesting area will thus affect growth rates of young-of-the-year (YOY) bass.

Smallmouth bass were introduced into the study lake, Lake Opeongo, Ontario, early in the 20th century (Martin & Fry 1972). Detailed information on the distribution of smallmouth bass nests in Lake Opeongo gathered over several years indicates that nest distribution is patchy. The concentration of nests is highest downwind in reference to prevailing winds with 67.5% of nests occurring within a littoral area of less than 10% of the shoreline (Rejwan et al.

1997). High concentrations of nests along the downwind shores have been observed in some other lakes (Carlander 1977). Nest-specific DNA fingerprints suggest that smallmouth bass are territorial and return to their natal sites to breed (Gross et al. 1994), thus raising the possibility that non-uniform nest distributions may be due to differential survival and growth of YOY bass in littoral areas of varying suitability. If local conditions enable high growth, which often leads to strong year classes (Sogard 1997), lower predation risk (Miller et al. 1988) and better winter survival (Shuter et al. 1980), then a tendency for subsequent generations to show site fidelity will lead to higher adult density and more nests.

Fish growth is determined by genetic and environmental factors, with temperature and food availability having the greatest effects (Jobling 1994). Spatial variability in nearshore water temperatures can be caused by wind-induced seiches that move warm surface waters towards downwind shores (Mortimer 1952, Verber et al. 1953). Downwind accumulation of epilimnetic water causes the thermocline to tilt and push cold metalimnetic water in the opposite direction into upwind littoral areas. Such an effect of wind on temperature in littoral areas has been observed in Lake Opeongo (Finlay et al. 2001). Wind can also transport zooplankton, the principal prey of YOY smallmouth bass (Fisher 1972, Wales 1981, Duns Moor et al. 1991), resulting in increased concentration of vertically swimming zooplankton along downwind shores and a corresponding reduction in upwind areas (Colebrook 1960, Langford & Jermolajev 1966, George & Edwards 1976). Downwind aggregation of zooplankton is most likely when winds of low or intermediate strength prevail for considerable periods of time (Haines & Bryson 1961).

The objective of this study was to test the hypothesis that growth rates of YOY smallmouth bass are lower in upwind than downwind sites due to wind-induced patterns in water temperature and zooplankton concentration. We show (a) that water temperature and zooplankton concentration are higher in downwind than upwind littoral areas, (b) that bioenergetic simulations based on measured field temperatures predict higher YOY growth rates at downwind than upwind sites, but (c) that mea-

sured YOY growth rates do not differ between downwind and upwind shores.

Methods

Study area

We conducted this study during 1999 in Lake Opeongo (45°42' N; 78°22' W) in Algonquin Provincial Park, Ontario, Canada. We sampled two basins of this medium-sized (area 58.6 km², maximum depth 52 m) oligotrophic lake (Martin & Fry 1972); the South Arm with a surface area of 22.1 km² and mean depth of 14.6 m, and the North Arm with an area of 14.0 km² and mean depth of 15.2 m (King et al. 1999). Sampling sites were in the shallow littoral zone (Figure 1), upwind and downwind in reference to prevailing southwesterly and northwesterly winds (Rejwan et al. 1997, Finlay et al. 2001).

Field and laboratory methods

We located nests by snorkeling in the nearshore areas at a depth of approximately 1 m. We sampled from mid-June, when the YOY swam up into the water column, until mid-July when the broods dispersed from the immediate vicinity of the nest. Several nests were lost during the course of the study and we replaced them with new nests in the same area. We sampled upwind and downwind sites within a basin during the same day at intervals of 2–4 days, but we sampled the South and North Arms on different days. During each sampling day, we randomly sampled approximately 5–6 YOY from study broods with a dip net and categorized the YOY bass into larvae (black fry) and juveniles (green fry). Larvae were dried with a paper towel in a standardized fashion and weighed to the nearest 0.1 mg using an analytical balance (Mettler AE50, Mettler Toledo Canada, Mississauga, ON).

We placed thermistors (Onset HOBO, Onset, Bourne, Maine) that automatically recorded water temperature every 0.5 h at a depth of 1.5 m in the upwind and downwind littoral sites of the South and North Arms (Figure 1). We supplemented these data with similar observations from other thermistors placed in the study areas (Figure 1)

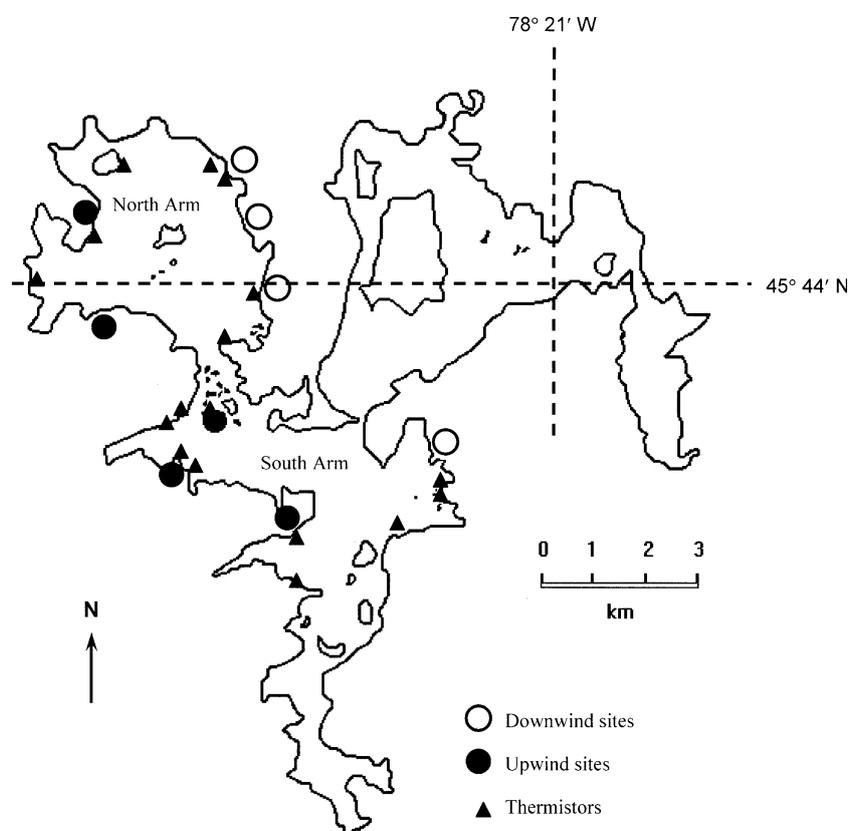


Figure 1. Map of Lake Opeongo, Ontario, Canada. The nesting areas sampled are designated with circles and the locations of thermistors with triangles.

that recorded every 8 or 16 min (H. Cyr, K. Finlay & BJS, University of Toronto).

We used a battery-powered pump to sample zooplankton near the study nests and from several predetermined nearshore sites where no nests were found. On each day, we sampled zooplankton from a randomly chosen subset of the sampling sites. The number of zooplankton samples varied among the sampling days as a result of weather conditions or time constraints. We obtained the samples from the mid-depth of the sampling site by pumping 60 l of water through a 43 μm mesh and preserving the zooplankton samples in 4% sucrose formalin. We filtered the samples, rinsed them with water, diluted them to a sample volume of 50 ml and homogenized them with a stir bar. We obtained a measured sub-volume from the solution, placed it into a counting wheel under the microscope, identified the zooplankton to genus and enumer-

ated them. If fewer than 250 organisms were in the initial sub-sample, we processed additional sub-samples and computed the concentration of zooplankton (no. l^{-1}).

Data analysis

We determined water temperatures during the study period from seven and three thermistors, respectively in upwind and downwind sites of the South Arm, and from three and four thermistors, respectively in the North Arm (Figure 1). To combine the data recorded every 8, 16 or 30 min, we calculated mean temperatures for each thermistor for consecutive 4 h intervals. We then averaged these values for thermistors within a given arm (North or South) and site (upwind or downwind) to produce a sequence of temperatures every 4 h for each. We determined the frequency distribution of differences between downwind and upwind temperatures for

each 4 h interval for both the North and South Arms. We did not statistically test the hypothesis that the mean difference was zero because the sequential 4 h observations are not independent. However we did contrast the distribution of temperature differences in the North and South Arms using a Kolmogorov Two-Sample Test (Sokal & Rohlf 1997).

We predicted that zooplankton concentration would be higher near the shores located downwind in reference to the prevailing winds. We examined the distribution of concentrations within sampling days using normal probability plots and logarithmically transformed the data (\log_e) to satisfy parametric assumptions. Some of the concentrations were low and we added the constant 1 to all values before transformation (Zar 1999). We used one-tailed t -tests with sequential Bonferroni corrections for multiple tests (Sokal & Rohlf 1997) to evaluate whether mean zooplankton densities were higher in downwind sampling sites on each sampling day. We combined p -values from t -tests for each sampling day to test for overall consistency in trends within a basin using the χ^2 distribution (Sokal & Rohlf 1997).

We used a bioenergetics model for smallmouth bass (Shuter & Post 1990) to simulate the growth of YOY based on field temperatures measured near the nests. The model is based on the principle of energy conservation with all consumed energy used for growth, metabolism, excretion or egestion:

$$G = C - (R + U + F)$$

where G is the specific growth rate ($\text{g g}^{-1} \text{d}^{-1}$) and C , R , U and F are the mass-specific rates of consumption, respiration (= metabolism), excretion and egestion (Kitchell et al. 1977). Metabolism has three components – standard metabolism for body maintenance, an activity multiplier to account for active metabolism and specific dynamic action for food absorption and digestion. Each of these components is a function of temperature and body mass while excretion, egestion and specific dynamic action also depend on the consumption rate. The model uses a series of species-specific rate parameters estimated from laboratory experiments to simulate the growth of a fish over a specified period starting with an initial body mass. To facilitate comparisons among arms and sites, we ran all simulations from 12 June to 8 July 1999

even though some of the field observations ended earlier than this. We assumed that the bass had an initial mass of 0.01 g, corresponding to the mean mass of fish observed in the field, and that they fed at maximum rates. We ran the model with the software STELLA (Version 2, isec systems, Lebanon, NH, USA) using a time step of one day.

We determined the instantaneous growth rate of YOY smallmouth bass, I (day^{-1}), from field observations using the least squares regression:

$$\ln W = a + I \times t$$

where W is body mass (g) and t is time (d). We defined a single observation as the mean mass of bass sampled from a brood on a given sampling day and assumed that YOY sampled from the same nest on the same day were of the same age and had been exposed to similar conditions for growth. We tested differences in the fitted parameters (a and I) between upwind and downwind sites of the South and North Arms using ANCOVA (Sokal & Rohlf 1997). Residuals in the ANCOVA models were normally distributed and there was no serial autocorrelation due to the time variate except for upwind data in the South Arm. All statistical analyses were done with the software STATISTICA (Release 5.1, StatSoft Inc., Tulsa OK, USA).

Results

In the South Arm, which has a long unobstructed fetch of approximately 12 km, mean temperatures during the observation period (12 June–8 July 1999) were $20.9 \pm 1.2^\circ\text{C}$ (mean \pm standard deviation) in the upwind sites and $22.2 \pm 1.6^\circ\text{C}$ in the downwind sites. In the North Arm, which has a shorter fetch of approximately 3.5 km, temperatures during the observation period 13–30 June 1999 were $20.7 \pm 1.4^\circ\text{C}$ in the upwind sites and $21.3 \pm 1.7^\circ\text{C}$ in the downwind sites. In the South Arm, the mean temperature difference between downwind and upwind shores was $1.3 \pm 0.8^\circ\text{C}$ and temperature was higher in downwind littoral sites 95.7% of the 4 h periods (Figure 2a). In the North Arm, the mean temperature difference was $0.6 \pm 0.7^\circ\text{C}$ and temperature was higher in the downwind sites 80.6% of the time periods (Figure 2b). The frequency distributions of tempera-

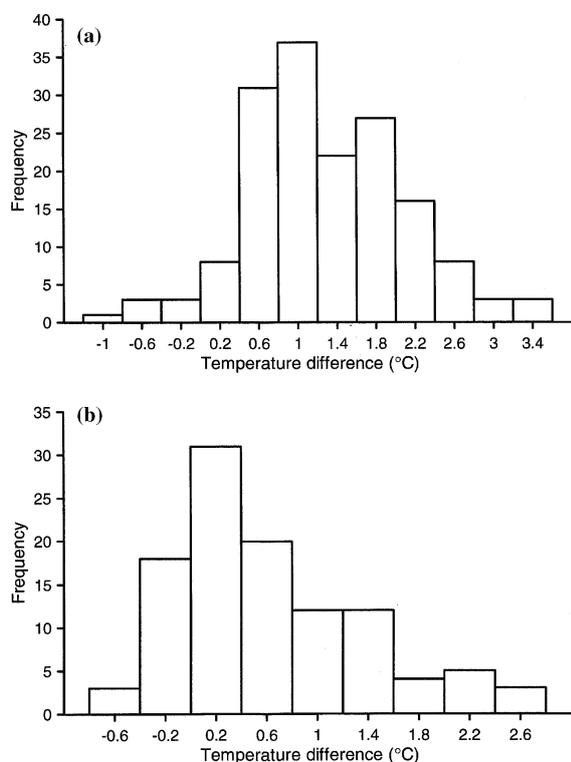


Figure 2. Temperature differences (downwind–upwind) between downwind sites and upwind sites every 4 h from 12 June to 8 July, 1999 in the South Arm (a) and from 13 June to 30 June 1999 in the North Arm (b).

ture differences are statistically distinct in the two basins (Kolmogorov two-sample test, $n = 108$ and 162 , $p < 0.001$), which is consistent with our prediction that the wind would induce greater temperature gradients across the longer fetch of the South Arm.

The zooplankton community in the North Arm consisted principally of cyclopoid and calanoid copepod nauplii (48% of total numerical abundance at all sites combined), cyclopoid copepod juveniles and adults (18%), and bosminid (8%) and chydorid (20%) cladocerans. In the South Arm, the community comprised principally copepod nauplii (25%), cyclopoid copepod juveniles and adults (31%), bosminid cladocerans (28%) and rotifers (9%). Low numbers of calanoid copepod juveniles and adults, *Polyphemus pediculus* (Linnaeus), *Diaphanosoma birgei* Kořinek, *Daphnia* spp., *Ceriodaphnia* spp. and *Holopedium gibberum* Zaddach made up the rest of the communities.

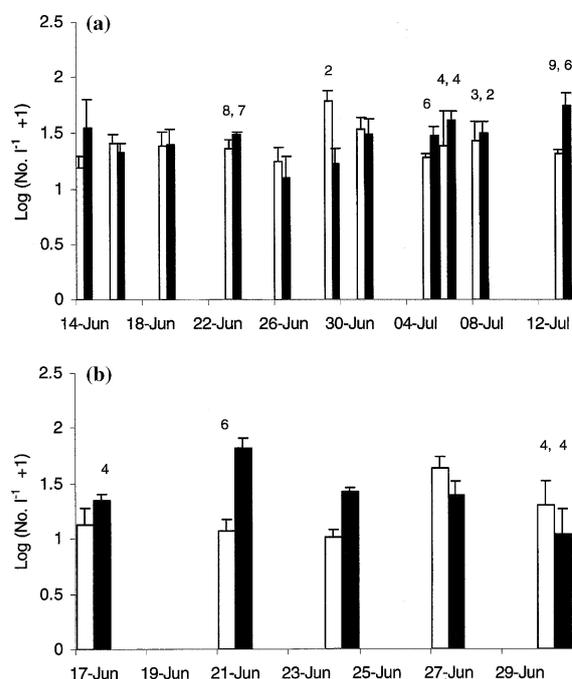


Figure 3. Mean zooplankton concentrations with standard errors for the downwind (dark bars) and upwind (light bars) sites of the South (a) and North (b) Arms. Sample sizes for each bar are five unless otherwise indicated.

Zooplankton concentration was higher in downwind sites on 7 of 11 sampling days in the South Arm (Figure 3a) but the only difference that was statistically significant was July 13 ($t = 3.32$, $df = 13$, $p = 0.003$). In the North Arm, zooplankton concentration was higher in downwind sites on 3 of 5 sampling days (Figure 3b) and statistically significant on June 21 ($t = 6.10$, $df = 9$, $p = 0.0001$) and June 24 ($t = 3.44$, $df = 8$, $p = 0.004$). When the probabilities from these independent tests were combined, the overall trend was statistically higher zooplankton abundance in the downwind sampling sites of both the South ($\chi^2 = 35.4$, $df = 22$, $p < 0.035$) and North ($\chi^2 = 34.2$, $df = 10$, $p < 0.0002$) Arms.

We used temperature sequences recording during the study period from the thermistors to model the growth of YOY bass in each of the North and South Arms (Figure 4) using the bioenergetics model. Except for one simulation in the North Arm, modelled masses of YOY bass at downwind sites were consistently higher than those at upwind sites (Figure 4). The largest fish at the end of the

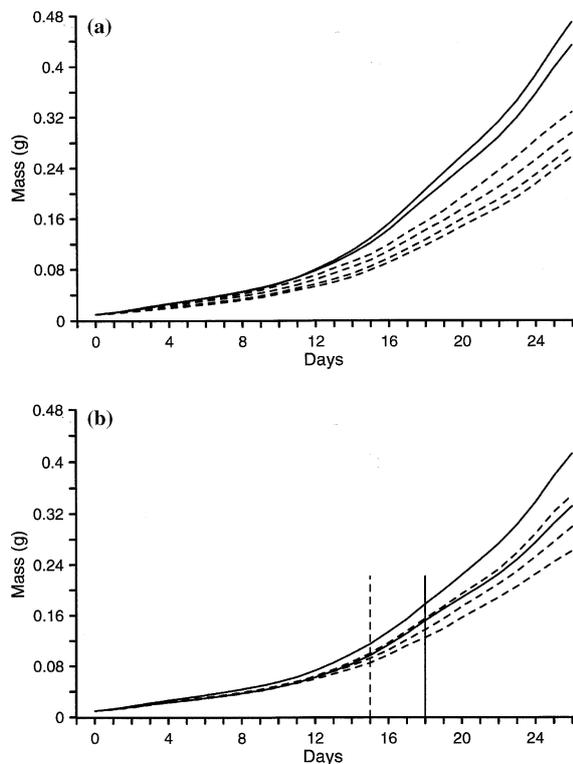


Figure 4. Modelled growth of YOY bass from bioenergetic simulations. Predicted body masses are shown for downwind (solid lines) and upwind sites (dashed line) in the South (a) and North (b) Arms. Each line is a simulation based on temperature data from a single thermistor. In panel (a) the simulations end on the last day of field observations whereas in panel (b) vertical lines indicate the days of last field observations for the upwind (dashed) and downwind (solid) sites. Data from some thermistors are not plotted for clarity but this does not affect maximum and minimum trends for the sites. Day 0 is 12 June 1999 in both panels.

simulation period occurred downwind in the South Arm and they ranged in mass from 0.43 to 0.47 g. By contrast, modelled larvae ranged from 0.33 to 0.41 g downwind in the North Arm where downwind temperatures averaged 0.9°C less than in the South Arm. It should be noted that field observations ended earlier in the North Arm because it became difficult to collect enough larvae for analysis (Figure 4b).

The instantaneous growth rate of YOY bass (based on observed body mass) at the downwind sites of the South Arm was slightly higher than the growth rate at upwind sites (0.15 vs. 0.14 day^{-1} , Figure 5a) but this was not statistically significant (ANCOVA, $F_{1,92} = 0.4$, $p = 0.53$). However the

body mass of YOY bass at downwind sites was consistently higher than that at upwind sites (Figure 5a; ANCOVA, $F_{1,93} = 10.8$, $p = 0.001$) probably reflecting earlier downwind spawning as a result of higher water temperatures (Shuter et al. 1980). In the North Arm, there were no differences in observed growth rates (ANCOVA, $F_{1,44} = 1.82$, $p = 0.18$) or intercepts (ANCOVA, $F_{1,45} = 0.79$, $p = 0.38$) between upwind and downwind sites (Figure 5b). At the end of the sampling period, larval masses observed in the field were roughly the same or slightly lower than those predicted from the bioenergetics model in the North Arm, whereas

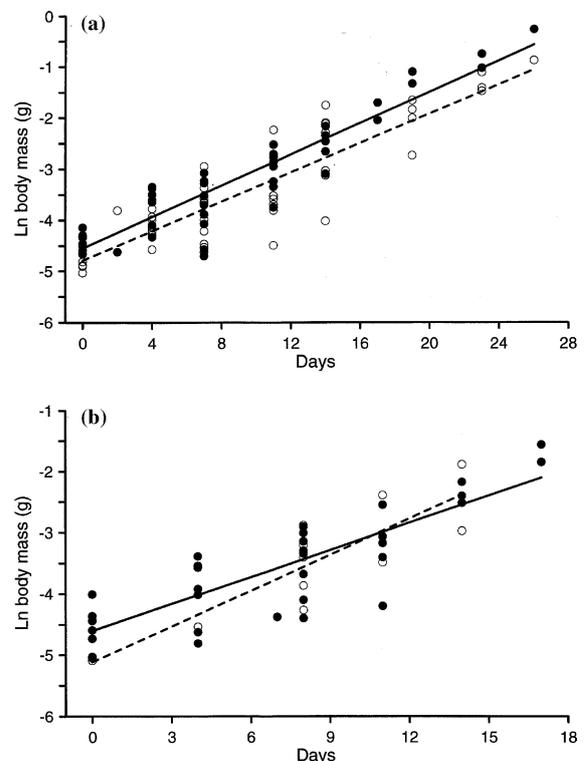


Figure 5. Growth of small mouth bass fry based on observed body masses in the South (a) and North (b) Arms. Upwind data are open symbols and dashed lines, and downwind data are filled symbols and solid lines. In panel (a) day 0 is 12 June and in panel (b) day 0 is 13 June 1999. Fitted least squares linear regressions are: South Arm upwind $Y = -4.79 + 0.144$ (± 0.012) X , $r^2 = 0.77$; South Arm downwind $Y = -4.55 + 0.153$ (± 0.009) X , $r^2 = 0.86$; North Arm upwind $Y = -5.12 + 0.196$ (± 0.032) X , $r^2 = 0.79$; North Arm downwind $Y = -4.60 + 0.147$ (± 0.016) X , $r^2 = 0.71$, where Y is \ln mass (g), X is time (d), r^2 is explained variance and standard errors of the coefficients are shown. All regressions are statistically significant.

Table 1. Observed and predicted maximum body masses of smallmouth bass larvae.

Location		Predicted	Observed	
			Raw data	Linear fit
North Arm	Upwind	0.09 (0.003, $n = 4$)	0.10 (0.05, $n = 3$)	0.093
	Downwind	0.17 (0.009, $n = 3$)	0.18 (0.03, $n = 2$)	0.12
South Arm	Upwind	0.30 (0.01, $n = 6$)	0.42 (–, $n = 1$)	0.35
	Downwind	0.44 (0.01, $n = 3$)	0.77 (–, $n = 1$)	0.57

All values for a location are calculated on the last day of field observations (27 and 30 June 1999 for North Arm upwind and downwind, respectively, and 8 July 1999 for both South Arm locations). Predicted values are means from the bioenergetic simulations, observed raw data values are means from field observations and observed linear fit values are computed from the linear regressions of observed body mass on time. Standard errors and samples sizes are shown where appropriate.

observed values were higher than predicted ones in the South Arm, particularly for the downwind site (Table 1). Except for the temperature sequences from individual thermistors, all parameters were identical in the simulations and hence these reflect pure temperature effects on larval growth. Effects of varying concentrations of zooplankton prey are not incorporated in the simulations and hence we interpret differences between observed and predicted larval masses to be due to this additional food effect on larval growth observed in the field.

Discussion

Our objective was to test the hypothesis that growth rates of YOY smallmouth bass are lower in upwind than downwind sites due to wind-induced patterns in water temperature and zooplankton concentration. Because prevailing winds over Lake Opeongo are westerly to south- and northwesterly, cooler upwelling water should occur along the western shores of the lake and warmer water along the eastern shores. Observed temperature patterns were consistent with this expectation since nests along the western shores (i.e. upwind sites) were exposed to cooler water than those in downwind sites for the majority of the observation periods in both the North and South Arms. We expected temperature gradients to be smaller in the North Arm where the effective fetch is shorter and the islands in the central area of the basin can restrict the establishment of uninodal seiches, and our data are also consistent with this prediction. Water temperature is considered to be an important habitat variable determining the location of

smallmouth bass nests (Rowan 1962) and the patterns we observe at least partially account for the higher density of bass nests found along downwind shores in Lake Opeongo (Rejwan et al. 1997).

Wind-induced water currents can result in the net displacement of zooplankton towards downwind shores (Colebrook 1960). We observed substantial variation in the spatial distribution of zooplankton from one sampling day to the next, and within a sampling day variation in zooplankton concentrations among nests was considerable. Nevertheless, there was an overall pattern of statistically higher zooplankton concentrations at the downwind nests compared to upwind nests in both the South and North Arms. The higher downwind concentrations result from the interaction of horizontal currents that move zooplankton downwind and their vertical migrations that take them out of the return currents flowing along the metalimnion (Colebrook 1960). Some species remaining near the metalimnion could be transported to upwind shores, but detailed observations on zooplankton spatial distributions from June to September 2001 indicate that zooplankton are concentrated at sites downwind of the prevailing winds for a high proportion of observations periods (Menza 2003). Lower upwind concentrations result when zooplankton are moved downwind, but upwelling of cool metalimnetic water containing fewer zooplankton also contributes on days with particularly strong winds. Higher zooplankton concentrations will increase feeding rates of YOY smallmouth bass at downwind sites because of enhanced predator-prey contact rates (Sundby & Fossum 1990). There is evidence that turbulence

resulting from moderate winds can also increase encounter rates between fish and zooplankton (Rothschild & Osborn 1988).

Bioenergetic growth simulations support our hypothesis that YOY growth is higher at downwind sites where the water is warmer. These simulations were based on the actual field temperatures recorded by thermistors but did not take account of variations in prey concentrations. Incorporating temporal and spatial variation in prey concentration would have made the simulation more realistic but such processes are not part of the bioenergetic model we used. Field measurements of YOY growth rates, on the other hand, showed no statistical differences between upwind and downwind sites in either the North or South Arms, although the downwind growth rate in the South Arm was numerically higher. Body mass of fry was also consistently higher at downwind than upwind sites in the South Arm, possibly because eggs hatched earlier there due to more rapid spring warming.

The lack of statistical pattern in measured growth rates is clearly due to the high variation, we observed in the body mass of fry from one nest to another within a single day. Such variation is likely due to strong spatial heterogeneity in physical and biological factors in these complex and shallow littoral zones. For instance, along the upwind shores where the nest density is generally low, only the most suitable microhabitats were probably used for nesting, resulting in higher measured growth rates in upwind areas than would be expected from spatially averaged temperature and zooplankton measures. Variability in the ages of larvae collected from the same nest, density-dependent growth compensation and variable sample sizes, particularly in the North Arm, could further add to uncertainty in our estimates of instantaneous growth rates. It is also possible that site-specific factors influencing juvenile bass at times of year other than our late spring-early summer study period could affect their growth and survival and hence adult nesting behaviour.

The final answer to our speculation that smallmouth bass should grow faster in the warmer, plankton rich downwind sites in Lake Opeongo is thus somewhat equivocal. Clearly higher, wind-induced temperatures exist in the downwind sites and, although more variable, overall zooplankton

concentrations were higher too. Such conditions should promote higher growth according to the bioenergetic simulations but we observed no statistical differences in our empirical estimates of larval growth between upwind and downwind sites. The fact is that smallmouth bass nests are much more common in sites that are downwind to prevailing winds in Lake Opeongo (Rejwan et al. 1997) and no other better explanation for this distribution than our wind-induced growth hypothesis exists as far as we know. Higher growth and associated lower mortality at downwind sites combined with fidelity to natal habitats (Gross et al. 1994) would produce non-uniform nest distributions in lakes with fetches large enough for effective wind action. This might be especially true of lakes such as Lake Opeongo which is near to the northern limit of smallmouth bass and in which this species may be especially sensitive to water temperature and food availability. Nevertheless additional research on effects of spatial gradients in physical and biological variables on smallmouth bass life history is required before a firm resolution of our speculations is achieved.

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