

Divergent life histories among smallmouth bass *Micropterus dolomieu* inhabiting a connected river–lake system

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Annual reproductive surveys monitored nesting location, reproductive success and the age and size of individually tagged male smallmouth bass *Micropterus dolomieu* that reproduced in Millers Lake, a 45 ha widening of the Mississippi River, Ontario, and in a 1.5 km pool and riffle section of the river directly upstream. The vast majority of males displayed fidelity to either the river or the lake as reproductive habitat throughout their lifetimes. Nearly, half of the males that reproduced in successive years exhibited strong nest-site fidelity by nesting within 20 m of their previous year's nest site. In most years, when compared to those in the lake, reproductive males in the river differed significantly in reproductive characteristics including age and size at maturation and nesting success rates. A 3 year telemetry project identified two distinct habitat use patterns: lake-resident fish remained in the lake throughout the year and potamodromous individuals migrated from the lake to upriver spawning habitat in the spring and then returned to the lake prior to the onset of winter. Integration of habitat use and reproductive data suggests that there are significant differences in the life-history strategies of fish that reproduce in the river v. the lake.

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INTRODUCTION

Decades of empirical and theoretical research have led to an understanding of how growth and mortality rates interact to affect key demographic variables such as abundance, biomass and maturation schedules of fish populations

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(Roff, 1984; Lester *et al.*, 2004; Shuter *et al.*, 2005). This knowledge has proven to be effective in identifying ecological and environmental factors underlying life-history variation within and among panmictic populations (Lester *et al.*, 2004; Dunlop *et al.*, 2005a). A number of studies have identified differences in growth and mortality rates between groups of fishes inhabiting the same system but mating assortatively (often due to differences in the habitats selected by the members of each group; Schluter, 2001), these examples illustrate the potential for unrecognized population structure to confound life-history studies, particularly when group members choose habitats with different selection pressures. As a result, it is now clear that determining whether a putative population exists in panmixia is a challenging but necessary first step towards understanding the basis of life-history variation.

Streams are recognized to include a number of habitats with varying biotic and abiotic conditions from the headwaters to the mouth (Vannote *et al.*, 1980), and even contiguous habitats have been shown to present significantly different environments for resident species (Schlosser, 1991). For organisms inhabiting connected river–lake systems, the physical, thermal and biotic environments can vary greatly between lentic and lotic habitats. For example, adaptation to flowing water has been proposed to account for morphological differences between river-dwelling and lake-dwelling populations of fishes, including pumpkinseed *Lepomis gibbosus* (L.) and rock bass *Ambloplites rupestris* (Rafinesque) (Brinsmead & Fox, 2002). Differences between lentic and lotic environments were linked to life-history variation between populations of pearl cichlid *Geophagus brasiliensis* (Quoy & Gaimard) inhabiting a connected river–lagoon system (Mazzoni & Iglesias-Rios, 2002). Additionally, riverine systems are recognized to be more vulnerable to stochastic hydrologic events than lacustrine systems; the frequency, magnitude and unpredictability of events can have strong effects on food availability and mortality (Lytle & Poff, 2004). In any spatially heterogeneous system, the extent to which life-history variation is the result of habitat-specific differences in growth and mortality depends on the degree to which individual fishes reside within a single habitat type. Life-history divergence can occur *via* plastic and genetic pathways when groups of fishes display fidelity to different habitat types, and the magnitude of environmentally induced life-history differentiation is expected to be inversely related to the frequency of gene flow between groups.

The *M. dolomieu* Lacepède is a common species in both lacustrine and riverine systems across North America (Scott & Crossman, 1973). Male age and size at maturation have been demonstrated to vary both within and among populations of *M. dolomieu* (Ridgway *et al.*, 1989; Raffetto *et al.*, 1990; Dunlop *et al.*, 2005b), and individual fish are recognized to display fidelity to specific reproductive habitats and home ranges over multiple years (Ridgway *et al.*, 2002). The species' reproductive ecology is characterized by the paternal construction and defence of nesting sites. Males use their caudal fins to scrape nests (shallow, saucer-shaped depressions) in the littoral zone substratum in the spring, when water temperatures approach 15° C (Turner & MacCrimmon, 1970). Females depart after depositing externally fertilized eggs into the nest, and males provide sole parental care of the brood, a period of time that can last for *c.* 4–6 weeks post-fertilization (Coble, 1975; Ridgway *et al.*, 1989).

Previous studies have proposed that variation in ages at maturation within a single population was directly related to body size; the largest members of a cohort matured at the earliest ages, while smaller individuals delayed until subsequent breeding seasons (Raffetto *et al.*, 1990; Dunlop *et al.*, 2005b). A recent inter-population comparison found that males inhabiting a lake with fewer large-bodied prey (resulting in slower growth at age ≥ 5 years) matured at younger ages and smaller sizes than males in a nearby lake with more large-bodied prey (Dunlop *et al.*, 2005a). It is also possible that because larger males within a population often have increased mating success compared to smaller males, sexual selection may influence age and size at maturation (Ridgway *et al.*, 1989; Suski *et al.*, 2003, Suski & Philipp, 2004). Despite the observation that male *M. dolomieu* display strong fidelity to specific reproductive habitats and home ranges over multiple years (Ridgway *et al.*, 2002), and genetic evidence suggestive of philopatry to natal sites (Gross *et al.*, 1994), there has been no evaluation of whether fish inhabiting connected river–lake systems have different life-history characteristics.

Robbins & MacCrimmon (1977) provide the most thorough description of a potamodromous population of *M. dolomieu* in a tributary of Lake Simcoe, Ontario. Just prior to the reproductive period, individuals migrated from the lake to spawning areas in the tributary, then most migrants returned to the lake shortly after the conclusion of parental care activities. The study, however, did not attempt to describe the reproductive characteristics of the population or to evaluate the relationship between potamodromous fish and fish spawning in the lake. For more than a decade, *M. dolomieu* reproductive activity has been studied in another connected river–lake system in eastern Ontario, Canada. A 3 year radio-telemetry project investigated movement patterns and habitat use of adult *M. dolomieu* in this system. The objective of this study was to integrate reproductive data and habitat use data to evaluate whether life-history variation among *M. dolomieu* inhabiting a continuous system was partitioned between fish spawning in these two distinct habitats (*i.e.* lake and river).

MATERIALS AND METHODS

STUDY SITE

The Mississippi River is a shallow, warm-water tributary of the Ottawa River (Frontenac County, Ontario, Canada; 44°56' N; 76°42' W), and this study was conducted on a section of river that encompasses two distinctly different habitats (Fig. 1). The upstream 1.5 km is riverine habitat, with eight pools separated by riffles and rapids of varying magnitudes. All pools have a maximum depth >6 m and surface areas ranging from 0.49 to 2.14 ha (mean \pm s.d. surface area 1.00 ± 0.57 ha). At the downstream end of this section, the river flows over a set of rapids into Millers Lake. None of the rapids between the uppermost pool and the lake are barriers to *M. dolomieu* movement. The lake is 1.75 km long and 0.25 km wide (45 ha), with a maximum depth of nearly 25 m. The study site is bordered upstream by *c.* 2 km of white-water environment (extremely marginal spawning habitat for *M. dolomieu*) that includes a natural waterfall with a 2 m vertical drop. This waterfall serves as a complete impediment to *M. dolomieu* emigration and probably limits immigration greatly as well. There is another series of rapids and waterfalls downstream of the study site with *c.* 2 m vertical declinations but each with somewhat of a more gradual grade suggesting that they might serve as less

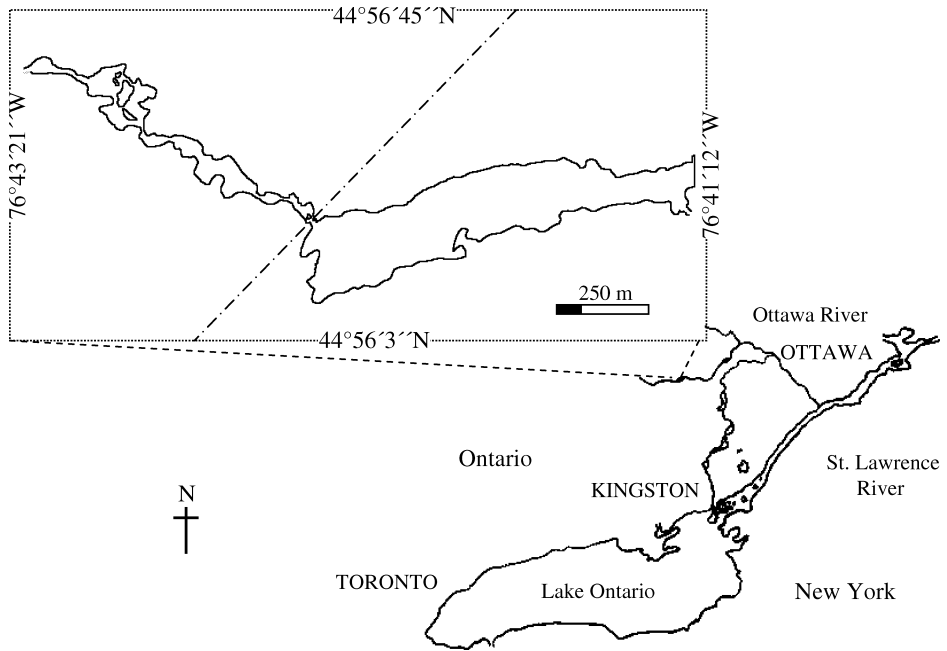


FIG. 1. Map of eastern Ontario showing the location of a section the Mississippi River studied. The inset box shows the locations and sizes of the river and lake sections of the study site. Water flows from the river into the lake.

than a total obstruction to *M. dolomieu* movement than the upstream falls. Telemetry studies, however, reported here did not detect fish movements out of the study site in either direction. The riverine section of the study site is only accessible by canoe portage and receives negligible angling pressure. There is public access to the lake, which does receive more angling pressure than the river but does not, however, attract a substantial number of anglers targeting *M. dolomieu* (Kubacki *et al.*, 2002). In this part of Ontario, the *M. dolomieu* angling season is closed until the last weekend in June, thereby protecting nesting *M. dolomieu* through the reproductive period.

TELEMETRY STUDY

A 3 year telemetry study was initiated in May of 2000, when radio transmitters (MBFT-6A, 36 month battery life, 3.7 g in water; Lotek Wireless Inc., Newmarket, Ontario, Canada) were surgically implanted into the peritoneal cavity of 16 male and 13 female adult *M. dolomieu* using methods described in Cooke *et al.* (2001). Individuals were captured by hook and line angling: nine females and two males were captured at the rapids between the river and lake habitats, two females and six males were captured near known nesting areas in the river and two females and eight males were captured near known nesting areas in the lake. To ensure transmitter size did not exceed 2% body mass and interfere with natural behaviour, larger individuals were selected to be part of the study (mean \pm s.d. total length, L_T , = 372 ± 49 mm, L_T range = 285–486 mm). Fish were located with a four-element Yagi antenna and SRX_400 receiver (Lotek Wireless Inc.) from either a boat or canoe during most of the year, but from shore or the lake surface when there was ice cover. Fish locations were triangulated using shore-based landmarks, while moving towards the estimated location and simultaneously reducing gain to ensure accurate locations. Radio-tagged fish were

tracked three times a week during the reproductive period and less frequently during the non-reproductive periods.

REPRODUCTIVE SURVEYS

Snorkelling surveys were conducted three times a week during the reproductive period (mid-May to early July) to monitor *M. dolomieu* reproductive activities (nesting, spawning and parental care) from 1990 to 2005. Snorkellers swimming the littoral zone of both the river and the lake placed a numbered plastic tag beside each nest as it was discovered and recorded its location on a detailed map. The following information was recorded for each nest: a visual estimate of male L_T (mm), nest depth (m), estimated spawn date and brood development stage. Subsequent swims searched for new nests and monitored previously tagged nests, thereby determining whether each male was successful or not in raising its brood. A male was considered successful if its brood developed to the point at which the offspring dispersed from the nest into shallow littoral zone structure, had transformed from black to green body colouration and were acting independently of the male (Philipp *et al.*, 1997). Nesting success was calculated as the proportion of spawning males that successfully raised a brood to independence, regardless of the number of surviving juveniles. Because of the clarity of the water in the system, a strong tendency of male *M. dolomieu* to nest at depths <2 m and the frequency of snorkelling surveys during the reproductive period (three to four per week), most if not all nests in each year were probably found.

MARK-AND-RECAPTURE STUDY

From 1996 to 2005, after each nest was located, nesting males were angled off their nests and tagged. The capture and handling process took <1 min, thereby minimizing stress. Exceptionally low numbers of brood predators in the littoral zone of this site resulted in negligible levels of brood predation in the short period that males were removed from their nests. Upon capture, L_T was measured to the nearest mm and scales were sampled below the lateral line, posterior to the dorsal fin for age determination. Each new nesting male had a passive integrated transponder (PIT) tag injected into its peritoneal cavity to allow for the identification of individual males over multiple years. If the captured male was found to have been PIT tagged in a previous year, the alphanumeric code was recorded. Males were released back onto their nests and they immediately resumed parental care behaviour. A male was considered to have matured in the year that it was first observed to nest. Between 1997 and 2004, males were captured from 866 of the 1037 nests constructed in the system (83.5%). Many of the males that were not captured had abandoned their broods quite prematurely, before being angled. The ages of the nesting male *M. dolomieu* were determined by counting scale annuli using scale impressions on acetate slides that were magnified using a microprojector (Jearld, 1983). Hoxmeier *et al.* (2001) found the accuracy of scale age estimation was positively related to latitude; the distinct winters of northern latitudes (such as those at the present study site) produced easily distinguishable annuli, resulting in high precision for age estimation (Kruse *et al.*, 1993). Furthermore, the recapture of individual males over multiple years allowed the accuracy of many age determinations to be validated.

DATA ANALYSIS

Telemetry study

Seasonal habitat use was evaluated by determining the proportion of tracking locations for each radio-tracked fish during each of five seasonal periods. Each seasonal period is a major ecological period encountered by *M. dolomieu* in northern environments. The 'prespawn' period is defined as beginning with the vernal equinox and

ending the day before the first nest is found to have eggs in the study site in each year. At the start of this period, *M. dolomieu* are relatively inactive in overwintering habitat and then become increasingly active as they move towards spawning habitats. The 'spawning' period is defined as those days between the first and last spawning events in the study system in each year and is characterized by female egg deposition into nests. The 'parental care' period begins the day after the last observed spawning event and continues through the last observation of males guarding broods in either study site. Males provide sole parental care of the brood after egg deposition, and females have completed their reproductive activity by this period. The 'post-reproductive' period follows the end of parental care period and lasts through the autumnal equinox. Activities of both males and females have turned to feeding prior to the onset of quiescence during cold temperatures. The 'autumn-winter' period occurs between the autumnal and vernal equinoxes. As previously mentioned, *M. dolomieu* are believed to show fidelity to an overwintering site during the winter (Webster, 1954).

Reproductive surveys

Nest-site fidelity of individual males was evaluated by measuring the physical distance between nest locations for all males nesting in multiple years between 1997 and 2004. All observed 'nesting decisions' (characterized by the distance between successive annual nest sites) in the river and lake were organized into a series of distance classes for statistical analysis. A test of marginal homogeneity was conducted to compare nest-site choice in the river and lake environments; the distributions of nesting decisions among distance classes (0–20, 21–40, 41–60, 61–80, 81–100, 101–200 and >200 m) were compared for males that spawned in the river v. those that spawned in the lake with Pearson χ^2 tests.

The number of reproductive seasons in which each male nested was calculated for those males that spawned either in the river or in the lake and had matured between 1997 and 2002. Those males that had spawned (or were likely to have spawned) prior to 1997 were omitted from the analyses, as were those males that matured in 2003 or later, due to the possibility that some of these males would still be reproducing in 2006. The number of reproductive seasons were compared for males spawning in the river v. those in the lake using a Pearson χ^2 analysis of spawning location (river or lake) and the number of reproductive seasons of individual males (1, 2, 3 and ≥ 4 years).

For each year between 1997 and 2004, the reproductive characteristics of males spawning in the river v. the lake were compared. Nesting success of males was compared with the Pearson's χ^2 test of spawning location (river or lake) and the proportion of males that successfully raised their brood in each year (1997–2004). Age distributions of males reproducing in the river v. in the lake were also compared using a test of marginal homogeneity, Pearson's χ^2 test of location and numbers of males that matured at each age in each year. The ages at which males matured in the river v. the lake were compared in each year between 1997 and 2004. In an effort to exclude males that had spawned in years prior to 1997, males that had been PIT tagged the previous year were not included.

The ages that fish matured in the two habitats were also compared by identifying the reproductive characteristics of individuals for 4 year-classes (those males that hatched in each year 1995–1998) that spawned either in the river or in the lake during the period of this study. For each year-class, male age at maturation distributions were compared for individuals that reproduced in each habitat (river or lake) using Pearson's χ^2 statistic. Then for each year-class, the L_T of males that matured at each age were compared using Wilcoxon rank sum tests. Some comparisons were not possible due to few or no males maturing in some age-classes.

Pre-maturation L_T -at-age were backcalculated for males that matured at ages 3–6 years in 4 year-classes (1995–1998). Backcalculations followed the procedure of Dunlop & Shuter (2006), which found a common body-scale relationship among 17 *M. dolomieu* populations in Ontario and Nova Scotia. These authors validated this procedure using marked-and-recaptured *M. dolomieu* from two populations in Ontario and successfully

applied the method to backcalculate ages of fish collected across the province (Dunlop & Shuter, 2006). Mean L_T -at-age curves were constructed independently for males spawning in the river and for those spawning in the lake in each of the 4 year classes using the backcalculated L_T at ages.

Mortality of nesting males was estimated by dividing the number of males that did not return to spawn in a subsequent year by the total number of males observed to spawn for the first time at each age between 1997 and 2004. This method was used in a similar study of two lake-dwelling populations of *M. dolomieu* in eastern Ontario (Dunlop *et al.*, 2005a). The high levels of nest-site fidelity exhibited by male *M. dolomieu* (Ridgway *et al.*, 2002) and the fact that no radio-tagged males left the study site during the telemetry study together suggest that very few males are likely to have strayed outside of the study site. Mortality rates of males spawning in the river and the lake were compared using Pearson's χ^2 tests.

All tests were conducted using JMP 4.0.4 (SAS Inc., Cary, NC, U.S.A.).

RESULTS

TELEMETRY STUDY

Two major habitat-use patterns were observed among radio-tracked fish, a lake-resident pattern characterized by movements restricted to the lake and a migratory pattern with potamodromous movements from the lake into the river in the spring, followed by a return to the lake prior to the onset of winter. Three of the tagged females were lake residents and 10 followed the migratory pattern (referred to as the potamodromous pattern from this point forward); the lake resident and potamodromous pattern were each exhibited by eight males (Table I). Fish that followed the two different patterns did not differ in mean L_T (Table I), and fish showed fidelity to a single pattern over the course of the study. The only exception to the general patterns described above was a single male tagged in the river that remained in the river through the first autumn and winter but then migrated and overwintered in the lake the following year. This was the only radio-tagged fish to overwinter in the river during the study period, and despite this uncharacteristic behaviour in the first year, it has been classed as a potamodromous male. This fish is the one responsible for the observation that some potamodromous males may remain in the river into the autumn and perhaps even the winter period. All tracked males displayed fidelity to either the river or the lake as reproductive habitat throughout the study period. Fish were not observed to overwinter in the river and migrate to the lake for reproduction; spring migrations were always from the lake to the river. The timing of all observed movements from the lake to the river coincided with the spawning period. For males, their nesting was confirmed; for females, it is assumed to be related to use of the river as reproductive habitat. Habitat use patterns in each seasonal period are described in further detail in the following sections.

Prespawn period

During this period, >75% of locations of potamodromous fish were in the lake. The system is covered with ice at the time of the vernal equinox (20–21 March), and this study agrees with previous observations that *M. dolomieu*

TABLE I. Telemetry results organized by the sex and the habitat-use pattern of each *M. dolomieu*, showing mean \pm s.d. total lengths (L_T) of tagged fish, the total number of locations during each of the five seasonal periods, and the number and percentage of locations of fish in the river habitat during each seasonal period

Movement pattern	Number of fish	L_T (mm)	Prespawm period locations		Spawning period locations		Parental care period locations		Post-reproductive period locations		Autumn and winter period locations						
			Total (n)	In the river %	Total (n)	In the river %	Total (n)	In the river %	Total (n)	In the river %	Total (n)	In the river %					
Potamodromous male	8	360.8 \pm 60.0	26	9	34.6	86	80	93.0	58	45	77.6	151	64	42.4	24	5	20.8
Potamodromous female	10	373.9 \pm 52.6	20	1	5.0	68	28	41.2	40	17	42.5	55	12	21.8	11	0	0
Lake-resident male	8	378.0 \pm 42.5	28	0	0	120	0	0	73	0	0	148	0	0	19	0	0
Lake-resident female	3	383.7 \pm 32.3	10	0	0	47	0	0	24	0	0	56	0	0	12	0	0

are relatively quiescent during winter (Kolok, 1991), residing in a particular overwintering habitat during winter (Langhurst & Schoenike, 1990). Fish became more active and moved towards spawning areas as water temperatures increased after ice-out. Potamodromous fish tended to be located at the river-mouth for a short period prior to migration into the river; lake-resident fish, however, did not show this behaviour and instead distributed themselves around the lake shoreline. Potamodromous males were observed to enter the river 8–13 days before the first spawn in the system (median = 11 days). Upriver movements prior to spawning are responsible for the locations of potamodromous males in the river during this period. Potamodromous females were located in the river as early as 13 days prior to the onset of spawning and as many as 16 days after the first spawn.

Spawning period

Potamodromous males were located in the river during this period, where they built, maintained and guarded nests. Nearly half of the locations of potamodromous females were in the river during this period. Surveys were not able to delineate female spawning activity (which probably lasts only a few hours or less), but the assumption that female movements into the river during this period were motivated by mating opportunities is supported by the lack of observations of females moving upriver during any other seasonal periods. The majority of females (60%) returned to the lake before the end of the spawning period, and all females returned to the lake shortly after this period. The date that females were observed to return to the lake ranged from as many as 30 days before the last spawn to 22 days after the last spawn (median return date = 3 days before the last spawn). No potamodromous males returned to the lake during this period.

Parental care period

Male *M. dolomieu* provide parental care for 4–6 weeks following egg deposition and 30% of potamodromous males were observed to return to the lake immediately following the conclusion of parental care (*i.e.* within 1–3 days). Other males (40%) returned to the lake only after a few weeks following their terminating parental care. The remaining 30% did not return to the lake until August, September or October, with the date ranging from 6 to 128 days after the last spawn date in the system (median = 30 days). Although many potamodromous females returned to the lake during the spawning period, a few remained in the river during the parental care period, presumably to feed. All potamodromous fish dispersed throughout the lake upon their return to the lake and appeared to use the same habitats as lake-resident fish.

Post-reproductive period

As previously stated, most potamodromous males returned to the lake shortly after concluding parental care, although some were located in the river during this period. A few potamodromous females were also still located in the river in the post-reproductive period but numbers declined substantially as

more females returned to the lake. The potamodromous fish that remained in the river were generally found in deeper areas at the head of pools and were associated with water flowing from upstream pools.

Autumn and winter period

By the time of the autumnal equinox (22–23 September), most potamodromous fish had returned to the lake. By late November, all but one male (in year one only) had moved to the lake, and 24 of the 29 tracked fish had aggregated in a relatively small area in the deepest portion of the lake (Bunt *et al.*, 2003). Half the lake-resident males overwintered in this aggregation, as did all the lake-resident and potamodromous females. All but one of the potamodromous males were also in this aggregation. Those fish that were not in the aggregation were dispersed throughout the lake and not associated with any obvious hydrological or physical characteristics during the winter.

NEST-SITE FIDELITY

During the course of the study, 526 individual males were captured while guarding nests in the river and 340 nesting males were captured in the lake. From these data it was ascertained that 543 individual males matured, spawned and completed (were no longer observed among the breeding population) their reproductive lives in the study system between 1997 and 2004. This number does not include individuals that matured in years prior to 1997 or individuals that had matured during the course of the study but spawned in 2005 (and may have nested in future reproductive seasons). The majority of these 543 males were effectively semelparous, spawning in a single reproductive season; only 128 males spawned in multiple years. Only four of these 128 males were observed to skip a reproductive season (*i.e.* not spawn in each successive year between maturation and their departure from the reproductive population). The vast majority of the 128 males that spawned in multiple years (123 males, 96%) returned to the same reproductive habitat (either the river or the lake) every year in which they spawned, 51 males showed complete fidelity to the lake as reproductive habitat and 72 males showed complete fidelity to the river as reproductive habitat. Only five males (4%) were observed to nest and spawn in both habitats during their lifetime.

Nest-site fidelity was evaluated within each habitat during the study period 1997–2004. The analysis included 110 nesting decisions of 82 males that were observed to reproduce during multiple years only in the river, and 112 nesting decisions of 67 males that reproduced during multiple years only in the lake. These data indicate that nearly half of the nesting decisions in the river, and just more than half of the nesting decisions in the lake resulted in males nesting within 20 m of their previous year's nest site (Fig. 2). Pearson's χ^2 test of nesting distances and location found that males that reproduced in the river tended to nest closer to their previous years nest site than males in the lake ($\chi^2 = 36.53$, $P < 0.001$; 85% of nesting decisions resulted in males nesting within 100 m of their previous years nest site in the river compared to 65% of nesting decisions in the lake; 98% of nesting decisions resulted in males nesting within

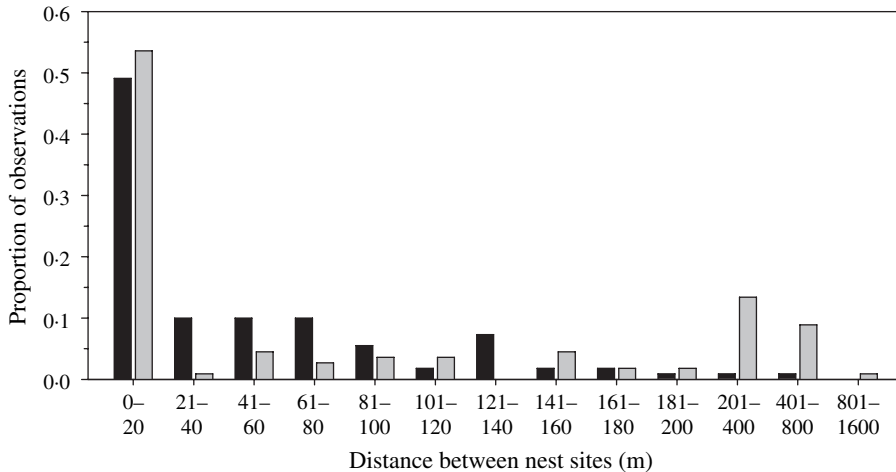


FIG. 2. Comparison of the distances between the nest sites of individual male *Micropterus dolomieu* that nested in two successive years in either the river (■) or lake (□) habitats of the Mississippi River study site. Data are presented for males that displayed fidelity to either the river (82 males, 110 observations of nests constructed in successive years) or the lake (67 males, 112 observations of nests constructed in successive years) as reproductive habitat between 1997 and 2004 and is organized as the proportion of nesting decisions that occurred within a series of distance classes.

200 m of their previous years nest in the river compared with 77% of decisions in the lake).

CHARACTERISTICS OF REPRODUCTIVE MALES

A greater number of nests were constructed in the river than in the lake in all but one of the years of the study (Table II). Nesting habitat does not appear to be a limiting resource in the river or in the lake because many nesting areas used in 1 year were vacant in others and the year with the greatest number of nests (2001) also had a high nest-success rate. The date of first spawn was very similar in the river and lake in each year (Table II), and spawning tended to be slightly more protracted in the river than in the lake (Table II). Although more males tended to raise their broods to independence in the lake than the river in each year of the study, there were only statistically significant differences in nest-success rates for 3 years (2000, 2001 and 2002; Table II). For each year of the study, across both habitats, the majority of males that reproduced were doing so for the first time, *i.e.* they matured in that year. More than two thirds of the males that matured in the system between 1997 and 2004 spawned in only a single reproductive year (Table III). The number of reproductive seasons in which a male spawned did not differ between the two habitats ($\chi^2 = 4.18$, $P > 0.05$).

Males that spawned in the lake were older on average than males that spawned in the river in all but 1 year of the study (2003) (Table IV and Fig. 3). Males that spawned in the lake were larger on average in every year (Fig. 4). Males in the river and lake had different age at maturation distributions in

TABLE II. The magnitude, timing and success rates of male *Micropterus dolomieu* reproductive activity in the river and lake habitats of the Mississippi River study site, 1997–2004. Dates of first spawn and last spawn are the first and last day that eggs were deposited into nests in each habitat, respectively. Dates are presented as the number of days from the start of the year (1 January). The number of days between the first and last spawn are recorded as the spawning period (this does not include the entire parental care period of most nests). The proportion of new males is the proportion of nesting males that were observed to spawn for the first time in each year. Nest success is presented as the percentage of nesting males that raised their broods to independence. The results of statistical comparisons of nest success in the two habitats are presented for each year (Pearson χ^2 tests of marginal homogeneity)

Year	Habitat	Nests (<i>n</i>)	Day of first spawn	Day of last spawn	Spawning period (days)	Proportion of new males	Nest success		
							%	χ^2	<i>P</i>
1997	River	72	152	165	14	0.732	83.3	0.40	0.528
	Lake	25	140	164	25	0.500	100		
1998	River	74	133	144	12	0.800	86.5	0.70	0.402
	Lake	47	129	143	15	0.848	91.5		
1999	River	63	133	156	24	0.696	93.7	0.02	0.904
	Lake	57	134	151	18	0.630	93.1		
2000	River	82	140	169	30	0.730	45.1	22.41	<0.0001
	Lake	69	137	161	25	0.569	82.6		
2001	River	94	137	159	23	0.747	70.2	14.48	0.0001
	Lake	99	137	160	24	0.753	91.8		
2002	River	74	146	172	27	0.821	43.2	15.56	<0.0001
	Lake	29	150	159	10	0.586	86.2		
2003	River	70	138	163	26	0.621	92.9	0.96	0.327
	Lake	61	137	163	27	0.667	96.7		
2004	River	78	136	157	22	0.703	92.3	0.42	0.519
	Lake	43	137	154	18	0.514	95.3		
Mean	River	76	139	162	24	0.731	75.9		
	Lake	58	138	157	20	0.633	92.2		

TABLE III. Comparison of the total number of reproductive seasons that individual male *Micropterus dolomieu* spawned in the river and lake habitats of the Mississippi River study site between 1997 and 2004. These data are for males determined to have matured, spawned and completed their reproductive lives during the course of the study

Reproductive seasons (<i>n</i>)	Males that reproduced in the river		Males that reproduced in the lake	
	<i>n</i>	%	<i>n</i>	%
1	195	75.0	119	69.6
2	42	16.2	26	15.2
3	13	5.0	14	8.2
≥4	10	3.8	12	7.0

TABLE IV. Statistical results for comparisons of ages and ages at maturation of male *Micropterus dolomieu* that reproduced in the river and lake habitats between 1997 and 2004. Distributions were compared using Pearson's χ^2 tests of marginal homogeneity

Year	Age of nesting males				Age at maturation			
	<i>n</i>		χ^2	<i>P</i>	<i>n</i>		χ^2	<i>P</i>
	River	Lake			River	Lake		
1997	56	12	13.82	0.032	30	7	10.92	0.027
1998	60	28	15.53	0.030	46	23	11.95	0.018
1999	58	53	20.47	0.015	39	33	17.22	0.002
2000	65	58	23.90	0.002	43	29	18.10	0.001
2001	75	68	23.39	0.001	59	53	30.69	<0.001
2002	66	25	30.20	<0.001	51	13	16.89	0.002
2003	67	52	15.45	0.051	33	29	5.63	0.131
2004	73	37	30.86	<0.001	34	12	5.13	0.274

all but 2 years (2003 and 2004; Table IV), and a greater proportion of males matured at older ages (5 and 6 years) in the lake than in the river (Fig. 3). Males that spawned in the lake had greater L_T at maturation than males that spawned in the river in each year (Fig. 4). Age at maturation distributions varied among years within each habitat (Fig. 3): the most abundant age at maturation tended to be age 4 years in the river, with the frequency of 3 and 5 year olds varying among years; the most observed age at maturation classes in the lake were 4, 5 and 6 years, with considerable interannual variation in the relative frequency of these age-classes.

There were differences in age at maturation distributions between male members of the same year-class that reproduced in the river and lake in 3 of 4 year classes analysed (Table V). These differences were a result of there being a greater proportion of males maturing at ages 5 and 6 years in the lake, while most males matured at age 4 years in the river (Fig. 5). There was considerable interannual variation within each habitat: the most frequent age class in the river was 4 years for all year classes, and 3 year olds were the second most abundant class in 3 of 4 year classes. Non-parametric tests detected a single significant difference in the L_T of males that matured at each age in the river v. the lake in the 4 year classes (age 4 years, year class 1996; Table V).

Pre-maturation L_T at age were very similar for males spawning in the river and lake habitats for all for 4 year classes (Fig. 6). Although this study was not able to determine the habitat in which males resided prior to maturation, these results indicate pre-maturation growth rates did not differ between males that spawned in the river and the lake (mean L_T of males that matured in the lake divided by mean L_T of males that matured in the river at each age ranged from 1.00 to 1.09 for the 1995 year class, 0.99 to 1.05 for the 1996 year class, 0.95 to 1.03 for the 1997 year class and 0.91 to 1.02 for the 1998 year class).

Males that spawned in the two habitats did not have statistically different return rates at any ages (Table VI), although it is possible that small sample

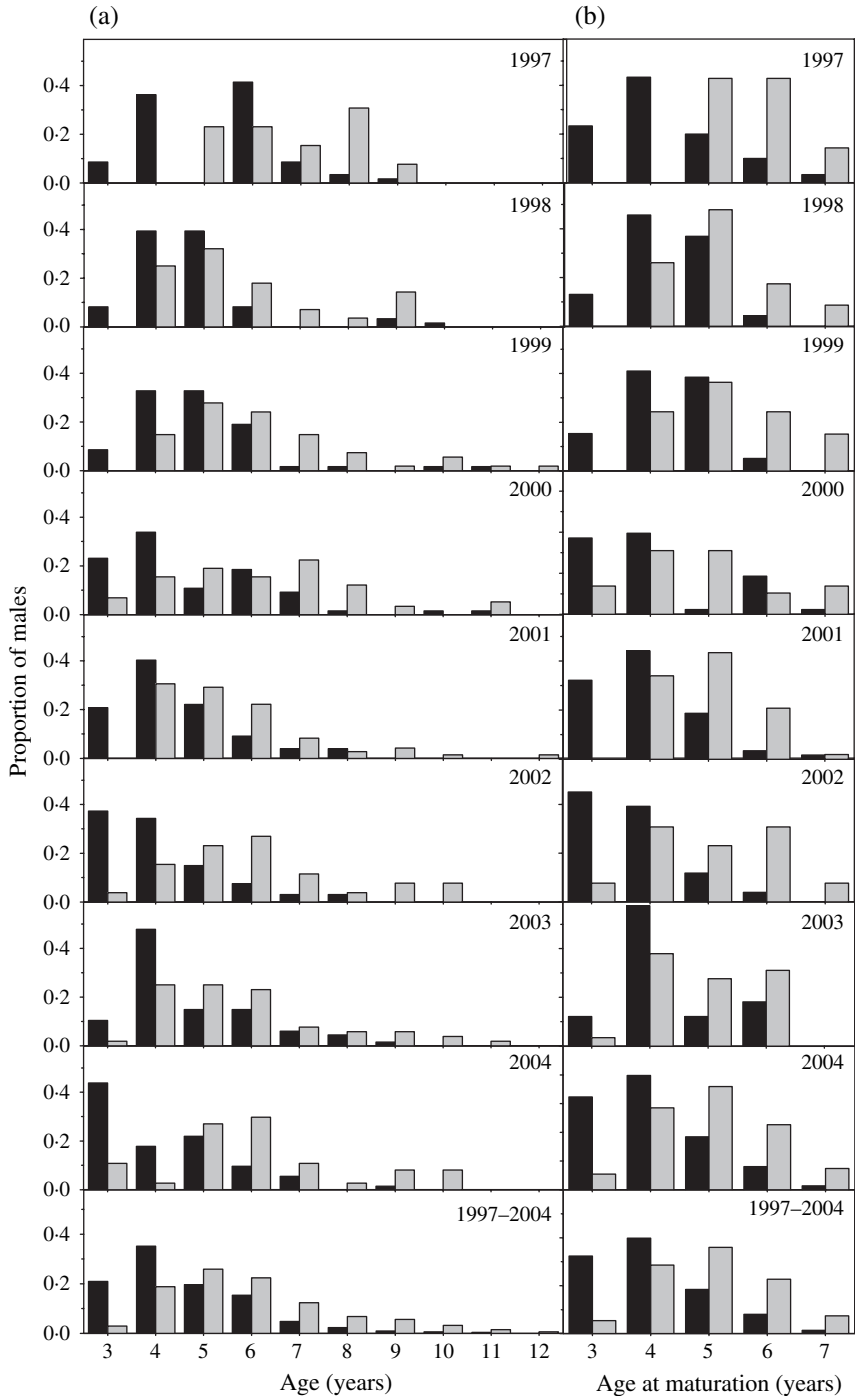


FIG. 3. Relative frequency distributions of (a) the ages and (b) ages at maturation for male *Micropterus dolomieu* that spawned in the river (■) or lake (□) habitats of the Mississippi River study site between 1997 and 2004. Sample sizes and statistical test results are given in Table V.

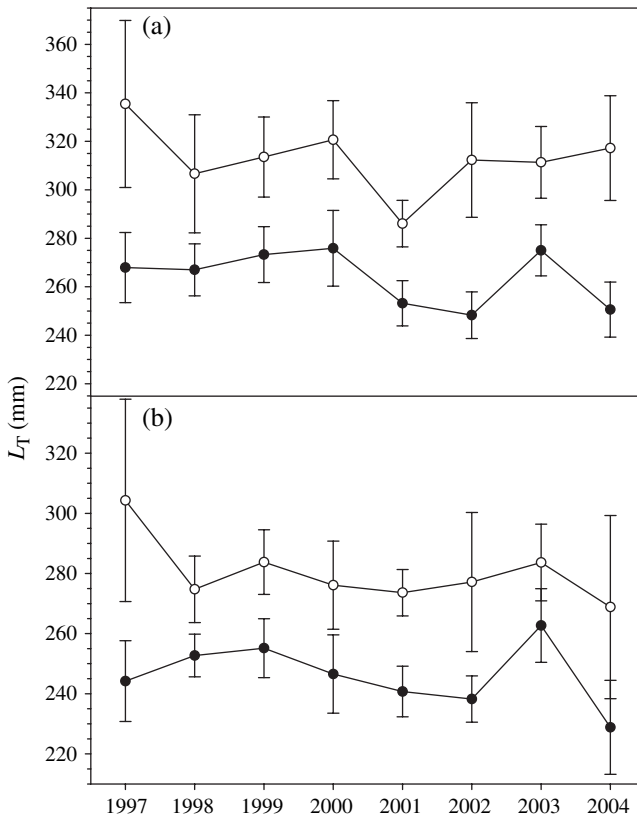


FIG. 4. Mean \pm 95% CI (a) total lengths (L_T) and (b) mean L_T at maturation for male *Micropterus dolomieu* that spawned in the river (●) or in the lake (○) habitats (see Table V for sample sizes).

sizes may have limited the ability to detect statistical significance, particularly for ages 6 and 7 years.

DISCUSSION

The integration of the reproductive activity data and habitat use data clearly indicates that life-history variation is not randomly distributed among the *M. dolomieu* inhabiting this small-scale system. Two lines of evidence suggest that life-history variation within the system was significant, consistent across years, and partitioned between fish that spawned in the river v. lake habitats.

First, both the habitat use and nest choice patterns of *M. dolomieu* indicated that the vast majority of fish displayed fidelity to either the river or the lake as reproductive habitat over multiple years (with most males displaying fidelity throughout their reproductive lives). All but one of the radio-tracked individuals displayed fidelity to one of the two major habitat use patterns during the telemetry study and 96% of males that reproduced in multiple years nested either in the river or the lake and not both during their lives. These results are significant because the consistent spatial segregation indicates that the fish of

TABLE V. Comparisons of the ages and total lengths (L_T) at maturation (mean \pm s.d.) of male *Micropterus dolomieu*, from 4 year classes that spawned in either the river or the lake habitats (1995–1998). Age at maturation distributions were compared for each year class using Pearson χ^2 tests. Wilcoxon rank sum tests were used to test whether males spawning in the river and lake had similar L_T at ages at maturation for all age classes with adequate sample sizes

Year class	River			Lake			Age at maturation (years)			Mean L_T at age of maturation		
	Age (years)	n	%	Mean L_T (mm)	n	%	Mean L_T (mm)	χ^2	P	Z	P	
1995	3	6	24.0	218.0 \pm 8.0	0	0.0		22.12	<0.001	na	0.177	
	4	16	64.0	240.3 \pm 12.4	8	26.7	248.3 \pm 4.7			1.351		
	5	1	4.0	297.0	10	33.3	281.4 \pm 10.6			na	0.691	
	6	2	8.0	304.5 \pm 7.8	11	36.7	309.8 \pm 15.6			-0.398		
	7	0	0.0		1	3.3	335.0			na		
	3	6	16.7	217.5 \pm 18.2	0	0.0		13.36	0.004	na	0.005	
	4	17	47.2	238.4 \pm 15.0	9	24.3	255.6 \pm 10.1			2.808	1.000	
1996	5	11	30.6	278.0 \pm 18.9	24	64.9	276.2 \pm 13.1			-0.0	0.817	
	6	2	5.6	314.0 \pm 5.7	4	10.8	304.0 \pm 27.7			0.232		
	7	0	0.0		0	0.0				na	0.394	
	3	16	29.1	213.8 \pm 14.5	4	11.4	219.0 \pm 6.1	6.78	0.148	0.805	0.382	
	4	26	47.3	240.5 \pm 14.1	19	54.3	245.4 \pm 11.4			0.863	0.439	
	5	6	10.9	273.5 \pm 14.3	3	8.6	280.3 \pm 19.4			0.646	0.768	
	6	6	10.9	314.3 \pm 13.4	9	25.7	317.7 \pm 16.2			-0.236		
1997	7	1	1.8	349.0	0	0.0				na		
	3	19	39.6	208.6 \pm 12.0	0	0.0		21.19	<0.001	na	0.182	
	4	21	43.8	243.8 \pm 16.6	4	25.0	251.3 \pm 12.8			1.336	0.671	
	5	4	8.3	279.8 \pm 15.9	8	50.0	282.4 \pm 20.9			-0.425	0.885	
	6	4	8.3	321.8 \pm 20.2	4	25.0	322.5 \pm 11.7			0.144		
	7	0	0.0		0	0.0				na		

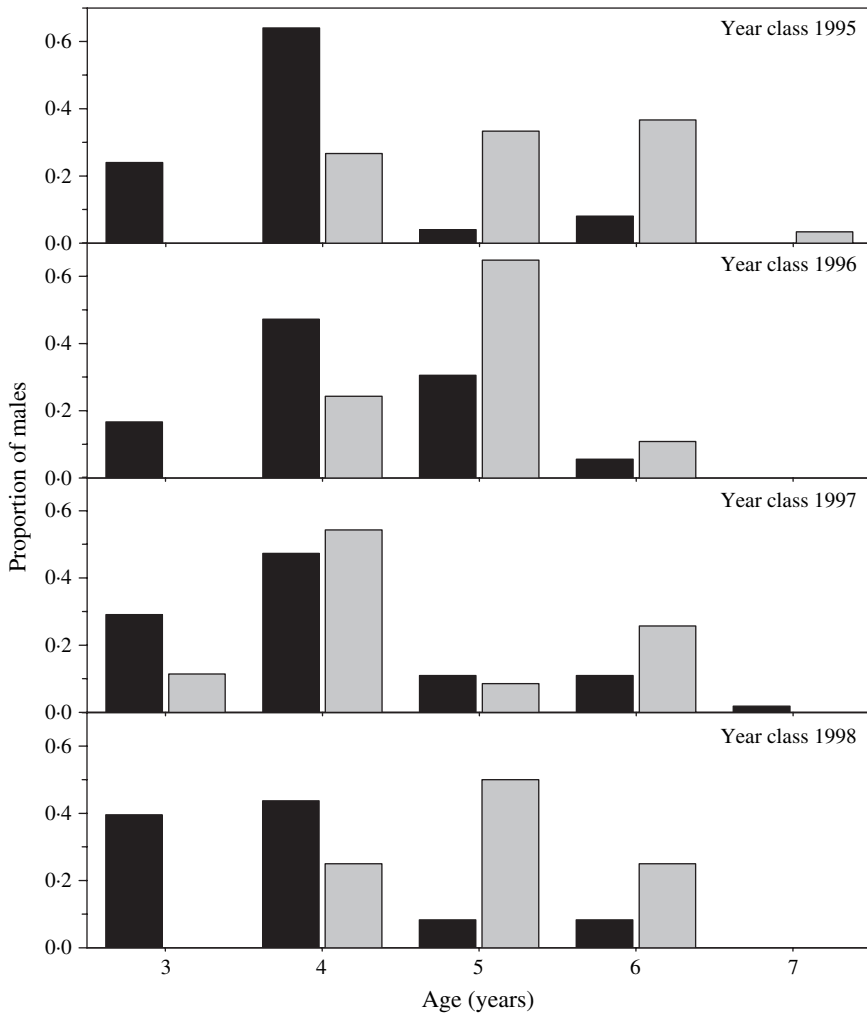


FIG. 5. Age at maturation relative frequency distributions for male *Micropterus dolomieu* from year classes 1995–1998 that spawned in the river (■) or the lake (□) habitats of the Mississippi River study site (see table V for sample sizes and statistical results).

the system do not exist in panmixia. This does not mean that there is reproductive isolation between groups of fish spawning in the two habitats (4% of males were observed to spawn in both habitats, and knowledge of female movement patterns is limited to only 13 radio-tagged fish), but these results suggest that fish following the same movement pattern are more likely to mate than are fish following different patterns. To date, only a single study has reported the rate and distance that juvenile *M. dolomieu* disperse from their nests: almost all age 0 year individuals were within 200 m of their natal sites when captured during the first week of September in Lake Opeongo (Ridgway *et al.*, 2002). There are no studies of dispersal beyond the first summer, although Ridgway *et al.* (2002) speculated that the distance that juveniles dispersed from natal sites

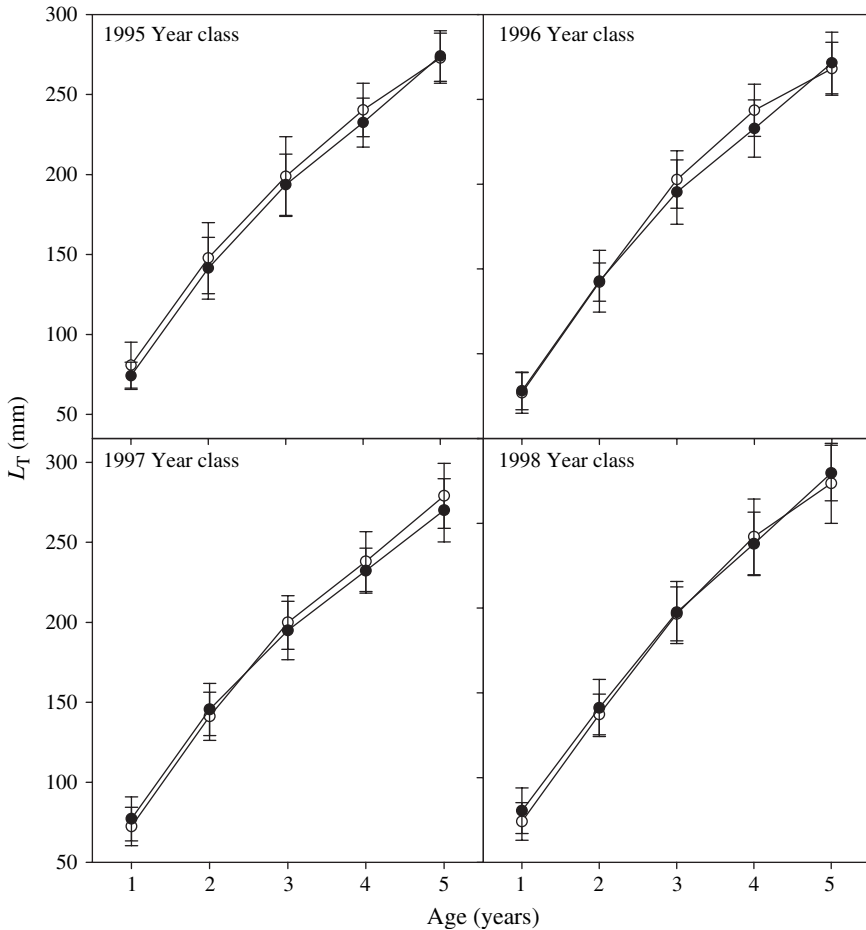


FIG. 6. Comparison of mean \pm S.D. pre-maturation total length (L_T) at age (ages 1–5 years) between male *Micropterus dolomieu* from 4 year classes that spawned in the river (●) or the lake (○) habitats of the Mississippi River study site.

was determined by the availability of suitable foraging territories. Natal homing (adults returning to spawn in the locations in which they hatched) was first proposed for *M. dolomieu* based on the genetic relationships of reproductive pairs of *M. dolomieu* in Lake Opeongo, Ontario, Canada (Gross *et al.*, 1994), where males were observed to have very similar levels of nest-site fidelity (Ridgway *et al.*, 1991) as were observed in the current study. Although it is not possible to discriminate between natal homing and nest-site fidelity at present, the habitat-use data have identified the spatial segregation of distinct groups of fish during the reproductive period, which is often a requisite condition for the development and preservation of life-history differentiation among groups of organisms.

The second line of support for life-history differentiation are the significantly different reproductive characteristics observed between fish that spawned in the two habitats, foremost among them different maturation schedules. Age and size at maturation are considered prominent life-history characteristics because

TABLE VI. Mortality (M) for male *M. dolomieu* that spawned for the first time in the river or lake habitats (1997–2004). M was estimated by dividing the number of males that did not return to spawn in a subsequent year by the total number (n) of males that spawned at that age. Statistical results for Pearson χ^2 tests that tested whether the mortality rates were the same or different for males that nested in the river and lake habitats are provided for each age

Age (years)	River		Lake		χ^2 test	
	n	M	n	M	χ^2	P
3	101	0.79	10	0.80	0.01	0.953
4	141	0.74	57	0.74	0.00	0.991
5	65	0.77	68	0.71	0.69	0.407
6	27	0.85	45	0.78	0.59	0.442
7	5	0.80	14	0.57	0.83	0.363

of their strong influence on most other life-history characteristics, including ultimate body size (particularly for organisms with indeterminate growth), survival and reproductive success (Bernardo, 1993; Roff, 2002). Male *M. dolomieu* that nested in the river were significantly younger at maturation than males that nested in the lake for all but 2 of the 8 years of the study. Similarly, males from 3 of 4 year classes were observed to mature at significantly younger ages in the river than the lake. Comparisons of the male L_T at ages prior to maturation (based on backcalculations) and at maturation (based on comparisons of male L_T at ages at maturation of 1995–1998 year classes) indicate that growth rates were very similar for males that reproduced in the river and the lake (the only significant difference was between males that matured at age 4 years in the 1996 year class). The greater L_T of males that spawned in lake, therefore, result from maturation at older ages rather than differences in growth rates.

Theoretical and empirical studies have shown that growth rates and mortality rates have a profound influence on the ages and sizes at which *M. dolomieu* mature (Lester *et al.*, 2004; Shuter *et al.*, 2005). Competition for food resources at high population densities has been proposed to be responsible for a negative relationship between the number of adult males present in a population and the number of males that mature in a given year in the *M. dolomieu* population of Lake Opeongo (Ridgway *et al.*, 2002). Differences in the maturation schedules of *M. dolomieu* inhabiting Lake Opeongo and a smaller Ontario lake were attributed to differences in the abundance of large-bodied prey: fish inhabiting the system with fewer prey had slower adult growth, higher adult mortality and earlier maturation than the population with greater abundances of large-bodied prey (Dunlop *et al.*, 2005a). In the present study, the fact that males that spawned in the two habitats had very similar growth rates suggests that differences in maturation schedules were not related to food availability. Although this study did not detect statistical differences in the mortality rates of fish that spawned in the two habitats, these results suggest that there are biologically significant differences in mortality, particularly at older ages. First, estimated mortality rates were very similar for males that spawned in the river and the lake at ages 3 and 4 years, but there was a trend (although non-significant)

towards greater divergence across ages 5, 6 and 7 years. Second, fewer males survived to spawn at ages ≥ 5 years in the river than did in the lake in each year of the study. The situation in which males that spawned in the river faced greater mortality rates at ages ≥ 5 years than males that spawned in the lake is consistent with theoretical predictions and empirical observations that adult mortality is inversely related to age at maturation in fish populations (Lester *et al.*, 2004; Shuter *et al.*, 2005; Dunlop *et al.*, 2007): in this study it appears that the males that spawned in the river had higher adult mortality rates and matured at younger ages than males that spawned in the lake.

The telemetry results indicate that many of the males that spawned in the river must have inhabited the lake during non-reproductive periods of the year, and, therefore, encountered the same environmental conditions as males that spawned in the lake for much of their lives. Although all of the radio-tagged fish that spawned in the river resided in the lake during non-reproductive periods, mature males have been captured in the river in mid-October (after the date that radio-tagged fish had returned to the lake) on the few occasions that autumn sampling has been carried out (unpubl. data). Neither of these infrequent sampling events or the small number of radio-tagged fish provide the data necessary to estimate the proportion of fish that might reside in the river throughout the year (rather than just during the reproductive period), but an elevated risk of mortality in the river environment relative to the lake could be responsible for the differences in survival. There has not been a quantitative comparison of predator densities in the two habitats, but the only piscine predator capable of consuming adult *M. dolomieu* would be pike *Esox lucius* L. that are present in both habitats. An alternative explanation for differences in mortality rates is an elevated cost to reproduction in the river environment relative to the lake. Parental care has been shown to be energetically expensive for nesting male *M. dolomieu* (Gillooly & Baylis, 1999; Mackereth *et al.*, 1999); if raising broods in the river requires a greater energetic investment than in the lake, a larger proportion of males that spawn in the river may fail to recover the energetic reserves necessary to survive to the next breeding season. This hypothesis would be better supported if this study had found statistically significant differences in mortality rates across all ages or if males that reproduced in the river had been observed to have shorter reproductive lifespans than those that spawned in the lake.

These data reveal that a relatively greater proportion of males that spawned in the lake raised their broods successfully than males that spawned in the river. Two factors are primarily responsible for this observation: (1) a positive relationship between male *M. dolomieu* L_T and nesting success has been observed in a number of populations (Reynolds & O'Bara, 1991; Suski & Ridgway, 2007) and (2) the fact that the river is more susceptible to stochastic hydrologic events than the lake. Extreme hydrologic conditions were responsible for the significantly lower nesting success of males nesting in the river in 2000 and 2002. Reduced hydrologic discharge and substantially receding water levels during the parental care period negatively affected a greater proportion of nests in the river than the lake during the reproductive period in 2000. A series of heavy rains in June 2002 produced a rapid increase in discharge that caused many (57%) of the nests in the river to be abandoned (essentially overnight)

by the parental male, while nests in the lake were relatively unaffected (86% of males were successful). Although a larger proportion of males raised their broods successfully in the lake than the river in all but 1 year, the magnitude of differences in nesting success rates were much smaller in years that were not affected by stochastic events (with the exception of 2001). Although nest predation has been reported to have a considerable effect on *M. dolomieu* reproductive success in other systems (Steinhart *et al.*, 2004), there are exceptionally low abundances of brood predators in the current study system, and males have only rarely been observed actively chasing predators from the area of their nests. The different body sizes of males that spawned in the two habitats may have contributed to differences in nesting success rates: smaller-sized male *M. dolomieu* have been shown to enter the reproductive period with fewer energetic reserves than larger males (Mackereth *et al.*, 1999), and energy expenditure has been shown to be positively correlated to nesting success (Gillooly & Baylis, 1999). As a result, differences in nesting success between habitats observed during hydrologically stable years might be explained by males in the river having had lower energetic reserves to invest in parental care than the generally larger males that spawned in the lake.

Life-history variation between sympatric groups of fishes can result from phenotypic plasticity, genetic divergence, or some combination of the two. Reproductive isolation and life-history variation have been documented among fishes inhabiting contiguous systems without physical barriers to gene flow. For example, morphological and genetic differences between parapatric pairs of three-spined sticklebacks *Gasterosteus aculeatus* L. cohabitating the same watersheds are believed to result from adaptations to stream and lake environments that occurred in at least three separate systems (Thompson *et al.*, 1997). In addition, *G. brasiliensis* (Qua & Gaimard) displayed adaptation and life-history differentiation between populations in a river and lagoon in a coastal watershed in Brazil (Mazzoni & Iglesias-Rios, 2002), and genetic divergence between sympatric anadromous and non-anadromous morphs of sockeye salmon *Oncorhynchus nerka* (Walbaum) has been identified throughout most of the species' range (Wood & Foote, 1996). To date, the only evaluation of the genetic relationships of river and lake-spawning *M. dolomieu* was conducted at a much larger spatial scale than the current study, but found that fish spawning in each of four tributaries of Lake Erie were genetically differentiated from each other as well as from fish spawning in the lake (Stepien *et al.*, 2007). Another recent study, however, determined that differences in the maturation schedules between two introduced lake-dwelling populations of *M. dolomieu* that were founded from a common stock in the early 20th century (and had been reproductively isolated for >50 years) were probably a result of phenotypic plasticity (Dunlop *et al.*, 2005b). Even under a situation in which individuals of both sexes returned to spawn in their natal habitats, the small proportion of males observed to spawn in both environments in the present study could have a significant genetic homogenizing effect if they successfully contributed to recruitment outside their natal habitats. The observations that a small number of males spawned in both habitats and that both river and lake-spawning fish not only cohabited in the lake during large portions of the year, and had very similar growth rates, all suggest that phenotypic plasticity is likely to play some

role in producing the observed differences in the maturation schedules among the two groups of males. To what extent genetic divergence might also be involved in producing these differences, however, is a question that can only be answered definitively through an evaluation of the maturation schedules of family lines with known genetic relationships throughout the system and over time. Even for cases in which the observed life-history differences among groups are plastic rather than genetic, the magnitude and temporal stability of differences between groups, particularly those that have river *v.* lake-spawning fish, could have important management and conservation implications, especially for heavily harvested populations (Dunlop *et al.*, 2007).

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