Spatial and temporal distributions of smallmouth bass (*Micropterus dolomieu*) nests in Lake Opeongo, Ontario¹

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Abstract: Smallmouth bass (*Micropterus dolomieu*) nests were patchily distributed within the littoral zone of Lake Opeongo at two spatial scales (1 km and 100 m shoreline segments). Nest locations were recorded by snorkelling along 155 and 6.3 km of littoral zone over 4 and 11 years, respectively. The degree of patchiness was greater and occurred more consistently at the 1-km than at the 100-m spatial scale. However, the degree of patchiness was not significantly affected by 200% differences in spawning population size, implying that competitive interactions did not strongly influence nest locations over the study period. High-density nesting areas remained stationary between years at the 1-km and 100-m scales. This suggests that habitat variables having stationary spatial characteristics, influence nest site choice. Since the locations of nest patches are less stationary and less consistent among 100-m than among 1-km scale sites, influential habitat variables at the 100-m scale are either less important to the locations of nests or less stationary from year-to-year in their effects on nest distributions. If stationary nest patches are typical of spawning smallmouth bass in lakes, permanent protection of known patch locations could enhance their reproductive success.

Résumé : Les nids d'achigan à petite bouche (*Micropterus dolomieu*) étaient répartis irrégulièrement dans la zone littérale du lac Opeongo à deux échelles spatiales (segments de rivage de 1 km et de 100 m). L'emplacement des nids a été consigné par plongée en apnée couvrant 155 et 6,3 km de zone littorale pendant 4 et 11 ans, respectivement. Le degré de morcellement était supérieur et survenait de manière plus uniforme à l'échelle spatiale de 1 km qu'à l'échelle de 100 m. Toutefois, le degré de morcellement n'était pas modifié de manière substantielle par des différences de l'ordre de 200 % dans la taille de la population des reproducteurs, ce qui indiquerait que la compétition n'a pas exercé une forte influence sur l'emplacement des nids au cours de la période d'étude. Les endroits où la densité des nids était élevée étaient fixes d'une année à l'autre aux échelles de 1 km et de 100 m. Cette constatation laisse entendre que des variables liées à l'habitat ayant des caractéristiques spatiales fixes influent sur le choix du site pour la construction du nid. Comme les emplacements des groupes de nids sont moins fixes et moins uniformes parmi les sites examinés à l'échelle de 100 m par rapport à l'échelle de 1 km, des variables de l'habitat qui jouent un rôle à l'autre pour ce qui est de leurs effets sur la distribution des nids. Si les groupes de nids fixes sont typiques de l'achigan à petite bouche en frai dans les lacs, une protection permanente des emplacements connus pourrait accroître leur succès de reproduction.

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Introduction

The growth rate and survival of smallmouth bass (*Micropterus dolmieu*) broods during the early stages of their development are major determinants of year-class strength (Shuter et al.

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1980; MacLean et al. 1981). During the first few weeks of life when the young smallmouth bass are particularly fragile, each brood is confined to the nest (a depression in the sediment that the male spawner creates, where spawning occurs) (Scott and Crossman 1973; Ridgway 1988). The fragility and immobility of smallmouth bass broods during this time, combined with typically heterogeneous littoral habitat conditions, may lead to patchiness in nest locations that reflects spatial and perhaps temporal differences in habitat suitability for maturation of eggs and larvae.

Evidence from Ridgway et al. (1991*a*) and Gross et al. (1994) provide further reason to expect that the nearshore area is not randomly colonized by spawning smallmouth bass and that nest locations are determined by microhabitat characteristics. Of male smallmouth bass who nested in more than 1 year, 65.9% were observed to nest within 100 m of their previous spawning site and virtually all nested within 1 km of their previous spawning site (Ridgway et al. 1991*a*). Furthermore, DNA fingerprinting analyses of males and their broods show that the spawners probably have high fidelity to their birth site (Gross et al. 1994). If nest patches exist and are stationary from year to year despite this imperfect nest site

Fig. 1. (A) Lake Opeongo, Ontario; 1 km long shoreline segments (used in calculations of nest density in Fig. 5A) are numbered clockwise, at the ends of 10-km intervals. (B) Jones Bay, Lake Opeongo; 100 m long shoreline segments (used in Fig. 5B) are numbered from south to north at the ends of 1-km intervals.



fidelity, breeding locations would likely be important to recruitment rates.

To investigate whether lake-dwelling smallmouth bass nest locations are indeed non-random, we examined nest locations within Lake Opeongo, Ontario (45°42'N, 78°22'W) (Fig. 1), a large oligotrophic lake, throughout the entire 155 km long littoral zone in 4 years and within a 6.3 km long section of the lake in 11 years. This unusually extensive data record provided a rare opportunity to examine the breeding distributions of an entire fish population and to refine the list of possible mechanisms influencing their distributions. Since organisms' distributions and the associated influential mechanisms frequently change with scale (Wiley and Wiley 1980; Duarte 1991; Orians and Wittenberger 1991; Levin 1992), nest distributions were examined over a duration exceeding the typical life-span of the species and across a large range in spatial scales, throughout the entire spawning territory of a population of lake-dwelling smallmouth bass.

Materials and methods

Field methods

Nest locations were detected by snorkellers who were familiar with the appearance of a smallmouth bass nest, who swam along the 1 m depth contour (the approximate depth of smallmouth bass nests in Lake Opeongo). The nearshore slope of the lake is generally sufficiently steep and visibility sufficiently good to allow snorkellers to see the entire depth range (approximately 0.3–2.5 m) of bass nests in the lake in a single pass. Nests were recorded only if they contained smallmouth bass young. Smallmouth bass nests could not be mistaken for those of the pumpkinseed (*Lepomis gibbosus*), the only other nest-building fish in the lake, whose young are approximately one quarter the size of smallmouth bass young.

Nest locations were recorded throughout Jones Bay, a 6.3 km long particularly high-density nesting area in Lake Opeongo in 11 years (1977-1979, 1984, 1988-1994). Particularly during the years 1988–1994, when nest locations were monitored every 3 days over the nest-guarding period, approximately 97% of the entire nesting population within Jones Bay was detected and mapped. Nest locations were also recorded along the entire 155 km long shoreline of Lake Opeongo in 4 years (1984, 1992-1994). To maintain maximum consistency in nest detections, all of these whole-lake surveys were made towards the end of the nest-guarding period. At this time, most nests contained young that had developed into more conspicuous grey or black fry. These surveys occurred within the last week of June or the first week of July. In each of the years the entire lake was surveyed within a maximum period of 3 days. This minimized both changes in the conspicuousness of the broods over the census period and in the nesting population size (owing to new nest appearances and nest abandonments).

The proportions of the total nesting population present during the whole-lake surveys were estimated for each of two whole-lake surveys by calculating the proportion of nests present in Jones Bay on the whole-lake swim dates, relative to the total number of nests found in Jones Bay over the entire nesting period. The average proportion of nests present in Jones Bay in the 2 years was 67.5%. Furthermore, of the nests present in the lake, approximately 62% were actually detected during the whole-lake swims. This proportion of nests detected was estimated by very meticulously re-surveying eight 1 km long areas of shoreline in Lake Opeongo within 3 days after the 1994 whole-lake swim to detect approximately all existing nests within

Fig. 2. Calculations of the two-term local quadrat variance (Hill 1973) in nest densities among adjacent segments of littoral zone along the shoreline in Jones Bay at segment lengths ranging from 100 to 700 m (at 100-m intervals), and in Lake Opeongo at segment lengths from 1 to 10 km (at 1-km intervals).



those areas. Thus, through nest abandonments prior to the whole-lake swims and undetected nests, the overall proportion of nests detected during the whole-lake surveys of Lake Opeongo was approximately 42% of the entire nesting population. Although these surveys include only part of the Lake Opeongo nest population, they represent one of the most comprehensive sets of measurements known for a spawning fish population.

Analyses

A preliminary assessment was made to determine whether dramatic changes in the degree to which nests are clumped occur at particular spatial scales. If dramatic changes as such do not occur, the selection of spatial scales for further more detailed analyses could be made more freely. To determine whether smallmouth nest distributions change dramatically across spatial scales, nest densities were measured within segments of littoral spawning habitat that were conceptually divided at constant intervals along the shoreline. Clumped distributions of nests would be characterized by high variability in nest densities among shoreline segments, relative to the mean nest density per segment (Ludwig and Reynolds 1988). The two-term local quadrat variance (TTLQV) method (Hill 1973) was used to calculate variability in nest densities among adjacent segments, across a range of segment lengths (spatial scales): at 100-m intervals from 100 to 700 m within Jones Bay, and at 1-km intervals from 1 to 15 km within the whole lake. These measurements were made in 4 years (1984, 1992–1994) at all spatial scales within Jones Bay and the whole lake.

The TTLQV analysis involves calculation of the variability (the sum of squares of the variances) in nest densities for all adjacent pairs of segments, divided by the total number of segments. Since the denominator of the TTLQV formula does not contain the mean nest density, some increase in the TTLQV variances will occur with increasing spatial scale even if the degree of patchiness does not change (Ludwig and Reynolds 1988; Kershaw 1964). Thus, gradual increases in TTLQV variance across increasing spatial scales may not reflect changing biological circumstances. Furthermore, variable shoreline reticulation (Kent and Wong 1982) creates difficulties in accurately identifying particular spatial scales. Nevertheless, the TTLVQ method is useful for identifying large changes in the degree of nest patchiness that may exist within the wide range of spatial scales of this study.

The TTLQV results showed no sharp change in the degree of

patchiness across the observed range of spatial scales (Fig. 2). This suggests that mechanisms most strongly influencing nest locations are not restricted to particular scales within the 100-m to 10-km range. Consequently, the selection of segment sizes for more extensive analyses were made according to shoreline lengths that would be likely relevant to lake management.

Extensive analyses of nest densities were made at two spatial scales (100-m and 1-km shoreline segments) to determine whether nest distributions are significantly patchy rather than random or uniform and to refine the possible mechanisms influencing nest locations. To test whether nest distributions along the shoreline are patchy, observed frequency distributions of nest counts per shoreline segment were compared with statistically random (Poisson) expected frequency distributions using *G*-tests (and William's corrections) (Sokal and Rohlf 1987) at two spatial scales. Frequency distributions of nest counts per shoreline segment were calculated for 155 large-scale (1 km long) and 63 small-scale (100 m long) segments (sites) in each of 4 and 11 years, respectively.

To facilitate comparisons of nest frequency distributions between years for each of the two spatial scales, the number of nest density categories was adjusted to 9 and 6 for all of the 4 and 11 G-tests at the 1-km and 100-m scales, respectively. Expected frequencies for the Poisson distribution that were less than 3 in any of the nest density categories were avoided by combining categories, since the power of the G-test is reduced at very low expected frequencies (Sokal and Rohlf 1987). Thus, the number of categories was made constant (at each of the two spatial scales) by combining the categories with the lowest frequencies. Bonferroni corrections were made for the 4 and 11 G-tests that were calculated at the 1-km and 100-m scales, respectively, to determine the G-test results without reference to specific years. To compare the level of patchiness between the 100-m and 1-km spatial scales, despite differences in the total sample size and the mean nests per site, Green's indices (Green 1966) were calculated at each of the two spatial scales, for each year.

In Jones Bay, nest locations were examined to determine whether changes in nesting population size over 11 years influence the degree of nest patchiness. The two measures of nest frequency distributions that were chosen to quantify the level of nest patchiness were the number of unoccupied 100-m sites, and the maximum number of nests per 100-m site. These measures represent the two extremes in nest distributions where density-dependent effects on nest locations should be clearest.

Comparisons were made between these observed annual measurements of patchiness and equivalent measures from Poisson frequency distributions. The number of unoccupied sites and the maximum number of nests per site calculated from the Poisson distribution were used as control values for comparisons, since the Poisson distribution maintains the same random structure despite changes in population size. For each year, the maximum number of nests per site was recorded from the Poisson frequency distribution as the highest nestdensity category having a frequency nearest to one (one site). The expected number of unoccupied sites was the simply the number of unoccupied sites in the Poisson frequency distribution. Differences between the observed and expected measures of the two indices of patchiness were calculated to determine whether the observed values changed relative to the values expected for random distributions, along a gradient of increasing spawning population size.

Results

Are nests clumped in space?

Nest distributions irrespective of the sampling year were significantly non-random at both the 1-km spatial scale in the whole lake (Fig. 3A) and at the 100-m scale within Jones Bay (Fig. 3B). Large significant differences from randomness were observed in each of the 4 years at the 1-km spatial scale (after

Table 1. Calculations of *G*-tests to determine whether observed frequency distributions are different from Poisson (random) frequency distributions for 4 years at the 1-km scale and for 11 years at the 100-m spatial scale.

Site	Year										
length (m)	1977	1978	1979	1984	1988	1989	1990	1991	1992	1993	1994
100 1000	15.0*	15.6*	12.8	3.6 167.2*	15.5*	7.3	7.6	5.4	0.7 147.6*	3.8 202.7*	20.8* 189.5*

Note: Frequency categories of nest density were consistent: nine density categories at the 1-km scale (density categories: 0, 1, 2, 3, 4, 5, 6, 7, 8+) and six density categories at the 100-m scale (density categories in 7 years: 0, 1, 2, 3, 4, 5; in 3 years: 0-1, 2, 3, 4, 5, 6+; and in 1 year: 0-2, 3, 4, 5, 6, 7).

*Significant G-test (p < 0.05) after Bonferoni adjustments for 4 years at the 1-km scale and for 11 years at the 100-m scale.



Fig. 3. An example of the observed and expected (Poisson) frequency distributions of (A) nests per kilometre from the 1994 whole-lake census of Lake Opeongo and (B) nests per 100 m from the 1994 census of Jones Bay

Bonferroni adjustment: $p \ll 0.001$ in all 4 years), while at the 100-m spatial scale, significant differences between observed and Poisson frequency distributions (after Bonferroni adjustment: p < 0.0045) occurred in only 4 of the 11 years (Table 1). Patchy frequency distributions of nests are characterized by more unoccupied sites than expected from a Poisson frequency distribution and a greater maximum number of nests per site than expected from a Poisson distribution. These characteristics of patchiness are observed at the 1-km and, to a lesser extent, at the 100-m spatial scales (Fig. 3). Differences among the two spatial scales are quantified by Green's Index (GI) calculations, which indicate that the degree of patchiness is

approximately four times greater at the 1-km scale in Lake Opeongo (mean GI = 0.031) than at the 100-m scale within Jones Bay (mean GI = 0.008).

These differences in the GIs are consistent with the higher measures of TTLQV variance in nest density among adjacent 1 km long segments than among 100 m long segments (Fig. 2). Thus, the gradual increase in variance among segment sizes from 100 m to 10 km (Fig. 2) cannot be entirely attributed to spurious increases in the TTLQV variance with increasing segment size. Instead, this gradual increase also indicates that the degree of patchiness of smallmouth bass nests increases across the spatial scales from 100 m to 10 km.

Does spawning population size influence the intensity of nest patchiness?

Within Jones Bay at the 100-m scale the lower degree of patchiness, and the inconsistent occurrence of statistical patchiness (Table 1) could be a product of (*i*) fluctuations in densities of spawning bass and associated density-dependent influences or (*ii*) year-to-year changes in influential habitat conditions. If density-dependent influences exist, they would confound effects of influential habitat conditions on nest distributions. Jones Bay (where particularly high densities of nests and some low-density areas occur) was an ideal location to determine whether conditions related to population size influenced the degree of nest patchiness. Within Jones Bay, nesting populations ranged from 111 to 309 individuals over the 11 years.

Differences in the known number of unoccupied sites and the maximum number of nests per site, relative to the equivalent frequencies from Poisson distributions, were calculated for the entire range in nesting population sizes in Jones Bay in each of the 11 years (Fig. 4). With increasing population size, increasing differences between the observed and expected measures of either or both of these two indices would suggest that positively density-dependent factors (such as in the attractions of adult spawners towards aggregations of other nesters), influence nest locations. Negatively density-dependent influences, such as the effects of shortages of nesting habitat under conditions of increasing nesting population size, would be likely if the reverse were true. However, there was no significant trend in either of the two measures of patchiness in response to changes in nesting population size in Jones Bay. Although the power of these tests were not high, the test results are further substantiated by small and probably biologically insignificant ranges in the two measures of patchiness.

Are the locations of nest patches consistent among years? Pearson's correlations of nest densities at each site were

Fig. 4. The observed (A) maximum nests per 100-m site and (B) percent unoccupied 100-m sites were subtracted from their associated expected (Poisson) measures for each of the 11 years of Jones Bay data. Simple linear regression lines were fit to each of these residual plots and indicated that there was no significant change between observed and expected measures with increasing population size (A) $r^2 = 0.20$, n = 11, p < 0.17; (B) $r^2 = 0.03$, n = 11, p < 0.61.



Fig. 5. Percent of total nests in the season (A) per 1-km quadrat, clockwise around the perimeter of Lake Opeongo, for each of 4 years (1984, 1992–1994) and (B) per 100-m quadrat along the shoreline of Jones Bay from north to south, for 4 of 11 years (1984, 1992–1994). See Fig. 1 to identify quadrat locations.



calculated between all pairs of years to determine whether each of the sites maintained similar nest densities from year to year. The Pearson's correlation coefficients were tested for significance after Bonferroni adjustments were made for the 6 and 55 pairwise comparisons at the 1-km (from 4 years) and 100-m (from 11 years) spatial scales, respectively. Nest densities were significantly positively correlated between years at both the 1-km and 100-m spatial scales within Lake Opeongo (range of correlation coefficients 0.75–0.80) and Jones Bay (range of correlation coefficients 0.05–0.65), respectively. For visualization of these results, the proportion of the nests per 1-km and 100-m site (measured as a percentage of total nests) were plotted, rather than plotting the absolute number of nests per site (the latter of which is confounded by large year-to-year changes in the size of the nesting population)(Fig. 5).

Spatial autocorrelation in nest densities per site would

complicate the interpretation of these results by reducing the effective number of degrees of freedom in the data. However, the degree of spatial autocorrelation of the smallmouth bass nest distributions is extremely difficult to quantify as a consequence of two general characteristics of the shape of lake shorelines. First, the degree of reticulation of lake shorelines varies across and within spatial scales (Kent and Wong 1982). Consequently, shoreline segments that are situated in highly reticulated areas of shoreline have very different distances among one another than is assumed in analyses for the detection of spatial autocorrelation. Second, the circular nature of the whole-lake nest records (which encompass the entire lake perimeter) complicate measures of the distance among all of the shoreline segments, that are assumed to occur along a straight line.

The existence of spatial autocorrelation would result in an overestimation of the true degrees of freedom. However, no increase in the correlation among years occurred as a direct consequence of spatial autocorrelation according to two simulation correlations; Pearson's correlation coefficients among years for 1 km long sites that were separated by 4 and 9 km, respectively, did not decrease in relation to the correlations generated from the complete data set.

Thus, large reductions in the degrees of freedom of the statistical tests were used to determine whether significant positive correlations in nest patch locations exist among years despite the effects of spatial autocorrelation. Despite this adjustment, nest densities remained significantly stationary among years. At the 1-km scale, significant positive correlations in nest densities existed after reducing the degrees of freedom by 15-fold (8 degrees of freedom rather than 153). Similarly, positive correlations at the 100-m scale were significant after the number of degrees of freedom were reduced by threefold (19 degrees of freedom rather than 61). Therefore, the extensive year-to-year consistency in nest distributions that exists could not be an artifact of spatial autocorrelation.

The year-to-year consistency in nest locations were examined over an increasing time lag (in years), to determine whether the positive correlation in nest densities were maintained over many years and even between generations of spawners. Thus, the Pearson's correlations that were calculated at the 100-m scale were plotted against the corresponding time lags. A simple linear regression analysis of the 100 m scale correlations was made to test whether a significant decline in relatedness among nest positions occurred over time. A very conservative estimate of 9 degrees of freedom was used in the analysis because the 55 correlations among years were all generated from the same 11 years of data and were, therefore, not independent from one another. At the 100-m scale within Jones Bay, the decreasing correlation among patch locations over increasing time gaps (in years) was not quite significant (p > 0.05). A similar analysis was not conducted at the 1-km spatial scale because only 4 years of data were available.

Discussion

Are habitat conditions influencing nest site selection?

One or all of three possible mechanisms may be used to explain the significantly clumped nest distributions that occurred consistently at the 1-km (Lake Opeongo) spatial scale and in 4 of 11 years at the 100-m (Jones Bay) spatial scale (Fig. 3). Nest distributions may be influenced by habitat conditions, by attractions of nesters to nest aggregations, or by an unintentionally patchy selection of nest locations by the small population of smallmouth bass that first colonized the lake, maintained over time through phylopatry (the return of adults to their birthplace to spawn). It is not possible to confirm or discredit the influence of the latter mechanism on nest distributions from this study.

However, habitat conditions probably do influence nest locations at the 1-km and 100-m spatial scales. Without stationary influential habitat conditions to stabilize the nest patch locations, nest aggregations would be expected to drift over time as a consequence of the imperfect nest site fidelity of returning males (Ridgway et al. 1991*a*) and the occasional presence of nesters in the sites that usually remain uncolonized. Since this drift is not observed at the 1-km scale (Fig. 5A) or (although less distinctly) at the 100-m scale (Fig. 5B), nest patch locations must be influenced, to some extent, by stationary habitat conditions.

Although significant patchiness and stationary nest patch locations existed at both the 100-m and the 1-km scales, the degree of patchiness at the 100-m scale was less extreme (Fig. 2) and less consistent from year to year (Table 1), and patch locations were less stationary (Fig. 5) than at the 1-km scale. These differences in nest distributions between the two spatial scales may be attributed to various factors. If habitat conditions are indeed important determinants of nest locations at both spatial scales, perhaps they have less stationary characteristics at the 100-m, than at the 1-km scale. Alternatively, habitat conditions may be less important to nest distributions at the 100-m scale in Jones Bay, thereby allowing greater variability in nest distributions.

Are habitat influences confounded by changes in nesting population size?

In addition to potential influences by habitat characteristics, low consistency in the degree of patchiness at the 100-m scale may be explained by the existence of density-dependent influences. Since the nesting population size within the lake (and Jones Bay) changes dramatically between years, positively or negatively density-dependent factors may influence the degree to which patchiness exists among years (particlarly at the smaller spatial stage) and could thereby explain the interannual variation in patchiness of nests in Jones Bay.

If the patchiness that existed within Jones Bay in 4 of 11 years at the 100-m scale is positively or negatively influenced by the nesting population size in the bay, relations between nest locations and influential habitat variables could be expected to be particularly complex and difficult to dissect statistically. Under density-dependent influences, the slopes in the relations between nesting population size and differences in the observed and expected maximum number of nests per site would be expected to deviate from zero. Likewise, significant changes in the difference between observed and expected (Poisson) numbers of unoccupied sites would be anticipated in response to changes in nesting population size in the bay. Our data indicate that changes in nest abundances do not have a significant influence on patchiness within Jones Bay (Fig. 4). This result simplifies examinations of the relationships between habitat conditions and nest locations within Jones Bay and further supports previous findings that space for nesting is not limited within Jones Bay (Ridgway et al. 1991b). These results also indicate that attractions of adults to spawn among aggregations of other nesters is not the primary determinant of the patchy nest distributions.

Applications

Although variability exists in the patchiness and consistency of nests in Lake Opeongo, nests are significantly patchy (Fig. 1), and patch locations are significantly stationary (Fig. 5) at both spatial scales. These findings suggest the existence of influential habitat conditions that have stationary characteristics among years (particularly in the case of the 1-km scale). In subsequent analyses we hope to identify the habitat variables influencing nest distributions at these two spatial scales to improve our understanding of the factors governing the reproductive success of smallmouth bass.

Smallmouth bass are probably particularly vulnerable to

various types of human disturbances as a consequence of their shallow nest locations and the long nest guarding periods (which commonly extend to between 2 and 4 weeks; Scott and Crossman 1973). The nest-guarding period is particularly long in areas such as central Ontario, near the northern limits of the bass' range, where relatively cool temperatures slow the rate at which the broods develop (Shuter et al. 1980; Serns 1982; Ridgway and Friesen 1992). In these cool environments, adult males are very susceptible to capture by anglers who are active either before or after the opening date of the fishing season (Kieffer et al. 1995; Philipp et al. 1997). During this time, even catch-and-release angling decreases the survival of broods very substantially (Kieffer et al. 1995; Philipp et al. 1997; Ridgway and Shuter 1997). The consistency of patch locations through time in this study suggests that protecting a few highdensity nesting areas in a lake could enhance the reproductive success of a large fraction of the bass population. Thus, if stationary nesting patches occur within lakes other than Lake Opeongo, it would seem prudent to attempt to identify or predict the locations of high density nest areas for their protection.

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