Spatial Ecology and Density-Dependent Processes in Smallmouth Bass: The Juvenile Transition Hypothesis

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Abstract.- Previous research from our long-term study of smallmouth bass *Micropterus dolomieu* ecology in Lake Opeongo revealed a negative density-dependent relationship between the number of adult males in the population that appeared mature and the number of males nesting in any given year. The availability of nesting habitat is not the limiting resource behind this observation. We present three lines of evidence to argue that the process of forming an adult home range is the key factor in determining what fish join the breeding population. First, the dispersal of age-0 fish from their nest site is limited in their first summer and, assuming that this reflects the location of age-1 juveniles, indicates that juveniles can be located relatively close to their nest of origin. Second, juvenile growth is density-dependent with the strength of this relationship increasing during the mid-juvenile period (ages 2, 3, and 4) and weakening at the end of the juvenile period (ages 5 and 6). Third, adult home ranges are large (200-400 ha), traveled extensively each day (1-9 km), established quickly after reproduction, rarely incorporate the nest site and overlap in location from one year to the next. The home range analysis of adults and dispersal of age-0 juveniles provides evidence of a strong spatial structure in smallmouth bass populations. We propose that density-dependent growth during the mid- to late juvenile period reflects a process of movement away from the natal area to locations where adult home ranges will be established. We further propose that this movement is a density-dependent process based on competitive abilities of individuals and possibly reflects social foraging that is observed to increase in juvenile bass after their first year. The spatial spread of juveniles presumably leads to adults establishing home ranges in various locations in the lake and, based on our observations of their behavior and fidelity in the home range, points to a spatial learning process that may be functioning to locate home ranges at the end of the juvenile period. The 95 percent kernel home range is larger for females than for males indicating that there may be differences between males and females operating within this spatial spread process. Acquiring a home range and successfully foraging in what may be social groups of adults and sub-adults may be a prerequisite for maturation and nesting. In conditions of high population abundance, activity necessary for successful foraging and establishment of home ranges may consume larger proportions of assimilated energy as a result of competition and this in turn could slow the maturation process leading to our earlier observation of a density-dependent relationship between adult abundance and the numbers of nesting males. This is the juvenile transition hypothesis.

Introduction

Two general aspects of smallmouth bass ecology are known from field observations of their seasonal movements. First, the movements of adults can be extensive with seasonal shifts in habitat use often involving large distances in river and lake systems (Forney 1961; Langhurst and Schoenike 1990). These movements often correspond to shifts from active foraging areas to overwintering sites where adults remain inactive for much of the winter period (Webster 1954; Kolok 1991), and rely on stored energy reserves to survive to the following spring (Keast 1968; Mackereth et al. 1998). Second, movements can be limited to a small area at certain times of the year. Adult male smallmouth bass return close to old nest sites in subsequent years (Ridgway et al. 1991b) and remain close to the nest site throughout the parental care period (Scott et al. 1997). Seasonal home ranges can be large (100-300 ha); however, adults displaced from summer home ranges will return within a few days to a few weeks (Ridgway and Shuter 1996). Studies of externally tagged smallmouth bass also indicate that fish remain within a limited area each year during their active summer period (Fraser 1955), and return close to sites of capture when displaced (Pflug and Pauley 1983).

In two intensively studied populations of smallmouth bass, only a small proportion of adults that are large enough to reproduce actually reproduce in any given year (Raffetto et al. 1990; Ridgway et al. 1991a). In the case of the Lake Opeongo population, nesting habitat is not a limiting resource (Ridgway et al. 1991a; Rejwan et al. 1997). Even though nesting habitat is not limiting, there is a negative density-dependent relationship in Lake Opeongo between the number of adult nesting males and the total male population (Figure 4c in Ridgway et al. 1991a). This negative density-dependent relationship led to the hypothesis that space-use in the nonreproductive period, the so-called "lake phase" (Ridgway et al. 1991a), may be important in determining recruitment to the breeding population.

The objective of this paper is to present three lines of evidence that point to the development of home ranges as an important step in recruitment to the breeding population. First, we summarize the extent of age-0 dispersal from the nesting period to the fall (Gross et al. 1994; Gross and Kapuscinski 1997). Second, we use kernel home range estimators to examine home range structure of adult smallmouth bass (Powell 2000). Third, we present long-term data on age-specific growth of

smallmouth bass in Lake Opeongo that identifies an important life history stage in the ecology of smallmouth bass (Shuter et al. 1987; Shuter and Ridgway, this volume). Together, the data point to the spatial ecology of juveniles, ages 2-4, as a key consideration in understanding recruitment to the adult breeding population, a process we refer to as the *juvenile transition hypothesis*. The general thrust of the hypothesis we develop was fully anticipated by John Funk (1957) in his conclusions based on an analysis of smallmouth bass tag returns from Missouri streams and rivers.

Background

The general pattern of seasonal movements in adult smallmouth bass has been known in outline for a number of decades. Webster (1954) summarized tag recovery and netting information for Cayuga Lake in New York that clearly indicated three general locations occupied by adults throughout the year. Adult males nested in similar areas in different years, moved away from nest areas to different locations in the lake during summer followed by fall movements to one common location for the winter (Figure 1). His conceptual model of adults moving from nest sites to summer home ranges and then to overwinter sites, each occurring in three different areas of the lake, was partially confirmed by other tagging studies occurring at that time. The
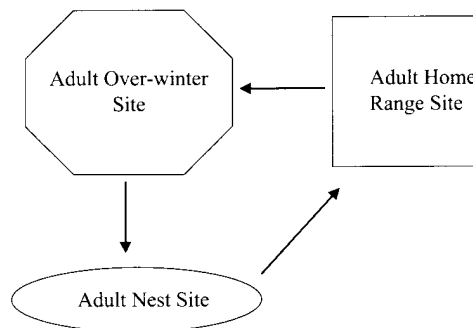

Figure 1. Schematic diagram of the spatial distribution of adult smallmouth bass based on early observations and tag returns. In this representation, males and females generally occupy different locations at different times in the year. Summer home ranges typically do not include nest sites and overwinter sites are located separate from summer home ranges. Nest sites are located in the shallow littoral zone separate from overwinter sites. This figure is a composite of information provided by Webster (1954), Fraser (1955), Forney (1961), Latta (1963), and Langhurst and Schoenike (1990).

late summer movement of adults that occurs prior to movement to the overwinter site was detected by increases in catch rates and tagged individuals moving into new areas (Fraser 1955). The home range area was thought to be large based on the extent of summer movements of tagged fish using a distance of 4-5 km between tag recaptures as a measure of restricted use of space (Fraser 1955; Forney 1961; Latta 1963). This metric was subsequently confirmed in a later ultrasonic tracking study when the length of smallmouth bass home ranges was shown to be on average 4.24 km (Ridgway and Shuter 1996). Webster's original idea that smallmouth bass remained in the overwinter site until the next spring was later elaborated by demonstrations that winter is a period of net energy deficit that generally leads to a reduction in the condition of smallmouth bass (Keast 1968; Mackereth et al. 1998).

Methods

Study Site
Data were collected from the smallmouth bass population in Lake Opeongo, Ontario (45°42'N; 78°22'W). Lake Opeongo is a large oligotrophic lake (area 5,860 ha) and the site of long-term study on the ecology of smallmouth bass. Smallmouth bass were introduced prior to the 1920's to supplement the angling fishery for native lake trout *Salvelinus namaycush*. The smallmouth bass population has been monitored since 1936 with an access point creel survey (Shuter et al. 1987) with data from the survey used to analyze age-specific growth in this study. Data on family-specific DNA fingerprints were collected in 1992 (Gross and Kapuscinski 1997) and data on the movements of adult smallmouth bass were collected from 1989 to 1993 (Ridgway and Shuter 1996).

Nest Site Fidelity
Smallmouth bass nests were monitored every three days throughout the nesting period and records maintained on the developmental phase of the brood and whether or not the nest was active or empty. Parental males were tagged with an external Hag beneath the soft dorsal fin and released. Individual nest sites were mapped each year and the nest location of returning tagged males was determined from one year to the next. Data reported on distances between subsequent nest sites represent minimum straight line distances following the shoreline contour.

Data for this summary of nest site fidelity covers the period of 1988-1998. A previous summary of nest site fidelity covered an earlier period in our long-term study (Ridgway et al. 1991b). An update of the nest site fidelity analysis was undertaken both to confirm the patterns observed in our initial study and to incorporate in the analysis recent improvements in the spatial resolution of the map of the study site.

Age-0 Diffusive Movements from Nest Sites
Nest-specific DNA fingerprints of age-0 fish were used to determine the dispersal distance of individuals from their nest site of origin to their location in September of 1992 (Gross et al. 1994). The locations of 139 age-0 fish collected as part of an assessment of male reproductive success (Gross and Kapuscinski 1997) were used to generate a frequency distribution of age-0 dispersal.

Briefly, age-0 smallmouth bass were collected along a 6 km length of shoreline (Jones Bay) that is a major spawning area in Lake Opeongo (Ridgway and Friesen 1992). Ten larvae were collected with an aquarium dip net from nests that had offspring survive to swim-up $(N = 116)$. All fish were placed separately in labeled vials, kept on dry ice and later stored at -70° C until DNA could be extracted. The details of whole larvae and fin tissue DNA analysis are provided in Gross et al. (1994) and Gross and Kapuscinski (1997).

Later in the same year, age-0 fish were collected in one week in September by an electro fishing survey along the entire length of the study area in Jones Bay (Gross 1995). The survey did not extend beyond 5 m from shore and was restricted to depths less than 1 m. This area along the shore provided for efficient and unbiased capture with the electrofishing gear (Gross and Kapuscinski 1997). Electrofishing extended approximately 1 km beyond each boundary of the Jones Bay study area to minimize under-sampling at the edges of the spawning area. Prior to returning each fish to the lake, the site of capture was noted on a topographic map and a fin tissue was obtained and stored in manner similar to the collection of swim-up larvae.

Eight larvae from the same nest were finger-printed on the same gel to generate family-specific marks. After fingerprinting all age-0 samples, each fall age-0 fingerprint was visually compared to each family fingerprint to determine its family of origin as illustrated in Gross et al. (1994). A match occurred when the overall banding pattern of a fall age-0 fish concurred with the overall banding pattern of a particular nest. The ability to successfully match

individuals back to their family of origin was verified with a double blind test (Gross et al. 1994).

The diffusive movements of age-0 smallmouth bass in the fall were compared to a normal distribution to determine if the movements generally reflected a homogeneous population (Skellam 1951). A population consisting of individuals following different movement tactics (i.e., fast or longdistance movers versus slow or short-distance movers) would produce a nonnormal movement distribution that would appear leptokurtic (high peak and long tail; Skalski and Gilliam 2000; Turchin 1998). Under conditions of a normally distributed, homogeneous movement pattern, the model of simple diffusion with advection can be used to describe their movements (Turchin 1998; equation A22):

$$u(x,t) = (N_o / 2\sqrt{\pi Dt}) \times \exp(-[x - \beta t^2] / 4Dt)$$

where $u(x,t)$ is the density of fish at x distance and time t, following a hypothetical release of N_0 individuals at a single point. Under normally distributed movements, the mean is βt where β is the advection or drift parameter (m/ d) and the variance is $2Dt$ where D is the diffusion coefficient (m^2/ d; Turchin 1998; Skalski and Gilliam 2000). The single point of release is the nest site location for individual juveniles with t being 70 days, a period of time extending from the last week of June until the first week of September when the juveniles were located by electrofishing. The one dimensional form of the simple diffusion equation was used since the juveniles are found along a narrow band of the shallow littoral zone near shore. The observed distribution of distances between nest site and fall 10-cations of juveniles was compared to a normal distribution using the Kolmogorov-Smirnov test.

In addition to the data on diffusive movement, the spawning date of age-0 fish captured in the fall could also be determined based on DNA analysis. The size of age-0 fish originating on different spawning dates was also compared.

Adult Home Range

Fish were located using ultrasonic tags surgically implanted in the body cavity. This technology was chosen rather than radio telemetry because of previous reports that smallmouth bass could, at certain time of their active season, live at depths beyond the range of radio telemetry (Winters 1996). Although smallmouth bass in Lake Opeongo begin breeding at age 5 and 6 (Ridgway and Friesen 1992), all adult males and females that received

ultrasonic tags were at least 38 em (forklength) because of the size of the tags (Sonotronics Inc., CTT83 tag; 60 mm 1ength x 16 mm diameter; weight = 8 g). Males were captured from their nest site and gravid females were captured in trapnets near the nesting area.

The surgical implanting of ultrasonic tags has been previously described (Ridgway and Shuter 1996). Following these procedures, fish were placed in a large container next to the boat and their recovery monitored by observers stationed in the water next to the boat. Fish were recovered from surgery when they had properly reoriented in the container. Nesting males were returned to their nest site in the container and released. All other fish were released at the boat. Normal activity for fish resumed soon after their return to the lake. For nesting males, parental fanning and guarding resumed within 30 minutes based on underwater observation. Nests of males that received ultrasonic tags were undisturbed during the capture, surgery and release procedures. For other fish, they appeared to swim away from the boat in a normal fashion and presumably had a brief period of recovery as observed in nesting males.

Locating Fish

All fish locations were based on the use of directional hydrophones and search procedures in the following way. After surgery, fish locations were not included in data collection for approximately one week to allow for the effects of surgery to pass. A search pattern that used the directional hydrophone to sweep embayments and points of land was used to locate tagged fish (range: 0.5-1.5 km). Once a fish was located the observer would begin to approach in the direction of the ultrasonic signal and continue the process of listening with the hydrophone and adjusting the boat position until the sound of the ultrasonic signal was omnidirectional (the pass-over technique; Winter 1996). This was taken as the location of the fish. This procedure was confirmed for a few fish by an observer in the water who visually located the tagged fish. From this point, the observer used a compass to triangulate their position from landmarks approximately 90° apart. In instances where a fish was in water too shallow for the boat, the directional hydrophone was used to determine the direction of the fish and to determine a location halfway between the boat and shore. Lake Opeongo, like many lakes on the Canadian Shield, possesses a relatively narrow shallow zone around the perimeter of the lake making it easy for boats to approach close to shore.

Throughout the summer, fish were located one to three times per day when observers were searching for fish. Location fixes were separated by a minimum of 1.5-2 hours in an attempt to minimize autocorrelation of location data. Location fixes were collected on 31 fish (mean number of fixes per fish = 98; minimum 79, maximum 123).

Movement activity within home ranges was compared to home range size for a subset of fish (N = 15) using quantities based on tracks. A track for an individual fish consisted of a set of sequential fixes that extended over at least a six hour period (range, 6-16 hours) with each fix separated by a 15 minute interval. The track statistics that will be used are: net displacement representing the shortest linear distance between the start and finish points of a track; maximum extent of a track representing the linear distance between the two fixes furthest apart in a track regardless of start and finish locations; total distance of a track representing the sum of all distances between sequential fixes; and maximum extent of a home range representing the maximum linear distance across the total home range area (see below). Tracks of at least five hours in duration did not show any correlation with total distance of a track $(r, = 0.01; P = 0.98)$.

Whether focusing on fixes for home range determination or for tracking the movements of individual fish, all compass bearings and triangulation data were transferred to maps (scale = 1:10,000) and stored as UTM coordinates. Location data were collected primarily during the active season after the nesting period from early July to September.

The movements of two fish were tracked for 24 hours to assess the amount of nocturnal movement. We found little or no movement in the evening so we confined our observations to the daylight period (approximately 09:00-17:00 hours). Early morning observations in mid- to late summer were not feasible because fog at this time of day prevented safe navigation.

Analysis

For the purposes of this study, we were interested in estimating postnesting home ranges for both male and female smallmouth bass and in examining the variability in both extent and location of home range between years for individual smallmouth bass. Location fixes for smallmouth bass used to define home range areas included all fixes after bass left the nest in the spring and included fixes until mid August (day of year = 218). After mid-August, water temperatures begin to decline

and smallmouth bass begin to leave their summer home range and undertake fall movements (Ridgway and Shuter 1996).

Home range estimates for smallmouth bass were calculated using the Home Range extension (Hooge et al. 1999) developed for use with Arcview GIS software (Environmental Systems Research Institute 1998). The kernel density estimator was used to describe the home range (Worton 1989, 1995; Seaman and Powell 1996; Powell 2000). The two-dimensional distribution of animal locations can be viewed as a utilization distribution with areas of many fix locations being areas of relatively high utilization compared to areas with fewer fix locations. Conceptually, kernel estimators operate based on placing a kernel (a probability density) over each fix location, imposing a grid pattern over all locations, and then determining the density of kernels at each grid intersection (Seaman and Powell 1996). Fix locations close to grid intersections will contribute more "kernel density" at those locations than fixes further from a particular grid intersection. Places with many fix locations will have high kernel density estimates. The size of kernels is an important consideration and is referred to as the bandwidth or smoothing parameter. Narrow bandwidths or kernels emphasize local detail because fix locations close to grid intersections have more influence on the density estimate than fixes further away. Broad bandwidths allow more influence from fix locations further away from a grid intersection and therefore provide an estimate of overall shape of a home range at the expense of local detail.

Following earlier evaluations of this home range estimator (Worton 1989; Seaman and Powell 1996), the least squares cross validation (LSCV) method of choosing bandwidth was used to estimate a fixed kernel home range for each tagged bass. Fixed kernel home range estimates using the LSCV method have performed well with respect to minimizing estimated error and reducing bias in home range estimates (Seaman et al. 1998; Seaman and Powell 1996). To achieve this level of performance, sample sizes of about 50 fix locations or greater are generally needed for kernel density estimates of home range (Seaman et al. 1999). The sample size of fixes for each smallmouth bass in this study exceeded this threshold.

To allow comparison of home range areas between fish and between years for individual fish, a second fixed kernel home range was also calculated for each tagged bass. The bandwidth used for these fixed kernel home range estimates was the median

value of all bandwidths chosen by the LSCV method in the initial analysis. The median bandwidth used was 285 with upper and lower quartiles of 454 and 170 respectively. The total home range was defined as the smallest area containing 95 percent of the utilization distribution (the 95% contour). The core area of the home range was defined as the smallest area containing 50 percent of the utilization distribution (the 50% contour). If data were available for a fish in more than one year, the percentage overlap between years for both the core home range and the home range extent were calculated to examine home range fidelity between years. Home range areas were clipped to exclude land areas initially incorporated in area estimates.

Age-Specific Growth and Abundance

Data for estimation of age, growth and abundance of smallmouth bass in Lake Opeongo were provided by an access point creel survey that has been in continuous operation since 1936 (Shuter et aL 1987). This survey stands as on of the longest and most complete sources of information on the dynamics of freshwater fish populations in the world. A full description of the creel survey and the analyses used to reconstruct the population abundance is described in Shuter et aL (1987). From each smallmouth bass observed in the creel survey, scales were removed from the side of the fish immediately posterior to the pectoral fin, mounted on glass slides or pressed onto acetate slides, and the annuli counted under magnification for age determination. Distances to annuli were measured and used to estimate annual growth rates using the back-calculation procedures outlined in Shuter et aL (1980).

Estimation of smallmouth bass abundance in Lake Opeongo based on the creel survey data required adjustment for creel effectiveness in addition to determining vital rates for the population (Shuter et aL 1987). Briefly, instantaneous rates of total mortality (2, per year) were estimated from catch-at-age data and from catch-per-effort data. Instantaneous natural mortality rates $(M,$ per year) were estimated from linear regressions of 2 on effort. This value of M was used to obtain estimates of the instantaneous fishing mortality rate $(F,$ per year) for each year using separable virtual population analysis (Pope and Shepherd 1982). With these estimates of M and F in hand, the recovery rates of tagged fish in the creel survey were used to check and, where necessary, correct the total harvest estimates provided by the creel survey. Annual estimates of abundance for smallmouth bass were then obtained by applying both separable as

well as virtual population analysis (Sims 1982) to the corrected total harvest at age data. These abundance estimates were cross-checked against independent abundance estimates obtained through mark-recapture experiments.

Results

Juvenile Stage

Age-0 Dispersal from Nest Sites: The movement of age-0 fish from their nest of origin in June to their location in the fall is limited (Mean, 87.63 m; SD, 60.67 m). Almost all age-0 fish were found within 200 m of their nest of origin (Figure 2). There is no difference between the observed distribution of diffusive movement and a normal distribution (Kolmogorov-Smirnov test), indicating population homogeneity in the movements of juvenile smallmouth bass in their first summer. The mean *(βt)* and variance *(2Dt)* of the distribution allows for the determination of the drift *(b)* and diffusion coefficient *(D)*. From swim-up in late June until the first week of September *(t* = 70 days), the diffusion coefficient is 26.3 m2 per day and drift is 1.3 m per day. These estimates include the parental care period during which the guarding male and brood remain close to the nest site for two to three weeks (Scott et al. 1997; Friesen and Ridgway 2000). Shifting the start time for diffusion to the end of parental care in mid-July reduces the number of days until the first week of September *(t* = 52 days) that in turn corresponds to a drift of 1.7 m per day and a diffusive coefficient of 35.4 m^2 per day.
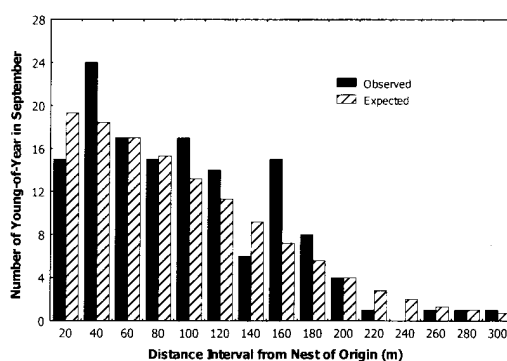

Figure 2. The observed distribution (dark bars) of dispersal distances for age-0 smallmouth bass in Lake Opeongo based on data from Gross (1995; N = 139 fish). Expected distribution (hatched bars) from a half-normal distribution is shown.

Age-0 Length in Fall: There was clear overlap in the length of age-0 fish in the fall with respect to spawning date (Table 1).. Because water temperatures are warmer in mid-June than early June, age-0 fish develop at faster rates from mid-June spawnings than early June spawnings which, in turn, reduces the observed 12 day spread in spawning dates relative to swim-up dates. However, for nests that made it to the swim-up stage, larvae from spawnings that occurred on June 1 swam-up earlier (Mean = 17 June; range 14-20 June; N = 8 nests) than larvae from spawnings in the 10-13 June period (Mean = 25 June; range 23-26 June; N = 6 nests). Therefore, despite warmer temperatures for late spawning males, age-0 fish from early spawnings retained an approximate eight day growth advantage over age-0 fish from spawnings in the 10-13 June period. This difference did not translate into a strong size advantage in the fall. Fish lengths from 1 June and 10 June have adequate sample sizes and do indicate a size advantage of approximately 4-5 mm for the early swim-up fish at the end of the growth season (Table 1).

Juvenile Abundance and Growth: Abundance of smallmouth bass ages 1-4 (first onset of adult stage) ranged from approximately 5,000-48,000 in the period of 1937-1990 (Figure 3; Shuter et al. 1987; Shuter and Ridgway, this volume). The range in abundance over this time span reflects changes in the bass population in three areas. First, increases in abundance are likely due, to some degree, in capturing the time series at a point when smallmouth bass are still expanding in the lake after their introduction after the turn of the century. Second, there was a decline in fishing mortality with the cessation of guided fishing in the 1950s resulting in a period of lower fishing mortality when anglers with a wider range in skilllevel fully participated in the fishery (Shuter et al. 1987). Third, the introduction of cisco
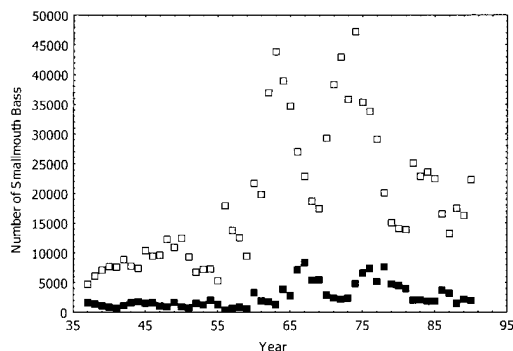

Figure 3. The abundance of smallmouth bass in Lake Opeongo from 1937 to 90. Open squares are estimates of abundance for juveniles ages 1-4. Closed squares are the estimates of abundance for bass ages 5-13. All data are based on the access point creel survey (Shuter et al. 1987).

(Coregonus artedi) in 1948 resulted in a fully established population of this species by the 1960s (Martin and Fry 1972). The abundance of adult smallmouth bass (ages 5-13) is also highly variable over this same time period shows but it exhibits periods of increase that correspond to the periods when juveniles also increased (Figure 3).

The time series from the Opeongo population generates a gradient for a comparison of growth in different age intervals relative to juvenile and early adult abundance (Table 2). Growth in the first year (age 0-1) was negatively correlated with abundance of fish age 1-4 *(r = -0.239; P = 0.082).* In the second and third years, this negative relationship between growth and abundance clearly strengthens for mid to late juveniles (Table 2; Figure 4). At the beginning of the adult period, the relationship between juvenile abundance (ages 1-4) and growth in the fifth and sixth year weakens considerably (Table 2; Figure 4). The density-dependent relationship between growth and abundance of juveniles

Table 1. The length of age-0 smallmouth bass in Jones Bay, Lake Opeongo based on known nest of origin and egg deposition date. Data from Gross (1995).

Spawning date in June	Mean TL (mm)	95% confidence inteval	N
1	53.4	51.7-55.1	20
4	49.8	46.6-53.0	13
7	51.5	49.9-53.1	34
10	47.7	47.5-47.9	65
13	51.8	49.8-53.8	5"
Combined	49.8	48.8-50.8	137

"All fish from the same nest (full siblings)

Table 2. The correlations between abundance of juvenile fish ages 1-4 (combined) and growth in length in each age interval. The data are from the long-term creel census on Lake Opeongo (1936-1990)

Age interval	Pearson's r	p-level	N (years)
0-1	-0.239	0.082	54
1-2	-0.685	<0.001	54
2-3	-0.589	<0.001	55
3-4	-0.349	0.009	55
4-5	-0.200	0.142	55
5-6	-0.102	0.643	23

for adults was 74 percent (95% Cl, :t 13.5%) from one year to the next (Figure 7). Too few females returned to make a meaningful comparison with males, but they tended to show less overlap (46%) from one year to the next than males (81 %; 95% Cl, :t 10.2%; Figure 7). The annual overlap for core areas was less than the total home range areas. For all

adults, core area overlap was 54 percent (95% Cl, :t 20.4%) with females again exhibiting less core area overlap (25%) than males (61 %; 95% Cl, :t 21 %).

The movements of individuals were extensive within their home ranges. The mean total distance traveled in tracks was 4.80 km with one fish traveling 9.01 km (Table 4). The mean rate of travel was 482.7 m per hour with one fish traveling a maximum rate of 1,120 m per hour (Table 4). Fish with high rates of travel covered greater total distances during their track *(rs = 0.85; P < 0.0001; N = 15)*. The total distance of a track and the maximum extent of a track were not strongly correlated with the maximum extent of home ranges *(rs = 0.436; p = 0.104* for total distance of a track; *rs = 0232; P = 0.405* for maximum extent of a track). However, home ranges sometimes consisted of separate component areas (Figure 6). The total distance of a track was compared with the maximum length of the component area in the home range in which the fish was swimming at the time (and not the maximum extent of the total home range). There was a significant positive correlation between total distance of a track and the maximum length of the relevant component area of the total home range *(rs = 0.536; P = 0.04)*. There was no correlation between maximum extent of a track and the length of the component area in the home range *(rs = 0.293; P = 0.289)*. The total distance of a track represented on average 110.6 percent of the maximum extent of the total home range. The maximum extent of a track represented 50.7 percent of the maximum extent of the total home range. When considering only the component area in which the track took place (versus the maximum extent of the total home range) then the maximum extent of a track repre
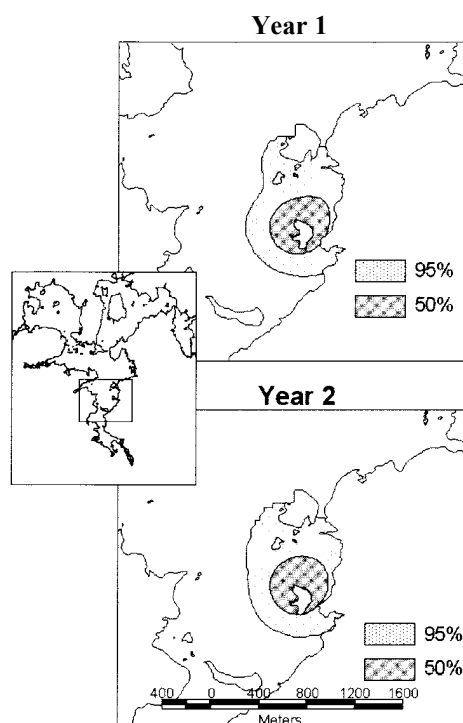

Figure 7. The 95% and 50% kernel estimates of home range configuration for a male smallmouth bass in two consecutive years.

sented on average 84.2 percent of the length of the component area of the home range. The net displacement of a track was relatively small in comparison to the maximum extent of a track and the rate of movement (Table 4). Taken together, the results point to extensive daily use of the adult home range in general with any given daily track covering substantial areas of a summer home range. The foraging behavior of the adults appears similar to the movements of age-O fish with extensive and relatively high rates of movements on a daily basis but with little displacement overall.

Only two fish, both males, incorporated their

Table 4. Movement characteristics of Smallm01]th h"ss *IN =* 1.'1\ tr"rkpn ""ithin thpir Sll mmpr hnmp r"nO'ps

	Hours tracked	Total distance of track (km)	Maximum extent of track (km)	Net displacement (km)	Rate of travel (m/hour) (km)	Maximum extent of homerange	Max. extent of track/max. extent home range x 100 (%)
Mean	11.38	4.80	1.90	1.23	482.7	4.47	50.73
Lower 95% CI	9.34	3.50	1.24	0.55	307.3	3.02	33.56
Upper 95% CI	13.34	6.10	2.55	1.92	658.1	5.92	67.91
Minimum	6.0	1.25	0.40	0.00	110.0	1.67	10.64
Maximum	16.0	9.01	4.10	4.20	1,120.0	11.43	119.0

spawning site within their summer home range and this occurred towards the end of the summer period. Other fish appeared to establish home ranges away from their spawning sites.

Discussion

The lines of evidence we present point to a strong spatial structure in smallmouth bass populations at the beginning of the juvenile stage and at the adult stage. Dispersal of age-O smallmouth bass in Lake Opeongo is limited with most fish remaining close to their nest of origin. Adult home ranges are large and are occupied by the same individual from one year to the next with most home ranges established away from the nesting areas. When displaced from their home ranges, most adult smallmouth bass return in a relatively short period of time (Ridgway and Shuter 1996). Adults show strong nest site fidelity in this population (Figure 5; Ridgway et al. 1991b). Given this fidelity to home ranges and nest sites, we conclude that foraging and reproduction are precisely located but spatially separate activities in adults. Similar levels of precision are suggested in movement studies of smallmouth bass in river systems (Langhurst and Schoenike 1990).

Both age-O fish and adults demonstrate extensive movement patterns. For age-O bass, the limited dispersal in the first summer is particularly interesting when considering that they are capable of sustained movement of 1-2 m per minute (Friesen 1998). For adults, a substantial area of the home range is used on a daily basis. For both life stages, foraging areas must be repeatedly covered for observed net displacement to be low while at the same time rates of movement remain relatively high.

The long-term data on growth and abundance demonstrates that the mid- to late juvenile period is characterized by strong density-dependent growth. Density-dependent growth weakens as fish enter the adult period. In general, the lines of evidence we present can be characterized by strong spatial structure in the early juvenile and adult periods separated by strong density-dependent growth in the mid- to late juvenile period. There is little information available on space use patterns for juvenile smallmouth bass after age 1 during the period of density-dependent growth. In a radio-telemetry study of smallmouth bass movements in a Maine lake, small adults (24.8‑27.9 cm TL) were found in shallow areas of the lake relative to larger adults and appeared to occupy intensely used core areas relative to the

wider ranging larger adults (Cole and Moring 1997). The size range of small adults in the Maine study represents the transition between late juveniles and young adults. Although the size range in the Maine study is not representative of two and three-year-old fish, the observations of small bass do provide an intriguing glimpse into basic differences between large and small sizes of smallmouth bass. The core areas that were heavily used by small adults were separated by relatively long distances where fixes were sometimes recorded indicating that the distances between core areas were travel routes (Cole and Moring 1997). Based on the movement and home range information in this and other studies, what general process is operating during the mid- to late juvenile period to account for density-dependent growth and adult home ranges that appear to be spatially separate from juvenile habitat?

We propose that density-dependent processes during the mid- to late juvenile stage are the link between space use at age-O and adult stages. Specifically, these processes lead to the net displacement of mid- to late juveniles away from nesting areas to areas where adult home ranges can be supported. Furthermore, this displacement is not simply one of ontogenetic changes in diet but rather one that includes a spatial learning component perhaps reinforced by foraging profitability. We interpret the core areas and fidelity to both the location and use of adult home ranges as a product of this spatial learning process. The fidelity to a home range shown by adult smallmouth bass following displacement reflects this spatial learning process (Ridgway and Shuter 1996). Acquiring an adult home range is a prerequisite to maturation. In conditions of high population abundance, activity necessary for successful foraging and establishment of home ranges may consume larger proportions of assimilated energy due to competition. This in turn could slow the maturation process leading to our earlier observation of a density-dependent relationship between adult abundance and the numbers of nesting males. The period of transition from natal to adult areas is what we refer to as the juvenile transition hypothesis (Figure 8).

The idea that natal and adult space use are linked in the ecology of smallmouth bass via a period encompassing net displacement of older juveniles is not new. Over forty years ago, Funk (1957) proposed a general process of shifting space use in stream fish including smallmouth bass. His contention was that early juveniles remained near their
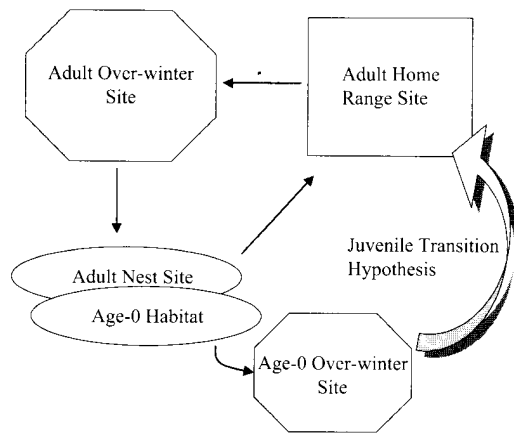
Figure 8. Schematic representation of the spatial distribution of adult and juvenile smallmouth bass emphasizing the juvenile transition hypothesis. The spatial distribution of adults is the same as outlined in Figure 1. Age-O smallmouth bass remain close to their nest of origin. From the perspective of nesting areas, age-O fish remain within or close to the nesting area through to the fall season. Following from this, we assume that overwinter habitat for age-O fish is similarly close to, or within nesting areas. After agel, and until maturation, juvenile smallmouth bass move away from natal and age-O habitat to occupy different areas of a lake or river system. Density-dependent growth occurs during this period of spatial spread in juveniles pointing to competitive mechanisms as a basis for developing adult home ranges in areas of lake or river systems away from nesting/ natal habitat. Field-based observations of social groups of juvenile smallmouth bass, ages 2-4, suggest that social processes (i.e., social foraging and group membership, territorial behavior, etc.) may be important considerations in the spatial distribution of fish prior to maturation.

natal area, ranged farther from this area as they grew in order to meet food requirements, and continued to move to less crowded conditions or established a suitable "territory" that was defended. Furthermore, based on more widespread movements of small to medium size fish as revealed by tag returns from anglers, Funk (1957, page 56) concluded that "competition for territories seems to be keenest among fish of intermediate size, therefore they are the greatest wanderers."

What mechanisms may be operating that result in net displacement of juveniles generating density-dependent growth and ultimately negative density-dependent recruitment to the reproductive sub-population? Literature on diet changes is probably too coarse to capture spatial changes. Indeed, during the first year, larger age-O smallmouth bass appear to be undergoing a change in trophic posi

tion that has not been detected by standard diet analysis (Vander Zanden et al. 1998). The social structure of foraging groups of fish may be important. The distribution and density of juvenile smallmouth bass in broods suggests that young fish under parental care maintain visual contact with neighboring fish while foraging in the broods (Friesen and Ridgway 2000). Sustaining visual contact can in turn set limits on how far individual fish venture away from the nest site and their siblings while in the brood. Later in the year, age-O smallmouth bass are observed as single fish or in small groups composed of a few fish. We now know these fish are close to their nest of origin (Figure 2), and consequently may be associating with siblings in their foraging movements. Mid- to late juveniles are often observed in small groups in the shallow littoral zone where they move in semicoordinated groups or generally occupy areas as a single group when not moving (Ridgway, personal observation). Since there are no natural predators capable of capturing mid- to late juveniles in Lake Opeongo, the level of sociality observed in the field presumably reflects gains based on foraging efficiency or perhaps a kleptoparasitic approach to foraging success among individuals of different size. Individual recognition in centrarchid fish has been demonstrated and the potential for individuals to associate with other individuals based on foraging success is real (Brown and Colgan 1986; Dugatkin and Wilson 1992). Whatever the precise nature of the competitive process that occurs during the juvenile transition period, we envision the process leading to the occupation of outer regions of the lake that have very low densities of nesters or none at all even though juvenile smallmouth bass are present (Rejwan et al. 1997). The low use of nesting areas in the home ranges of adults we observed may be due to the level of competition among juveniles of different ages occupying the nesting area or it may reflect an adaptive response to minimize

potential competition with what could be their off-spring.

Another hypothesis regarding mechanisms governing recruitment to the breeding sub-population of smallmouth bass emphasizes the swimup date as the key factor in determining whether individual fish reach adulthood early or late within the life of a cohort (Baylis et al. 1993). There is a critical and narrow timing window that drives this perspective because the period of swim-up from nests ranges from one to three weeks in duration (Ridgway and Friesen 1992). Our results clearly indicate that there is much more competitive interac

tion over a number of years in the juvenile stage than previously realized and this in turn suggests a more complex picture of the processes that determine when individual fish breed. It is not clear that the 45 mm difference in size between early swim-up fish and late swim-up fish we observed would translate into a sustained advantage into adulthood for larger age-O fish under these conditions.

The kind of competitive mechanism we outline, in which social behavior determines natal dispersal, has been identified as a key process in the population regulation of brown trout in small streams (Elliott 1989, 1990a, b). For brown trout *Salmo trutta,* acquiring a feeding territory was a key process that determined whether fish remained in the stream or dispersed. The competitive process was clearly size-based and the seasonal timing shifted with population density such that large cohorts reached this competitive bottleneck earlier in the season relative to smaller cohorts. This level of insight into the social mechanisms of population regulation in brown trout is a rare event in field-based studies of fish ecology. However, a similar approach is required if we are to advance on two significant unanswered questions in ecology, namely mechanisms governing population density and the spatial structure of populations (May 1999). For different *Micropterus* species occupying different habitats, such an approach offers the promise of deeper insight into the mechanisms regulating population size, growth rate and maturity. Determining the linkages between the social behavior of individuals and population regulation in fish ecology was a recommended approach outlined by a prominent fish ecologist over forty years ago (Gerking 1959).

Acknowledgments

References

Baylis, J. R, D. D. Wiegmann, and M. H. Hoff. 1993. Alternating life histories of smallmouth bass. Transactions of the American Fisheries Society 122:500-510.

Brown, J., and P. Colgan. 1986. Individual and species recognition in centrarchid fishes: evidence and hypotheses. Behavioral Ecology and Sociobiology 19:373-379.

Cole, M. B., and J. R Moring. 1997. Relation of adult size to movements and distribution of smallmouth bass in a central Maine Lake. Transactions of the American Fisheries Society 126:815-821.

Dugatkin, L. A, and D. S. Wilson. 1992. The prerequisites for strategic behaviour in bluegill sunfish, Lepomis macrochirus. Animal Behaviour 44:223-230.

Elliott, J. M. 1989. Mechanisms responsible for population regulation in young migratory trout, Salmo trutta. I. The critical time for survival. Journal of Animal Ecology 58:987-1001.

Elliott, J. M. 1990a. Mechanisms responsible for population regulation in young migratory trout, Salmo trutta. II. Fish growth and size variation. Journal of Animal Ecology 59:171-185.

Elliott, J. M. 1990b. Mechanisms responsible for population regulation in young migratory trout, Salmo trutta. III. The role of territorial behaviour. Journal of Animal Ecology 59:803-818.

Environmental Systems Research Institute. 1998. ArcView GIS Version 3.1.

Forney, J. L. 1961. Growth, movements and survival of smallmouth bass *(Micropterus dolomieui)* in Oneida Lake, New York. New York Fish and Game Journal 8:88-105.

Fraser, J. M. 1955. The smallmouth bass fishery of South Bay, Lake Huron. Journal of the Fisheries Research Board of Canada 12:147-177.

Friesen, T. G. 1998. Effects of food abundance and temperature on growth, survival, development and abundance of larval and juvenile smallmouth bass. Doctoral dissertation, University of Guelph, Ontario, Canada.

Friesen, T. G., and M. S. Ridgway. 2000. Brood size does not influence the behaviour or density of larval and juvenile smallmouth bass under parental care. Behaviour 137:61-74.

Funk, J. L. 1957. Movement of stream fishes in Missouri. Transactions of the American Fisheries Society 85(1955):39-57.

Gerking, S. D. 1959. The restricted movements of stream fish populations. Biological Reviews 34:221-242.

Gross, M. L. 1995. Family-specific DNA fingerprints: a powerful tool to assess reproductive success of a natural population of smallmouth bass *(Micropterus dolomieu).* Doctoral dissertation, University of Minnesota, Minnesota.

Gross, M. L., and A R Kapuscinski. 1997. Reproductive success of smallmouth bass estimated and evaluated from family-specific DNA fingerprints. Ecology 78:1424-1430.

Gross, M. L., A R Kapuscinski, and A J. Faras. 1994. Nest-specific DNA fingerprints of smallmouth bass in Lake Opeongo, Ontario. Transactions of the American Fisheries Society 123:449-459.

Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The animal movement program, USGS, Alaska Biological Sciences Center, Alaska.

Keast, A. 1968. Feeding of some Great Lake fishes at low temperatures. Journal of the Fisheries Research Board of Canada 25:1199-1218.

Kolok, A. S. 1991. Temperature compensation in two centrarchid fishes: do winter-quiescent fish undergo cellular temperature compensation? Transactions of the American Fisheries Society 120:52-57.

Langhurst, R. W, and D. L. Schoenike. 1990. Seasonal migration of smallmouth bass in the Embarrass and Wolfe rivers, Wisconsin. North American Journal of Fisheries Management 10:224-227.

Latta, W. C. 1963. The life history of the smallmouth bass, *Micropterus d. dolomieui,* at Waugoshance Point, Lake Michigan. Bulletin of the Institute for Fisheries Research No.5, Michigan Department of Conservation, Michigan.

Mackereth, R. W, D. L. G. Noakes, and M. S. Ridgway. 1998. Size-based variation in somatic energy and parental expenditure by male smallmouth bass *Micropterus dolomieu.* Environmental Biology of Fishes 56:263-275.

Martin, N. v., and F. E. J. Fry. 1972. Lake Opeongo: effects of exploitation and introductions on the salmonid community. Journal of the Fisheries Research Board of Canada 29:75-805.

May, R. 1999. Unanswered questions in ecology. Philosophical Transactions of the Royal Society, London B 354:1951-1959.

Pflug, D. E., and G. B. Pauley. 1983. The movement and homing of smallmouth bass, Micropterus dolomieui, in Lake Sammamish, Washington. California Fish and Game 69:207-216.

Pope, J. G., and J. G. Shepherd. 1982. A simple method for the consistent interpretation of catch-at-age data. Journal du Conseil International pour I'Exploration de la Mer 40:176-184.

Powell, R. A. 2000. Animal home ranges and territories and home range estimates. Pages 65-110 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York.

Raffetto, N. S., J. R. Baylis, and S. L. Serns. 1990. Reproductive success in a closed population of smallmouth bass *(Micropterus dolomieui):* the significance of accurate estimates. Ecology 71:15231535.

Rejwan, c., B. J. Shuter, M. S. Ridgway, and N. C. Collins. 1997. Spatial and temporal distributions of smallmouth bass *(Micropterus dolomieu)* nests in Lake Opeongo, Ontario. Canadian Journal of Fisheries and Aquatic Sciences 54:2007-2013.

Ridgway, M. S., and T. G. Friesen. 1992. Annual variation in parental care in smallmouth bass, *Micropterus dolomieu.* Environmental Biology of Fishes 35:243-255.

Ridgway, M. S., and B. J. Shuter. 1996. Effects of displacement on the seasonal movements and home range characteristics of smallmouth bass in Lake Opeongo. North American Journal of Fisheries Management 16:371-377.

Ridgway, M. S., B. J. Shuter, and E. E. Post. 1991a. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieu* (Pisces: Centrarchidae). Journal of Animal Ecology 60:665-681.

Ridgway, M. S., J. A. MacLean, and J. C. MacLeod. 1991b. Nest site fidelity in a centrarchid fish, the smallmouth bass *(Micropterus dolomieu).* Canadian Journal of Zoology 69:3103-3105.

Skalski, G. T., and J. F. Gilliam. 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. Ecology 81:1685-1700.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrika 38:196-218.

Scott, R. L M. S. Ridgway, and D. L. G. Noakes. 1997. The nest range of smallmouth bass *(Micropterus dolomieu):* parental care after swim-up. Canadian Journal of Zoology 75:2058-2062.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Seaman, D. E., B. Griffith, and R. A. Powell. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95-100.

Seaman, D. E., J. J. Millspaugh, B. J. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernal home range estimates. Journal of Wildlife Management 63:739-747.

Shuter, B. J., J. E. Matuszek, and H. A. Regier. 1987. Optimal use of creel survey data in assessing population behaviour: Lake Opeongo lake trout *(Salvelinus namaycush)* and smallmouth bass *(Micropterus dolomieui)* 1936-83. Canadian Journal of Fisheries and Aquatic Sciences 44 (Supplement 2):229-238.

Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1-34.

Sims, S. E. 1982. Algorithms for solving the catch equation forward and backward in time. Canadian Journal of Fisheries and Aquatic Sciences 39:197-202.

Turchin, P. 1998. Quantitative analysis of movement. John Wiley, New York.

Vander Zanden, M. J., M. Hulshof, M. S. Ridgway, and J. B. Rasmussen. 1998. Application of stable isotope techniques to trophic studies of age-O smallmouth bass. Transactions of the American Fisheries Society 127:729-739.

Webster, D. A. 1954. Smallmouth bass *(Micropterus dolomieui)* in Cayuga Lake. Part 1. Life history and environment. Agricultural Experiment Station Memoir 327. Cornell Univeristy, Ithaca, New York.

Winters, J. 1996. Advances in underwater biotelemetry. Pages 555-590 *in* B. R. Murphy and D. W Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Worton, B. J. 1989. Kernel methods for estimating the utility distribution in home-range studies. Ecology 70:164-168.

Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794-800.