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POPULATION SIZE AND RECOVERY CRITERIA OF THE THREATENED LAKE ERIE WATERSNAKE: INTEGRATING MULTIPLE METHODS OF POPULATION ESTIMATION

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Abstract: The Lake Erie watersnake, *Nerodia sipedon insularum*, occurs only in the island region of western Lake Erie, an area less than 40 km in diameter. Restricted geographic distribution and declining population size resulted in this snake's classification as Threatened in the U.S. and Endangered in Ontario and Ohio. A combination of mark-recapture methods, capture rate information, and interpolation were used to estimate the current U.S. population size of Lake Erie watersnakes. A total of 121 point estimates were generated using both 'closed' population (Lincoln–Petersen, Schumacher's) and 'open' population (Jolly–Seber, Bailey's triple-catch) methods to analyze data collected from 1980–2004. Paired t-tests, comparing estimates obtained using alternative methods, were consistently non-significant. Although standard errors and confidence intervals of individual estimates were often large, standard errors of mean estimates, obtained by averaging across methods and sets of consecutive years, were markedly smaller, averaging 14% (range = 5–25%). These analyses demonstrate the utility of mark-recapture methods even in cases where sample size and recapture rates are low, as may often be true for threatened and endangered species. Another 60 estimates were obtained by applying the Lincoln–Petersen method to samples collected in consecutive years. As expected if recruitment occurs between samples, these estimates were significantly larger than those obtained using other methods. By comparing these recruitment-biased estimates to unbiased estimates, annual adult recruitment (and by extension, adult survivorship) was estimated to be 0.63.

At 11 study sites for which recent (2000–2004) mark-recapture estimates were available, population density (adults/km) was highly correlated with capture rate. The regression relationship between density and capture rate was thus used to estimate watersnake population size at 19 additional sites for which only capture rate was known. Interpolations of watersnake population size were made at another 29 sites, thus encompassing the entire U.S. range of the Lake Erie watersnake. Interpolations were based on habitat suitability, land-use practices, the observed presence of watersnakes, and density at sites for which mark-recapture or capture rate estimates were available.

Lake Erie watersnake densities exceeded those of many other snakes. At 30 sites for which recent estimates were available, median density = 141 adults/km of shoreline (range = 11–1107 adults/km). Mark-recapture estimates encompassing 15.8 km and capture rate estimates encompassing 19.6 km of shoreline on the U.S. islands totaled more than 6500 adult watersnakes. Including interpolated numbers at 28.3 km of uncensused shoreline to encompass the entire U.S. distribution of the Lake Erie watersnake brought this total to nearly 7700 adults. This exceeds 5555 adults, the number specified in the *Population Persistence* criterion of the Lake Erie Watersnake Recovery Plan. Estimates also exceeded island-specific criteria for Kelleys, South Bass, and Middle Bass Island. On North Bass Island, estimated population size (385 adults) fell short of the island-specific recovery criterion (410 adults) unless interpolated numbers at uncensused sites were included (total = 443 adults).

Other criteria for delisting the Lake Erie watersnake include *Habitat Protection and Management* and *Reduction of Human-induced Mortality*. Recent land acquisitions, development of watersnake-friendly land management plans, and outreach efforts seeking to foster public appreciation and minimize watersnake-human conflicts have contributed to achievement of these goals. These actions, together with this snake's capacity for rapid population growth, make recovery and eventual delisting of the Lake Erie watersnake a real possibility.

Key words: Capture rate; Conservation; Density; Islands; Lake Erie; Mark-recapture population estimation; *Nerodia*; Population size; Recovery; Recruitment; Survivorship; Threatened and Endangered species; Watersnake.

Quantitative estimates of abundance are central to the recognition, management, and recovery of vulnerable, threatened, and endangered populations and species. Unfortunately, obtaining such estimates is often difficult, especially for rare and secretive organisms. Estimates of animal populations frequently rely on mark-recapture techniques (Caughly, 1977; Krebs, 1998; Seber, 1982). Although simple in concept, these techniques

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sometimes require restrictive assumptions such as closed population structure and equal catchability. Furthermore, sample sizes and recapture rates required for accurate estimates (e.g., confidence limits that fall within 10% of the true population size) may be unattainable for many organisms. More sophisticated techniques for the analysis of mark-recapture data make less restrictive assumptions but are primarily intended to generate estimates of population vital statistics (e.g., survivorship, population growth), not population size, and require even more complete capture histories (White and Burnham, 1999).

The primary objective of this paper is to provide quantitative estimates of current adult population size for the Lake Erie watersnake (*Nerodia sipedon insularum*), a U.S. federally threatened and state (Ohio) and provincially (Ontario) endangered species (Fazio and Szymanski, 1999), using data collected from 1980 to the present. This paper builds on work described in King (1986) and a series of unpublished reports to the Ohio Department of Natural Resources Division of Wildlife (ODNR DOW) and U. S. Fish and Wildlife Service (USFWS) (King, 1998*a*, 1998*b*, 2001*b*, 2002*a*, 2002*b*, 2002*c*, 2004). Population estimates included in those documents contributed to the decision to list this snake (Fazio and Szymanski, 1999) and to the development of the Lake Erie Watersnake Recovery Plan (U. S. Fish and Wildlife Service, 2003). In achieving this primary objective, we compare the performance of alternative estimation techniques when sample size and recapture rates are sometimes low. This comparison allows estimation of the degree of bias introduced by recruitment between sample periods when using techniques that assume closed population structure. We also develop an alternative estimation technique based on capture rate. This technique allows quantitative population monitoring at more sites than might be possible (e.g., due to logistic or financial constraints) using only mark-recapture methods.

The Lake Erie watersnake is a nonvenomous live-bearing medium-sized colubrid snake that occurs only in the island region of western Lake Erie, straddling the U.S.–Canada international boundary (Fig. 1). There are 18 islands in western Lake Erie consisting of dolomite and limestone bedrock that resisted glaciation. They are overlain by shallow soils and range in size from less than 1 to more than 4000 ha (Forsyth, 1988). The islands span an area less than 40 km in diameter, giving the Lake Erie watersnake one of the most restricted geographic distributions of any North American vertebrate taxon. Excluding Johnson and Mouse Island, where watersnakes are not protected (Fazio and Szymanski, 1999), Starve Island, which is too small and low to provide over-wintering habitat, and West Sister Island, where the population status of watersnakes remains uncertain (see Discussion), the U.S. islands in Lake Erie comprise about 64 km of shoreline and 2440 ha of inland habitat. The Canadian islands comprise another 41 km of shoreline and 4310 ha of inland habitat. Outside of hibernation, watersnake activity is largely restricted to island shorelines (R.B. King, K.M. Stanford, and D. Wynn; unpublished). Thus, worldwide, potential Lake Erie watersnake summer habitat is comprised of about 105 km of shoreline.

Lake Erie watersnakes differ in color pattern from mainland northern watersnakes (Conant and Clay, 1937), a difference maintained by a dynamic balance between natural selection favoring uniformly gray unbanded snakes in island populations and gene flow from mainland populations where banded snakes are favored (Hendry et al., 2001; King, 1993*b*, 1993*c*; King and Lawson, 1995, 1997). Historically, the diet of Lake Erie watersnakes consisted of native fishes and amphibians (mudpuppies) captured from the nearshore waters of Lake Erie (King, 1986, 1993*a*; King et al., 1999). A dramatic change in diet composition took place starting in the mid-1990's and Lake Erie watersnakes now feed almost exclusively on round gobies, an invasive fish now abundant in the island region (King et. al., 2006). Watersnake courtship and mating occur in spring and early summer and offspring are born in late summer and fall. Lake Erie watersnakes are sexually dimorphic with females exceeding males in adult body size. Sexual maturity is reached in 2–3 years and longevity may exceed 10 years (Gibbons

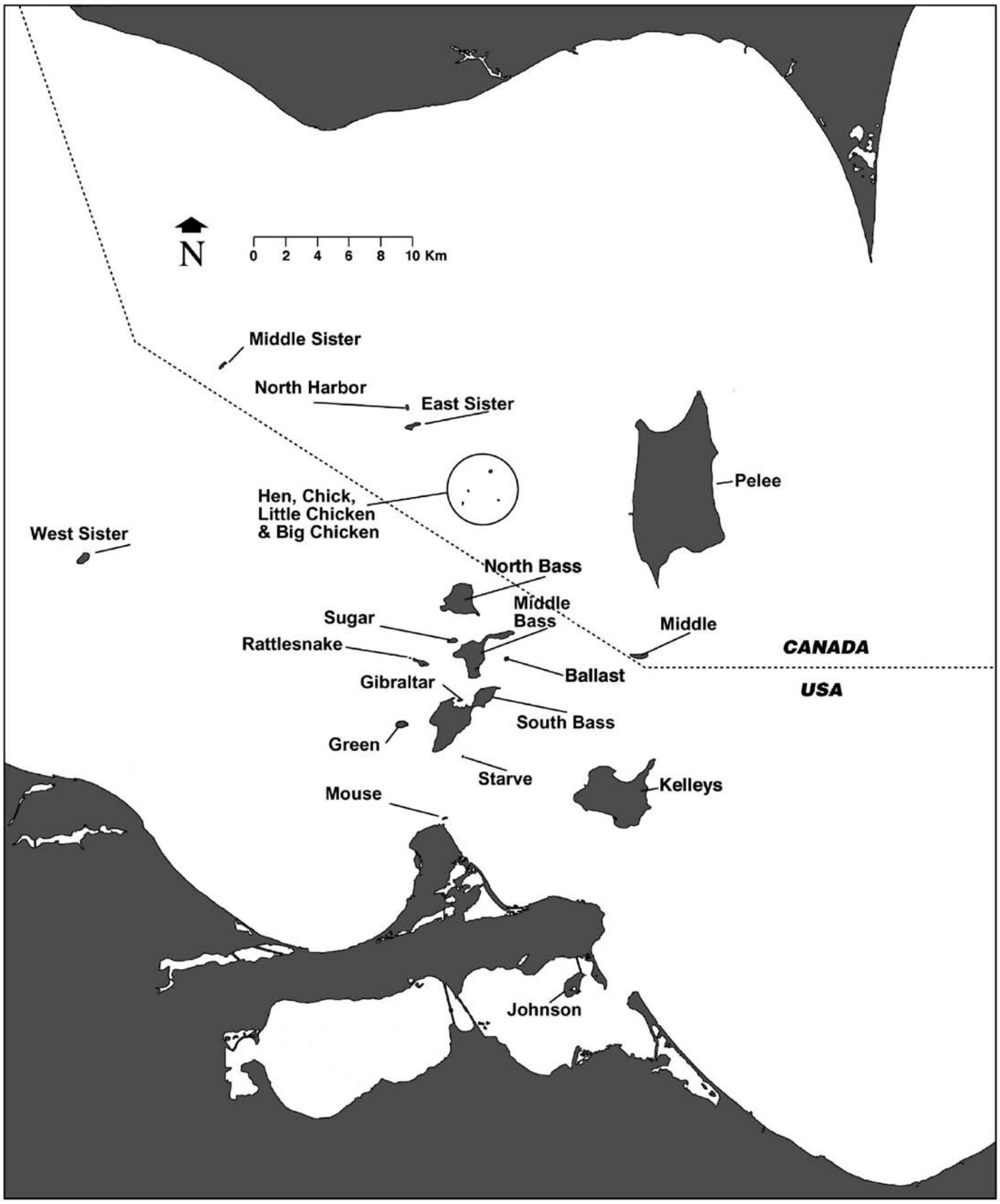


FIG. 1. The island region of western Lake Erie.

and Dorcas, 2004; King, 1986; Walley et al., 2006).

Early European visitors were impressed with the abundance of snakes in the region, dubbing the islands the "Les Isles aux Serpentes" and reporting "myriads of water-snakes basking in the sun" (Langlois, 1964, p. 11; see McDermott, 1947 for additional narratives). Pigs, released by settlers, may have reduced snake populations to some degree (Hatcher, 1945; McDermott, 1947) but scientific investigators in the early- to mid-

1900's reported high watersnake densities; three workers caught 234 in just four hours in 1935 (Conant and Clay, 1937) and seven workers caught about 400 in five hours in 1949 (Camin and Ehrlich, 1958). Published reports raising concerns that watersnake populations were declining first appeared in the 1960s when Ehrlich and Camin commented that "[a] campaign of extermination is being waged against the snakes" on Middle Island (Ehrlich and Camin, 1960, p. 136) and Langlois noted that "[t]he Lake Erie Water Snakes appear to be much less abundant now around the islands than they were in 1936" (Langlois, 1964, p. 18). The effectiveness of earlier efforts by island residents to eliminate snakes from Rattlesnake Island is described by Conant (1982, 1997). Based on multiple visits to the four largest U.S. islands in 1979 and 1980, Kraus and Schuett (1982) classified the Lake Erie watersnake as rare (very restricted in range and numbers), noting that "population densities of insular *Nerodia* have been drastically reduced over the past 40 years" and suggesting that "building and clearing activities along the shoreline and the increased influx of tourists . . . are contributing to the degradation of the shoreline habitat that *Nerodia* inhabits" (Kraus and Schuett, 1982, pp. 38–39). Such observations were echoed in comments to RBK by biologists teaching at the Ohio State University F. T. Stone Laboratory on South Bass Island in the early 1980's.

The first quantitative estimates of Lake Erie watersnake population size were based on field work at 12 study sites on 7 islands from 1980–1984 (King, 1986). A combination of mark-recapture and capture rate techniques were used, resulting in an estimate for all sites combined of 1262 adults (upper and lower bounds = 523 and 4064, table 2 in King, 1986). Of this total, an estimated 586 adults occurred on those U.S. islands where watersnakes are currently protected under the U.S. Endangered Species Act, an estimated 549 adults occurred on Canadian islands, and an estimated 127 adults occurred on Johnson Island in Sandusky Bay. Concerns that these estimates were incomplete and had become outdated led to additional field work on the U.S. islands, commencing in 1996. This work revealed that Lake Erie watersnakes were present along a greater extent of island shoreline than previously realized and that total population size was somewhat larger than suggested by King (1986). Mark-recapture techniques, capture rate data, and inferences regarding population size in shoreline areas where intensive field work was not possible indicated that the U.S. Lake Erie watersnake population numbered between 1530 and 2030 adults (Fazio and Szymanski, 1999; King, 1998*a*, 1998*b*).

Although it is difficult to compare these estimates directly with qualitative reports regarding historic watersnake densities, evidence of declining Lake Erie watersnake populations include the following: (1) Capture rates during 1980–1985 were far lower than those reported by earlier workers (King, 1986). (2) The adult population on Middle Island, a small island sampled in its entirety, numbered ca. 35 adults in the early 1980's, whereas about 400 watersnakes were captured there in 1949 (Camin et al., 1954, Erhlich and Camin, 1960). (3) No watersnakes were found on four small islands (Green, West Sister, North Harbour, Middle Sister) during repeated visits between 1980 and 1997 despite their documented presence in the 1930's and 1940's, suggesting that they had been extirpated from these islands (King et al., 1997).

Legal protection of the Lake Erie watersnake was first extended to Canadian populations in 1977 under the Ontario provincial Endangered Species Act. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) listed it as endangered in 1991 (http://www.cosewic.gc.ca/index.htm). In the U.S., the USFWS designated the Lake Erie watersnake as a category 2 candidate species in 1985, a category 1 species in 1991, and proposed it for listing as threatened in 1993. Listing was delayed when, in 1995, Congress enacted a moratorium on all final listing actions under the U.S. Endangered Species Act. In 1999, a USFWS final rule designated the Lake Erie watersnake as threatened (Fazio and Szymanski, 1999). The Ohio Department of Natural Resources Division of Wildlife listed the Lake Erie watersnake as state endangered in 2000. Restricted geographic distribution and declining population size, attributed to human persecution and habitat loss, were identified as primary factors in extending legal protection to the Lake Erie watersnake (Fazio and Szymanski, 1999; McKeating and Bowman, 1977; U.S. Fish and Wildlife Service, 2003).

A recovery plan with the goal of removing the Lake Erie watersnake from the Federal list of Endangered and Threatened Wildlife was approved by the USFWS in 2003 (U.S. Fish and Wildlife Service, 2003). Three criteria for delisting were identified. The first, *Population Persistence*, sets overall and island-specific population size requirements for the U.S. islands. The second, *Habitat Protection and Management*, sets overall and island-specific habitat protection requirements. The third, *Reduction of Human-induced Mortality*, seeks to reduce intentional and accidental human-induced mortality to the point where such mortality no longer represents a significant threat. Recovery tasks designed to achieve these criteria include population monitoring, land acquisition, habitat management, and public outreach (U.S. Fish and Wildlife Service, 2003).

It is the population persistence criterion that is of particular relevance to this paper. This criterion specifies that "[e]stimated population size reaches or exceeds 5,555 adult Lake Erie watersnakes on the U.S. islands combined (Kelleys, South Bass, Middle Bass, North Bass, Rattlesnake, West Sister, Green, Ballast, and Gibraltar) for a period of six or more years" (U.S. Fish and Wildlife Service, 2003, Criterion 1a, p. 28). The rationale for this criterion comes from the International Union for Conservation of Nature and Natural Resources (IUCN) Red List Categories and Criteria: Version 3.1 (IUCN, 2001). One IUCN criterion for the Endangered classification (this classification corresponds to the USFWS designation of Threatened, U.S. Fish and Wildlife Service, 2003) is that *effective population size* is less than 2500 adults (IUCN Criterion EN C, IUCN, 2001). Effective population size, N_e, refers to the size of an ideal population (one with 1:1 sex ratio, random mating, equal contribution of all adults to subsequent generations, constant size over time) that has the same genetic characteristics as the real population of interest (Crandall et al., 1999; Frankham, 1995; Nunney, 2000; Nunney and Elam, 1994). In Lake Erie watersnakes, the ratio of effective population size to census population size, N_e/N, has been estimated to be approximately 0.45 (U.S. Fish and Wildlife Service, 2003). This estimate is based on information on adult sex ratio, frequency of reproduction, annual survivorship, variation in offspring production, and temporal variation in population size for both Lake Erie watersnakes and northern watersnakes (Brown and Weatherhead 1999; King, 1986; Prosser, 1999; Prosser et al., 2002) as detailed in the Lake Erie Watersnake Recovery Plan (U.S. Fish and Wildlife Service 2003). In Lake Erie watersnakes, an effective population size of 2500 thus corresponds to a census population size of 5555 (U.S. Fish and Wildlife Service 2003).

The population persistence criterion further specifies that "[s]ubpopulations on each of the 5 small islands capable of supporting Lake Erie watersnakes year-round (Rattlesnake, Sugar, Green, Ballast, and Gibraltar) persist during the same six or more year period as Criterion 1a, and the estimated population size reaches or exceeds the population size stated below for the four largest islands simultaneously during the same six or more year period as Criterion 1a" (U.S. Fish and Wildlife Service, 2003, Criterion 1b,
p. 29). Island-specific population criteria are: 1
1. Kelleys Island—900 adults, 2. South Bass Island—850 adults, 3. Middle Bass Island—620 adults, and 4. North Bass Island—410 adults. These criteria are intended to ensure that multiple Lake Erie watersnake subpopulations persist as a hedge against population decline or extinction due to catastrophic or stochastic events. These size criteria were selected such that 50% (2780) of the total adult population size required for delisting is distributed among the four largest U.S. islands in proportion to the amount of shoreline habitat that they provide. The remaining 2775 adults might be found on any of these islands or the smaller U.S. islands in Lake Erie (U.S. Fish and Wildlife Service, 2003).

The requirement that total and island-specific population criteria are met for six or more years is intended to ensure that there is sufficient time for recruitment of new adults within the recovery period (U.S. Fish and Wildlife Service, 2003). Because Lake Erie watersnakes can reach sexual maturity in 2–3 years (King, 1986), six years should provide enough time for at least two generations of snakes to mature.

Methods

General

Fieldwork on Lake Erie watersnakes occurred in four blocks of consecutive years with differing primary research objectives. During 1980–1985, efforts focused on analyzing the role of natural selection on color pattern variation on U.S. and Canadian islands (King, 1987, 1992). During 1988–1992, efforts focused on collection of tissue samples and estimation of rates of gene flow among U.S. and Canadian island and mainland populations (King and Lawson, 1995). Population ecological data were collected during these periods and were used to generate population estimates (King, 1986), but this was not a primary objective. During 1996–1998, efforts focused on determining Lake Erie watersnake distribution and abundance on the U.S. islands (King, 1998*a*, 1998*b*). From 2000–2004, efforts focused on population estimation and on documenting watersnake movements and hibernation site usage (King, 2000, 2001*a*, 2001*b*, 2001*c*, 2002*a*, 2002*b*, 2002*c*, 2003*a*, 2003*b*, 2004).

During the initial years of this project, much of the perimeter of the larger islands (Pelee, Kelleys, South Bass, Middle Bass, North Bass) and the entire perimeter of a number of smaller islands (Middle, Gibraltar, Green, East Sister, West Sister) was surveyed for the presence of water snakes. Initial surveys involved walking searches of continuous stretches of shoreline or, where shoreline access was limited, point-based visual searches separated by unsearched areas. Based on these initial surveys, study sites were established at locations that appeared to have high water snake densities and were relatively undisturbed by humans. Additional small islands (Rattlesnake, Sugar, Ballast, Middle Sister, Hen) were surveyed in later years as were shoreline areas outside study sites established in the early 1980s. This led to the discovery of high-density water snake populations overlooked or unappreciated in earlier years and resulted in establishment of additional study sites. Sites on Canadian islands were not visited after 1991 except for a single visit in 2003. In addition to Lake Erie watersnake study sites on islands in western Lake Erie, one site on Johnson Island in Sandusky Bay and one site on the Ohio mainland were studied. The Johnson Island site is inhabited by watersnakes similar in color pattern to Lake Erie watersnakes but this island is not included among populations protected under the U.S. Endangered Species Act (Fazio and Szymanski, 1999). The Ohio mainland study site is inhabited by northern watersnakes (*Nerodia sipedon sipedon*). Johnson Island and mainland sites were included to increase sample size in comparisons among population estimation methods. Study sites and other shoreline segments on the U.S. islands referred to in this study are illustrated in Fig. 2.

Watersnakes were captured by hand during area constrained searches of suitable shoreline habitat within defined study sites. Searches were typically conducted by a single field worker during 1980–1991 (RBK) and by one to four workers in 1992–2000 (led by RBK or AQ-R). In 2001, a program of intensive annual spring censuses was initiated. These censuses spanned two-week periods (late May to mid-June) and involved up to three teams of two to four workers (led by RBK and KMS). Fieldwork outside of annual census periods during 2001–2004 typically involved two workers (led by KMS or J. Ray). Upon capture, snakes were classified by sex, measured to obtain snout-vent length (SVL), and weighed. Watersnakes were individually marked by scale clipping (1980–1992) or passive integrated transponders (PIT tags, 1996–present) and released at their site of capture. Watersnakes were classified as adults using size criteria from King (1986; male SVL $\geq$ 430 mm, female SVL $\geq$ 590 mm).

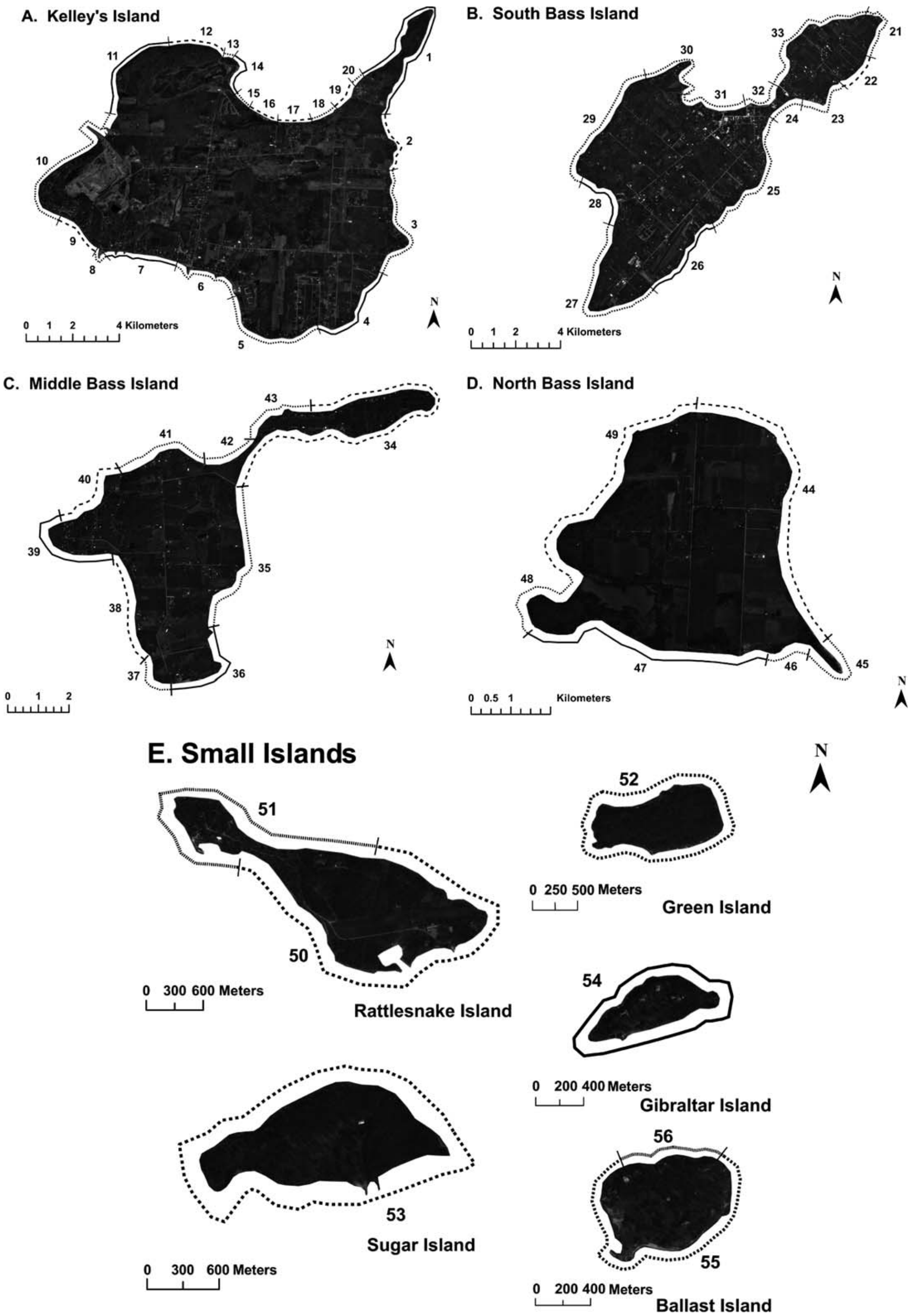
Population Estimation Using Mark-Recapture Techniques

Mark-recapture techniques were used to estimate adult population size as follows.

Within-year estimates were generated for sites censused two or more times within a year. At sites censused twice within a year, the Lincoln–Petersen method was used (as modified by Bailey in Caughley, 1977, p. 142); at sites censused three or more times within a year, Schumacher's method was used (Caughley, 1977, p. 145). These methods assume that recruitment of new individuals between census periods is negligible (i.e., they are designed for 'closed populations'). This assumption seems reasonable for watersnakes when censuses are separated by a few months or less; watersnakes require 2–3 years to reach sexual maturity, reproduce just once per year, and may live for 10 or more years (King, 1986, unpublished). *Between-year* estimates were generated for sites censused in three or more years using the Jolly–Seber method (as modified by Manley in Krebs, 1998, p. 42) and Bailey's triple-catch method (Caughley, 1977, p. 146). These methods are appropriate when recruitment occurs between census periods (i.e., for 'open populations'), as is likely when censuses span multiple years. This combination of secondary (within year) and primary (between year) sampling periods constitutes the "robust design" of Pollock (Krebs, 1998; Pollock et al., 1993). The robust design offers practical advantages with respect to investigator effort and provides multiple estimators of population size without assuming equal catchability (these and other advantages are described in Pollock et al., 1993). Between-year estimates were also generated using the Lincoln–Petersen method despite the likely occurrence of recruitment between years. This was done for two reasons: (1) For some sites and time periods, this was the only method by which population estimates could be generated. (2) When recruitment occurs between censuses, the Lincoln–Petersen method is expected to be biased upward by an amount proportional to recruitment rate (as discussed below). Thus, comparison of between-year Lincoln–Petersen estimates with those generated by other methods allows estimation of this bias.

Sample sizes necessary to generate accurate and unbiased estimates of population size using mark-recapture techniques are often large. For example, when using the Lincoln–Petersen method, obtaining estimates with only 50% accuracy requires capture of a large proportion of the total population, especially when population size is small (e.g., about 2/3 of the population when $n = 100$ and about 1/3 when $n = 1000$; fig. 2.3 and 2.4 in Krebs, 2
1998). Furthermore, this method produces biased estimates, tending to overestimate true population size, when sample size is small or the number of recaptures is less than seven (Krebs, 1998). Sample size requirements for other methods of population estimation have been less well characterized but "Jolly–Seber estimates are very imprecise unless the number of marked animals in each sample is more than 10" (Greenwood, 1996, p. 33). Because one of the objectives here was to provide an empirical comparison of the performance of alternative estimation techniques when sample size and recapture rates are sometimes low, the following sample size criteria were used in generating population estimates. (1) The Lincoln–Petersen method was used only when 10 or more adults were captured in both censuses and there was at least one recapture in the second census. (2) Schumacher's method was used only when a total of 30 or more adults were captured and recaptures were present in two or more censuses. Captures separated by up to 29 days were sometimes pooled together and treated as a single census when using Schumacher's method. (3) Jolly–Seber and Bailey's triple-catch methods were used only when 10 or more adults were captured in the census year prior to, of, and following the year for which population size was estimated. For some Jolly–Seber and Bailey's triple-catch estimates, there was a gap of one year between censuses (e.g., estimates were based on censuses in 1997, 1998, and 2000).

Population estimates were limited to adults because recaptures of marked snakes consisted almost entirely of this age class and because it is adult population size that is of greatest concern for conservation and management. Twenty-two watersnakes initially marked as juveniles were recaptured as adults. These snakes were treated as new captures when first captured as adults for the purposes of population estimation. Out of more than 1000 recaptures of adult water-


A. Kelley's Island
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E. Small Islands
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0 300 600 Meters
Rattlesnake Island
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0 250 500 Meters
Green Island
54
0 200 400 Meters
Gibraltar Island
53
0 300 600 Meters
Sugar Island
56
55
0 200 400 Meters
Ballast Island

snakes, eleven were of snakes marked at one study site and recaptured at another. These snakes were treated as having been recaptured when calculating population estimates for sites at which these snakes were initially marked; they were treated as new captures when calculating population estimates for sites at which they were recaptured. Nine watersnakes were recaptured whose individual identity could not be resolved either because not all scale clips could be discerned or because of apparent errors in recording PIT tag codes. These snakes were treated as new captures for purposes of population estimation.

When population estimates could be generated by multiple methods or for more than one year at a given site, they were averaged to obtain a single estimate for a given block of years (1980–1985, 1989–1992, 1996–1998, 2000–2004). Blocks of years were treated separately because of changes in the extent of shoreline sampled and because of possible changes in adult population size over time. Between-year Lincoln–Petersen estimates were not included in these averages unless this was the only method of estimation possible for a given site and block of years. To compare population estimates generated by different methods, means were computed for each site and block of consecutive years separately for each estimation method. These means were compared among methods using paired *t*-tests.

Unless populations are naturally bounded, the population being estimated using mark-recapture data occupies a larger area than that used for data collection. This is because some individuals have home ranges that extend outside of the study area. If home range size is known, the actual area to which population estimates apply can be determined and used to estimate population density. For Lake Erie watersnakes, information on home range size comes from a multi-year radiotelemetry study involving 61 adult animals (R.B. King, K.M. Stanford, and D. Wynn; unpublished). During the active season, home range of these animals was linear, consisting of a narrow band of shoreline that averaged 256 m in length (range = 70–1360 m). Therefore, the extent of shoreline to which mark-recapture population estimates apply was determined by adding one-half home range (128 m) to each end of shoreline segments included within study sites (256 m total) for all study sites except Gibraltar and Middle Island, which were sampled in their entirety. Population density was estimated by dividing mark-recapture population estimates by this adjusted length.

Recruitment Bias and Annual Adult Survivorship

When recruitment occurs between census periods, population estimates generated using the Lincoln-Petersen method are biased upwards (Caughley, 1977). This is because recruitment (and immigration) adds new individuals to the population that were not present during the first census and thus the proportion of marked individuals in the second sample is reduced. In contrast, mortality between census periods does not result in biased estimates provided mortality rates are the same for marked and unmarked individuals (Caughley, 1977). When both recruitment-biased and unbiased estimates of population size are available, recruitment (and by extension, survivorship) can be estimated as follows. Let M be the number of individuals marked and released during the first census, let n be the number examined for marks in the second census, and let m be the

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Fig. 2. Aerial views of the U.S. islands in Lake Erie included in this study: (A) Kelleys Island, (B) South Bass Island, (C) Middle Bass Island, (D) North Bass Island, (E) small islands. Numbers denote sites refereed to in this paper (see text and Tables 1, 2, and 4). Scale varies among islands. Solid lines identify sites for which recent (2000–2004) population estimates based on mark-recapture techniques are available (Table 1). Dashed lines identify sites for which recent population estimates based on capture rate are available (Table 3). Dotted lines identify sites for which population size was interpolated (Table 4).

number of marked individuals recaptured in the second census. If recruitment occurs between censuses, then the standard Lincoln–Petersen method provides a recruitment-biased estimate of population size:

$$N_{biased} = [M(n + 1)]/(m + 1). \quad (1)$$

Furthermore, the n individuals examined for marks at the second census should consist of the proportion $(1 - r)$ that was present during the first census and the proportion r that consists of new recruits. If r were known, an unbiased estimate of population size could be calculated as:

$$N_{unbiased} = [M(n(r - 1) + 1)]/(m + 1). \quad (2)$$

If population size remains constant such that survivorship, $s = 1 - r$, an alternative formulation is provided by:

$$N_{unbiased} = [M(ns + 1)]/(m + 1). \quad (3)$$

The ratio of unbiased to biased population estimates is then:

$$N_{unbiased}/N_{biased} = [M(ns + 1)]/[M(n + 1)] \quad (4)$$

and

$$s = [(N_{unbiased}/N_{biased})(n + 1) - 1]/n. \quad (5)$$

That is, survivorship (and recruitment) can be estimated from knowledge of unbiased and recruitment-biased estimates of population size and the number of individuals examined for marks during the second census. Here, between-year Lincoln–Petersen estimates represent recruitment-biased estimates whereas unbiased estimates are provided by other methods (including within-year Lincoln–Petersen estimates). Multiple estimates of $N_{unbiased}$, N_{biased}, and n for a given site and period of successive years were averaged to facilitate calculation of s.

Population Estimation Based on Capture Rate

To estimate population size at sites for which mark-recapture estimates could not be generated, the relationship between population size and capture rate was analyzed for those sites for which mark-recapture estimates could be generated. This relationship was then used to estimate population size for sites for which only capture rate data were available. Raw data consisted of the number of adult Lake Erie watersnakes captured per area constrained search during intensive spring censuses conducted 2001–2004. From these data, the mean and maximum number of captures was calculated for each site. These were converted into rates (adults captured per km) by dividing by the extent of shoreline included within each study site. Correlation and linear regression were used to characterize the relationship between population density and capture rate at 11 sites for which both kinds of information were available. This relationship was used to generate density estimates for sites for which mark-recapture estimates were lacking. Capture rate data for the majority of these latter sites came from intensive spring censuses conducted 2001–2004 but also included some censuses that occurred later in the summer.

Results

Population Estimation Using Mark-Recapture Techniques

Mark-recapture techniques were used to generate population estimates for 19 study sites on eight islands in western Lake Erie, one site on Johnson in Sandusky Bay, and one site on the Ohio mainland (Table 1) based on 5441 captures of 4168 adult watersnakes between 1980 and 2004. Most recaptures occurred within one or two years of marking but as many as eight years sometimes elapsed between first and final capture. Individual study sites consisted of 250–2750 m of shoreline habitat. Excluding the Johnson Island and Ohio mainland sites, a total of 25 km of shoreline habitat was included, about 18 km on U.S. islands and 7 km on Canadian islands (these totals include 128 m added to either end of study sites other than Gibraltar and Middle Island, which were sampled in their entirety). When only estimates from 2000–2004 were considered, a total of 15,830 m of shoreline at 11 sites on five U.S. islands were included.

A total of 171 point estimates of population size were generated (Table 1, summary tables showing each estimate are available by request from RBK). Of these, 60 were Lincoln–

Petersen between-year estimates and hence were expected to overestimate true population size due to recruitment. When population estimates were averaged across methods and within blocks of consecutive years, 31 mean estimates were obtained (Table 1). Lincoln–Petersen between-year estimates were excluded from these calculations except for seven combinations of sites and blocks of years (11 estimates total) for which they were the only estimates available.

Mean population estimates ranged from 39 to 1036 adults per study site and density estimates ranged from 18 to 1107 adults/km (Table 1). Estimates generated using Lincoln–Petersen (L–P), Schumacher (S), Jolly–Seber (J–S), and Bailey's triple-catch (B) methods did not differ significantly from each other, even without adjusting P values for multiple comparisons (P = 0.061–0.506, Table 2). Similarly, within-year estimates (generated using Lincoln–Petersen and Schumacher's methods) did not differ from between-year estimates (generated using Jolly–Seber and Bailey's methods) (P = 0.368, Table 2). Although it is possible that differences among methods went undetected, power to detect a medium effect size (Cohen, 1988) was moderate to high (Table 2). Furthermore, the lack of consistent directional differences (L–P > S in 3 of 10 comparisons, L–P > J–S in 6 of 13 comparisons, L–P > B in 5 of 13 comparisons, S > J–S in 6 of 11 comparisons, S > B in 4 of 10 comparisons, J–S > B in 8 of 16 comparisons, within-year estimates exceeded between-year estimates in 9 of 16 comparisons) suggests that alternative methods performed equally well.

Recruitment Bias and Annual Adult Survivorship

In contrast to comparisons among methods described above, Lincoln–Petersen between-year estimates (recruitment-biased estimates) exceeded estimates generated using other methods (unbiased estimates) in 21 of 23 comparisons (mean = 350 vs. 235 adults, $P <$ 0.001, Table 2). Using equation 5, the estimated mean annual adult survivorship, s, was 0.63 (range = 0.32–1.06). Using this value, unbiased between-year Lincoln–Petersen estimates were generated by equation 3. These unbiased Lincoln–Petersen estimates were similar to estimates generated by other methods (mean = 224 vs. 235 adults, P = 0.364, Table 2).

Population Estimation based on Capture Rate

Estimated population density, mean capture rate, and maximum capture rate were available for 11 sites in 2000–2004. Population density estimates were based on two to nine mark-recapture estimates and mean and maximum capture rates were based on three to eight censuses at each site. Natural log transformations of all three variables were computed to linearize their relationship and to normalize error variance.

Both mean and maximum capture rates were significantly correlated with population density (mean capture rate: r = 0.851, P = 0.001; maximum capture rate; r = 0.807, P = 0.003). Because it was more strongly correlated with population density, mean capture rate was used as the dependent variable in regression analysis relating capture rate and population density with the result that:

$$Ln(\textit{Mean Capture Rate}) = -0.87 + 0.81(\ln(\textit{Population Density})) \quad (6)$$

Backtransforming,

$$\textit{Mean Capture Rate} = 0.42 * \textit{Population Density}^{0.81} \quad (7)$$

and

$$\textit{Population Density} = 2.93 * \textit{Mean Capture Rate}^{1.23} \quad (8)$$

Graphical analysis suggested that one site represented an outlier with respect to this relationship (Fig. 3). Specifically, the density estimate at the Kelleys Island South Shore site (site 7 in Fig. 3) was more than two times higher than the next highest density estimate yet mean capture rate at this site was similar to that of sites with much lower density estimates. Regression diagnostics (Christensen, 1996) also suggested that this site was an outlier in that it exceeded all other sites in

TABLE 1.—Estimates of adult Lake Erie watersnake population size based on mark-recapture methods. 'Length' refers to the length of shoreline habitat included within a given study site. 'Effective Length' refers to the length of shoreline to which a given population estimate applies and was obtained by adding 256 m to Length for all sites except islands sampled in their entirety. Within-year estimates are based on 2 or more censuses in the same year. Between-year estimates are based on censuses in two or more years. Method of estimation is abbreviated as follows: L–P = Lincoln–Petersen, S = Schumacher's, J–S = Jolly–Seber, B = Bailey's triple catch. 'Mean' refers to the mean of estimates generated by all methods within a block of successive years. Between-year estimates generated using the Lincoln–Petersen method were not included in calculating these means unless no other estimates were available (between-year Lincoln–Petersen estimates excluded from such calculations are shaded in gray). Unbiased between-year Lincoln–Petersen estimates (see text) are shown in parentheses. Density estimates were generated by dividing the mean estimate by effective length. Note that the extent of shore sampled at a given site sometimes varied among years. Locations of sites on U.S. islands are indicated by site number on Fig. 2.

					Within-year estimates		Between-year estimates				
Site #	Island	Site name	Length (effective length) (m)	Year	L–P	S	J–S	B	L–P	Mean	Density (adults per km)
1	Kelleys	Long Point	1480 (1736)	1980	75				104 (67)		
				1981			75	39	156 (103)		
				1982			80	60	83 (54)	66	38
			2750 (3006)	2001			208	112	248 (160)		
				2002					248 (159)	160	53
4	Kelleys	Southeast Shore	1000 (1256)	2001		389			617 (391)		
				2002			408	383	591 (375)		
				2003		461	449	686	663 (420)		
				2004	281					439	350
5	Kelleys	Marina Entrance	0[1] (256)	1997					106 (68)	106	414
7	Kelleys	South Shore	200 (456)	1996					90 (60)	90	197
			680 (936)	2001		652			997 (633)		
				2002	598		1013	967	1241 (788)		
				2003			1680	1379	2837 (1806)	1036	1107
11	Kelleys	Minshall	1450 (1706)	1996					124 (80)		
				1997	88		98		127 (84)		
				1998			62	44		73	43
			1250 (1506)	2000			68		185 (119)		
				2001		123				96	64
14	Kelleys	State Park	300 (556)	2000			96	45	94 (60)		
				2001		124	39		173 (111)		
				2002	132		113	63	186 (118)		
				2003	122	133	169	252	201 (128)		
				2004	320	261				144	259
26	South Bass	East Shore	1030 (1286)	2002	550		204		581 (369)		
				2003	733	780		504	508 (323)	554	431
28	South Bass	State Park	650 (906)	1996					75 (48)		
				1997			60	86	264 (169)		
				1998			260			135	149
			650 (906)	2001			427	450	394 (251)		
				2002	300		264	356	630 (399)		
				2003	105	346	404	539	455 (289)		
				2004	279	405				352	389
34	Middle Bass	East Point (part)	750 (1006)	1983			53		105 (69)	53	53
			750 (1006)	1996					138 (89)		
				1997	72					72	72
36	Middle Bass	State Park	1045 (1301)	1982					203 (131)		
				1983					238 (156)	221	170
			1630 (1886)	2002					309 (197)		
				2003	163	323	473	418	623 (397)		
				2004	266	401				341	181
39	Middle Bass	West End	320 (576)	1996	34				132 (86)		
				1997			42	36	105 (69)		
				1998			42			39	68
			320 (576)	2001			37	168	288 (184)		
				2002	100		128		247 (160)	108	188

TABLE 1.—Continued.

Site #	Island	Site name	Length (effective length) (m)	Year	Within-year estimates L–P	Within-year estimates S	Between-year estimates J–S	Between-year estimates B	Between-year estimates L–P	Mean	Density (adults per km)
			1100 (1356)	2002		561			1034 (657)		
				2003	429		934	1009	914 (580)		
				2004	587					704	519
47	North Bass	South Shore	1775 (2031)	1980		134			324 (206)		
				1981		288	232	136	328 (210)		
				1982	199		130	175	470 (300)		
				1983	270		195	231	396 (253)		
				1984		138				193	95
			1775 (2031)	1989	122				209 (133)		
				1990		212				167	82
			1980 (2236)	2001					350 (224)		
				2002	108		226	240	289 (184)		
				2003			121	161	367 (234)		
				2004	275					189	85
53	Sugar	SI2, SI3A, SI3B	900 (1156)	1996					86 (56)	86	74
55	Gibraltar	Entire island	900 (900)	2003		73			248 (158)		
				2004	173					123	152
	Middle[2]	Entire island	2200 (2200)	1980					39 (25)	39	18
	Pelee[2]	Fish Point-west	900 (1156)	1989					76 (49)		
				1990					153 (100)	115	99
	Pelee[2]	Fish Point-south	750 (1006)	1980					164 (106)		
				1981		268		181	243 (156)		
				1982		341	138		252 (166)	232	231
	Pelee[2]	Lighthouse Point	1700 (1956)	1989					115 (74)	115	59
	Pelee[2]	Sheridan Point	500 (756)	1983	40					40	53
	Johnson[3]	Quarry 'fingers'	250 (506)	1981					78 (51)		
				1982				65	176 (115)	65	128
	Ohio mainland[4]	Willow Point	740 (996)	1989		58			131 (84)		
				1990		63	74	69	98 (64)		
				1991			91			71	71

[1] Snakes captured at this site were all captured from beneath a single sheet of plywood, hence Length = 0.
[2] Middle and Pelee Island are Canadian.
[3] Johnson Island is located in Sandusky Bay; watersnakes here are unprotected.
[4] Northern watersnakes, *Nerodia sipedon sipedon*, are found at the Ohio mainland site.

Cook's D, a measure of the change in residuals if a particular case were excluded ($D = 0.99$ for Kelleys Island South Shore vs. 0.00–0.80 for other sites), and leverage, a measure of the influence of a point on the fit of the regression (leverage = 0.28 for Kelleys Island South Shore vs. 0.00–0.23 for other sites). When the Kelleys Island South Shore site was omitted from analysis, the correlation between mean capture rate and population density increased to 0.903 ($P < 0.001$) and regression analysis yielded:

$$\text{Ln}(\textit{Mean Capture Rate}) = -1.87 + 1.02(\ln(\textit{Population Density})), \quad (9)$$

$$\textit{Mean Capture Rate} = 0.15 * \textit{PopulationDensity}^{1.02} \quad (10)$$

and

$$\textit{Population Density} = 6.32 * \textit{Mean Capture Rate}^{6.32}. \quad (11)$$

Equation 11 was used to estimate population density and population size (the product of population density and extent of shoreline) at 19 additional sites for which only capture rate data were available from 2000–2004 (Table 3). These included 12 sites on the four large U.S. islands, three sites on Pelee Island (a Canadian island) and all or the majority of

TABLE 2.—Paired t-tests comparing population estimates generated using different methods. Shown are methods being compared, mean ± the standard error of the mean (range) adult population size via each method, number of sites for which estimates by both methods are available (n), Pearson correlation coefficient between methods (r), paired t statistic (t), P value, and power to detect a medium effect size (Cohen 1988). Method of estimation is abbreviated as follows: L–P = Lincoln–Petersen, S = Schumacher's, J–S = Jolly–Seber, B = Bailey's triple catch. Means, standard errors, and ranges vary among comparisons for a given method because sites included in comparisons vary.

Comparison		Mean ± SE (range)						
Method 1	Method 2	Method 1	Method 2	n	r	t	P	Power
L–P	S	319 ± 60 (122, 642)	380 ± 72 (73, 780)	10	0.93	−2.14	0.061	>0.84
L–P	J–S	260 ± 55 (34, 642)	344 ± 106 (42, 1311)	13	0.72	−1.09	0.298	0.65
L–P	B	260 ± 55 (34, 642)	376 ± 101 (36, 1173)	13	0.85	−1.87	0.087	0.87
S	J–S	364 ± 69 (61, 780)	391 ± 120 (68, 1310)	11	0.64	−0.29	0.777	0.45
S	B	388 ± 71 (61, 780)	464 ± 118 (69, 1173)	10	0.78	−0.99	0.349	0.60
J–S	B	297 ± 83 (42, 1311)	314 ± 82 (36, 1173)	17	0.96	−0.68	0.506	>0.99
Within-year (L–P & S)	Between-year (J–S & B)	260 ± 51 (34, 688)	311 ± 87 (40,1242)	16	0.80	−0.93	0.368	0.79
Mean of unbiased estimates	Between-year L–P	235 ± 51 (39, 1036)	350 ± 75 (105, 1692)	23	0.97	−4.06	0.001	>0.99
Mean of unbiased estimates	Unbiased between-year L–P	235 ± 51 (39, 1036)	224 ± 47 (68, 1076)	23	0.97	0.93	0.364	>0.99

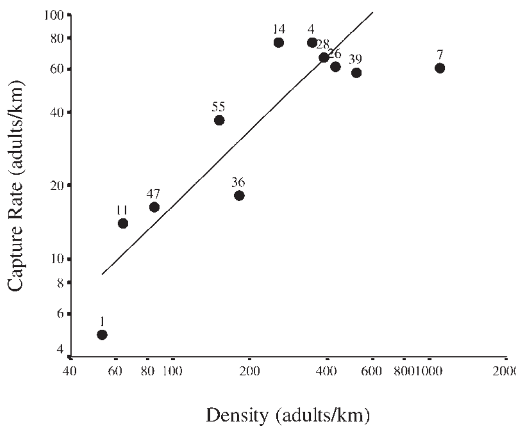

FIG. 3. Relationship between population density and capture rate based on data collected during intensive surveys in May and June 2000–2004. Line represents the simple linear regression of ln(capture rate) on ln(density) for all sites except site 7, Kelleys Island South Shore (see text). Sites are labeled as follows: 1—Kelleys Island Long Point, 4—Kelleys Island Southeast Shore, 7—Kelleys Island South Shore, 11—Kelleys Island Minshall, 14—Kelleys Island State Park, 26—South Bass Island East Shore, 28—South Bass Island State Park, 36—Middle Bass Island State Park, 39—Middle Bass Island West End, 47—North Bass Island South Shore, 55—Gibraltar Island (site numbers correspond to those in Fig. 2 and Table 1).

four small U.S. islands. Individual sites included 420–3980 m of shoreline (nearly 23 km in total; about 20 km on U.S. islands and 3 km on Pelee Island), density estimates ranged from 11–396 adults/km, and estimated population size ranged from 13–650 adults per site (2762 adults total; 2427 adults at sites on U.S. islands and 335 adults at sites on Pelee Island). Using the regression relationship between population density and capture rate for all 11 sites to estimate population size (equation 8) gave a total of 2921 at these 19 sites. Thus, equation 11 provides a more conservative estimate of watersnake population size with respect to meeting recovery goals.

DISCUSSION

Population Estimation Using Mark-Recapture Techniques

Alternative mark-recapture techniques (Lincoln–Petersen, Schumacher, Jolly–Seber, Bailey's triple-catch) gave similar population estimates for Lake Erie watersnakes as indicated by a lack of significant differences

TABLE 3.—Estimates of adult Lake Erie watersnake population size based capture rate. Capture rate data come from intensive spring censuses 2001–2004 except as noted. Locations of sites on U.S. islands are indicated by site number on Fig. 2.

Site number	Island	Site name	Extent of shore (m)	# of censuses	Mean # of captures (rate)	Density estimate (adults/km)	Population estimate
2	Kelleys	East Shore	950	1	6 (6)	39	37
9	Kelleys	Trailer Park and East	700	1	13 (19)	112	78
12	Kelleys	State Park North Shore	860	1	7 (8)	50	43
16	Kelleys	State Park Beach	450	1	7 (16)	94	42
17	Kelleys	East of State Park Beach	420	1	9 (21)	129	54
19	Kelleys	Camp Patmos	450	1	6 (14)	83	36
22	South Bass	East Point	500	1	21 (42)	250	125
34	Middle Bass	East Point	3300[1]	3	39–78 (28)	163	650
38	Middle Bass	West Shore	1100	1	2 (2)	11	13
40	Middle Bass	West End/Burgundy Bay	1060	1	34 (32)	192	203
44	North Bass	NE, E, SE Shore	2400	2	19 (8)	48	116
49	North Bass	NW, W Shore	1920	3	13 (7)	41	80
50	Rattlesnake	East	1500	1	51 (34)	203	304
52	Green	Entire island	1150	1[2]	9 (8)	48	55
53	Sugar	South	900	2[2]	55 (61)	358	322
56	Ballast	S, W, and E Shore	670	1	45 (67)	396	266
	Pelee	Fish Point South	750	1[2]	37 (49)	293	219
	Pelee	Lighthouse Point	1700	1[2]	10 (6)	36	61
	Pelee	Mill Point	800	1[2]	9 (11)	68	55

[1] Because extent of shoreline censused varied among years, density estimates were generated separately for each year, averaged, and applied to the total extent of shoreline censused to generate a population estimate.
[2] Includes capture rates from one or more censuses outside of intensive spring census periods of 2001–2004.

between pairs of methods (Table 1, 2). Furthermore, closed and open-population techniques (Lincoln–Petersen and Schumacher vs. Jolly–Seber and Bailey's triple-catch) gave similar results (Table 2), suggesting that the assumption of no recruitment between within-year samples was reasonably well met.

Despite consistency among estimation techniques, population estimates for a given site within a given time period often differed by a factor of two or more (Table 1) and standard errors of individual estimates (available from RBK) were frequently large. For example, standard errors of 26 within-year Lincoln–Petersen estimates averaged 38% of the estimate (range = 13–54%) and standard errors of 28 estimates generated using Bailey's triple-catch method averaged 67% of the estimate (range = 29–100%). Large standard errors are expected when number of recaptures and sample size are low. Here, number of recaptures exceeded seven in only four of 26 within-year Lincoln–Petersen estimates and total number of captures never exceeded the population estimate. Numbers of recaptures were ≥10 for the years prior to, of, and following the year of estimate in just three of 35 Jolly–Seber estimates. Thus, strict application of sample size recommendations of some (Greenwood, 1996; Krebs, 1998) would suggest that few if any meaningful population estimates could be generated for Lake Erie watersnakes.

Use of multiple methods to estimate population size and then averaging these estimates across consecutive years appears to have generated more precise estimates of population size. At 15 combinations of sites and time periods for which 4 or more mark-recapture estimates were available, the standard error as a percent of the mean estimate averaged 14% (range = 5–25%). However, accuracy of these estimates is uncertain. Simulation results suggest that small sample size and low recapture rate can result in upwardly biased estimates (Krebs, 1998). In contrast, population estimators used here consistently underestimated true population size in painted turtles (Koper and Brooks, 1997). Some insight into the accuracy of the estimates presented here can be gained by comparing them to numbers of individual adult watersnakes known to be alive. Summing across the 11 sites for which recent mark-recapture estimates are available, the number of individual adult watersnakes captured each year was 50 (2000), 472 (2001), 794 (2002), 901 (2003), and 966 (2004). Assuming annual survivorship of 0.63 (see Results), the minimum number of adult watersnakes alive at these 11 sites in 2004 is estimated to be 1975. In comparison, mark-recaptures estimates for these 11 sites are 2.1 times larger, totaling 4107 (Table 4). Given that minimum number alive is almost certainly an underestimate, it seems unlikely that mark-recapture techniques greatly overestimate the true population size of adult Lake Erie watersnakes at these 11 sites.

Recruitment Bias and Annual Adult Survivorship

Between-year Lincoln–Petersen estimates were significantly larger than estimates generated by other methods (Table 2) as expected due to recruitment between years. Assuming constant population size (recruitment = mortality), this difference suggests annual adult survivorship of Lake Erie watersnakes is about 0.63. This value is similar to that estimated from mark-recapture data for northern watersnakes in southern Ontario by Brown and Weatherhead (1999), who found that survivorship was 0.61 in two year old snakes, 0.63 in three year olds, and 0.48 in older adults. Estimates of annual adult watersnake survivorship fall between those typical of early-maturing colubrids (seven species, mean = 0.49, range = 0.35–0.63) and late maturing colubrids (six populations of five species, mean = 0.71, range = 0.62–0.80;
3 table 9–5 in Parker and Plummer 1986) (see Bronikowski and Arnold 1999, Stanford and King 2004 for additional survivorship estimates). Direct estimation of Lake Erie watersnake survivorship, based on mark-recapture data presented here, is in progress.

Population Estimation based on Capture Rate

Capture rate and population density were highly correlated at sites where both types of data were available (Fig. 3), making it possible to estimate population size at sites where only capture rate was known (Table 3). These estimates assume that variation in capture rate is due primarily to differences in population density. However, other factors may

Table 4.—Island-by-island summary of current (2000–2004) adult Lake Erie watersnake population size. Details for mark-recapture and capture rate estimates are shown in Table 1 and 3, respectively. Extrapolated population sizes for uncensused sites (Table 4) and totals that include 5
these extrapolations are shown in parentheses.

Island	Method	Length (km)	Population
Kelleys	mark-recapture	7.3	1875
	capture rate	3.8	290
	uncensused	7.2	(269)
	total	18.3	2165 (2434)
South Bass	mark-recapture	2.2	906
	capture rate	0.5	125
	uncensused	13.8	(538)
	total	16.5	1031 (1569)
Middle Bass	mark-recapture	3.2	1045
	capture rate	6.1	866
	uncensused	4.3	(179)
	total	13.6	1911 (2090)
North Bass	mark-recapture	2.2	189
	capture rate	4.3	196
	uncensused	1.9	(58)
	total	8.4	385 (443)
Rattlesnake	capture rate	1.5	304
	uncensused	1.0	(48)
	total	2.5	304 (352)
Sugar	capture rate	1.5	325
Green	capture rate	1.2	55
Ballast	capture rate	0.7	266
	uncensused	0.3	(12)
	total	0.9	266 (278)
Gibraltar	mark-recapture	0.9	123
9 U.S. Islands	mark-recapture	15.8	4138
	capture rate	19.6	2427
	uncensused	28.3	(1104)
	total	63.7	6565 (7669)

contribute to variation in capture rate. In particular, variation in habitat characteristics may result in differences in watersnake catchability among sites. Examination of the 11 sites for which both capture rate and density estimates are available suggests that this is true. As noted earlier, the Kelleys Island South Shore site (site 7 in Fig. 3) differed from other sites in having an unusually high population density but a mean capture rate comparable to sites with much lower population density. This site includes a number of rock filled metal or wood crib docks. Such docks provide abundant basking and retreat sites but also make it relatively easy for watersnakes to evade capture by diving into the lake or crawling into rock crevices, perhaps resulting in reduced capture rate. It is also possible that this site includes a larger proportion of transient individuals than do other sites; recapture rates here were relatively low despite moderate to large sample sizes. The Middle Bass State Park site (site 36 in Fig. 3) includes a section of rock rip-rap where watersnakes were frequently seen but where escape into the water or rock crevices was also common. In contrast, a cluster of discarded pipes at the Kelleys Island Southeast Shore site (site 4 in Fig. 3) provided a favored retreat site for large numbers of watersnakes and dozens of adults could be easily captured. Variation in catchability and low numbers of censuses (frequently just one) doubtless influence estimates of population size at sites for which only capture rate data are available. Despite the errors inherent in these estimates, they are of value in providing a more complete picture of current Lake Erie watersnake population size.

It is worth noting that capture rate estimates include Green Island, an island where Lake Erie watersnakes were present in the 1930's and 40's but from which they were extirpated prior to 1980 (none were observed during repeated searches from 1980–1997) (King et al., 1997). The renewed presence of Lake Erie watersnakes on Green Island was confirmed during fieldwork conducted by C. Caldwell and S. Butterworth (ODNR–DOW) on 25 June 2002 when about 20 individuals were observed (C. Caldwell, personal communication) and by KMS, M. Andre (Northern Illinois University), A. Zimmerman, M. Seymour (USFWS), and J. Spaeth (Ohio State University) on 23 July 2002 when nine adults were captured and marked with PIT tags (King, 2002*c*). Green Island lies about 1.6 km west of South Bass Island (Fig. 1) and about 1.9 km from South Bass State Park, a site where Lake Erie watersnakes occur in high density (site 28 on Fig. 2). As noted earlier, watersnakes were also extirpated from West Sister Island prior to 1980 (King et al., 1997). Fieldwork conducted on this island by KMS, M. Andre (NIU), M. Thomas, and T. Thorne (Ohio State University F. T. Stone Laboratory) on 26 July 2002 resulted in the capture of a single adult female (King, 2002*c*). The color pattern of this snake was dark and distinctly banded as is typical of mainland populations of northern watersnakes (*Nerodia sipedon sipedon*). Furthermore, West Sister Island is closer to the Ohio mainland (13.4 km) than it is to the nearest island occupied by Lake Erie watersnakes (Rattlesnake Island, 21 km) (Fig. 1). Hence, it is possible that this snake represents an immigrant from a mainland northern watersnake population rather than a Lake Erie watersnake (King, 2002*c*). Further fieldwork is planned for both of these islands to clarify the status of watersnakes found there.

Lake Erie Watersnake Population Density

The density of Lake Erie watersnakes exceeds that of many other snake species. In a review of 57 density estimates for 40 species tabulated by Parker and Plummer (1987, table
9–1), 21 were less than or equal to 1/ha and 4
the median density was just 5/ha (range = ≤1–1289/ha). Densities of New World natricines (which include watersnakes) were higher with a median of 22/ha (range = 1–1289/ha in 14 populations of 9 species). Although watersnake densities are reported here in adults/km, radiotelemetry indicates that Lake Erie watersnakes are rarely found more than 10 m from shore outside of hibernation (R.B. King, K.M. Stanford, and D. Wynn, unpublished). Thus, density estimates reported here in adults/km are roughly comparable to those reported in adults/ha. Median Lake Erie watersnake density at 30 sites for which recent (2000–2004) estimates are available is 141 adults/km (range = 11–1107 adults/km) (Table 1, 3). This exceeds the median for snakes generally and for natricines in particular (table 9–1 in Parker and Plummer, 1987). Even species known for high population density fall below the Lake Erie watersnake; tiger snakes on Carnac Island, Western Australia have a density of 22 adults/ha (Bonnet et al. 2002) and brown tree snakes on Guam achieve a maximum density of about 50/ha (G. Rodda in Beltz, 2005). Lake Erie watersnake densities also exceed those of conspecifics elsewhere. Population densities of northern watersnakes at two ponds in Ontario were 25 adults/ha and 28 adults/ha (Brown and Weatherhead, 1999). Along 6.4 km of a Kansas stream, Beatson (1976) collected 197 watersnakes and estimated this to be 75–90% of the total population, giving a density of 34–41 juveniles and adults per

TABLE 5.—Characteristics of uncensused segments of shoreline on U.S. islands and extrapolated adult Lake Erie watersnake population size. Population estimates for sites where habitat characteristics are unsuitable for watersnakes (sites #42 and 45) or where land use practices makes protection unfeasible (sites #6, 8, 15, 24, 31, 32) were set to 0. For other sites, population estimates were based on a density of 48 adults/km. Locations of sites are indicated by site number on Fig. 2.

Site #	Island	Length (m)	Years of watersnake sightings/captures (other information on watersnake status)	Population estimate
3	Kelleys	1570	2001	75
5	Kelleys	1515	1997–1998	73
6	Kelleys	1110	2000–2004 (downtown Kelleys Island)	0
8	Kelleys	225	2001 (commercial ferry dock)	0
10	Kelleys	1940	2000–2004	93
13	Kelleys	60	(present at adjacent sites)	3
15	Kelleys	220	(State Park swimming beach)	0
18	Kelleys	400	(present at adjacent sites)	19
20	Kelleys	120	(present at adjacent sites)	6
21	South Bass	750	2002	36
23	South Bass	905	(present at adjacent site)	43
24	South Bass	485	(Perry's Victory & International Peace Memorial)	0
25	South Bass	2040	1996, 1997, 2000–2004	98
27	South Bass	2270	1996–1997, 2004	109
29	South Bass	1900	(present at adjacent sites)	91
30	South Bass	1400	2000–2004	67
31	South Bass	1550	(downtown Put-in-Bay)	0
32	South Bass	520	(Perry's Victory & International Peace Memorial)	0
33	South Bass	1950	1996–1997	94
35	Middle Bass	1640	2003	79
37	Middle Bass	320	1996–1997	15
41	Middle Bass	1015	1997	49
42	Middle Bass	525	(sand shoreline)	0
43	Middle Bass	750	1998	36
45	North Bass	650	(sand shoreline)	0
46	North Bass	330	1996–1998, 2002	16
48	North Bass	885	1980–1984	42
51	Rattlesnake	1000	(present at adjacent site)	48
56	Ballast	250	(present at adjacent site)	12

km. Reasons for the high local densities of Lake Erie watersnakes are unclear but may include the ameliorating effects of Lake Erie on local climate (Albrecht, 1988; Bolsenga and Herdendorf, 1993), the ready availability of suitable hibernation sites perhaps facilitated by deep fissures in the bedrock that underlies the islands, and an abundance of prey in the nearshore waters of Lake Erie.

Current Lake Erie Watersnake Population Size and Recovery Objectives

Population estimates presented here can be used to evaluate the degree to which the Population Persistence criterion of the Lake Erie Watersnake Recovery Plan (U.S. Fish and Wildlife Service, 2003) has been met. On the U.S. islands, recent (2000–2004) population estimates encompass 35.3 km of shore (15.7 km for which mark-recapture estimates and 19.6 km for which capture-rate estimates are available). Population estimates of either type are lacking for another 28.3 km. To extrapolate possible watersnake numbers, the remaining 28.3 km was divided into 29 shoreline segments ranging in length from 60 to 2270 m (Fig. 2) and information on habitat characteristics and watersnake status were tabulated (Table 5). Sites where current land use practices precluded watersnake protection or habitat characteristics and field observations suggested that watersnakes were rare or absent were assigned a density of 0 (Table 5). Sites where habitat characteristics were similar to suitable watersnake habitat elsewhere and field observations confirmed the presence of watersnakes were assigned a density of 48 adults/km (Table 5). This value represents the median of the 10 sites with the lowest Lake Erie watersnake density based on mark-recapture and capture-rate estimates (range = 11–68 adults/km). For comparison, median density at the 10 sites having intermediate watersnake density = 141 adults/km (range = 83–203) and median density at the 10 sites having the highest watersnake density = 370 adults/km (range = 217–1107) (Tables 1, 3). By using the median of the lowest density sites, it is intended that extrapolated population numbers for uncensused sites should be conservative with respect to Lake Erie watersnake recovery objectives.

Together, mark-recapture and capture rate estimates exceed 6500 adult watersnakes on the U.S. islands (Table 4), more than meeting the overall population size criterion of 5555 adults specified in the Lake Erie Watersnake Recovery Plan (U.S. Fish and Wildlife Service, 2003). Including uncensused sites brings the total population size to nearly 7700 adults (Table 4). Mark-recapture and capture rate estimates also exceed island-specific criteria on three of four islands, totaling more that 2100 adults on Kelleys Island, 1000 adults on South Bass Island, and 1900 adults on Middle Bass Island (Table 4) (island-specific population size criteria for these islands are 900 adults, 850 adults, and 620 adults, respectively, U.S. Fish and Wildlife Service, 2003). Mark-recapture and capture rate estimates total 385 adults on North Bass Island, falling somewhat short of 410 adults, the population size criterion for this island. However, including uncensused sites brings the total population size estimate for this island to 443 adults (Table 4), suggesting that even on this island, population size criteria may be met. Unfortunately, formal confidence limits on overall and island-specific population estimates are not available, based as they are on multiple methods of estimation. However, it is perhaps instructive to note that if the standard error of 14%, reported above for mean estimates based on mark-recapture data, is taken as a guide, then the overall estimate of nearly 7700 adults exceeds the recovery criterion of 5555 adults by about two standard errors.

The population persistence criterion of the Lake Erie Watersnake Recovery Plan also specifies that population size goals be met for 6 or more years (U.S. Fish and Wildlife Service, 2003). Intensive spring population censuses, begun in 2001, are continuing and will allow estimation of population trends, taking into account potential differences in vital rates among sites, sexes, and years. Assuming population sizes remain stable or increase and other recovery criteria (*Habitat Protection and Management*, *Reduction of Human-induced Mortality*) are met, delisting of the Lake Erie watersnake might commence in the near future. Although delisting of recovered species under the U.S. Endangered Species Act has not been common, some notable examples exist, including the American alligator, peregrine falcon, and brown pelican (http://www.fws.gov/endangered/). In addition, the USFWS is currently determining the appropriateness of delisting another threatened watersnake, the Concho watersnake, *Nerodia paucimaculata* (R. Pine, personal communication). Although caution is warranted lest delisting take place prior to true population recovery, provisions of the U.S. Endangered Species Act require population monitoring for a minimum of five additional years and mandate relisting should populations fall below criterion levels during that period (Endangered Species Act, Section 4; http://endangered.fws.gov/esa.html). The delisting process itself also includes multiple safeguards, including a public comment period and review at regional and national levels. In addition, protections at the state level may remain should federal protection end.

Considerable progress has been made in achieving the Habitat Protection and Management criterion specified in the Lake Erie Watersnake Recovery Plan (U.S. Fish and Wildlife Service 2003). Much Lake Erie watersnake habitat is privately owned with human population centers on Pelee, Kelleys, and South Bass Island, smaller numbers of permanent residents on Middle Bass, North Bass, and Rattlesnake Island, and summer residents on Sugar, Ballast, Gibraltar, Hen, and North Harbour Island (historically, year-round or summer residents also occupied West Sister, Middle, and Green Island). However, public lands managed by the ODNR are found on the four larger U.S. islands (South Bass Island: 25 ha, 0.6 km of shoreline; Kelleys Island: 274 ha, 1.9 km of shoreline; Middle Bass Island: 50 ha, 0.9 km of shoreline; North Bass Island: 238 ha, 4.0 km of shoreline). These include significant recent watersnake habitat acquisitions on Middle Bass and North Bass Island (totaling ca. 87% of the latter island). In addition, Green Island is managed by the ODNR and West Sister Island is part of the Ottawa National Wildlife Refuge. Public lands on the Canadian Islands include the entirety of Middle Island and East Sister Island and multiple preserves on Pelee Island. Management plans are being developed for public lands on the U.S. islands by both the ODNR DOW and USFWS (U.S. Fish and Wildlife Service, 2003) and once adopted, should aid in ensuring the persistence of the Lake Erie watersnake. Further progress in habitat management and protection is being achieved through federally sanctioned Habitat Conservation Plans and state sanctioned Conservation Easements involving private landowners.

Although listed as threatened, local populations of Lake Erie watersnakes are sometimes remarkably dense, creating a dichotomy of perceptions regarding protection. Some island residents and visitors, aware of its local abundance, view the Lake Erie watersnake as interfering with recreational activities and its protection as imposing limits on local land use practices. In contrast, other residents, visitors, and wildlife managers recognize the Lake Erie watersnake as a unique component of the local biota that, despite its local abundance, is rare on a global scale. To these people, Lake Erie watersnake protection is seen to benefit other species and ecological communities and promote awareness of local environmental resources. Resolving these contrasting views is no small task and can probably never be fully achieved. However, through outreach efforts and land use recommendations, management agencies are seeking to foster greater appreciation of the Lake Erie watersnake and provide guidelines minimizing watersnake-human conflicts (U.S. Fish and Wildlife Service, 2003).

Lake Erie watersnakes seem tolerant of many human activities. Medium to high density populations occur in close proximity to summer homes (e.g., Kelleys Island Southeast Shore, South Bass Island East Shore; sites 4 and 26 on Fig. 2) and high traffic areas (e.g., adjacent to public boat launches at Kelleys Island State Park and South Bass Island State Park; sites 14 and 28 on Fig. 2). In addition, Lake Erie watersnakes appear capable of rapid population growth. Many females produce large numbers of offspring annually and sexual maturity is attained in 2–3 years (King, 1986). These characteristics, combined with management activities outlined in the Lake Erie Watersnake Recovery Plan (U.S. Fish and Wildlife Service, 2003), should promote population persistence of this Lake Erie endemic.

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