Bass in Time and Space: Operational Definitions of Risk

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Abstract.-Findings from both a long term, single population study and a short-term, regional, multi-population comparison were used to develop extensive and reliable insights into the nature of the abiotic and biotic factors that shape the dynamics of smallmouth bass populations over ecological time scales and over regional spatial scales. From a 58-year study on the bass population of Lake Opeongo Ontario, both individual growth and recruitment are shown to be strongly affected by variations in summer air temperatures and by variations in bass population abundance: growth rates among pre-reproductive age groups are higher when summers are warmer and when population abundance is reduced; recruitment is higher when summers are warmer and when adult abundance is higher. In a regional study of spawning timing that included the Lake Opeongo population, plus populations in nine additional lakes, a single relationship was found that could predict both temporal and spatial variations in the timing of spawning, using information on spring water temperatures and the size distribution of mature males. This relationship was used, along with historical patterns of variation in both spring water temperature regimes and male size distributions, to predict long-term, regional patterns of variation in spawning times. These expected patterns of variation were used to define objective measures of the risks associated with different opening dates for the fishing season. We discuss the respective roles of scientist and policy maker in establishing management regulations for individual populations, and for groups of populations in geographically distinct regions.

Introduction

The conservation of fish and the sustainability of fisheries are essential goals of fisheries management regulations. For recreational fisheries, regulations governing size of harvested fish, creel limits, and season openings and closings have been used both to protect populations and provide preferred sizes of fish to anglers. Size and creel limits may be the most widespread regulatory mechanisms employed in managing black bass populations in North America. These kinds of regulatory control for bass populations are largely focused on restricting fishing practices in the hope that compliance will indirectly, but effectively, cap total harvest and focus it on preferred segments of the population. Season closures to protect spawning fish are less widely employed for managing black bass populations (Quinn, this volume). Whether developed for constraining exploitation, codifying angler preferences, or limiting access at critical life stages, regulatory complexity is proliferating in a site-specific manner and at a rate greater than gains in our un

derstanding of the ecological mechanisms controlling most fish populations at broader spatial and temporal scales (Radomski et al. 2001).

This paper represents a departure from this pattern. We use findings from both a long term, single population study and a short-term, regional, multi-population comparison to develop extensive and reliable insights into the nature of the abiotic and biotic factors that shape the dynamics of smallmouth bass populations over ecological time scales and over regional spatial scales. We then go on to demonstrate the role that this kind of knowledge can play in clarifying the policy decisions required to rationally justify the imposition of a specific regulatory measure (i.e., the fishing season opening date) over relatively broad spatial and temporal scales.

This combination of population ecology and regional policy relies on findings from both empirical and modeling studies. First, we provide an empirical assessment of the relative roles of biotic factors (particularly density) and abiotic factors (particularly temperature) in shaping the degree of long and short-term variability in the growth patterns of individuals and the abundance of different age groups observed in the smallmouth bass *Micropterus dolomieu* population of Lake Opeongo, Ontario Canada (Figure 1). Second, we provide an

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assessment of the degree to which some of the predictive relationships developed for the Lake Opeongo population can be applied to other Ontario smallmouth bass populations. Finally, we use an individual-based population model to translate historical patterns of temporal and spatial variability in these controlling factors into forecasts of variability patterns for spawning timing at both the population level and the regional level. These expected patterns of variability are then used to assess the various levels of risk associated with different opening dates for the fishing season.

Methods

Lake Opeongo (45°42'N, 78°22'W; Figure 1) is located about 400 km North West of Toronto in Algonquin Provincial Park. Lake Opeongo is a large (area = 58.6 km2), clear (See chi disk reading = 6 m), oligotrophic (TDS = 29 mg/L) lake. Smallmouth bass were introduced into Lake Opeongo sometime between 1900 and 1920 to supplement the recreational fishery for native salmonids. The first record

of their presence in the lake comes from 1927 (Christie 1957). This population has supported a recreational fishery of varying size since at least the mid -1930s. The Lake Opeongo smallmou th bass population has been extensively studied since 1936 when an access point creel survey was initiated at the only point of departure from the lake. The angling fishery is closed for most of the parental care period (May and June) but opens in late June and continues into September each year. Beginning in 1936, the creel survey operated daily on weekends and randomly selected weekdays. Fish sampled during the survey are measured, weighed, aged by the scale method and examined for sex and maturity. More detailed information on Lake Opeongo is provided in Martin and Fry (1972).

Lake Opeongo Data Base

Data collection programs on the Lake Opeongo smallmouth bass population that started in 1936 and have continued annually to the present. The programs can be divided into two primary categories
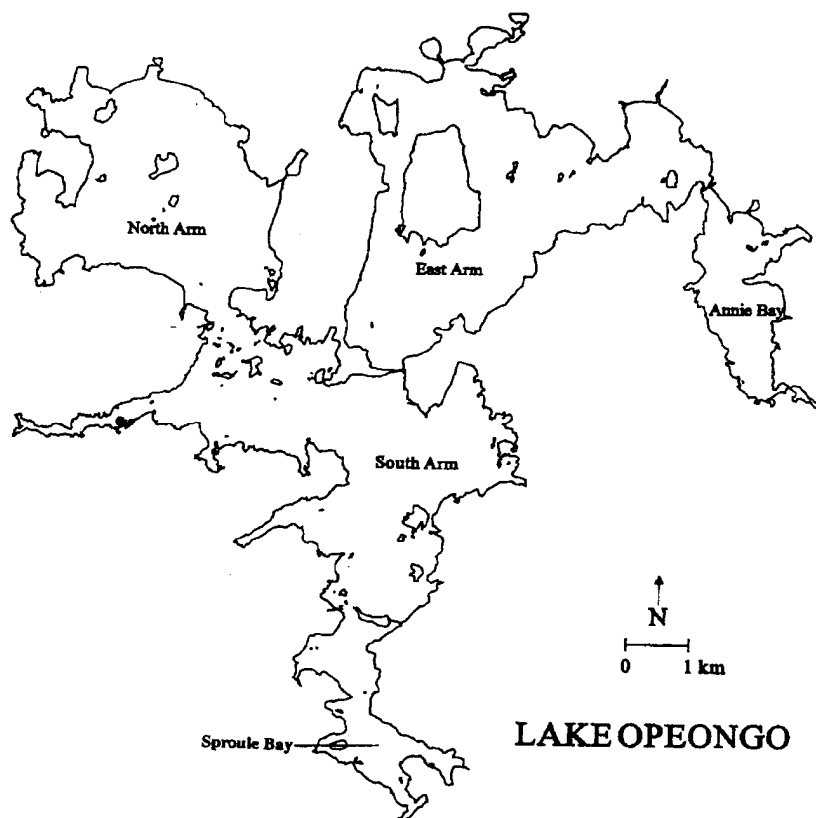

Figure 1. Map of Lake Opeongo

(Figure 2). First, there are indirect studies of bass population dynamics as seen through the creel survey of the angler harvest (McMurtry and Shuter 1985; Shuter et al. 1987). Second, there are direct studies of various aspects of bass behavior and ecology involving field and laboratory observations, experiments and simulation studies (Emery 1975; Shuter et al. 1980; Cunningham and Shuter 1986; Ridgway et al.1991; Ridgway and Friesen 1992; Ridgway and Shuter 1994, 1996, 1997; Rejwan et al. 1997, 1999; Friesen and Ridgway 2000). Direct studies in the field have typically focused on the main spawning area of Jones Bay, in the South Arm of the lake.

In this paper, the creel survey data were used in harvest-at-age analysis, coupled with mark-recapture studies (Shuter et al. 1987), to reconstruct almost the entire history of the colonization of Lake Opeongo by smallmouth bass. Annual estimates of population abundance, by age-class, were generated for the period 1937-1992. Back-calculation techniques (Shuter et al. 1980), applied to the scale collections provided by the creel survey, were used to estimate annual growth rates prior to maturity for each year-class from 1932 through 1993. Beginning in the late 1940s, state of maturity assessments were made of almost all bass seen in the creel survey. These data were used to estimate length at 50 percent maturity for each sex for consecutive five year intervals.

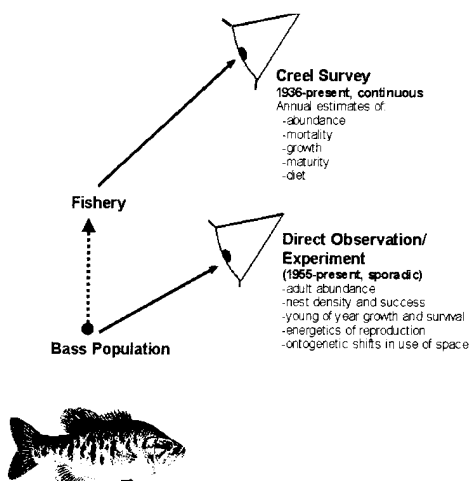Existing air temperature records from the nearest Canadian government weather station

Figure 2. Studies that have contributed to current understanding of the dynamics of the Lake Opeongo smallmouth bass population. Annual systematic surveys of the creel harvest began in 1936 and have continued until the present. Direct observational and experimental studies began in 1955.

(Madawaska, about 50 km southeast of Lake Opeongo) were summarized for the period 1932 through 1993. Continuous water temperature recorders were used to document daily variation in the surface water temperature of Lake Opeongo, spring through fall, from 1964 through 1993.

Multiple regression analysis was used to assess the statistical significance of associations between year-to-year variation in growth and recruitment and year-to-year variation in climate and abundance. In these analyses, the following definitions were used: (i) growth of age i fish in year j: the change in fork length from spring to fall in year j, exhibited by fish born in year $j-i$; these quantities were estimated by back-calculating length at age from scales collected from at least 25 fish sampled from the appropriate cohort after they had completed at least five years of life; (ii) recruitment in year j; (iii) the abundance at age 1 of the cohort born in year j, as determined from harvest-at-age analysis; and abundance of mature adults in year j: the abundance of all fish aged five years and over in the spring of year j, as determined from harvestat-age analysis; throughout the time series, the age at 50 percent maturity was less than (or equal to) five years for both males and females.

For dependent variables that exhibited significant associations with both climate and abundance, the resulting multiple regression equation was used to 'correct' the dependent variable for variation in one factor in order to provide a clear, visual display of its relationship to the other factor.

Data and results from direct observational studies in Lake Opeongo were used to: assess the relationship between the abundance of mature males alive in a particular year and the number of

males that fertilize a clutch of eggs (Ridgway et al. 1991; Rejwan et al. 1997); and assess the relationship between timing of spawning, spring water temperature patterns and the size distribution of reproductively active males (Ridgway et al. 1991; Lucas and Orth 1995).

Full details on the creel survey and its history are provided in Shuter et al. 1987. Detailed descriptions of the underwater survey methods and re

productive ecology of nesting males are provided in Ridgway et al. (1991), Rejwan et al. (1997), and Friesen and Ridgway (2000).

Comparative Survey Data Base

In 1990, a comparative study of the timing of spawning in 10 separate smallmouth bass populations (nine lake populations and one river population; Figure 3) was conducted according to the fol

lowing protocol. In each population, a continuous water temperature recorder was placed at 1-2 m depth in a known spawning area soon after iceout in spring. Swimmers with mask and snorkel searched each spawning area several times in late May and June and nests with young were noted and the developmental state of the young was recorded. The spawning dates and swim up dates for each nest were back-calculated from the observed developmental state using the daily water temperature record for the spawning area and the temperature-dependent development rate equations presented in Shuter et al. (1980). The nine lake populations resided in relatively small (median surface area, 536 ha; range, 214-5860 ha), shallow (mean depth: median, 10.6 m; range, 5.5-24.7 m) lakes with relatively similar basic productivity levels (TDS: median = 34 mg/L; range 22-138).

Lake Opeongo Results

Changes in Abundance

The abundance estimates for the Lake Opeongo population make up a time series that is fairly typi

cal of an invader (Levin 1989; Morton 1997). There is a period of slow growth as the invader becomes established in its new environment, followed by a period of explosive growth or expansion, followed by a period of contraction to a new, lower range of abundance, as the invader 'accommodates' to its new environment (Figure 4). The population more than tripled from the establishment phase through to the expansion phase in the 1960s and 1970s (Figure 4). In all the Figures that follow, these three phases of acclimation, expansion and accommodation are identified using a common set of symbols depicting each of the three phases. This permits a quick visual assessment of the temporal consistency of statistical associations across the entire time series.

Individual Growth

For age groups 1 through 4, year-to-year variation in annual growth rate is large (range for coefficient of variation: 12% to 18%), similar and consistent in each of the three phases of the time series. Variation in growth during the first year of life is smaller (C.v. = 9%) and is not consistently associated with variation in other age groups (Table 1). Only during the
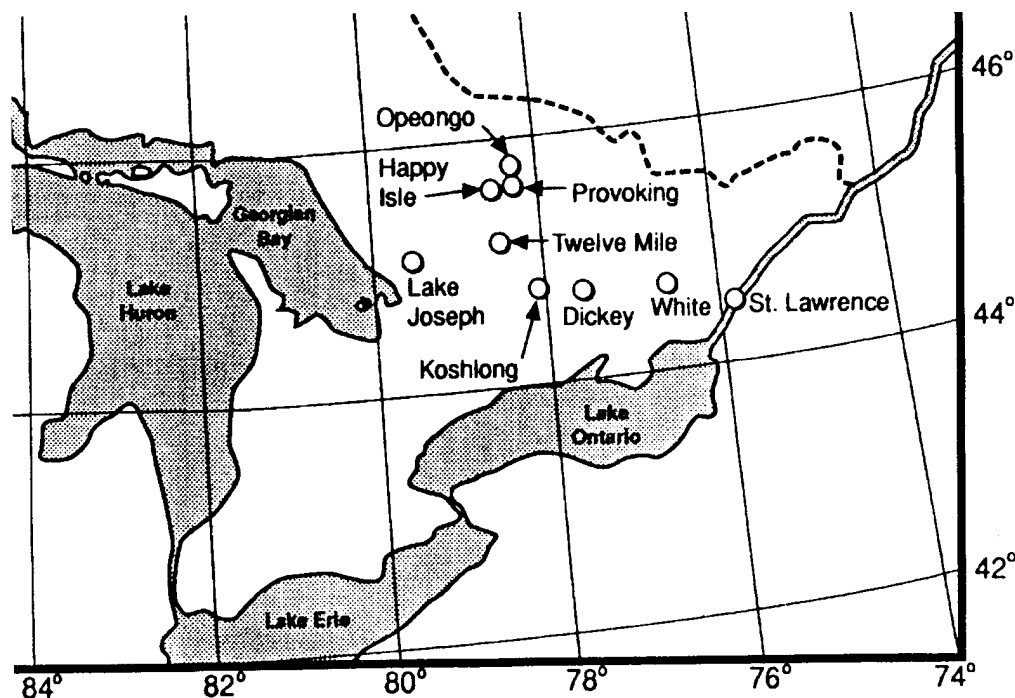

Figure 3. Map of southeastern Ontario showing locations of 9 of the 10 smallmouth bass populations (9 lake populations, 1 river population) included in the comparative study of spawning timing in 1990. The tenth lake (Crooked Pine, 48.47 lat, 91.04 long) is located in the northwest of the province, about 1,000 km from the others.
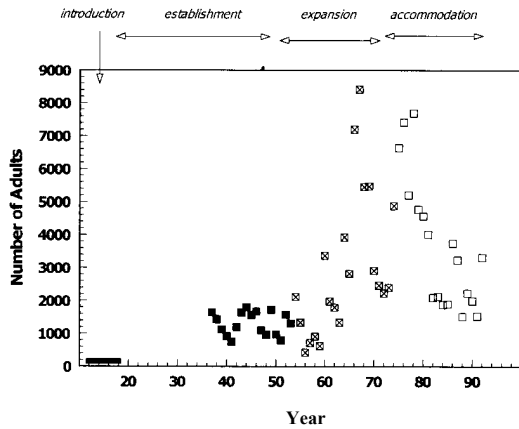
Figure 4. Variation in abundance of adult smallmouth bass 1937-1992. Smallmouth bass were introduced to the lake sometime between 1900 and 1920; the observed variation in abundance can be split into the establishment, expansion and accommodation phases that are typical of many invasion situations (Levin 1989). The three symbols representing each of these phases are used consistently in subsequent figures.

Table 1. Pearson correlations between annual growth increments of adjacent age groups in the same year. N = number of years in each phase. Figures in bold are statistically significant at the 0.05 level, 2 sided test.

Phase	N	o vs 1	1 vs 2	2 vs 3	3 vs 4
		- Age groups			
Establishment	18	-0.39	+0.63	+0.67	+0.51
Expansion	21	+0.56	**+0.65**	+0.54	**+0.37**
Accommoda tion	12	+0.20	**+0.60**	+0.73	**+0.62**

expansion phase is there a statistically significant association between young-of-year (YOY) growth and growth in older age groups (Table 1). This pattern of concordance among older age groups, and discordance with young of year, is to be expected, given that the food resources of age groups 1 through 4 are similar (larger benthic invertebrates, smaller littoral fish) and quite separate from those exploited by y~y (zooplankton and smaller benthic invertebrates).

Two general factors likely contribute to growth variation among the older age groups. First, variation in the abundance of the age groups over the entire time series is large and could impact growth negatively through increased competition for shared food resources. Second, the positive effect which longer, warmer summers have on the growth of individuals in northern smallmouth bass populations could result in clear differences in growth given the level of climatic variation in recent years (e.g., Shuter and Post 1990).

Both these effects were evident in the multiple regression analyses of growth variation in age groups 1 through 4. The analyses for each age-group were similar but not identical (Table 2). A negative association between growth and the total summed abundance of all four age groups was present in each of the age groups (ages 1-4) and was statistically significant in three (all except growth by age 4 fish; Table 2). In addition, a positive association between growth and mean summer air temperature was

present in each of the four age groups (ages 1-4) and was statistically significant in three (all except growth by age 1 fish; Table 2). These relationships between growth and both density and climate are illustrated in Figures Sa and 6a.

Since the primary food resources for y~y are quite distinct from those of older age groups, competitive effects on y~y growth will most likely be expressed as a negative association between y~y growth and initial cohort abundance. A positive effect of warmer summers would also be anticipated. Multiple regression analysis of y~y growth variation over the entire time series revealed a variant of this expected pattern (Table 3). There was a strong negative association between an index of initial cohort abundance (number of mature adults alive immediately prior to spawning) and a strong positive association with June air temperatures. However, these associations were not expressed consistently in each of the phases of the time series. No effects were evident in the establishment phase, whereas both effects were detectable in the expansion and accommodation phases. There appears to have been a general decline in growth in the accommodation phase that is not explained by either factor very well (Figure Sb).

Table 2. Regression coefficients from multiple regression analyses of variation in annual growth increments for different age groups. Figures in bold are significant at the 0.05 level (one-sided *p-values* in brackets). Variables: In (Gri) = natural logarithm of annual length increment (cm) for age i fish; In (NI3) = natural logarithm of number of fish in age groups 1 through 4; HAS = mean summer air temperature, June through September (DC).

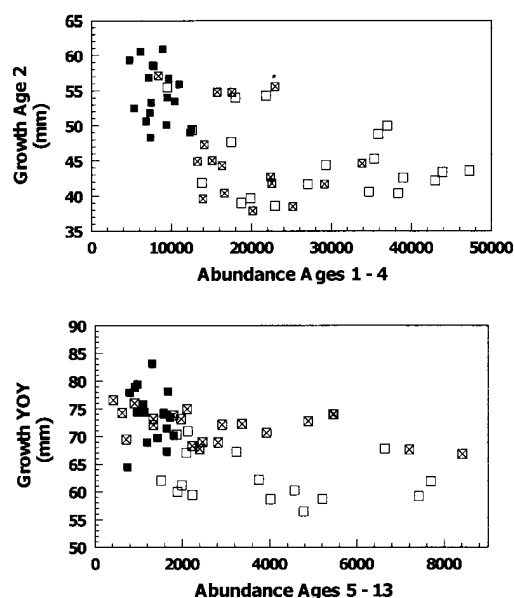| Dependent variable	N	Adjusted R'	Independent variable In(NL4)	HAS
In(GRl)	54	0.56	**-0.220** (0.0000)	+0.0147 (0.2800)
In(GR2)	55	0.49	**-0.155** (0.0000)	**+0.0643** (0.0021)
In(GR3)	55	0.32	**-0.083** (0.0006)	**+0.0834** (0.0002)
In(GR4)	55	0.22	-0.038 (0.0501)	**+0.0773** (0.0003)

Figure 5. Effects of abundance on individual growth. Growth estimates have been adjusted for inter-annual variation in climate in order to provide a clear picture of their link to abundance A) Growth in length over the third year of life versus abundance of those age groups (1 through 4) that compete for the same food resources. B) Growth in length over the first year of life versus an index of the abundance of young of year at the start of their first year of life. For each data set, the appropriate multiple regression equation from Tables 2 or 3 has been used to adjust each increment to the value expected for the average climate conditions observed over the entire time series;
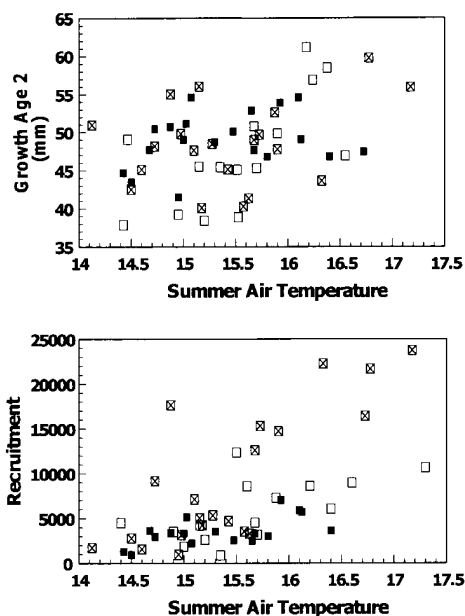

Figure 6. Effects of climate on individual growth and recruitment. Growth and recruitment estimates have been adjusted for inter-annual variation in abundance in order to provide a clear picture of their links to climate. A) Growth in length over the third year of life versus mean summer air temperature. Each length increment has been adjusted to the value expected for the average abundance level observed over the entire time series, using the 'all phases' regression equation from Table 3. B) Recruitment (cohort abundance at start of second year of life) versus mean summer air temperature. Each recruitment value has been adjusted to the value expected for the average abundance level observed over the entire time series, using the 'all phases' regression equation from Table 4.

Recruitment

Recruitment was highly variable (Figure 7). Over the entire time series, maximum and minimum observed values differed by 34 fold and within each phase of the time series, the variation was about 10 fold. Factors likely to be associated with this variation in recruitment include: variation in climatewarmer summers have often been associated with stronger year classes in northern smallrnouth bass populations; and variation in number of adults-in principle, recruitment should be positively linked to the abundance of breeding fish, particularly at very low levels of abundance. Multiple regression analysis revealed that a significant amount (- 45%) of the observed variation was linked to these factors: a strong positive temperature effect was evident overall, and was detectable in each phase of the time series; a strong positive effect of adult abundance was evident overall, and was recognizable in two of the three phases (Table 4). The temperature relationship was relatively tight and consistent

Table 3. Regression coefficients from multiple regression analyses of variation in annual length growth (cm) for YOY. Dependent Variable: natural logarithm of y~y growth. Independent variables: Ln($N5\_13$) $=$ naturallogarithrn of annual spring abundance of age groups 5 through 13--those age groups that are over 50 percent sexually mature; June $=$ average air temperature for June (oC). Figures in bold are significant at the 0.05 level; I-sided *p-values* are provided in brackets. The R' value for the establishment phase is so low that the coefficient estimates are meaningless and hence are not given.

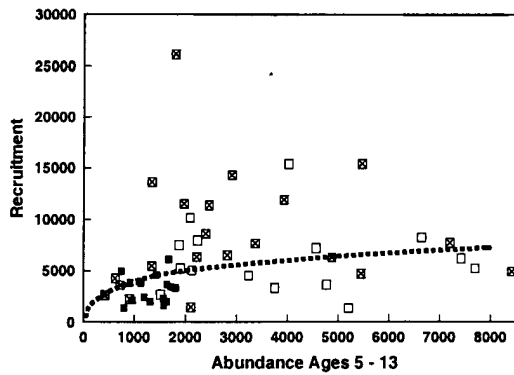| Phase	N	R'	ln *(N5_13)*	June
			Adjusted Regression coefficient	
All phases	54	0.284	-0.0658	+0.022
			(0.0000)	(0.010)
Establishment	17	0.007	**	**
Expansion	21	0.241	-0.0232	+0.011
			(0.015)	(0.049)
Accomodation	16	0.202	-0.0469	+0.031
			(0.099)	(0.021)

Figure 7. Co-variation in recruitment and abundance of adult (ages ::0:5) smallmouth bass. Recruitment estimates have been corrected for year-to-year variation in summer air temperatures. Dashed line is the regression line fitted to the data after log transforming both variables.

throughout the time series (Figure 6b). In contrast, the abundance relationship was quite variable (Figure 7). However, data from relatively low abundance levels « 2000 individuals) were available from all three phases of the time series and most of these points appeared to cluster in the same area of the graph, independent of phase.

Maturity and Reproduction

Both males and females exhibited strong and consistent positive relationships between juvenile growth rate, as represented by growth in the third

Table 4. Regression coefficients from multiple regression analyses of year-to-year variation in recruitment. Dependent variable: natural logarithm of estimated abundance of each cohort at the start of its second year of life; Independent variables: Ln $(N5~13)$ = natural logarithm of annual spring abundance of age groups 5 through 13-- those age groups that are over 50 percent sexually mature; HAS average air temperature for June through September (0C). Figures in bold are significant at the 0.05 level; I-sided pvalues are provided in brackets. In the Accommodation phase, inclusion of the density term actually reduces the adjusted R2 value--hence only results from the univariate regression on the temperature measure are reported.

| | | | Adjusted Regression coefficient | |
Phase	N	R'	In $(N5\_13)$	HAS
All phases	53	0.455	0.366	0.751
			(0.003)	(0.000)
Establishment	17	0.415	0.442	**0.498**
			(0.163)	(0.015)
Expansion	21	0.528	0.303	0.888
			(0.064)	(0.0001)
Accommodation	15	0.193	**	0.567
				(0.028)

year of life, and length at 50 percent maturity (Figure 8a). Males and females showed similar patterns of decline in size through the time series when the data were aggregated in five-year intervals. Length at 50 percent maturity for both sexes declined through the expansion phase, reaching an overall reduction of 2 cm in the accommodation phase.

Ridgway et a1. (1991), in their direct study of Opeongo spawning males, noted that as the abundance of mature males rose, there was a systematic decline in the fraction of those males that actually acquired a clutch of eggs to fertilize. This observation still remains after using updated population estimates from recent creel census data (Figure 8b). This decline becomes apparent in the expansion phase of the colonization and continues to be observed throughout the accommodation phase (Figure 8b).

Comparative Study Results

Ridgway et a1. (1991) demonstrated that timing of spawning, size of breeding males and spring water temperatures were all interrelated according to a relationship of the following form:

size of males spawning on day i = a x eb x ddi

Where a and b are constants and ddi is the number of degree days greater than 10°C that have accumulated by day i.

The same empirical relationship was observed in a river population of smallmouth bass in Virginia (Lucas and Orth1995). Data on spawning timing in 1990 from the comparative database of ten lakes was used to determine if a single relationship of this form could be used to generate accurate predictions of spawning timing across a number of populations. The ten lakes differed widely in both water temperatures and in male size distributions (Figure 9). The single relationship based on the eight year Opeongo analysis carried out by Ridgway et a1. (1991) was capable of generating accurate predictions for both the start and end of the spawning season in all ten of the lakes (Figure 10).

Discussion

Long- and Short- Term Variability in the Population Dynamics of Opeongo Smallmouth Bass

The stock-recruit curve shown in Figure 7 exhibits a progressive decline in the ratio of recruits to

Figure 9. Cross-population variation in the comparative data set. A) Water temperatures. B) Size distributions of spawning males, population identified by the first two letters of its water body (see Figure 3).
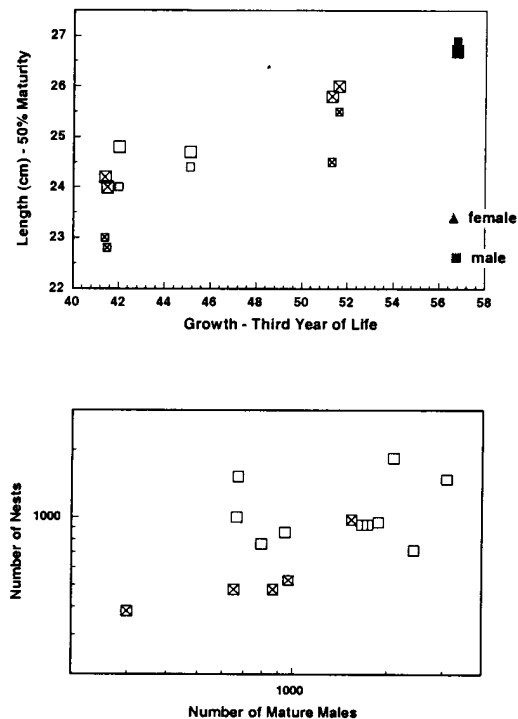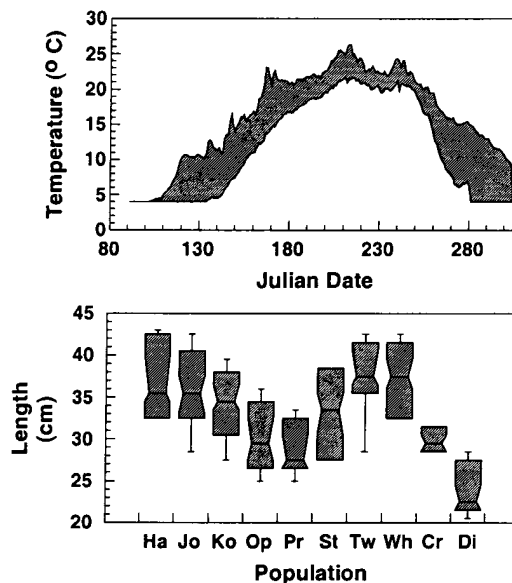
Figure 8. Individual size and number of breeding adults. A) Length at 50% maturity versus growth in the third year of life for both sexes---each point represents an average value over five consecutive years. Arrows indicate order of values in the time series for males; a similar sequence applies for females. Large and small squares represent females and males, respectively. Symbols for different phases as in Figure 4. B) Total number of nests with eggs versus number of mature males aged 5 or over: solid line is the 1:1 line, dashed line is the fitted regression line.

adults (fish aged 5 and over) as the number of adults increases. This pattern is consistent with the density-dependent changes in growth, maturity and breeding success evident in Figures 5 and 8. The decline in growth rate among age groups 1-4 occurred early in the expansion phase (Figure 5a) and was followed immediately by declines in size at maturity for both males and females (Figure 8a). Since age at maturity did not change substantially, the decline in size at maturity produced declines in the size of typical breeding males and females with resultant declines in median egg production per individual (Carlander 1977; Gillooly et al. 2000) and median levels of nest defense capability (Mackereth et al. 1999). Later in the expansion phase, and in the accommodation phase, the fraction of mature males that actually fertilized a clutch of eggs declined with increasing numbers of ma

ture males (Figure 8b). This decline is consistent with the hypothesis that increasing competition by adult bass for their specific food resources (i.e., primarily crayfish) will lead to a situation where only the larger males are successful in fertilizing a clutch of eggs (Ridgway and Shuter 1994; Baylis 1995; Mackereth et al. 1999). In the accommodation phase, (Figure 5b), overall growth in the first year of life declined and the negative effects of density on growth in this life stage appeared to strengthen (Table 3). One would expect such changes to lead to an overall decrease in winter survival (Shuter and Post 1990).

The appearance of each of these effects, as higher densities are reached during the progress of the time series, is consistent with the negative curvature evident in the stock-recruit plot presented in Figure 7. This leads to a picture of population regulation (Figure 11) that consists of the successive imposition of density-dependent bottlenecks on recruitment at various points in the life cycle (Shuter 1990). At least three bottlenecks appear to be operative in the population by the end of the accommodation phase. First, juvenile growth declines with increasing juvenile density (Figure 5a), leading to a downward shift in the size distribution of mature fish (Figure 8a). Considering the near universal pattern of size-related fecundity in fish, this downward
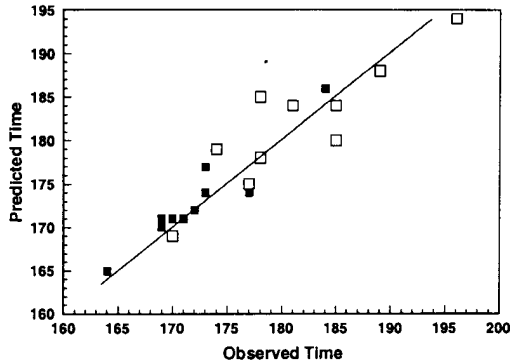
Figure 10. Predicted and observed start (black square) and end (gray square) Julian dates for spawning seasons in the comparative data set.
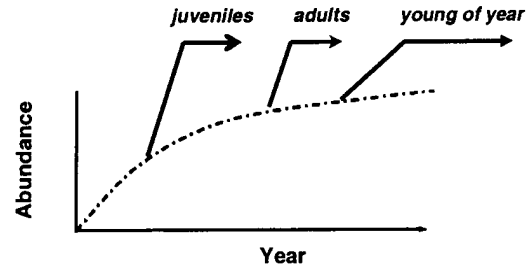

Figure 11. The progressive appearance of density-dependent effects at different stages in the smallmouth bass life cycle during the course of its invasion of Lake Opeongo.

shift in size reduces both the median gamete production per typical adult female and the effectiveness of parental care provided by the typical adult male. Second, the proportion of mature adult males that are successful in fertilizing a clutch of eggs declines with increases in the number of mature males (Figure 8b). This reduces the fertilization efficiency of a typical mature male. Third, a decline in overall growth in the first year of life plus an intensification of a negative relation between growth and y~y abundance (Figure 5b), reduces y~y (Shuter et al. 1980) survival and hence further decreases the overall reproductive success of a typical adult.

These density effects are modified by a strong abiotic, climate effect (Figure 6). The interactive effects of temperature on both growth and survival in early life have been described in terms of separate processes (i.e., the cueing of reproduction in spring, larval development, young of year feeding and growth, winter starvation and consequent mortality-Figure 12) that have been isolated and quantified in both laboratory and field settings (e.g., Oliver et al. 1979; Shuter et al. 1980; Shuter and Post 1990; Ridgway et al. 1991). Integrating these processes with the density effects described above leads to an overall picture in which both biotic and abiotic factors shape the dynamics of the Opeongo bass population (Figure 12). The lake-specific availability of each of the quite different food and habitat resources required by at least three distinct life stages interact to determine the size structure, number and reproductive output of breeding adults; the size structure of the breeders interacts with spring temperatures to generate both between and within year variation in spawning time; and spawning time itself further interacts with summer and winter temperatures to

determine summer growth, winter survival and ultimately reproductive success.

A previous examination of smallmouth bass growth patterns in Lake Opeongo attributed declines in the size of sub-adult fish to direct competition with cisco *Coregonus artedi* (Emery 1975). There is no evidence that cisco, as a pelagic planktivore, overlaps in either space or diet with juvenile smallmouth bass that forage in the littoral zone for benthic prey and small fish. In this current analysis, the start of the expansion phase in the time series of adult abundance in Opeongo coincided with two independent events. First, there was a full establishment of cisco in the lake in the late 1950s and early 1960s that followed a successful introduction a decade earlier (Martin and Fry 1972). Second, there was a decline in fishing mortality that corresponded to the disappearance of guided fishing during the late 1950s and early 1960s (Shuter et al. 1987). Declines in juvenile growth detected in the earlier summary (Emery 1975), and again in this summary, can be accounted for by changes in bass abundance without any appeal to interspecific competition. Specifically, changes in the abundance of juvenile smallmouth bass that appear to correspond in part to changes in adult abundance can account for declines in growth in early life stages. How this change in abundance came about is unclear. The invasion process itself was certainly in part responsible. In addition, declines in fishing mortality could have lead to overall increases in population abundance. Also, the establishment of cisco, a very efficient pelagic predator, could have caused an increase in the rate of nutrient recycling in the pelagic, with consequent increases in productivity throughout the lake. A primary objective of our future research will be to develop the Opeongo databases in ways that will increase our understanding of stock-recruitment processes in smallmouth bass.
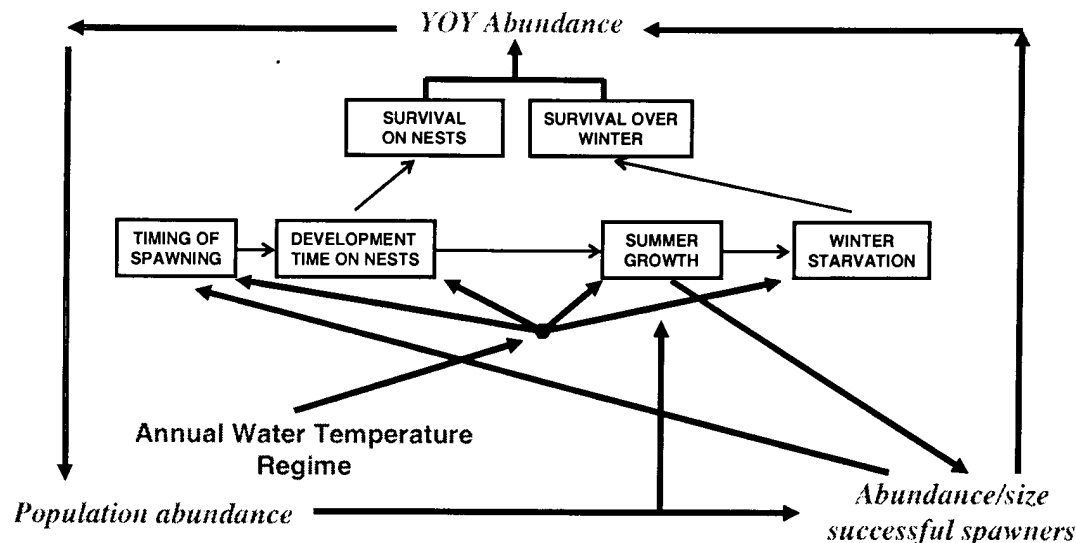
Figure 12. Interrelations among water temperature, population density, and the various processes that interact to determine the abundance of individual year classes.

Population Knowledge and Conservation Management-operational Definitions of Risk and the Importance of Protecting Spawners

A primary principle of conservation in fisheries management is the protection of spawning fish (Olver et al. 1995; Shuter et al. 1997). This principle should predominate in situations where fine scale control of annual harvests (e.g., Stock-specific quota management) is neither feasible nor desirable. It becomes particularly important in stocks where natural variation in recruitment is very high and density dependent effects come and go in an unpredictable fashion. The Lake Opeongo smallmouth bass population is just such a stock, and it is by no means unique-high variability in recruitment is endemic in the bass populations that are found in the northern half of the species' zoogeographic range (Shuter et al. 1980; Shuter et al. 1985; Shuter and Post 1990). A common management tool for extending such protection to spawners is the fishing season. In Ontario, a spring fishing ban has been a primary tool for bass conservation management for many years. The opening date for the season is common across the south-central area of the province (the last weekend in June) and is based on an informal assessment of spawning timing among a few well studied, local populations. The Opeongo and comparative databases described in this paper will be used to illustrate a more formal procedure for establishing regional opening dates based on operational definitions of risk developed

directly from biological assessments of recruitment variability in specific populations.

In smallmouth bass and other species that engage in parental care, protection of spawners must extend beyond the spawning act itself. Male smallmouth bass expend large amounts of energy (Mackereth et al. 1999) and accept considerable risk to their individual survival (Ridgway and Shuter 1994) in order to defend their young. The existence of this behavior pattern only makes evolutionary sense if typical smallmouth spawning habitat contains many effective egg and larval predators. This is certainly the case in Lake Opeongo, where removal of the guarding male early in the life of a brood inevitably leads to brood destruction within a few hours (Post. 1982). Once YOY begin to feed independently, their dependence on the protection of the guarding male begins to decline (Ridgway 1988; Ridgway and Friesen 1992). In a typical brood, independent feeding begins on the same day for all members (Friesen and Ridgway 2000)-this date will be referred to as the swim-up date. The distribution of swim-up dates varies widely, both within and between years, and much of this variation can be accounted for by the interaction between the spring water temperature regime and the size distribution of spawning males (Figure 13). For a given year, the distribution of swim-up dates can be used to define the level of protection offered by a particular season opening date. For example, given the distribution of swim-up dates expected for 1990 in Lake Opeongo

(Figure 14), eliminating fishing prior to Julian Date 180 would ensure that 80 percent of broods would not be exposed to the risk-of male removal until after swim-up: an 80 percent protection level. Earlier or later opening dates would provide lower or higher protection levels, respectively.

Risk at the Population Level
Both the within and between year variability in swim up dates for a particular population can be accurately simulated using an individual based model (DeAngelis et al. 1991) if the variability in both spring temperatures and male size distributions can be defined (Figure 13). Empirical definitions of these distributions are available if the population in question has been the subject of long term study, since each year of study produces a description of spring temperatures and male sizes which accumulate over time, effectively producing an empirical distribution for each. Given the ability to simulate both within and between year varia

tion in swim up date, it then becomes possible to assess the long term 'risk' associated with a particular season opening date in terms of the annual probability that the 'acceptable' protection level will not be met (Figure 15). For example, the longterm distribution of annual opening dates that provide an 80 percent protection level for the Opeongo population was generated as follows. First, a temperature pattern and a male size distribution from the set of 20 patterns and distributions observed over the accommodation phase of the time series were randomly and independently selected. Second, the selected temperature/size combination was used as input to the individual based model to generate a distribution of swim-up times for the simulated year (DeAngelis et al. 1991). Third, the Julian date where 80 percent of the broods have reached swim up-the 80 percent protection date *(d80)* was determined. Finally, the first three steps were repeated 100 times to generate the distribution of *d80* values (Figure 16).

Within and between year variation in spawn and swim-up dates

Individually-based model

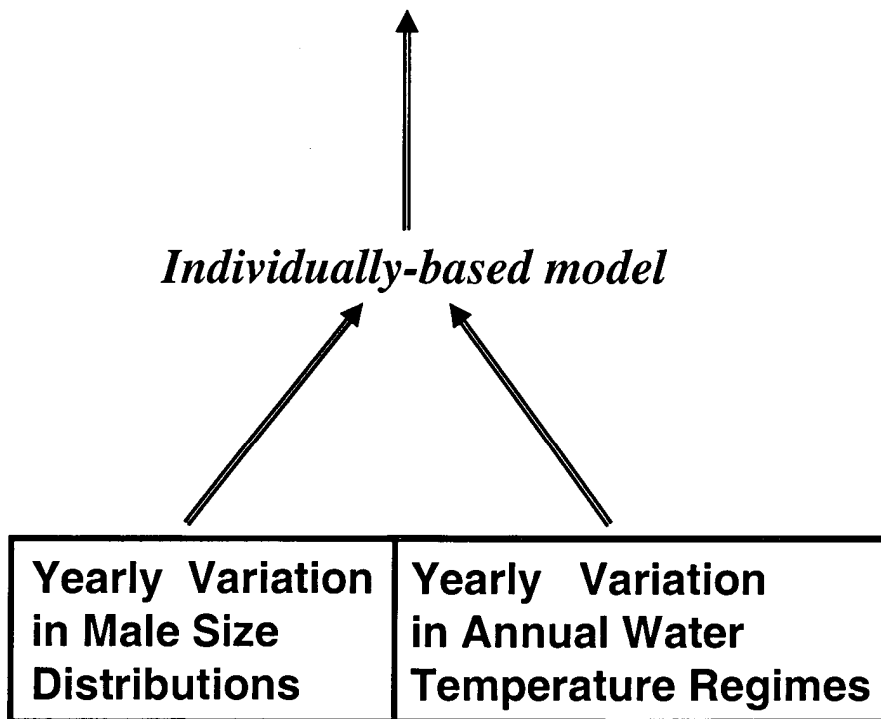| Yearly Variation in Male Size Distributions	Yearly Variation in Annual Water Temperature Regimes

Figure 13. Use of empirical distributions for temperature and spawner size to simulate swim-up time distributions.

Once the *d80* distribution has been generated, then the level of risk (Le., the probability that the acceptable protection level is not met) associated with each possible season opening date is then estimated as (1 - *C[d])*, where *C(d)* is the value, on day *d,* of the cumulative distribution for *d80* (Figure 15).

Risk at the Regional Level
A similar procedure can be applied to the empirical distributions of spring temperatures and male sizes derived from the 1990 regional survey of 10 populations in eastern Ontario (Figure 3). Randomly sampling temperature/size combinations from these empirical distributions will provide an estimate of the *d80* distribution for this geographical region in 1990 (Figure 16). Under the assumption that the inter-annual variation in *d80* observed in Lake Opeongo is typical of all the populations in the region, then the long-term Opeongo distribution and 1990 regional distribution can be combined to yield a long-term *d80* distribution for the region (Figure 16). The cumulative version of this *d80* distribution can then be used to derive, for each potential opening data, a regional measure of long term risk: the annual probability that a lake in the region will not receive the' acceptable' level of pro

tection. For example, opening the fishing season on Julian date 190 would expose a typical lake in the region to a 10 percent risk that the desired protection level of 80 percent would not be met.

The approach adopted here, to explicitly characterize the risk associated with different season opening dates, moves toward reducing the gap between scientific knowledge and policy practice (Bradshaw and Borchers 2000). It clarifies the respective roles of policy and biology in setting opening dates. Policy makers establish the levels of protection and risk that must be met by the opening date. Here, ethical and economical considerations are the primary determinants of the levels ultimately judged to be acceptable. Once these acceptable levels have been established, species-specific biological knowledge (mobilized using the techniques illustrated in Figure 16) is used to determine the earliest possible opening date that would meet the required levels of both protection and risk. Two components help in this effort. First, the ability to predict the spawning and parental care period reduces uncertainty with respect to the timing of these important events and the consequent seasonal vulnerability of nesting bass (Ridgway and Shuter 1997). Second, docu
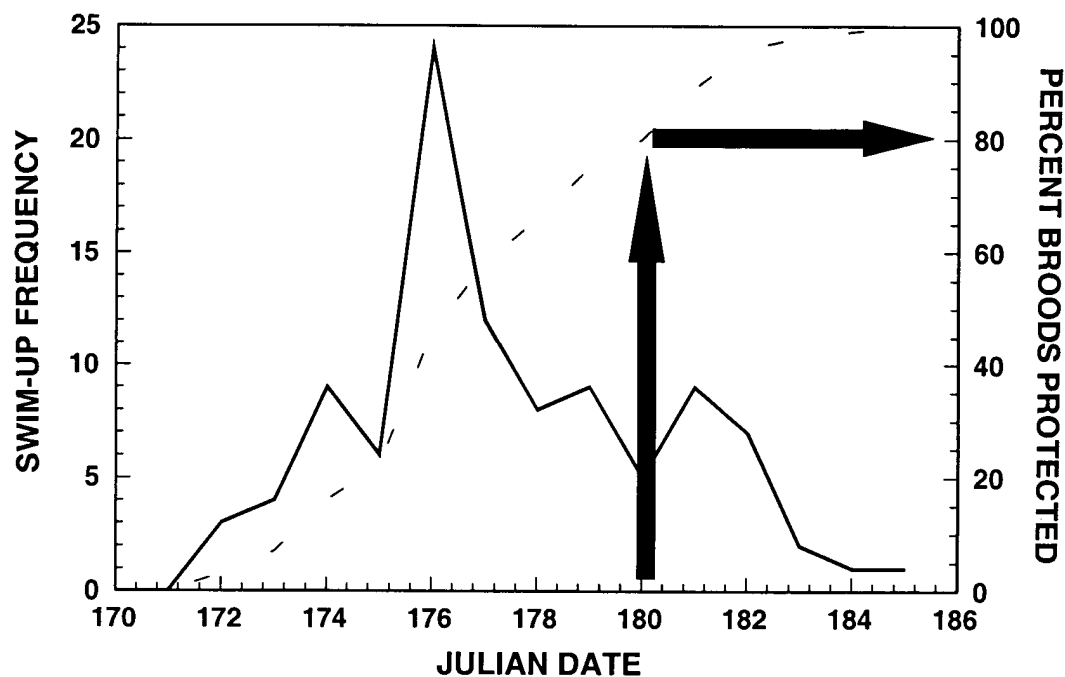

Figure 14. Simulated distribution of swim-up dates for Lake Opeongo in 1990: solid line = frequency distribution, dotted line = cumulative distribution. The arrows show that eliminating fishing prior to Julian Date 180 would ensure protec
tion for 80% of broods - €arlier dates provide lower protection levels.

Operational Definitions of Risk

Risk at the Population Level: -long term studies of a specific population derme year-to-year variation in temperature, male size and spawning time

Risk at the Regional Level: - comparative studies of many populations define inter-population variationinte~ature,malesize and spawning time
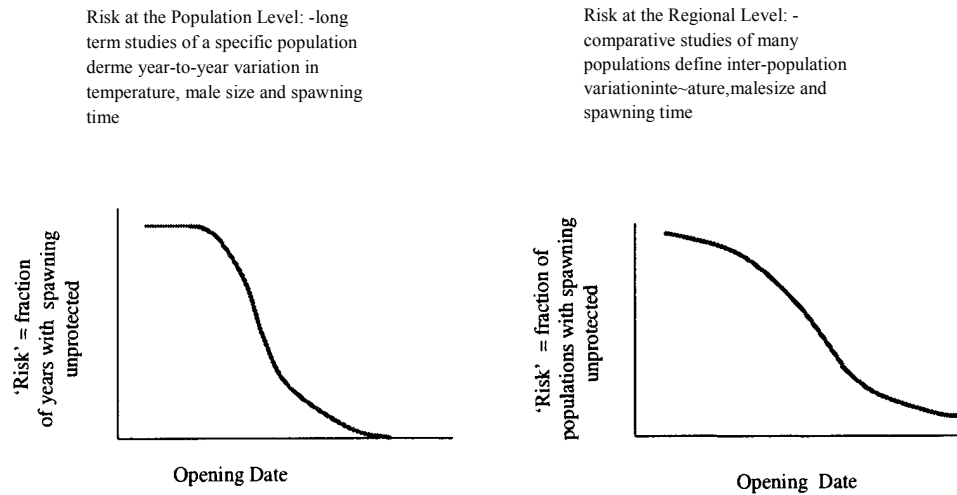

Figure 15. Operational definitions of risk at the level of an individual population and at the regional level, involving a group of populations. At the population level: risk is defined as the fraction of years expected to experience a level of protection less than the level established as acceptable by the policymaker. At the regional level: risk is defined as the fraction of populations expected to experience a level of protection less than the acceptable level.
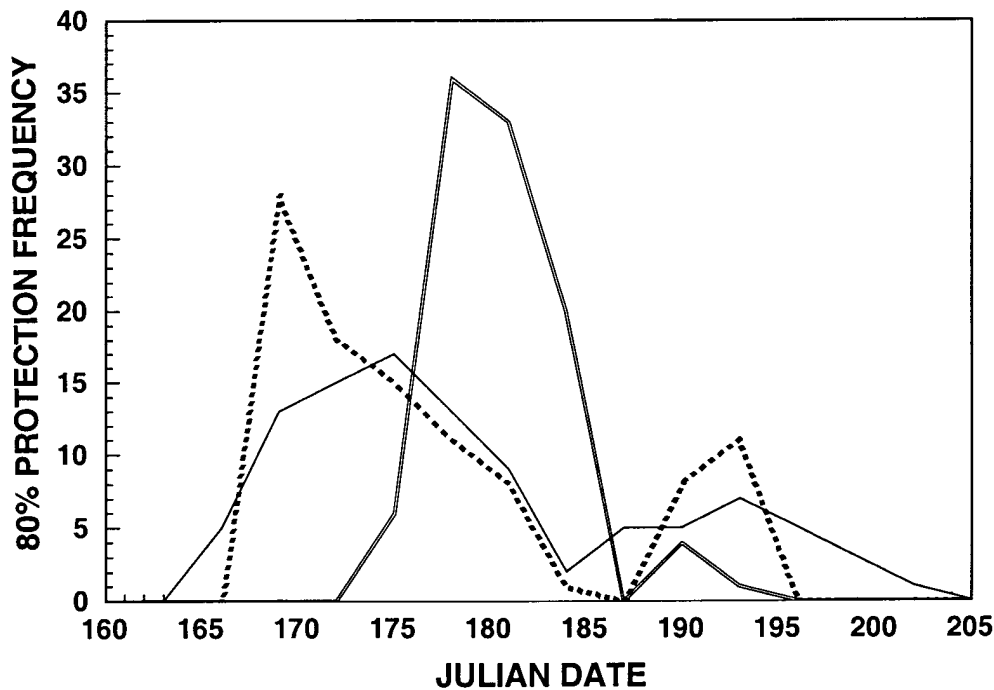

Figure 16. Simulated frequency distributions for dates providing 80% brood protection for: the Lake Opeongo population over the long term, 'eastern Ontario' populations in 1990, 'eastern Ontario' populations over the long term.

mentation of historical patterns of variation in both spring temperature regimes and male size distributions permits an evaluation of risk (loss of nesting males) associated with different opening dates within the parental care period. Thus, predictive ability and historical bounds on uncertainty are the key elements in developing a regional context for regulatory actions that seek to conserve spawning stocks.

Acknowledgments

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