EFFECTS OF FOOD ABUNDANCE AND TEMPERATURE ON GROWTH, SURVIVAL, DEVELOPMENT AND ABUNDANCE OF LARVAL AND JUVENILE SMALLMOUTH BASS

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ABSTRACT

EFFECTS OF FOOD ABUNDANCE AND TEMPERATURE ON GROWTH, SURVIVAL, DEVELOPMENT AND ABUNDANCE OF LARVAL AND JUVENILE SMALLMOUTH BASS *(MICROPTERUS DOLOMIEU)*

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The objective of my research was to determine the importance of prey availability and temperature to abundance and vital rates of young-of-the-year (YOY) smallmouth bass (SMB) during the parental care period of development. Results of this research suggested that food limitation is a relatively minor phenomenon in SMB populations during the larval and early juvenile periods of development and that the most important cause of mortality may be predation. Swimming speed, foraging rate, agonistic interactions and nearest neighbour distance of individual YOY were unrelated to brood size, suggesting that competition for prey resources did not increase with brood size. Dispersion of broods within the nesting territories was positively related to both body size and brood size, but YOY density within broods did not differ across brood size. Zooplankton sampling within and adjacent to natural broods revealed no evidence for resource depression by YOY bass. The size of first-feeding larvae differed significantly among years. The average duration of the embryonic and larval periods of development differed significantly among years. Brood-specific growth rates of larvae were positively associated with water temperature in 4 of 5 years. The relationship between mean annual growth rate and water temperature was significantly correlated among years. In contrast, brood-specific growth rates of larvae were not significantly related to the seasonal peak in prey biomass, nor did prey biomass account for much of the inter-annual variability in larval growth rates. Brood-specific mortality rates differed significantly among years. Mortality rates of early larvae were generally equal to, or below, those of late larvae within years and the critical period hypothesis in first-feeding larvae was rejected. Mortality rates of larvae were not significantly related to the seasonal peak in prey biomass offering little support for the match-mismatch hypothesis. Cumulative mortality was unrelated to phase duration during the early larval phase, but was significantly positively associated during the late larval phase. My results suggested that temperature can strongly influence both growth and developmental rates, size attained at metamorphosis and cumulative mortality rates of larvae. Growth and mortality rates of larvae were negatively associated in all years, supporting the growth-mortality hypothesis.

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Table of Contents

Chapter 5: Effects of Stocking Density and Prey Abundance on Growth and Survival of Young-of-Year Smallmouth Bass: an Experimental Evaluation Using In Situ Enclosures 218

LIST OF TABLES

List of Figures

Chapter 1

General Introduction

Two of the major themes discussed in 'larval fish' literature are growth and survival. Fishes suffer high mortality during the first few months of life, with survival rates in many species reported to be less than 5% in natural populations (May 1974). Many fish species exhibit large year-to-year fluctuations in recruitment, defined here as the number of offspring surviving to the age of first reproduction. Such large fluctuations, often orders of magnitude in range (Rothschild 1986), may lead to considerable variability in annual population abundance. Ultimately, fluctuations in population abundance of many species are believed to be determined through events occurring during early development (Sissenwine 1984; Rothschild 1986). Identifying the factors that determine growth and survival at these early periods is critical to identifying the processes that contribute to variability in recruitment and population abundance.

Starvation and predation have been considered the principal causes of larval mortality in most fish species (Hunter 1981). Consequently, a knowledge of impacts of starvation and predation to mortality during early life history are important areas of fisheries research. The effects of starvation and predation are exerted through numerous biotic and abiotic factors, acting independently or in combination. Biotic factors may include the quality, size and distribution of prey resources (Theilacker 1986; Cushing 1990), competition for food (Frank and Leggett 1986; Jenkins, et al. 1991; Dettmers and Stein 1992; Welker, et al. 1994), and size, density and distribution of predators (Hunter

1981; Taggart and Leggett 1987a; Bailey and Houde 1989; Luecke, et al. 1990; Purcell and Grover 1990), whereas abiotic factors may include factors such as direction and speed of wind and temperature (Crecco, et al. 1986; Taggart and Leggett 1987b; Mooij and Tongeren 1990; Brown, et al. 1993; Bailey, et al. 1995; Michaletz 1997). Biotic factors typically affect populations in a density-dependent manner as opposed to abiotic factors which often exert their effects in a density-independent manner. Density-independent means that population growth (i.e., number or biomass) is unrelated to population density; density-dependent means that there is a relationship between population growth and population density (Sissenwine 1984). Despite an extensive list of research studies on mortality of fishes during early life history, no clear agreement exists on the relative importance of key factors governing growth and survival. Part of the reason for this stems from the complexity of the problem itself, but also because relationships among key factors likely vary among species, with fecundity and between years.

Evidence for density-dependent mechanisms in regulating growth and survival of larval fishes in the field has remained elusive (Savoy and Crecco 1988; Jenkins, et al. 1991; Shi, et al. 1997). Theoretically, larval growth rates may be affected by density-dependent mechanisms (Ware 1975; Shepherd and Cushing 1980; Sissenwine 1984); however, with the absence of supporting field data, density-dependence has remained a key assumption in models of larval fish ecology. This presents problems for theoretical ecology as well. For instance, the ability of larvae to reduce prey abundance below that required for maximum growth is an assumption used in some theoretical models testing density-dependent control of recruitment (Rutherford 1992). However, starvation of larvae in the field has been documented in only a few studies (O'Connell 1980; Hewitt, et al. 1985; Theilacker 1986; McGurk 1989) and prey densities in natural conditions often appear adequate to support maximum growth of larvae (Houde 1978; Kiorboe, et al. 1985; Oiestad 1985; Purcell and Grover 1990).

Early studies on growth, mortality and recruitment focused on the nutritional condition of young fishes to demonstrate the degree of food limitation experienced by larvae (Laurence 1974; Lasker 1975). Hjort (1914), studying stock dynamics of Norwegian herring *Clupea harengus* and cod *Gadus morhua*, first proposed the 'critical period' concept, suggesting that newly feeding larvae are especially prone to starvation, and that recruitment reflected the survival rate during this critical period. Early reviews found the evidence for a critical period to be inconclusive (Marr 1956; May 1974; Dahlberg 1979). In a recent review, Leggett and Deblois (1994) conclude that available evidence does not support Hjort's 'critical period' as an important factor in recruitment variation in marine fishes.

Cushing (1974a) introduced the 'match-mismatch' hypothesis, which proposes that larval survival is dependent on the match between abundance of prey and larval production. This hypothesis compliments Hjort's 'critical period' concept but removes the restriction that the match between prey and larval production be restricted to a critical time during the larval period. However, evidence from subsequent studies, including recent reviews by Cushing (1990) and Leggett and Deblois (1994) suggest that matching of prey resources with larval abundance is less important than previously thought.

With starvation as an unlikely source of mortality, emphasis shifted to predation as the principal cause of mortality in larval fishes (Hunter 1981). The importance of predation as an important source of mortality in larval fish is widely accepted (Bailey and Houde 1989); however, quantifying its impact in the field remains difficult. Measuring predation in the field is difficult due to sampling problems associated with the patchy nature of predator distributions, the high diversity of potential predators and the rapid digestion of fish larvae by predators (Greene 1985; Bailey and Houde 1989; Heath 1992). Several field studies have attempted to overcome these difficulties by estimating mortality due to predation indirectly, as the difference between total mortality rate and age-specific starvation (Hewitt, et al. 1985; Theilacker 1986). It is perhaps unreasonable to expect predation to account for all of the non-starvation mortality and the relative importance of starvation and predation as causes of mortality in young fishes remains unresolved (Bailey and Houde 1989; Leggett and Deblois 1994).

Searching for a single solution to the complex problem of growth, survival and recruitment may be unreasonable (Sissenwine 1984; Anderson 1988; Leggett and Deblois 1994). Miller et al. (1988) stressed the need for a conceptual framework to both integrate existing ecological information and focus future studies. As many of the factors critical to larval survival and growth (starvation and predation) appear to be size-dependent, Miller et al. (1988) proposed an integrating framework based on body size. The essence of this conceptual framework was not entirely new, for ecologists had earlier realized how size-specific growth and mortality rates could interact to determine survivorship in fish populations (Cushing 1974b; Ware 1975; Shepherd and Cushing 1980).

Most recently, emphasis has shifted towards integrating the roles of starvation, food availability and predation (Ware 1975; Shepherd and Cushing 1980). Termed the 'growth-mortality hypothesis' (Anderson 1988), it proposes that predation decreases with increasing size and therefore, survival is directly related to growth rate. This hypothesis emphasizes the interaction of growth and predation; predation functions as the primary source of mortality, but food availability remains critical through its positive influence on growth rates (Rice, et al. 1987; Miller, et al. 1990). That mortality rates are generally size-dependent has been shown both inter-specifically (Peterson and Wroblewski 1984; McGurk 1986) and intra-specifically in both marine (Veer and Bergman 1987; DeVries, et al. 1990; Pepin, et al. 1992) and freshwater (Post and Prankevicius 1987) fishes. Also, several field studies have shown mortality rates of larval cohorts to be inversely related to growth rates (Graham and Townsend 1985) and food availability (Castro and Cowen 1991).

The 'stage duration hypothesis' (Chambers and Leggett 1987; Houde 1987), closely allied with the growth-mortality hypothesis, proposes that larvae which find adequate food will achieve high growth rates and therefore reach metamorphosis at an early age; the sooner individuals achieve metamorphosis, the higher their probability of survival. This hypothesis predicts that groups (year-classes, cohorts) achieving metamorphosis at earlier ages will experience lower cumulative mortality (Chambers and Leggett 1987; Houde 1987; Pepin 1991; Rice, et al. 1993). This proposition depends on the influence of growth rate on stage duration; larvae with the highest growth rates also develop more rapidly. Early development and growth are influenced by a variety of factors, most notably food availability, temperature and initial size (Chambers and Leggett

1987; Pepin 1991; Pepin 1997). Under this hypothesis, fast-growing larvae have a higher probability of survival simply because of shorter larval period duration, even if mortality rates are not size dependent. However, assuming size-selective mortality is operating, faster growing individuals may benefit from the combined effects of shorter larval period duration and lower predation risk during the larval period.

Vulnerability of larval fish to predation is influenced by numerous factors, especially the relative sizes of prey and predators (Bailey and Houde 1989; Pepin, et al. 1992; Paradis, et al. 1996), but also on the guild of predators present and predator-prey seasonal cycles. The commonly expressed view that older and larger larvae are less vulnerable to predation has recently been challenged (Litvak and Leggett 1992). The proposition was based principally on experiments that examined the probability of capture of larvae by predators, but failed to include other components of the attack cycle, including encounter and attack probabilities (Fuiman and Margurran 1994; Paradis, et al. 1996). Several laboratory studies examining predation risk in relation to length show vulnerability curves of larvae to predators to be dome shaped, with maximal vulnerability occurring at some intermediate size (Bailey and Houde 1989; Paradis, et al. 1996). Others, (Litvak and Leggett 1992; Pepin, et al. 1992), examine the effects of length for equal-aged individuals on vulnerability to predation and show that early larval capelin *Mallotus villosus*, have higher survival in trials with stickleback predators *Gasterosteus aculeatus* than do larger larvae of the same age. Bertram and Leggett (1994), in contrast, found no difference in the number of captures of 'small and large' and 'young and old' recently metamorphosed winter flounder *Pleuronectes americanus*, by individual predatory shrimp *Crangon septemspinosa*, after separating the effects of prey size and age. Results from several field studies also suggest that larger larvae may not have a survival advantage. Studies applying recent otolith-reading technology found no evidence for size-selective mortality (Laidig, et al. 1991; Brown and Bailey 1992). Also, survival rates were higher for small, late-hatching American shad *Alosa sapidissima*, than larger, early-hatching individuals (Hoenig, et al. 1990). Bertram and Leggett (1994) caution that the subtle differences in predation risk observed in their study are potentially ecologically inconsequential, and conclude that there is, at present, no firm support for the argument that being larger, or smaller, at a given age is superior.

Little progress has been made in solving the causes of mortality of larval and juvenile fish since Hjort (1914) first proposed starvation as a possible mechanism (Anderson 1988; Leggett and Deblois 1994). Failure to detect consistent relationships between food abundance and/or predation and survival persists, in part, due to the complexity of the problem, the number of variables that may influence growth and survival, and inappropriate technology for sampling larval fish. Recent developments in otolith technology have, for example, resulted in more accurate estimates of larval ages, compared to traditional studies that relied upon presumed stage durations (Crecco and Savoy 1985; Essig and Cole 1986).

Notwithstanding the technological aspects, previous studies have suffered from several common problems and/or omissions. First, practical difficulties have restricted many field studies to particular life stages, often carried out at large spatial scales. Thus, the discrepancy between scale of sampling and proposed mechanisms governing recruitment and larval ecology is vast (Frank 1988). Studies undertaken at inappropriate spatial scales may obscure density-dependent relationships that might exist at smaller scales (Heath 1992). Recent studies (Rice, et al. 1987; Ehlinger 1989; Rice, et al. 1993) suggest that our understanding of recruitment processes may be more rapidly enhanced by considering the effects of individual variability and the attributes of survivors. Furthermore, Blaxter (1986) states that small scale processes believed to be important in recruitment, have not been thoroughly examined in large scale studies.

Obtaining accurate estimates of larval mortality rate in the field presents another formidable problem. Taggart and Leggett (1987a) described the difficulty in obtaining accurate estimates of larval mortality for capelin *Mallotus villosus*, in a small embayment as more than just a trivial problem, and suggested that obtaining accurate estimates of larval mortality in larger ocean systems is doubtful. The difficulties associated with determining growth and mortality rates in the field may account, in part, for the abundance of laboratory studies. Results from laboratory studies may be difficult to extrapolate to the field, and one of the more intriguing aspects of these studies has been the apparent discrepancy between prey density required for adequate growth by larvae in laboratory aquaria compared to observed values under natural conditions. Prey concentrations required for high survival under laboratory conditions are often much greater than levels present in nature (Houde 1978; Sissenwine 1984) and suggests that zooplankton densities in nature must be much lower than previously thought for starvation to occur. The discrepancy between prey densities required for larval fish growth in field and laboratory studies may be explained by the failure of laboratory studies to adequately reflect natural conditions experienced by larval fish (MacKenzie, et al. 1990).

The challenge of field studies is not simply to document changes in growth and mortality rates of larval fishes, but to understand the principal processes that influence the dynamics of growth and mortality. Resolving the importance of prey availability to growth and survival and determining the relationship between growth and survival are relationships that must be determined in the field and not simply extrapolated from laboratory studies.

Food availability and predation risk are major processes influencing growth and mortality of most animals. Yet many animals are forced to compromise between food acquisition and predator avoidance (Lima and Dill 1990). The purpose of my dissertation is to determine the importance of food limitation to variability in growth and mortality of young-of-the-year (YOY) smallmouth bass, *Micropterus dolomieu.* Food limitation can affect growth and mortality in three ways: (1) by starvation; (2) through reduced growth rates and (3) by enhanced vulnerability to predation, or by any combination of these factors. If YOY are not food-limited, then survival of smallmouth bass should be predominantly affected by predation.

My dissertation is organized into 6 chapters. In chapter 1, the literature on growth and survival of larval and juvenile fishes is critically reviewed. Chapter 2 provides a general description of the methods used throughout the dissertation.

Chapter 3 presents the results of a study on the behavioral ontogeny of smallmouth bass. The objective of this chapter was to measure changes in swimming speed, foraging rate, and agonistic interactions among individuals and to measure size-based (total length) differences in these behaviours across brood size. If young are competing for food resources, I predict that agonistic interactions will be significantly higher in large broods relative to smaller broods, and that agonistic behaviour will increase with body size as energetic needs increase. Further, I predict that foraging rates will be lower in large broods relative to smaller broods. I also measure the area of water occupied by broods (dispersion) across body size and brood-size category, as the degree of competition for food resources may depend, in part, on the size of parental male territories.

Chapter 4 presents the results of a long-term field study to determine the importance of prey availability to first-year growth and mortality in a natural population of smallmouth bass. Data for my dissertation were collected from 1991 to 1993. Additionally, a retrospective analysis of data I collected on this same population in 1988 and 1989 is included to present a more comprehensive examination. If growth rates of offspring are a function of their foraging behaviour (see chapter 3) and prey density, then I predict growth rates will be higher and mortality rates lower in years when peaks in prey biomass most closely match the spawning period of smallmouth bass.

A second objective of this chapter is to address several main questions about larval fish growth and mortality that are not fully understood. For instance, what is the relative contribution of temperature to variation in growth and mortality rates of smallmouth bass offspring within a nesting season. Temperature can be an important factor controlling metabolism, growth and development in larvae, and may ultimately affect the time period that young bass remain susceptible to predation (Pepin 1991; Chambers and Leggett 1992). With this long-term data set, I hope to gain a better understanding of how temperature may affect larval growth and mortality under natural conditions. As smallmouth bass spawn over a relatively wide temperature range (13-21 °C; pers. obs.), and owing to the large seasonal variation in water temperatures, it is likely that temperature could have profound effects on growth rates, developmental times and survival within a nesting season.

Finally, I test several other key predictions underlying hypotheses of growth and survival that have dominated thinking in this area. For instance, I examine: 1) the relationship between growth and developmental rates and survival to metamorphosis. Given that metamorphosis in larval fishes is generally size- rather than age-related, I predict that cumulative mortality to metamorphosis will be higher in slower-growing larvae; 2) whether survival rates are directly related to growth rates. I predict that if growth rates are important to survival in larvae then, instantaneous mortality rates of larval broods will be negatively related to instantaneous growth rates.

In Chapter 5 I investigate, further, the role of food limitation on growth and survival of young smallmouth bass through the use of two field experiments. Using in situ enclosures I ask; what is the effect of stocking density (1992) and prey abundance (1993) on growth and mortality rates? If growth rates of larval and early juvenile smallmouth bass are food limited, I predict that growth rates will be negatively related to larval stocking density and positively related to prey abundance. Also, assuming a positive relationship between food abundance and larval survival I predict survival rates to be negatively related to stocking density (1992) and positively related to prey density (1993). Growth and mortality rates of enclosure-held fish are compared with those from the lake population.

In chapter 6, results from the study are summarized and conclusions are presented.

1.1 The Study Species

The smallmouth bass is a large, carnivorous fish (Scott and Crossman 1973) and in Lake Opeongo nesting males range from 4 to 12 + years old and measure between 20 and 45 cm in fork length (Ridgway and Friesen 1992). Historically, smallmouth bass inhabited rocky lakes and streams in eastern and central North America. More recently, the range of the species has expanded considerably in North America, through stocking efforts aimed at increasing recreational fishing opportunities. The diet of adults is comprised primarily of crayfish and small fish.

Males typically appear in the shallow littoral zone (< 2 m) in late-May to establish territories and build nests, when water temperatures rise to 15 °C (Shuter, et al. 1980). Nests consist of shallow, circular depressions formed through the sweeping action of the male's caudal and pectoral fins (Coble 1975; Ridgway, et al. 1989). In Lake Opeongo, age of first maturity ranges from 4 to 9 years (Ridgway, et al. 1991).

Following courtship, males begin a period of solitary parental care that may last 5 weeks or more (Ridgway, et al. 1989; Ridgway and Friesen 1992). Smallmouth bass undergo indirect development (Balon 1981; Balon 1985b) and progress through the embryonic, larval and juvenile periods while under parental care. Thresholds that separate periods are often very distinct events in fishes and are truly decisive events of ontogeny (Balon 1985a). In smallmouth bass, the threshold between the embryonic and larval periods is characterized by the onset of exogenous feeding, while the threshold between the larval and juvenile periods is characterized, among other things, by a rapid change in body colour from black to green/brown and the appearance of fully differentiated fins.

The duration of the parental care period is highly variable within and among years and reflects the temperature mediated developmental rate of embryos and larvae (Hubbs and Bailey 1938; Shuter, et al. 1980). For instance, the duration of the embryonic period has been shown to range between 8 and 21 days in Lake Opeongo (Shuter, et al. 1980; Ridgway and Friesen 1992). Following initiation of exogenous feeding, duration of parental care ranges from 1 to 27 days (Ridgway and Friesen 1992). During the first few months of life, larvae and juveniles feed largely on suspended zooplankton. Juveniles switch to benthivory soon after dispersal from their natal nests. In fall, when temperatures drop below 10 °C, smallmouth bass become inactive and rely on accumulated food reserves to maintain metabolism through the winter (Oliver, et al. 1979; Shuter, et al. 1980). As a consequence, survival of offspring through the first winter may be largely dependent on accumulating sufficient energy reserves during the first summer of life.

Chapter 2

General Methods

Data for this dissertation were collected from 1991 to 1993 and include field observations, behavioral studies and field experiments on larval and juvenile smallmouth bass (hereafter SMB). In addition, a retrospective analysis of data I collected in 1988 and 1989 on this same population is included, to provide a more comprehensive analysis of factors influencing growth and mortality. Preliminary behavioral studies conducted in 1991 served as a guideline for a more intensive examination of behavioral ontogeny during the last two reproductive seasons. In situ enclosures were employed to investigate the relationship of larval density (stocking density experiment) and prey abundance (supplemental feeding experiment) with first-year growth and mortality. In this chapter I discuss general methods applicable to the entire thesis. Methods that pertain only to certain sections or experiments of the dissertation are discussed where appropriate.

2.1 Study Site

Field work was conducted on Lake Opeongo (45° 42'N, 78° 22'W), situated in the southeastern region of Algonquin Provincial Park, Ontario, Canada. Lake Opeongo has a surface area of approximately 59 km^2 with a maximum depth of 52 m (Martin and Fry 1973). The lake is moderately oligotrophic and consists of four major basins joined by narrow channels. SMB were introduced into the lake in the 1920's (Martin and Fry 1973), largely to supplement the existing salmonid fishery (Ridgway, et al. 1991), and have since established a self-sustaining population.

Data for this research were collected on SMB nesting within Jones Bay, Lake Opeongo (Figure 2.1). Historically, researchers have divided the bay into three sections (South, Central and North); data for this thesis were collected from males nesting in the south section of the bay. Field work began in mid May, just prior to the onset of spawning, and continued until offspring from all nests had dispersed.

SMB spawn in the narrow littoral zone of Lake Opeongo (Ridgway, et al. 1991), preferring silt, gravel or boulder substrate, with low to moderate slopes. Fallen trees, boulders and aquatic plants provide cover in the littoral zone. Males nest at depths ranging from 0.25 to 2.5 m and from 1 to 50 m from the main shoreline (personal observation). Ridgway et al. (1991) have shown that nesting space in this population is not a limiting resource for adult males. This observation has been supported by an examination of factors that may govern nest density at large and small scales within Lake Opeongo (Rejwan, et al. 1997). SMB spawn throughout the lake, but surveys have shown that 25 - 52% of all nests occur in Jones Bay each season (Ridgway 1986).

The littoral zone within Jones Bay is diverse with regard to both its physical and biological attributes. I divided the littoral zone into three habitats: Exposed, Protected and Intermediate. All three habitats were used by nesting males, however, large males preferred exposed habitat while most small males nested in protected habitat.

Exposed habitat was characterized by shoreline areas directly exposed to prevailing northwest winds with a fetch greater than 1 km. Sediments are generally not deposited in wind-swept areas, and crevices between the rocks and large boulders overlying the substrate provide ideal hiding sites for offspring. Protected habitat can be characterized as areas sheltered from the prevailing northwest winds. Protected habitat is most often found on the lee side of small islands, or in sheltered bays along the main shoreline. The fetch from prevailing northwesterly winds on protected habitat is less than 50 m, and often no more than a few meters. Protected areas can further be characterized as depositional areas, with soft clay or muddy sediments overlying the rocks and boulders. Aquatic vegetation and submerged tree trunks are numerous in this habitat. Intermediate habitat is characterized by shoreline areas having a fetch between 50 and 1000 m relative to the direction of prevailing winds. Additionally, nests in the intermediate habitat may be situated downwind of gravel or rocky shoals, that serve to dissipate wave action.

2.2 Nesting Male Survey

Shoreline surveys, using mask and snorkel, were conducted daily beginning in late-May and continuing throughout the reproductive season. Once located, nests were individually marked with a numbered brick placed adjacent to the nest and locations recorded on a map. Nesting males were captured by angling, tagged, measured for fork length and scales collected for aging. Individually numbered Floy anchor tags (Floy Tag and Manufacturing Inc., Seattle, WA, USA) were embedded in the dorsal musculature beneath the last soft fin ray of the dorsal fin. A second diver remained in the water while the nesting male was processed to prevent predation of offspring in the nest. The tagging procedure required approximately 3 - 5 minutes to complete, after which the male was released in the immediate vicinity of his nest.

2.3 Brood Size Measurements

The number of offspring in a nest (hereafter referred to as 'brood size') was estimated using the methods of Friesen (1990). Daily, visual estimates of brood size began on the first day of the larval period and continued until no offspring remained in the nest. Brood size was estimated using visual counts of individuals, or groups of individuals, while snorkelling. I counted each individual in small broods (< 200) and counted groups of individuals (10, 25, or 50 individuals per group) in larger broods. Three estimates of brood size were made on each date and brood size was recorded as the mean of the three estimates. In conducting behavioral observations (Chapter 3), I grouped brood sizes into three brood-size categories: small (< 500), medium (500 - 1500), large (> 1500) broods.

I verified brood size estimates on a subset of nests (n = 20) from outside my study area. After completing a visual estimate, a large hoop net was used to capture the entire brood. All individuals in a netted brood were subsequently counted (real brood size) and then returned to their nest. I used simple linear regression to determine if brood size estimates accurately reflected real brood size (Fig. 2.2). Least squares regression resulted in the following relationship between real and estimated brood sizes:

$$BS_r = 33.65 + 1.12 \cdot BS_{est};$$

where BS_r equals real brood size and BS_{est} is estimated brood size ($r^2 = 0.87$). With few exceptions, I consistently underestimated real brood size. Estimates ranged from 5 to

19% below real values, the deviations increasing with increasing brood size.

2.4 Young-of-Year Sampling and Measurement

In order to determine brood-specific growth rates I sampled offspring from nests at 4 day intervals beginning on the first day of the larval period. Samples of 8 - 15 individuals were randomly collected with an aquarium dip net and placed in a 5% buffered formalin solution. Total length (TL; tip of snout to tip of tail) and standard length (SL; tip of snout to tip of the notochord) of individuals were measured to the nearest 0.1 mm, using a Wild dissecting microscope fitted with an ocular micrometer. Older juveniles were measured with the same precision using hand calipers. Following metamorphosis, juveniles collected for sampling from nests having <200 individuals were measured at the nest site using a 4x magnifying lens and hand calipers and immediately returned to the nest.

The life-history model for fishes proposes a hierarchical system of intervals, consisting of periods, phases and steps which are separated by thresholds (Balon 1975; Balon 1981). In this dissertation I have determined growth and mortality rates using all three intervals. At the period interval, rates have been determined for larvae and juveniles. Growth and mortality rates were also determined for the protopterygiolarval and the pterygiolarval phases of the larval period (Balon 1975). The former phase begins at first-feeding and ends with the absorption of the yolk sac and the differentiation of the embryonic median fin fold; the latter phase begins at the termination of the first phase and ends when the embryonic median fin fold is entirely differentiated. In SMB, termination of the final larval phase is also accompanied by a rapid change in body colour from black to a brown/green characteristic of adults. For the purposes of this dissertation, I will refer to the protopterygiolarval and pterygiolarval phases as 'early' and 'late' larval phases and the larvae within these phases as 'early larvae' and 'late larvae', respectively. At the shortest interval (steps) I have measured growth and mortality rates at 4-d intervals within the larval and juvenile periods. In fishes that undergo indirect development, such as SMB, the juvenile period encompasses the interval between metamorphosis and first reproduction (Balon 1975; Flegler-Balon 1989). In this study, I examined growth and mortality of juveniles only during the first few weeks of the juvenile period. I refer to this interval as the 'early juvenile phase'.

2.5 Water Temperature Recording

Water temperature was recorded from late May to July 1991-1993, with a continuous recording thermograph at a fixed site within the littoral zone of Jones Bay. The thermograph was placed at a depth of 80 cm, which approximated the mean depth of SMB nests in Lake Opeongo. Littoral zone water temperatures were recorded daily in 1988 and 1989 at Harkness Laboratory, situated at the southern end of Lake Opeongo, and daily means calculated. A strong linear relationship between temperature at Jones Bay and Harkness Laboratory existed:

1992; Jones Bay T °C = $-0.76 + 1.03 \times$ (lab T °C), $n=91$, $r^2=.94$

1993; Jones Bay T °C = $-4.69 + 1.20 \times$ (lab T °C), $n=53$, $r^2=.93$

I used these relationships to derive the following equation to predict temperatures in Jones Bay from temperatures taken at Harkness laboratory in 1988 and 1989:

$$\text{Jones Bay T°C} = -2.73 + 1.12 \times (\text{lab T °C})$$

Using the developmental history of each nest, including date of spawning, hatch, first-feeding, metamorphosis and dispersal, in combination with the mean daily water temperature data recorded for all five nesting seasons, I calculated mean brood-specific water temperatures for each of the embryonic, larval and juvenile periods of development.

2.6 Zooplankton Sampling

Zooplankton samples were collected from mid-May to late-July, encompassing the entire SMB reproductive season. Samples were collected from a fixed station in each of the exposed and protected habitats in Jones Bay in 1988 and again from 1991 to 1993. The location of sampling stations remained the same each year. Fixed stations were located in the littoral zone in approximately 1 m of water (typical location for SMB nests).

Samples were collected at 4-d intervals in 1988 and 1 or 2 wk intervals in other years. Seven samples were collected on each sampling date in each habitat. Samples were horizontally spaced at 2 m intervals, aligned parallel to the shoreline. The location of each sample was marked using white plastic vials, anchored near the substrate. The vials facilitated sampling, owing to the small inter-sample distance and also allowed samples to be collected at the same location throughout the season.

The patchy nature of zooplankton distributions is well documented (Malone and McQueen 1983; Pinel-Alloul, et al. 1988; Pinel-Alloul and Pont 1991); however, the implications of patchiness for population processes in larval fishes remains controversial. My objective in designing a strategy for sampling zooplankton was to determine variability in zooplankton abundance at spatial scales pertinent to SMB. As larval fish-prey interactions typically occur at fine scales (MacKenzie, et al. 1990), I chose to sample zooplankton at a horizontal spatial scale of two metres. Previous research has shown that the dispersion of broods away from their natal nests increases dramatically with offspring development, reaching a mean maximum distance of 12 m during the juvenile period (Friesen 1990). The cumulative distance between the 7 zooplankton samples in a site equalled 12 m, approximating the maximum dispersion distance for broods in Lake Opeongo.

Zooplankton samples (20 l) were collected using an electric bilge pump (ITT Fluid Products, Guelph, ON, with a capacity of 40 l min^{-1}) mounted in the bow of a boat. Sampling at a site proceeded in an upwind direction to minimize disturbance to the surrounding waters. The bow of the boat was manually guided into position by an individual standing alongside the boat. Upon reaching a plastic marker, a second individual, standing in the bow of the boat, lowered a 2 m length of opaque tubing (20 cm diameter) onto the substrate, directly over the plastic vial. This effectively isolated zooplankton organisms within the tubing. A long length of flexible tubing (2.5 cm diameter), attached to the intake port of the pump, was used to collect a 20 l sample.

Samples were filtered through 40 micron nitex netting and preserved in 5% buffered formalin solution. In the laboratory samples were sub-sampled and a minimum of 250 specimens were identified. A Wild-Leitz microscope, mounted to a black and white camera and interfaced with a computer work station was used to enumerate samples. Results were expressed as density (numbers $\times$ L^{-1}) and dry weight biomass (mg $\times$ m^{-3}). Biomass of specimens was calculated from published (Dumont, et al. 1975; Rosen 1981) length-weight regressions.

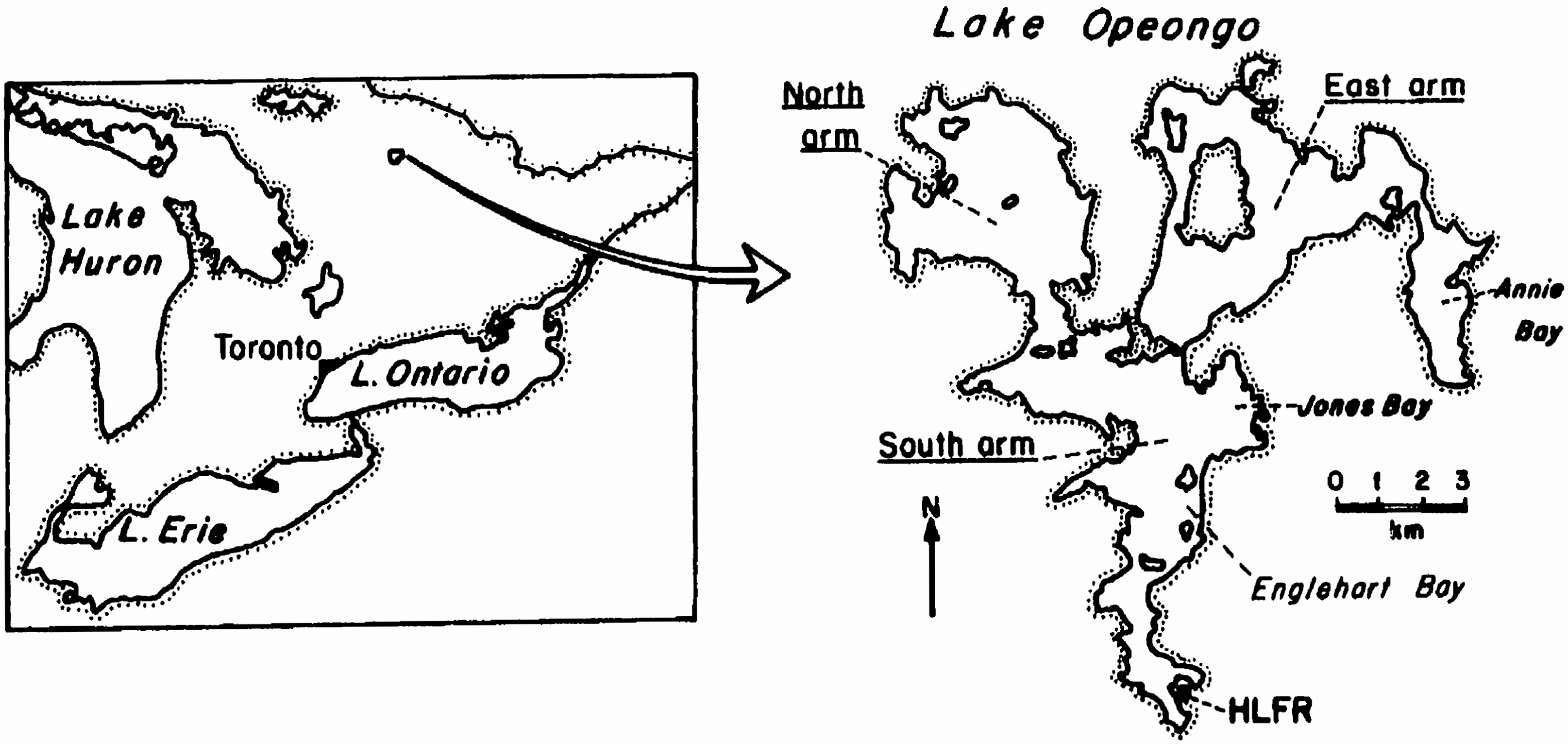

Figure 2.1. Map of southern Ontario showing the location of Lake Opeongo. The field study was conducted in Jones Bay, situated in the South arm of Lake Opeongo. HLFR refers to the Harkness Laboratory of Fisheries Research (OMNR).

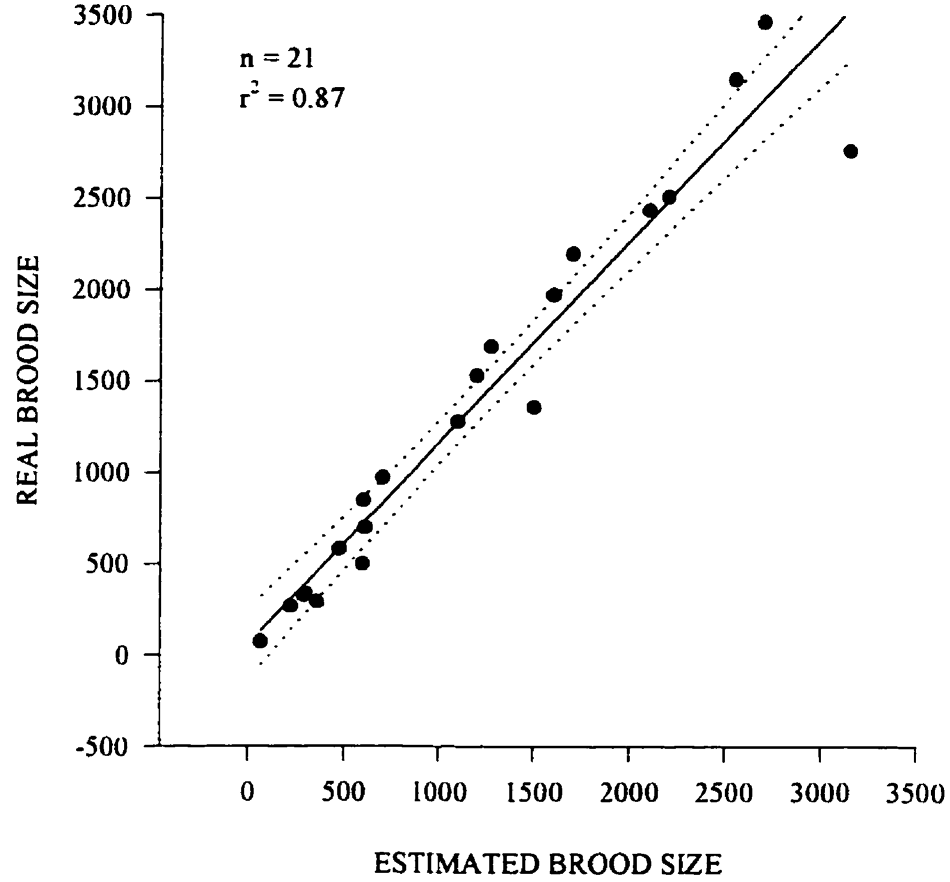

Figure 2.2. The relationship between estimated brood size (number of individuals in a brood) and real brood size for smallmouth bass in Lake Opeongo. Dashed lines indicate 95% confidence limits. Sample size and coefficient of determination are indicated.

Chapter 3

Behavioral Ontogeny in Larval and Early Juvenile Smallmouth Bass: Influence of Body Size and Brood Size

3.1 Introduction

Research into the causes of variability in fish growth has generated interest in size-related changes in foraging behaviour (Miller, et al. 1992). The foraging abilities of fish change considerably between first-feeding and metamorphosis (Werner and Gilliam 1984) and the importance of successful feeding to growth and survival during early life history in fishes is generally accepted (Hunter 1981; Houde 1987). In numerous fish species, early development is characterized by extensive morphological, physiological and behavioral changes (Blaxter 1986; Govoni, et al. 1986; Noakes and Godin 1988; Youson 1988; Mark, et al. 1989; Huntingford 1993; Post and Lee 1996; Poling and Fuiman 1997). Following the onset of exogenous feeding, foraging efficiency improves rapidly in many fishes (Houde and Schekter 1980; Miller, et al. 1992), and changes in foraging ability can dramatically influence growth and survival of young-of-year (YOY) fishes (Luecke, et al. 1990; Wu and Culver 1992; Rice, et al. 1993; Olson 1996).

Ontogenetic niche shifts, characterized by changes in habitat use and diet, are common in many species of fish (Werner and Gilliam 1984). For example, size-related diet shifts enable individuals to capture and consume progressively larger prey (Osenberg and Mittelbach 1989; Olson 1996), while ontogenetic habitat shifts are related to foraging rate-predation risk trade-offs (Werner, et al. 1983a; Werner, et al. 1983b). Diet shifts have been shown to dramatically increase first-year growth in related centrarchids (Osenberg and Mittelbach 1989; Olson 1996) and other species (Stergiou and Fourtouni 1991; Buijse and Houthuijzen 1992). Importantly, high growth during early development is critical to both the occurrence and timing of ontogenetic diet shifts (Olson 1996).

Smallmouth bass (*Micropterus dolomieu*, henceforth SMB) also undergo an ontogenetic diet shift, as juveniles shift from planktivory to benthivory shortly after dispersal from male territories (Clark and Mancini 1980; Easton, et al. 1996). The diet shift in SMB may also be dependent on early growth rates of larvae. One of the potential factors affecting growth rates during the larval and early juvenile periods of development is intraspecific competition for food resources. As larvae grow, the benefits of shoaling may decrease relative to and become out-weighed by the costs of competition for food. Despite the extensive literature available on SMB, there are few detailed examinations of behavioral ontogeny during the early life history periods. Moreover, to my knowledge, no long-term field studies of first-year growth and mortality have quantified the behavioral ontogeny of YOY in relation to local food densities, body size or brood size effects at a fine scale.

This chapter investigates the dynamics of behavioral ontogeny of larval and juvenile SMB during the parental care period of development. Observations were recorded at two levels: individual fish and entire broods. At the individual level, I examined changes in swimming speed, foraging rate, agonistic interactions and nearest neighbour distance. At the brood level, I examined changes in dispersion (m^2) of larvae between first-feeding and metamorphosis. Behaviour at both levels were examined across body size and brood-size category, and describe and quantify the ontogeny of social behaviour in a natural population of SMB. The behavioral observations were designed to determine the effect of body size and brood-size category on variation in behavioral ontogeny of larval and early juvenile SMB. If YOY SMB are food-limited I predicted that foraging rates would be lower and agonistic rates higher in large broods than in small broods. In addition, I compared prey abundance within and adjacent to SMB broods to evaluate the impact of foraging by YOY on prey resources. If YOY SMB are food-limited, I predicted that they would have a negative effect on prey densities near the nest.

This study addresses important aspects of the ecology of YOY fish, since foraging success at these early life history stages determines growth and survival rates and ultimately, can affect recruitment to the adult population. In addressing these objectives, I adopt a non-traditional approach in larval fish studies and base the study entirely on underwater sampling and observations.

3.2 Methods

Data were collected in the South section of Jones Bay from 1991 to 1993 during the SMB reproductive season. Beginning in late May, daily shoreline swims, using mask and snorkel, were conducted to locate new nests and determine the status of established nests. New nests were marked with a numbered brick placed on the substrate adjacent to the nest. Parental males were captured by angling and were measured, tagged and released near their nests.

3.2.1 General Procedures

I analyzed behaviour of SMB offspring at two levels: brood (family) and individual. A synopsis of the behavioral studies conducted in 1991, 1992 and 1993 and the associated independent variables are listed in Table 3.1. Size-related (total length = TL) changes in behaviour were recorded with fish with average TL's of 9.5, 14.0, 18.5 and 28 mm. YOY averaging 9.5 and 14.0 mm represented larvae in the early and late larval phases of development and are here referred to as early and late larvae, respectively (see Chapter 2 for description of development intervals). YOY averaging 18.5 and 28 mm were recently metamorphosed and pre-dispersal juveniles, respectively. Estimates of brood dispersion were conducted in 1992 on similar-sized offspring. Length at age of YOY differed slightly among years, due to variation in developmental rates related to temperature. The interval of time over which behavioral recordings were conducted within a season ranged from 3 - 4 weeks, due to inter-nest variation in both the spawning date of males and developmental rate of offspring. Sample sizes for all behaviour recorded are listed in Table 3.2. I estimated brood size (number of offspring in a brood) for all broods in the study area (described in Chapter 2). For the purposes of this chapter, brood size estimates were grouped into three brood-size categories as follows: small (< 500), medium (500 - 1500) and large (> 1500) individuals.

3.2.2 Behaviour of Individuals

During the 1991 and 1993 nesting seasons, swimming speed, foraging behaviour, agonistic interactions and nearest neighbour distances of YOY SMB were recorded. All behaviour recorded was conducted in Lake Opeongo under natural conditions and followed a standard procedure. Broods, in which I recorded individual behaviour, were randomly selected from the set of all active nests in the study area. Observations were made using the focal animal technique (Altmann 1974). During each focal period (2 min) the behaviour of only one fish was recorded. A focal period commenced by randomly selecting a fish for observation. Time was logged with a stopwatch and the focal period commenced 10 s after initial identification of the trial fish. All observations were recorded with an underwater slate and grease pencil by a swimmer using mask and snorkel. Young SMB did not appear to be disturbed by the presence of the swimmer (the author), who remained nearly motionless while observing.

Swimming Speed

In 1991 I examined the effect of brood-size category (small vs. large) on YOY swimming speed. During the 1993 reproductive season I examined swimming speed in relation to body size (TL) and habitat type (exposed vs. protected). Because of the enormous practical difficulties associated with measuring sustained swimming speed under natural conditions (Beamish 1978), I used a simple experimental approach that would provide meaningful data in an ecological sense and also be of value to the broader field of larval fish ecology. I estimated sustained swimming speed, defined here as total distance (cm) travelled along the swimming path divided by the duration (seconds) of the observation. The horizontal and vertical components of the swimming path of randomly chosen fish were measured independently (see Table 3.2 for sample sizes). For a given brood, I first recorded the horizontal movement of focal fish, after which the vertical movement of other focal fish was measured. Swimming speeds were recorded in cm s^{-1}.

To measure the horizontal swimming path, a rectangular grid, constructed of 3 cm PVC tubing, and measuring 2.5 x 3.5 m, was placed on the substrate near the nest. Lead-core line was used to divide the grid into 25 cm^2 units. To record the horizontal swimming path of fish, a grid pattern identical to the large grid positioned on the littoral substrate was etched onto the slates. The path of a fish was continuously recorded on an underwater slate using a grease pencil.

To facilitate tracking the vertical swimming path of fish, 7 metal rods, 150 cm in length and 2 cm in diameter, were positioned upright in the water near the nest. The length of each rod was divided into 15 cm segments, each segment marked a different colour using water-resistant paint. The vertical position of a fish could be determined more easily by noting its position relative to the coloured segments. To record the vertical movement of fish, the depth profile of the littoral zone was etched onto the slates. The depth profile on the slates was divided vertically so as to mimic the 15 cm coloured segments of the metal rods positioned in the lake.

In the laboratory, I copied the swimming paths of fish from the slates onto graph paper. To determine sustainable swimming speed, I overlaid the graph paper onto a screen monitor and traced the swimming path. After adjusting for scale, the path length of the tracing was sent to a microcomputer by a digitizing tablet (Terminal Display Systems Ltd). Swimming path length was divided by focal period duration to determine sustainable swimming speed for each fish. Mean sustainable swimming speed for a brood was calculated as the sum of the mean sustainable speeds of individual fish divided by the total number of fish observed and was calculated independently for the horizontal and vertical components.

Foraging Behaviour

No attempt was made to estimate foraging success of YOY SMB, because of the small size of prey organisms they consumed. I examined the foraging behaviour of fish across body size (TL) and brood-size categories (small, large). For each body size-brood-size category combination, I examined the behaviour of 10 randomly chosen fish in each of three broods. A total of 180 fish were observed. Behaviour recorded were determined during preliminary observations conducted in 1991 and follow those described by Brown and Colgan (1984). Foraging behaviours are described as follows:

1) *Orientate*: Response of fish to a prey item involving alignment of the fish to face toward the prey.
2) Fixate: Pause between orientation and capturing act, with flexing of the body axis.
3) *Lunge*: A prey-capture response in which the body of the larvae assumes an S-shaped position followed by the rapid forward movement of the larvae toward its prey.
4) *Bite*: A rapid lunge at prey item; however, no s-strike posture precedes it.
5) *Attack rate*: Equals the sum of s-strikes and bites divided by the foraging time.

Agonistic Interactions

Preliminary observations in 1991 were conducted to determine the effect of brood-size category (small vs. large) on the frequency of agonistic behaviour in recently metamorphosed juveniles (Table 3.1). I next investigated how agonistic behaviour differed across body size (TL = 9.5, 18.5, 28.0 mm) and year (1992, 1993). Since I was examining the development of agonistic behaviour in very young fish, behaviour recorded consisted of simple modal action patterns (MAPs) (Cole and Noakes 1980). Due to the low frequency of agonistic interactions among larvae in 1991, I decided to measure agonistic behaviour only once during the larval period in 1992 and 1993, but twice during the juvenile period, when agonistic behaviour appeared to increase. I examined the behaviour of 10 randomly chosen fish from each of 5 broods for each body size (TL)-year combination in 1992 and 1993 (Table 3.2). Behaviours recorded were:

1) *Chase*: A rapid darting approach toward another fish without making direct contact.
2) *Escape*: A fish accelerated away from a threatening fish.
3) *Avoid*: An obvious change in direction of movement of the focal animal away from another fish that was approaching or being approached by the focal animal.

Nearest Neighbour Distance

I examined the nearest neighbour distance (NND) of fish across body size (TL) and brood-size category (small and large) at two locations (central and peripheral) within broods (Table 3.1). Fifteen fish were randomly selected for observation in both the central and peripheral positions in each of three broods for each body size (TL) × brood-size category combination (Table 3.2). A fish was defined as central if the distance between it and the estimated central point of the brood was less than the shortest distance between the fish and the nearest edge of the brood. For a fish to be defined as peripheral, the distance between it and the nearest outer edge of the brood could be no greater than 1/4 the distance between it and the centre of the brood. Defined in this way, a buffer region existed between centrally and peripherally positioned fish.

I estimated nearest neighbour distance as the distance between the nose of the focal fish and the nearest part of the closest neighbouring fish. I expressed this distance in terms of 'YOY body lengths' and then assigned it to one of four nearest neighbour intervals (Table 3.3). Each interval corresponded to 4-body lengths and the mid-point for the four intervals corresponded to 2, 6, 10 and 14 body lengths. NND's > 16 body lengths were arbitrarily adjusted to 16 to maintain consistency among intervals. I expressed NND in millimetres for each sample time-nearest neighbour interval by multiplying YOY TL by the midpoint for each nearest neighbour interval.

3.2.3 Brood Dispersion

I recorded brood dispersion during the 1992 nesting season. By brood dispersion I refer to the surface area of water occupied by a brood within the territory of a parental male. Brood dispersion was measured across two independent variables: body size (9.5, 14.0, 18.5 mm) and brood-size category (small, medium, large). Ten nests in each brood-size category were randomly selected from the entire set of active nests in the study area for measurement at each of the three sampling times. An insufficient number of nests in the large brood-size category at the final sample time resulted in an unbalanced ANOVA design (Table 3.2). I also examined the influence of body size and brood-size category on YOY density within SMB broods. Density estimates were obtained by dividing brood dispersion estimates by brood size estimates for each nest.

Brood dispersion was measured between 1000 and 1600 h by a team of two divers using mask and snorkel. Upon locating a brood, the divers swam slowly around the periphery of the brood, placing 10 to 15 coloured markers on the substrate to indicate the brood's position. After all markers were positioned, the bearing (degrees) and distance (cm) of each marker from the centre of the guarding male's nest was measured using a compass and tape measure. Bearing and distance measurements were converted to Cartesian coordinates and a fortran coded algorithm was used to determine the minimum convex polygon as an estimator of brood dispersion.

3.2.4 Behaviour Analyses

Two-way ANOVA models that included the interaction term, were used to analyze individual-level behaviour, with the following exceptions. In 1991 I used a two-sample T-test to test for the one-tailed hypotheses that mean swimming speed and mean frequency of agonistic acts of juvenile SMB (TL = 18.5 mm) in the small brood size category ≤ that of juveniles in the large brood-size category. To analyze nearest neighbour distance (NND) I used a repeated measures ANOVA, with two grouping factors (body size and brood-size category) and one trial factor (location). In all analyses, individual fish selected for observation were treated as sub-samples and mean brood values for each behaviour were used in further analyses. A two-way ANOVA model was also used to analyze brood dispersion data. When necessary, behaviour data were log transformed (ln (x+1) to normalize for analyses (Zar 1984). In all analyses the level of significance was set at 5% (alpha = 0.05). Tukey's a posteriori multiple comparison test was used to distinguish between treatment means.

3.2.5 Prey Abundance

Zooplankton samples were collected at weekly or bi-weekly intervals during the 1993 field season (see Chapter 2 for methods). Samples were collected from two fixed stations within the SMB spawning habitat and analyzed for total biomass and density.

In 1993, I also measured zooplankton biomass within, and immediately adjacent to, SMB broods for evidence of resource depression by YOY SMB. Zooplankton samples were collected at five nest sites at metamorphosis and again five days later. Two samples were collected from each nest site, one from directly within the foraging brood and a second from outside the brood. The within- and outside-brood samples were intended to be representative of zooplankton biomass prior to and following exposure to feeding by YOY SMB, respectively. Samples collected from outside the broods were always located upwind of the brood. Samples consisted of three 10 l replicates which were pooled, filtered through a 40 μm screen and placed in 5% buffered formalin solution. Sample replicates taken from within the brood were collected from 3 different areas within the brood. Samples collected outside the brood were taken at a point approximately 15 m from the brood, with replicates spaced 2 m apart, parallel to the shoreline. Zooplankton samples were sub-sampled and a minimum of 250 specimens were identified. Results are expressed as density (individuals l^{-1}) and dry weight biomass (mg m^{-3}).

I used a one-tailed, paired comparison T-test on logarithmic ($\log_e$) transformed data to determine if foraging by juvenile SMB caused a reduction in prey density and biomass. Zooplankton density and biomass were compared among groups (within- and outside- brood samples) at metamorphosis (TL = 18.5 mm) and again just prior to dispersal (TL = 28.5 mm). A significance level of 5% (alpha = 0.05) was chosen as the critical level of difference among groups.

3.3 Results

3.3.1 Brood Size

In 1992, 92 nests were found in South Jones Bay, of which 72 reached the larval period (first-feeding) of development. Brood size estimates at first-feeding ranged from 17 to 5900 and the size distribution of broods was highly skewed towards lower numbers (Fig 3.1). Of the nests in which young survived to first-feeding, 15% had < 500 (category 1), 28% contained 500 - 1500 (category 2) and 57% had > 1500 individuals (category 3).

3.3.2 Behaviour of Individuals

Swimming Speed

Mean sustained swimming speed of juveniles did not differ between small and large brood-size categories in either the horizontal (T = 1.86, p = 0.275) or vertical (T = 1.130,

$p = 0.291$) direction. Also, mean horizontal swimming speed of YOY increased significantly with YOY TL ($F_{2,30} = 421.68$, $p < 0.0005$). Mean horizontal swimming speed of 9.5, 14.0 and 18.5 mm YOY averaged 8.3, 16.3 and 24.6 mm s^{-1}, respectively (Figure 3.2). Tukey's multiple comparison test showed that horizontal swimming speed differed significantly among all three body sizes. Mean swimming speed in the horizontal component also differed significantly across habitat type ($F_{1,30} = 8.85$, $p = 0.006$). In the exposed habitat, mean horizontal swimming speed increased by 118% between the early larval (TL = 9.5 mm) and late larval phases (TL = 14.0 mm), but increased by only 40% between the late larval phase and the early juvenile period (TL = 18 mm). Similarly, in the protected habitat mean horizontal swimming speed increased by 127% between the early and late larval phases, but only by 29% between the late larval and early juvenile period. Although the percentage increase in mean horizontal swimming speed with body size was similar across habitats, the average horizontal swimming speed of YOY in the protected habitat remained higher than values in the exposed habitat at all three body sizes.

The mean vertical swimming speed also differed significantly across body size ($F_{2,30} = 365.46$, $p < 0.0005$). Tukey's multiple comparison test indicated that vertical swimming speed differed significantly at all three body sizes. Mean swimming speed in the vertical component also differed significantly across habitats ($F_{1,30} = 11.69$, $p = 0.002$), such that mean swimming speeds of offspring in the protected habitat were higher at all three body sizes. The percentage increase in mean vertical swimming speed showed the same general pattern observed in mean horizontal swimming speed. In the exposed habitat, mean vertical swimming speed increased by 109% and 48% between the 9.5-14.0

and 14.0-18.5 mm length intervals, respectively, while values increased by 138% and 17% for the same body length intervals in the protected habitat.

YOY utilized the entire water column while foraging; however, the length of the horizontal swimming path always exceeded that in the vertical plane. This was not surprising, given the shallow depth (< 1 m) of littoral-zone water occupied by SMB broods. The length of the vertical swimming path equalled 40, 45 and 37% of the length of the horizontal swimming path for 9.5, 14.0 and 18.5 mm YOY, respectively. Given that the average depth of water occupied by broods was < 10% of the average maximum dispersion distance of broods from their nests (Friesen 1990), the length of the vertical swimming path, relative to the horizontal path, was considerable.

Foraging Behaviour

There was considerable variation in first feeding date among broods which reflects the consistent inverse relationship between male size and the seasonal timing of spawning (Ridgway, et al. 1991). Offspring from nests spawned early in the season began active feeding on June 18, while young from nests spawned late in the season initiated feeding on July 02. Less than 10% of first-feeding larvae made no feeding attempts during the two minute focal period and the percentage of non-feeders declined to nearly zero in late larval and early juvenile YOY.

All five foraging behaviours differed significantly across YOY TL (Table 3.4). In contrast, no significant effect of brood-size category on any of the observed foraging behaviours was found. Frequency of *Orientate* increased positively with YOY TL and

Tukey's test showed that the frequency of *Orientate* of 9.5 mm larvae was significantly lower than that observed in 14.0 and 18.5 mm YOY, which did not differ (Fig. 3.3a). *Fixate* increased during the larval period, but declined dramatically following metamorphosis (Fig. 3.3b). Tukey's test showed that the frequency of *Fixate* was significantly lower in juveniles than larvae at both sampling times, which did not differ from each other. The frequency of *Lunge* showed a very similar pattern to that observed for *Fixate* (Fig 3.3c). However, as fish did not lunge at all prey items on which they fixated, the number of lunges occurring during a focal period was often lower. Tukey's test showed that frequency of *Lunge* differed among all three body sizes. The frequency of *Bite* increased with YOY TL and differed significantly among all three size classes (Fig. 3.3d). *Attack rate* increased positively with YOY TL (Fig. 3.3e). Tukey's test showed that *Attack rate* of 9.5 mm larvae was significantly lower than observed in 14.0 and 18.5 mm larvae and juveniles, which did not differ.

Agonistic Interactions

Larvae foraged actively at first-feeding, but interacted little with siblings. Consequently, few or no agonistic behaviours were recorded among first-feeding larvae, and analyses were conducted only for the two juvenile sample times in 1992 and 1993. All three agonistic behaviours differed significantly across YOY TL (Table 3.5). Between the two juvenile sampling periods, the frequency of *Chases*, *Escapes* and *Avoids* increased by 125, 157 and 126%, respectively. Agonistic behaviours increased linearly with YOY TL (Fig 3.4); however, the daily rate of increase in agonistic behaviours was considerably higher following metamorphosis. This was due to the high absolute growth rate of juveniles, relative to larvae.

In contrast to YOY TL, the frequency of agonistic behaviours did not differ among years, nor was the frequency of *Chases* (T = 1.91, p = 0.100), *Escapes* (T = 1.89, p = 0.094) and *Avoids* (T = 1.17, p = 0.273) in recently metamorphosed juveniles significantly related to brood-size category. My results demonstrated a consistent annual pattern in the frequency of early agonistic behaviours, despite large differences in the chronological age of fish at progressive developmental intervals.

Nearest Neighbour Distance

There was a significant positive increase in NND with increasing body size (Fig. 3.5), however brood-size category had no significant effect on NND (Table 3.6). There was also a significant difference in NND between offspring located near the centre of the brood and those located near the edge. The NND for 9.5, 14.0 and 18.5 mm YOY located in the periphery of the brood was 57, 35 and 33% greater than that of YOY located in the centre of the brood. The location-TL interaction term was marginally significant and likely resulted from the extremely small sample size.

3.3.3 Brood Dispersion

During the 1992 nesting season, I recorded foraging movements of 98 broods during three developmental intervals in South Jones Bay; 30 broods at each of the two larval sampling intervals and 28 broods at the juvenile sampling interval, resulting in an unbalanced 2-way ANOVA.

The area of water occupied by broods increased significantly with YOY TL ($F_{2,81} = 149.55$, $p < 0.001$) and brood-size category ($F_{2,81} = 67.21$, $p < 0.001$). At first-feeding (TL = 9.5 mm), brood dispersion averaged 0.8, 2.6 and 5.8 m^{-2} for the small, medium and large brood-size categories, respectively. Upon reaching metamorphosis, brood dispersion had increased dramatically, averaging 14.8, 36.7 and 64.1 m^2 for the small, medium and large brood-size categories. Thus, area of water occupied increased by an order of magnitude between first-feeding and metamorphosis, regardless of brood-size category. The dispersion of broods increased linearly with body size across all brood-size categories (Fig. 3.6). Tukey's test showed that area of water occupied by broods differed among all three body sizes. Similarly, Tukey's test showed that the area occupied by broods differed across all 3 brood-size categories.

Brood density showed a significant seasonal decline with body size ($F_{2,81} = 196.52$, $p < 0.0005$); however, brood density did not differ across brood-size category at any of the developmental intervals ($F_{2,81} = 2.31$, $p = 0.29$). The, seasonal decline in brood density appeared to be brought about through the concomitant increase in brood dispersion and a decline in brood size.

3.3.4 Prey Abundance

The period from late May to mid-July was marked by large changes in zooplankton density and biomass. Values peaked in early June, approximately 2 weeks prior to the initiation of exogenous feeding of YOY SMB. Peak density and dry weight biomass on

09 June averaged 23 individuals l^{-1} and 155 mg m^{-3} respectively. At this time, the cladoceran, *Polyphemus pediculus*, comprised 85% of the total biomass. In late June, at which time SMB offspring had initiated exogenous feeding, zooplankton density and biomass had dropped sharply, averaging 15 l^{-1} and 45 mg m^{-3}, respectively (Fig. 3.7).

During the larval period of SMB development, zooplankton density in the exposed habitat was higher than that measured in the protected habitat (Table 3.7). In contrast, zooplankton density during the juvenile period of development was higher in the protected habitat. Zooplankton biomass was higher in the exposed habitat during both the larval and juvenile periods of SMB development. This seasonal variation in prey abundance contributed to a significant interaction between habitat type and sample date for zooplankton density and biomass (Table 3.8).

I measured the impact of foraging by juvenile SMB on zooplankton density and biomass twice during the parental care period of development (Fig. 3.8). The diet of young SMB at this time consisted primarily of zooplankton found within the water column (pers. obs.). I found no significant difference in either the density or biomass of zooplankton between treatments (inside versus outside brood) at either of the sample times (Table 3.9).

3.4 Discussion

3.4.1 Behaviour of Individuals

Swimming Speed

Results showed that sustained swimming speeds of juvenile SMB did not differ across brood-size category. As focal observation times were standardized for experimental fish (2 min), my results also indicated that the mean length of the swimming path did not differ across brood size category. Also notable was that feeding rates of young SMB did not differ across large and small brood-size categories (discussed below). Given the large difference in the number of individuals per brood between small and large brood-size categories and the low prey densities in Lake Opeongo (25-30 l^{-1}), I had anticipated longer swimming paths and/or higher swimming speeds for individuals in large broods. Lack of an effect of brood-size category on mean swimming speed may have been a consequence of spacing between individuals to reduce competition for prey resources, as individual-level (nearest neighbour distance) and brood-level (density) estimates showed no difference across brood-size categories.

When expressed in body lengths s^{-1} (BL s^{-1}), sustained swimming speeds of young SMB increased approximately proportionally to body length during the larval and early juvenile period of development, similar to the pattern generally observed in larval fish (Blaxter 1986). The pattern of increasing swimming speed (mm s^{-1}) with body size is consistent with that of other species, including northern anchovy *Engraulis mordax* (Hunter 1972), Atlantic herring *Clupea harengus*, plaice *Pleuronectes platessa* (Ehrlich, et al. 1976), and black sea bream *Acanthopagrus schlegeli* (Fukuhara 1987). Like SMB, these marine species swim nearly constantly. Zebra danios *Danio rerio*, in contrast, travel much greater distances per unit time, despite spending relatively less time swimming (Fuiman and Webb 1988). Such large differences in swimming speed may be attributable to differences in morphological development (Fuiman and Webb 1988) or swimming mode

(Webb and Weihs 1986). SMB larvae appear to be relatively slow swimmers at first feeding and this may be due to their large yolk sac and the presence of the continuous median fin fold. However following differentiation of the median fin fold, sustainable swimming speed increased by 120%. This is comparable to the increase in sustainable swimming speed of walleye *Stizostedion vitreum*, which doubles between first feeding and complete yolk absorption (Houde 1969).

Estimating swimming speed under natural conditions required that movement in the horizontal and vertical planes be measured separately. Notable in my study was that distance travelled in the vertical plane equalled 35-40% of the distance travelled in the horizontal plane, comprising a significant component of the total distance travelled. Thus, results of my study suggest that young SMB may be capable of searching larger volumes of water than previously reported in laboratory studies. These results have important implications for prey encounter rates under natural conditions, as swimming speed, together with reactive distance, determines the volume of water young fish are capable of searching (Hunter 1981; Blaxter 1986).

Sustainable swimming speed of young SMB in the horizontal plane compared closely with values estimated for similar-sized largemouth bass juveniles under laboratory conditions (Larimore and Duever 1968). However, no studies have estimated swimming speeds of larval and early juvenile centrarchids in the field and comparisons between laboratory and field situations must be made cautiously. Laboratory estimates of swimming speeds of larval fish in tanks may generally be low (Houde and Schekter 1980), as spatial constraints, imposed by container size, in conjunction with sensory deprivation, may serve to restrict fish movement in laboratory settings (Blaxter 1970). For example, von Westernhagen and Rosenthal (1979) show swimming speed of the Pacific herring *Clupea harengus pallasi* larvae in the laboratory to be nearly 50% below the value obtained under natural conditions. Comparison of YOY swimming speeds in the field with those conducted in swimming flumes must be made with equal caution, as swimming speeds of larvae in flumes, measured in BL s^{-1}, are generally 3x higher than those for larvae moving freely in tanks (Blaxter 1986). Not surprisingly, horizontal sustainable swimming speeds (BL s^{-1}) of SMB in my study were lower than average sustainable swimming speeds of other freshwater perciformes in swimming flumes, including largemouth bass (Laurence 1972), yellow perch *Perca flavescens* (Houde 1969) and striped bass *Morone saxitilis* (Meng 1993).

Swimming speeds of YOY in the protected habitat were consistently higher than those in the exposed habitat. Previous studies have demonstrated that larval fish alter their swimming speeds in response to changing prey conditions (Hunter and Thomas 1974) and may increase encounter rates by swimming faster at low prey densities (Munk and Kiørboe 1985). Although zooplankton biomass tended to be higher in the exposed habitat, values did not differ significantly. Thus, prey biomass alone did not explain the difference in swimming speed across habitat types.

For the purposes of this study, Jones Bay was divided into two major habitat types, based on their exposure to prevailing north-westerly winds (see Chapter 2). Although I did not conduct systematic measurements of water turbulence, the impact of wind-generated turbulence on the foraging behaviour of young SMB was observed underwater. Under all but the most severe wind conditions, young SMB in exposed habitat often oriented directly into the current, intercepting prey items delivered by wind-generated turbulence. This type of foraging behaviour was rarely observed in young SMB from broods located in the protected habitat. To confirm these observations, I determined the direction of surface water flow for broods in both protected and exposed habitats and then estimated the orientation of individual fish (n =30 per brood) with respect to the direction of surface water flow (data not analyzed). Subsequent analyses of these data will clarify whether the orientation of individuals with respect to the prevailing inshore current differs between broods located in exposed and protected habitat.

Rothschild (1986) suggests predator-prey contact rates based only on the relative density of predator and prey underestimate contact rates, since contact depends on both the relative density and the relative velocity of predator and prey . Rothschild and Osborn (1988) show analytically that even under moderate water turbulence, predator prey contact rates are higher than those computed for relative density alone. Similarly, MacKenzie and Leggett (1991) using simulations, found that encounter rates between marine fish and nauplii were seriously underestimated by excluding the contribution of small-scale turbulence, especially at low prey densities (i.e. $\leq 35\ l^{-1}$).

The contribution of small-scale turbulence to feeding rates of larval fish is supported by recent field studies. Sundby and Fossum (1990) show that the feeding rate of larval cod *Gadus morhua*, increases dramatically with increasing wind speed, while MacKenzie et al. (1990) determine that the feeding rates of larval fish collected at sea are higher than predicted laboratory values in which turbulence is absent. Kiørboe and Saiz

(1995) demonstrate that cruising predators, like many fish larvae, benefit from turbulent fluid motion only at relatively high turbulent intensities. This suggests that the effect of turbulence on contact rates between young SMB and their prey may be greatest in the exposed habitat.

Small-scale turbulence can act to increase predator-prey contact rates and the discrepancy between findings in the laboratory and field may result from the failure to account for small-scale effects (MacKenzie and Leggett 1991). However, most larval fish studies undertaken on large spatial scales have not considered, or have been unable to determine the importance of larval behavioral responses to prey dynamics at these smaller scales (Hunter and Thomas 1974; Munk and Kiørboe 1985). In my study, measures of swimming speed, foraging behaviour and prey abundance were undertaken at fine scales. Further studies are needed to evaluate the importance of water turbulence to swimming speeds and prey encounter rates of young SMB at these fine scales.

Foraging Behaviour

The frequency of *Lunge* dropped significantly following metamorphosis, consistent with previous results for SMB (Brown and Colgan 1985a). As *Bite* replaced *Lunge* as the prey capture mode, the manner of feeding by post-metamorphic juveniles more closely resembled that of older juveniles and adults. *Fixate*, a behaviour associated with early development in fish (Braum 1978) and possibly incorporated into the act of *Orientate* in later development (Brown and Colgan 1984) generally preceded *Lunge*. Unlike the consistent decline in the frequency of *Fixate* with development reported in SMB by

Brown and Colgan (1985a), Fixate increased between the early larval and late larval phase, prior to dropping significantly following metamorphosis. The difference in the results of the two studies may be due to the turbulent lake environment, compared to the static conditions of the laboratory. The need to *Fixate* prior to striking at prey may be greater in a turbulent environment, when swimming ability is poorly developed in larvae, and abiotic conditions and prey abundance interact to create dynamic feeding conditions.

Changes in the frequency of feeding behaviours of young SMB were strongly associated with YOY total length. Moreover, changes in the frequency of behavioral acts corresponded with specific thresholds that separated developmental intervals during early ontogeny. For instance, the frequency of Fixate and Lunge decreased significantly following metamorphosis. I also observed a consistent year-to-year pattern in the onset and decline in foraging and agonistic behaviours with body size, despite large differences in developmental rate among years. This is consistent with the finding that age is much more variable than size at metamorphosis in this population Friesen (1990). My results support the suggestion by Brown and Colgan (1985a) and Miller et al. (1992) that research related to behavioral ontogeny of fishes be addressed within a size-based framework, as opposed to one based on age.

Following dispersal, juveniles remained nearshore, where they foraged in a solitary manner close to the protective cover of boulders. This foraging mode contrasted sharply with the shoaling behaviour of younger SMB while under parental care. Prior to dispersal, young SMB fed primarily on suspended zooplankton. These observations are consistent with earlier research on this population, showing that the diet of recently metamorphosed juveniles consists primarily of cladocerans (Wales 1981). However, the frequency of benthic foraging by juveniles increased just prior to dispersal in all years (pers. obs.), as previously noted by Ridgway (1989). Wickliff (1920) also report a shift from a diet composed entirely of zooplankton to a mixed diet composed of increasing numbers of immature insects as young SMB reached 16 mm in length. Others (Coble 1975; Clark and Mancini 1980; Easton, et al. 1996) also note the increasing seasonal importance of immature insects in the diet of YOY SMB. Thus, the change in feeding mode following metamorphosis may signal an ontogenetic shift in resource use (Werner and Gilliam 1984). Post and McQueen (1994) demonstrate that variability in growth rates of YOY perch, and subsequent shifts in diet or habitat use, may be mediated through density-dependent competition for prey.

Agonistic Interactions

The pattern of increasing frequency of simple aggressive modal action patterns (MAPs) with offspring size is consistent with earlier observations on closely related centrarchids (Brown and Colgan 1985b). The frequency of *Chases* and *Escapes* in young SMB in my study was much lower however, than that determined for laboratory-reared largemouth bass (Brown and Colgan 1985b). For fish of similar size (ie. 28 mm), the frequency of *Chase* and *Escape* in SMB was lower than values observed in largemouth bass by nearly an order of magnitude. Additionally, the total length of SMB when agonistic behaviour first appeared was lower than that recorded for largemouth bass by Brown and Colgan (1985b). The low frequency of agonistic acts in SMB broods under natural conditions may have been a consequence of spacing among individuals to reduce aggression. The average density in SMB broods at metamorphosis was 88 individuals m^{-3}. In contrast, the stocking density in Brown and Colgan's (1985b) 90 l experimental tanks ranged from 150 (1660 m^{-3}) individuals initially to 30 (330 m^{-3}) per tank by the end of the experiment. Thus, the density of juvenile SMB in my study was at least 4 times lower than that of largemouth bass in Brown and Colgan's (1985b) study.

The distribution of prey resources in Lake Opeongo may also have contributed to the low frequency of agonistic behaviour observed in young SMB. Zooplankton density and biomass showed high variability, both temporally and spatially. The concept of economic defendability states that animals will only defend resources when the benefits exceed the costs of defence (Brown 1964). Syarifuddin and Kramer (1996) suggest that the blue gouramis *Trichogaster trichopterus*, adjusts its level of contest and scramble competition according to the costs and benefits of aggression as determined by the number of competitors and by the potential for missed feeding opportunities. Due to the patchy distribution of zooplankton and the ephemeral nature of the patches in lakes (Pinel-Alloul, et al. 1988; Pinel-Alloul and Pont 1991), monopolization of clumps by individuals would be highly unlikely (Grant and Kramer 1992). Under these conditions, YOY SMB may achieve higher foraging efficiency by remaining in family groups that allow for faster discovery of food patches through local enhancement or social facilitation (Pitcher 1986). For example, juvenile walleye pollock *Theragra chalcogramma*, exploit ephemeral food patches more effectively in the presence of conspecifics (Baird, et al. 1991).

Complex threat/appeasement behaviour, that typically develops from simple aggressive behaviour (Dill 1977; Noakes 1978; Cole and Noakes 1980), was not exhibited by any trial fish. In contrast, Brown (1985) and Brown and Colgan (1985b) noted the appearance of complex threat/appeasement behaviours, including lateral displays, tailbeat and opercular spread during the first 2 months of development. Sabo et al. (1996), in studying the development of agonistic behaviour in juvenile largemouth and smallmouth bass in laboratory and field conditions found few differences between the species. However, behavioral differences were evident between laboratory-reared fish and wild fish. For instance, the frequency of certain agonistic behaviours were generally higher in the laboratory in both species. Also, a higher diversity of agonistic behaviours were exhibited by fish in the laboratory. The early appearance of complex threat/appeasement behaviour exhibited in juvenile largemouth bass (<35 mm, TL) reported by Brown and Colgan (1985b) may have been due, in part, to the high density of fish in the experimental tanks, being nearly an order of magnitude higher than values reported by Sabo et al. (1996) for older juveniles (TL = 79-165 mm).

I observed SMB for the occurrence of agonistic behaviour soon after the initiation of exogenous feeding, and conclude: (1) agonistic behaviour, in the form of simple agonistic behaviour (*Chase*, Escape, *Avoid*) was non-existent, or occurred at very low frequencies during the larval period, (2) the frequencies of simple agonistic behaviour increased following metamorphosis, especially just prior to the dispersal of young from nesting territories; (3) complex agonistic behaviour was not exhibited by offspring during the parental care period of development. The appearance of these simple behaviours so early in life may signal the appearance of more complex agonistic behaviour observed in post-dispersal juvenile bass (Winemiller and Taylor 1987; Sabo, et al. 1996), as shown in other species (Noakes 1978).

The dramatic increase in agonistic behaviour among young SMB just prior to dispersal supports Brown's (1985) hypothesis that agonistic behaviour may be an important mechanism for initiating dispersal in young SMB. Similarly, the onset of aggression in stream salmonids resulting from limited space for feeding territories, may initiate the dispersal of young parr (Cole and Noakes 1980). Juvenile SMB may have dispersed from broods because of an increased tendency to avoid other juveniles and/or a decreased attraction to other individuals. An increase in the frequency of agonistic behaviour makes sense for a species that is switching from a shoaling existence to a solitary one. In contrast, an increase in the frequency of agonistic behaviour with body size would not be predicted for species that spend their lives in shoals. Thus, Morgan et al. (1995) show that during early development of shoaling behaviour in capelin *Mallotus villosus*, the frequency of avoids decreases with increasing larval size.

Nearest Neighbour Distance

NND's increased significantly with body size, but did not differ across brood-size category. These results were consistent with changes in dispersion and density measured at the level of the brood (discussed below). My results also showed that NND's of peripherally located fish were significantly greater than those of centrally located fish at each body length. There was a significant location × body size interaction, indicating that the effect of body size was not consistent across location (ie. peripheral vs. central). The significance of the interaction term may have resulted from the small sample size.

The position an individual occupies within a shoal can have important implications for foraging success and survival in the presence of predators (Lima and Dill 1990). For instance, under limited prey resources, larger NND's between peripherally located fish may result in a foraging advantage over more centrally located fish. Feeding benefits derived through position preference within a shoal have recently been demonstrated in three-spined sticklebacks *Gasterosteus aculeatus* (Buman and Krause 1993), in a mixed shoal comprised of roach *Rutilus rutilus* and chub *Leuciscus cephalus* (Krause 1993) and in a large shoal of migrating Atlantic cod *Gadus morhua* (DeBlois and Rose 1996). In each case, leading fish or peripherally located fish, gained feeding benefits. Alternatively, studies have shown that stragglers and individuals on the periphery of shoals suffer significantly higher mortality rates than average group members (Morgan and Godin 1985; Parrish 1989). Parrish (1992) shows that the relative safety of a position in a shoal depends to a large degree on the attack strategy of the predator; fish in peripheral positions are more vulnerable to marginal predators while invasive predators that enter prey aggregations are just as likely to attack centrally located individuals. Juvenile SMB from older year-classes appeared to be the principle diurnal predators of YOY SMB in Lake Opeongo (pers. obs.). These older juveniles typically positioned themselves around the periphery of a brood, and attacked YOY positioned near the outer edge of the brood. Thus, peripherally located YOY may experience a slightly higher risk of predation than more centrally located fish. Clearly, prey distribution and the presence of predators affected the foraging and social behaviour of young SMB.

3.4.2 Brood Dispersion

Dispersion of SMB broods increased significantly with body size during the first 20 days of exogenous feeding. The increase in the area of water occupied by broods was greater during the second sampling interval, during which time metamorphosis occurred. Shoaling from the time of first-feeding is common in centrarchids, but few studies have examined the dynamics of brood dispersion under natural conditions. Several studies, including Tester (1930) on SMB and Elliott (1976) on largemouth bass, have provided qualitative descriptions of the movement of YOY broods within the vicinity of the nest site, but measurements of brood dispersion or density within broods were not recorded. More recently, Friesen (1990) found that the maximum dispersion distance of SMB broods from their nests was positively related to brood-size category.

As sole parental care givers, do nesting male SMB influence the dispersion of broods within their territories? Defence activities of males peak at the onset of the larval period, but decline steadily to very low levels at metamorphosis (Ridgway 1988). Also, the amount of time nesting males spend with their young and total defence behaviour decline following metamorphosis (Mackereth 1995), suggesting that males reduce parental expenditure during the juvenile period. The role males might have on brood foraging movements would therefore be greatest during the larval period. However, Scott (1997) shows that territory size in nesting males changes in response to the dynamics of brood movements, and not visa versa, especially during the larval period. These results suggest that brood foraging dynamics are not strongly influenced by the behaviour of parental males.

My results also showed that dispersion of broods was positively related to brood-size category. However, after adjusting for brood size, the density of YOY SMB on a per area basis did not differ across brood-size category at any of the sampling times. Assuming uniform zooplankton abundance within the littoral zone, the pattern of brood dispersion observed in this study suggested that (1) the ratio of prey abundance to YOY SMB remained relatively constant on a per area basis among brood size categories, and (2) the prey encounter rate per individual increased during development.

Fish density within SMB broods declined dramatically between first feeding and metamorphosis. The decline in density was due primarily to the combined effects of natural mortality and brood dispersion. Following metamorphosis, fish density within broods remained relatively stable at 25-40 individuals m^{-2}, and may have represented a trade-off between energetic gains from foraging and predation risk. Indeed, mortality rates of young SMB in Lake Opeongo were high, ranging between 10 and 20% d^{-1} each year (see Chapter 4). Spatial and temporal variation in predation risk greatly affect the behavioral decisions of individuals (Lima and Dill 1990). Studies by Werner and Hall (1988) on bluegill *Lepomis machrochirus*, Gilliam and Fraser (1987) on creek chub *Semotilus atromaculatus*, and Foster et al. (1988) on three-spined stickleback *Gasterosteus aculeatus*, have demonstrated that fish are able to assess differences in food level and predation risk. In the presence of predators, experimental studies have shown that foragers switch habitats (Werner and Hall 1976; Mittelbach 1986) or limit their foraging movements (Dill 1983; Dill and Fraser 1984; Milinski 1986; Skutelsky 1996), often at the cost of diminished foraging returns.

For individuals living in groups, the impact of predation risk may be observed at both the individual and group level. For instance, stragglers suffer significantly higher mortality rates than average group members (Magurran and Pitcher 1987; Parrish 1989; Parrish, et al. 1989). In some fish species, *Lecaspius delineatus*, (Andörfer 1980) and various minnows (Magurran and Pitcher 1987; Morgan 1988), shoals become more concentrated in the presence of predators. Lima and Dill (1990) suggest that increased compaction of shoals may result from individuals reducing the frequency or duration of straggling from shoals in the presence of predators. Indeed, predation risk may function to maintain the integrity of groups as the tendency for individuals to leave the safety of a group diminishes with increasing predation risk (Parrish 1992).

In discussing the optimal strategy fish should adopt in balancing feeding requirements with predation risk, Gilliam and Fraser (1987) suggest a simple rule: 'minimize the ratio of mortality rate to foraging rate' (minimize the risk of mortality per unit energy eaten). Gilliam and Fraser (1987) use this rule to successfully predict the food density at which minnows *Semotilus atromaculatus*, shift from a low-food safe habitat to a high-food risky habitat. Also, Gotceitas (1990) was also able to predict the food density level at which bluegill sunfish *Lepomis macrochirus*, switched habitats in the presence of a predator. Future studies need to address the importance of risk-sensitive foraging to better understand the foraging dynamics of SMB broods. The simple rule of 'minimizing the ratio of mortality rate to foraging rate' (Gilliam and Fraser 1987) could be used to predict foraging decisions of individuals or to predict the timing of dispersal of young from the nesting territories.

3.4.3 Prey abundance

Although average density and biomass of zooplankton in outside-brood samples were lower than inside-brood samples, my results suggested that young SMB have little impact on their prey resources. Earlier work on this population, using the same sampling procedure, showed no evidence of resource depression by larval or early juvenile SMB (Friesen 1990). In Friesen's (1990) study, the average date of production of first-feeding SMB larvae closely matched the seasonal peak in zooplankton production. Under the matched larval-prey conditions, the probability of detecting resource depression would have been low. In this study, peak zooplankton production occurred 2 wks prior to the appearance of first-feeding larvae. Failure to detect evidence of resource depression under these mismatched larval-prey conditions, suggested that YOY SMB were not food-limited.

Given the low production of zooplankton in Lake Opeongo, the high density of young SMB within broods and the fixed spatial position of broods within nesting male territories, the high growth rates (see Chapter 4) achieved by young SMB are intriguing. The patchy nature of prey resources, brood shoaling dynamics and size-based changes in behaviour of individuals certainly contribute to their high growth rates. I propose that wind-generated nearshore water motion in freshwater lakes (Davidson-Arnott and McDonald 1989), through its potential to influence predator-prey contact rates (MacKenzie, et al. 1990; Kiorboe and Saiz 1995), may also play a critical role in regulating growth in YOY SMB, and may also explain the lack of effect of foraging by young SMB on prey resources. Consider the following example. The volume of water occupied by an average-sized brood (1000 individuals) at metamorphosis in Lake Opeongo was 15 m^{-3} (based on a mean territory depth of 0.5 m). Attack rate for juveniles in this study averaged 3.5 min^{-1}. Assuming capture success to be 80% (conservative), 2,800 prey would be consumed in one minute. At an average prey density of 25,900 m^{-3}, approximately 388,500 zooplanktors occurred in the 15 m^{-3} of water. Based on these estimates, it would have taken a brood this size 2.5 h to consume all of the prey. Young SMB feed throughout the day (Wales 1981) and forage for approximately 14 h each day in Lake Opeongo (Friesen 1990). At these feeding rates, the entire assemblage of zooplankton in the volume of water occupied by the brood would have to be replaced a minimum of 6 times each day. This example underlines the potential importance of wind-generated water turbulence to feeding rates in young SMB. The importance of water movement to prey renewal in nearshore zones in lotic systems may not be so unlike the situation in lentic systems, where many fishes depend on the unidirectional flow of water for delivery of terrestrial food items.

Numerous studies have investigated the impact of planktivorous fishes on zooplankton communities (Brooks and Dodson 1965; Lazzaro 1987). Consumption estimates by marine fish larvae in the field indicate that individual species may have little impact on the abundance of their prey (Cushing 1983; Jenkins 1987). Moreover, Fortier and Harris (1989) show that the ichthyoplankton assemblage as a whole has little impact on prey biomass. Mills and Forney (1983) however, studying yellow perch *Perca flavescens*, suggest that large YOY year-classes can deplete their prey resources. Determining the impact of predators on their prey resources is difficult in the field, due to the vast number of factors effecting prey abundance. For instance, a negative correlation between predator and prey abundance does not necessarily imply cause-effect. Within- and outside-brood zooplankton samples in my study were collected nearly instantaneously and therefore, may have removed many of the potential confounding effects. My results suggest that young SMB have a minimal effect on their prey resources. The impact of YOY fish on prey resources in the field remains unresolved and the degree to which discrepancies in results reflect methodological differences as opposed to species-specific differences remains to be determined.

In bringing together the vast literature on larval ecology, Miller et al. (1988) proposed that body size be used as an organizational scale. Size-dependent changes in the behavioral ontogeny of YOY SMB in this study support Miller et al.'s (1988) suggestion. The results of this study contribute to understanding more fully the ontogeny of foraging and its relationship with body size in SMB. This information forms an important part of the early life history component of SMB populations and will contribute to understanding SMB growth, survival and recruitment. In the next chapter I examine the contribution of prey abundance and water temperature to variability in growth and survival of YOY SMB.

Table 3.1. Summary of specific behaviours recorded of YOY smallmouth bass in 1991, 1992 and 1993. Independent variables and their associated levels are indicated with the symbol (x). Brood Size Category was a categorical variable and consisted of the following levels; small (< 500), medium (500 - 1500) and large (> 1500) individuals. The location of individuals in a brood was designated as cent =central or perif = peripheral. Habitats types are designated as exp = exposed and pro = protected.

	Independent Variables												
Behaviour	YOY Total Length, (mm)				Brood Size Category			Habitat		Year		Location	
	9.5	14.0	18.5	28.5	small	med	large	exp	pro	1992	1993	cent	perif
Individual Level													
swimming speed													
1991 (preliminary)			x		x		x						
1993	x	x	x					x	x				
foraging behaviour	x	x	x		x		x						
agonistic behaviour													
1991 (preliminary)			x		x		x						
1992/93	x		x	x						x	x		
nearest neighbour	x	x	x		x		x					x	x
Brood Level													
dispersion	x	x	x		x	x	x						

Table 3.2. Summary of sample sizes used to record individual and brood level behaviour of YOY smallmouth bass during three field seasons (1991-1993) in Lake Opeongo.

Behaviour	Sample Sizes		
	Broods	Fish/Brood	Total Fish
Individual Level			
swimming speed (1991)	10	16	160
swimming speed (1993)	36	16	576
foraging behaviour	18	10	180
agonistic behaviour (1991)	10	10	100
agonistic behaviour (92/93)	30	10	300
nearest neighbour	18	30	540
Brood Level			
dispersion	88		

Table 3.3. Summary of method to determine nearest neighbour distance (NND) in YOY smallmouth bass during the parental care period of development. Near Neigh Interval = Nearest Neighbour Interval, Body Lengths Per Interval = size of nearest neighbour intervals expressed as YOY body lengths and Mid Int = the midpoint of each nearest neigbour interval expressed as YOY body lengths. TL x Mid Int = NND (millimeters) for each Nearest Neighbour Interval- sampling time combination. See Table 3.2 for sample size.

			YOY Total Length (TL)		
			9.5	14.0	18.5
Near Neigh Interval	Body Lengths Per Interval	Mid Int	TL x Mid Int (mm)	TL x Mid Int (mm)	TL x Mid Int (mm)
1	0 - 4	2	19	28	37
2	4 - 8	6	57	84	111
3	8 - 12	10	95	140	185
4	12 - 16	14	133	196	259

Table 3.4. Results of two-way ANOVA on the effects of YOY total length (mm) and brood size category (small, large) on the frequency of five feeding behaviours in YOY smallmouth bass. See text for full description of independent variables. Interaction term (not shown) was not significant for any behaviour. Asterisk indicates a significant ($p < 0.05$) difference. See Table 3.2 for sample sizes.

	ANOVA			
Behaviour	Source	df	F	P
Orientate	total length	2	38.23	$p < 0.0005^*$
	brood cat	1	1.40	NS
Fixate	total length	2	45.86	$p < 0.0005^*$
	brood cat	1	0.71	NS
Lunge	total length	2	26.16	$p < 0.0005^*$
	brood cat	1	0.47	NS
Bite	total length	2	60.48	$p < 0.0005^*$
	brood cat	1	0.08	NS
Attack rate	total length	2	31.55	$p < 0.0005^*$
	brood cat	1	0.02	NS

Table 3.5. Results of two-way ANOVA on the effects of YOY total length (mm) and year (1992, 1993) on the frequency of three agonistic behaviours in YOY smallmouth bass. Total length of YOY at the three sample times averaged 9.5, 18.5, and 28.5 mm. Interaction term (not shown) was not significant for any behaviour. Asterisk indicates a significant ($p < 0.05$) difference, NS = not significant. See Table 3.2 for sample sizes.

	ANOVA			
Behaviour	Source	df	F	P
Chase	total length	1	41.26	$p < 0.0005^*$
	year	1	0.63	NS
Escape	total length	1	62.39	$p < 0.0005^*$
	year	1	1.01	NS
Avoid	total length	1	92.18	$p < 0.0005^*$
	year	1	1.46	NS

Table 3.6. Results of repeated measures ANOVA on mean nearest neighbour distance between smallmouth bass offspring. The ANOVA model contained two grouping factors, YOY total length (tl = 9.5, 14.0, 18.5 mm) and brood size category (brdcat = large and small) and one trial factor, location (loc = centre and periphery). Asterisk indicated a significant ($p < 0.05$) difference. See Table 3.2 for sample sizes.

	ANOVA			
Source	SS	df	F	P
Between subjects				
tl	93215.18	2	559.78	$p < 0.0005$*
brdcat	334.74	1	4.02	$p = 0.08$
tl × brdcat	251.03	2	1.50	$p = 0.26$
Within subjects				
loc	7320.51	1	103.40	$p < 0.0005$*
loc × tl	1317.22	2	9.30	$p = 0.01$*
loc × brdcat	1.09	1	0.02	$p = 0.91$
loc × tl × brdcat	9.76	2	0.07	$p = 0.94$

Table 3.7. Density (l^{-1}) and biomass (mg m^{-3}) of littoral-zone zooplankton in Jones Bay, Lake Opeongo during the smallmouth bass nesting season. Weekly samples (seven replicates per sample) were collected from a fixed station in both exposed and protected habitats during the larval and juvenile developmental periods. 'Average' indicates average zooplankton values for both habitats.

Develop Period	Density (number l^{-1})			Biomass (mg m^{-3})		
	Exposed	Protected	Average	Exposed	Protected	Average
Larval	28	13	20.5	70	40	55.0
Juvenile	20	32	26.0	38	33	35.5

Table 3.8. Results of two-way ANOVA on the effects of habitat (exposed, protected) and calender date (date) on the density (individuals l^{-1}) and dry weight biomass (mg m^{-3}) of zooplankton during the smallmouth bass nesting season in Lake Opeongo, 1993. Seven zooplankton samples were collected in each habitat on each of five weekly sampling dates ($n = 70$). Calender date (date) is a categorical variable and reflects average zooplankton values during the smallmouth bass larval and juvenile periods of development. Asterisk indicates a significant ($p < 0.05$) difference. Note significant interaction term for both analyses.

	ANOVA				
Dependent Variable	Source	SS	df	F	P
Density	habitat	0.14	1	0.86	NS
	date	5.31	4	8.08	$p < 0.0005^*$
	hab x date	15.03	4	22.89	$p < 0.0005^*$
Biomass	habitat	1.07	1	5.19	0.026^*
	date	3.10	4	3.74	0.009^*
	hab x date	10.98	4	13.27	$p < 0.0005^*$

Table 3.9. Results of one-tailed, paired t-tests to determine if the density (l^{-1}) and biomass (mg m^{-3}) of zooplankton collected outside bass broods were ≥ values within waters occupied by foraging broods at two different times during the juvenile period of development. Total length (mm) of juveniles at the two sampling times were; Juvenile_1 = 18.5 mm and Juvenile_2 = 28.5 mm. Observed t-values (t_{obs}) are indicated and the critical t-value ($t_{0.05(1),4}$) = 2.132.

Sampling Time	Independent Variable	n	df	t_{obs}	p
Juvenile_1					
	density	5	4	0.75	0.49 (NS)
	biomass	5	4	0.60	0.58 (NS)
Juvenile_2					
	density	5	4	0.47	0.66 (NS)
	biomass	5	4	0.56	0.61 (NS)

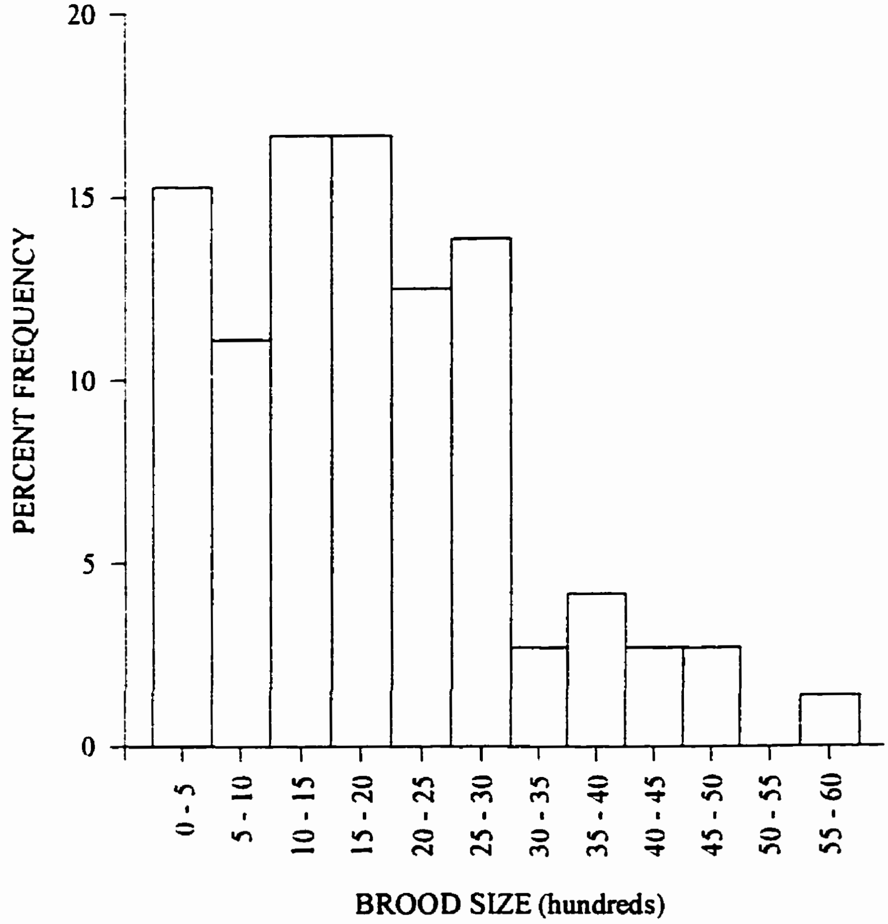

Figure 3.1. Estimated mean brood size (number of individuals in a brood) at first-feeding for smallmouth bass nests in Lake Opeongo, 1992. Sample size (n = 72) refers to the number of active nests in the study area.

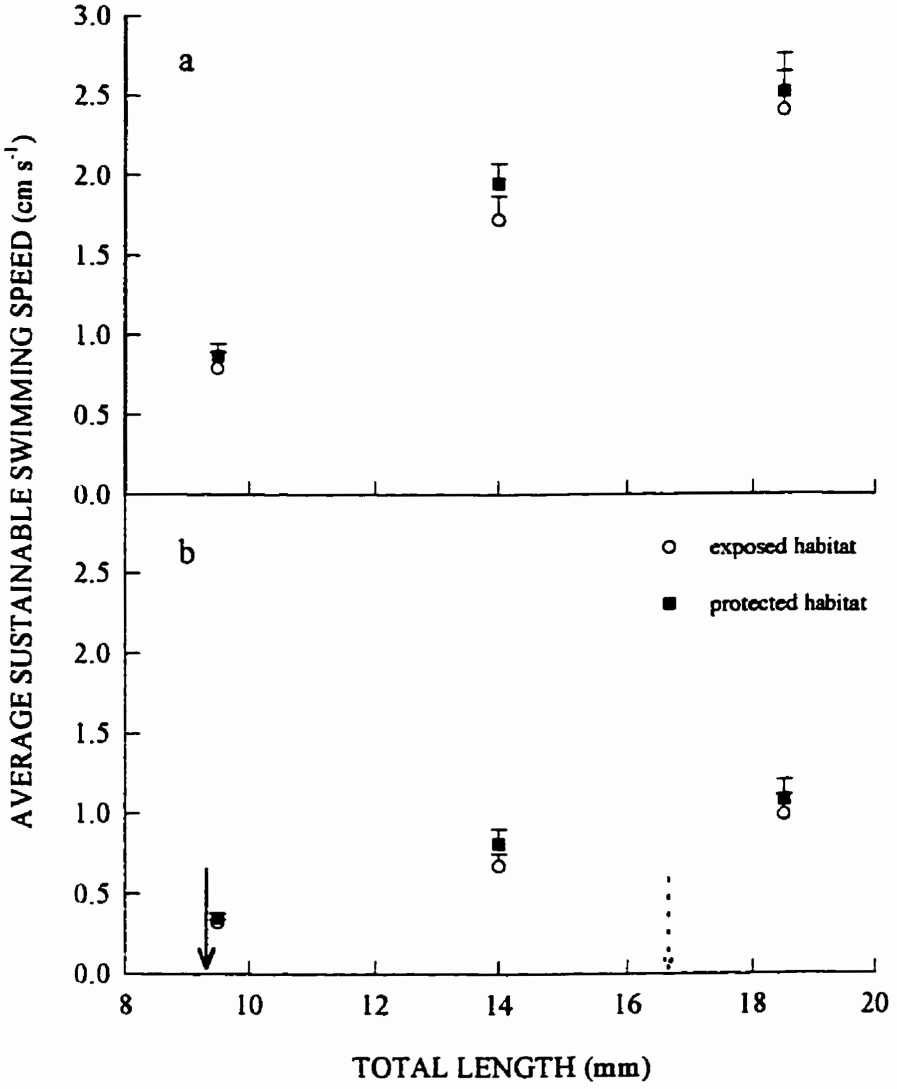

Figure 3.2. Average sustainable swimming speeds (cm s^{-1}; +SD) of YOY smallmouth bass in the (a) horizontal and (b) vertical plane in exposed (white circle) and protected (black square) habitat plotted against total length. The average total length of the offspring at the three sampling times was 9.5 (early larval), 14.0 (late larval) and 18.5 (early juvenile) mm. The solid vertical arrow marks the average length of larvae at the onset of exogenous feeding while the dashed vertical arrow indicates the average length of juveniles at metamorphosis for bass in lake Opeongo, 1993. Sample sizes as presented in Table 3.3.

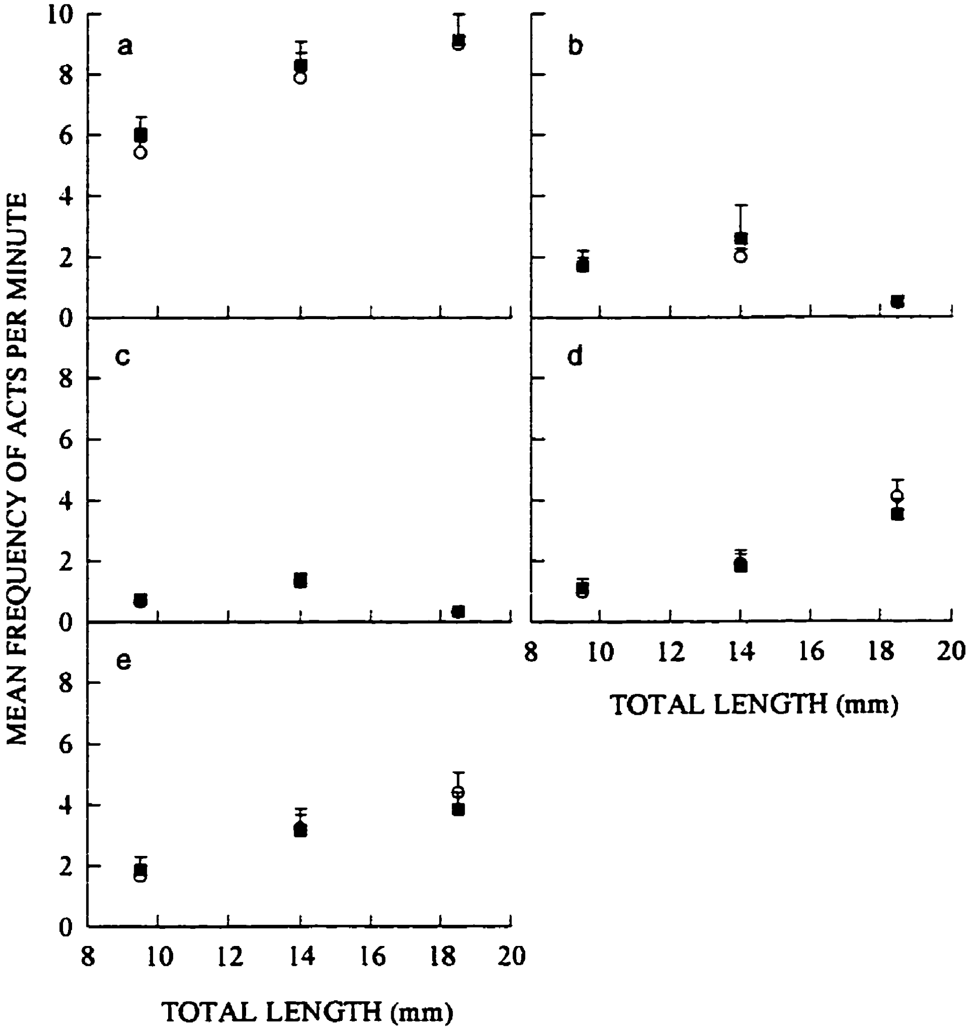

Figure 3.3. The mean frequency (+SD) of (a) orientations, (b) fixates, (c) S-strikes, (d) bites and (e) attack rate for small (open bars) and large (hatched bars) brood size categories plotted against body size (total length). The average total length of YOY at the three sampling times was 9.5 (early larval), 14.0 (late larval) and 18.5 (early juvenile) mm. See Table 3.3 for sample sizes.

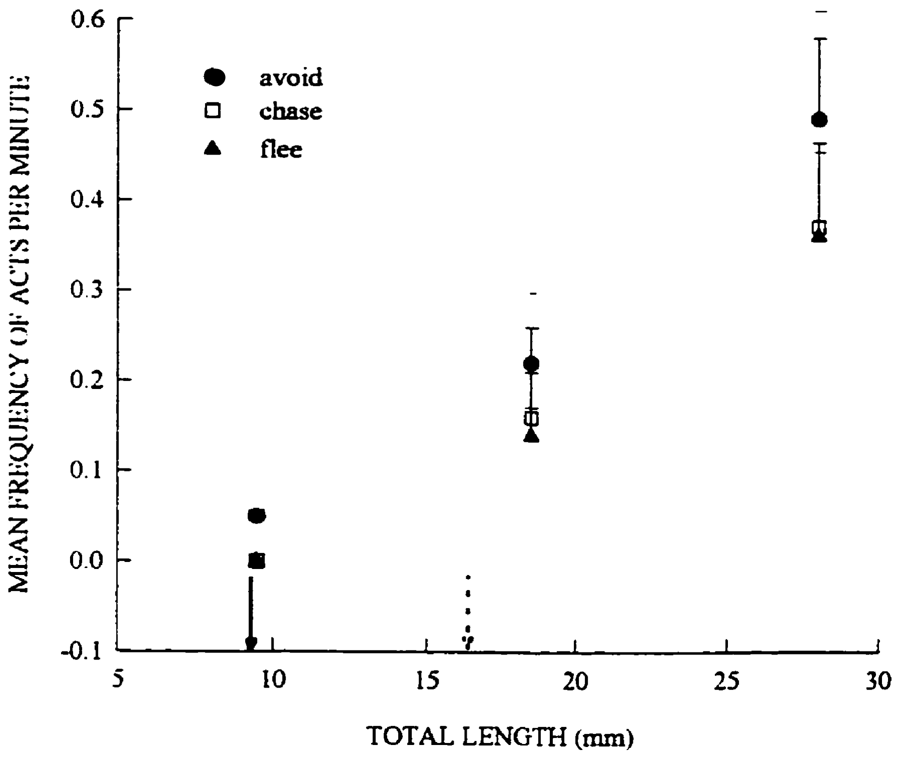

Figure 3.4. The mean frequency (+SD) of *Avoids* (black circle), *Chases* (white square) and *Escapes* (black triangle) of smallmouth bass YOY in Lake Opeongo plotted against body size (total length). Data were combined for 1992 and 1993, as no significant difference was found among years. The solid and dashed vertical arrows marked the average length of larvae at first-feeding and metamorphosis, respectively. Behaviour was recorded on ten broods at each of the three sample times (n = 30).

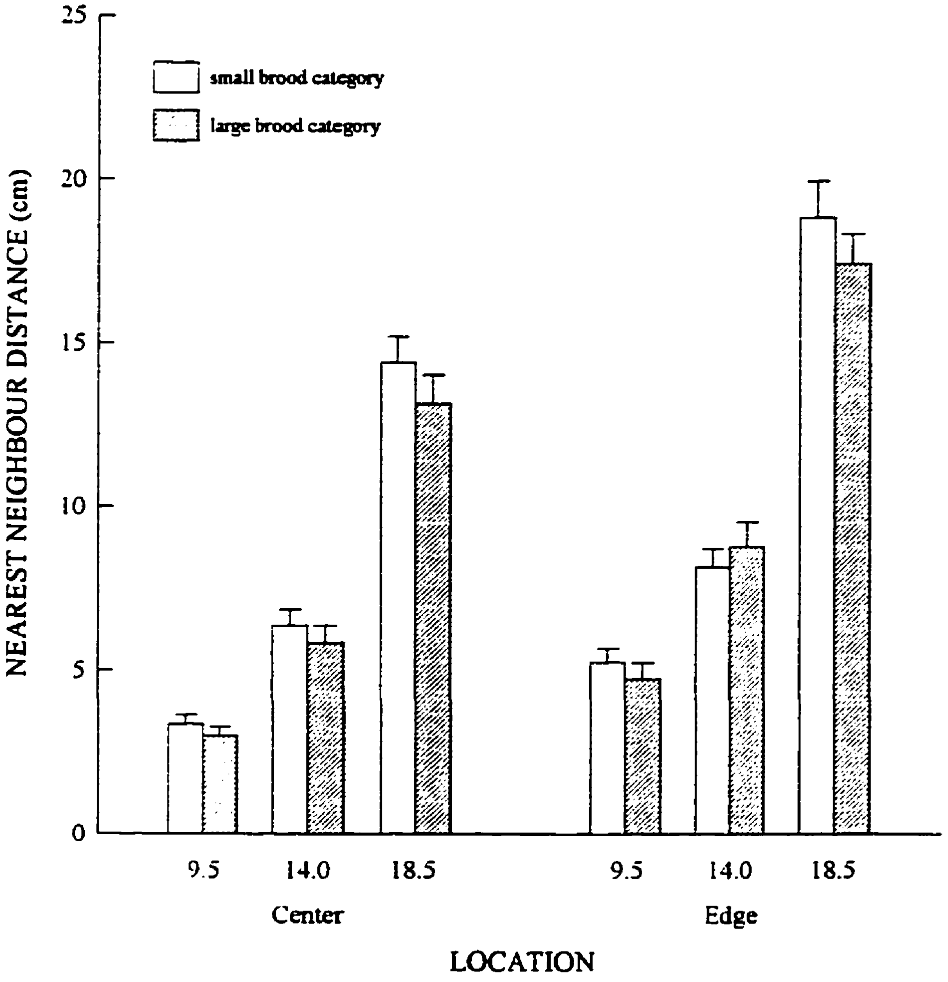

Figure 3.5. Mean nearest neighbour distance (+SE) of YOY smallmouth bass plotted against brood size category (small, large), YOY total length (9.5, 14.0, 18.5 mm) and location (centre, edge) within the brood. See Table 3.2 for sample sizes.

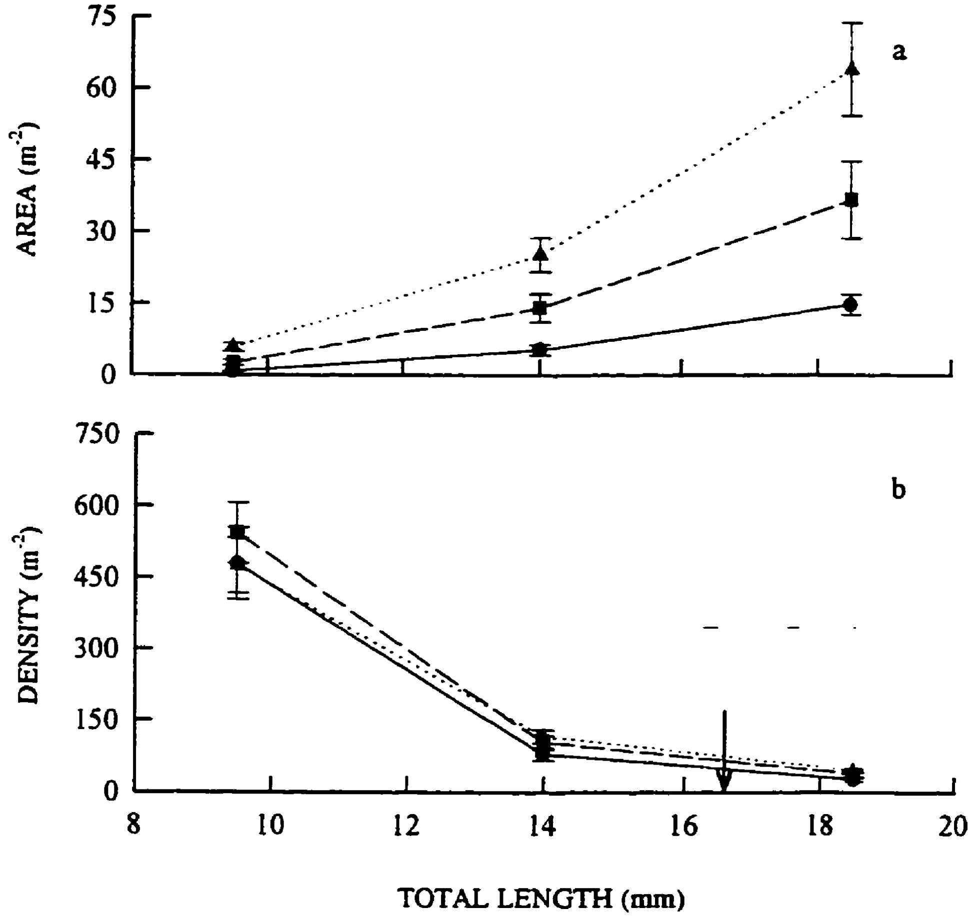

Figure 3.6. The mean (a) surface area of water occupied by broods and (b) density of YOY within broods plotted against body size (TL) for small (closed circles), medium (closed squares) and large (closed triangles) brood size categories. The small (9.5 mm), medium (14.5 mm) and large (18.5 mm) body sizes corresponded with the early larval, late larval and early juvenile intervals of development, respectively. Sample sizes for small, medium and large brood size categories, respectively, were 9.5 mm TL (10/10/10); 14.0 mm (10/10/10) and 18.5 mm (10,10,8). The vertical arrow indicates the mean size at metamorphosis. Error bars indicate ± SE.

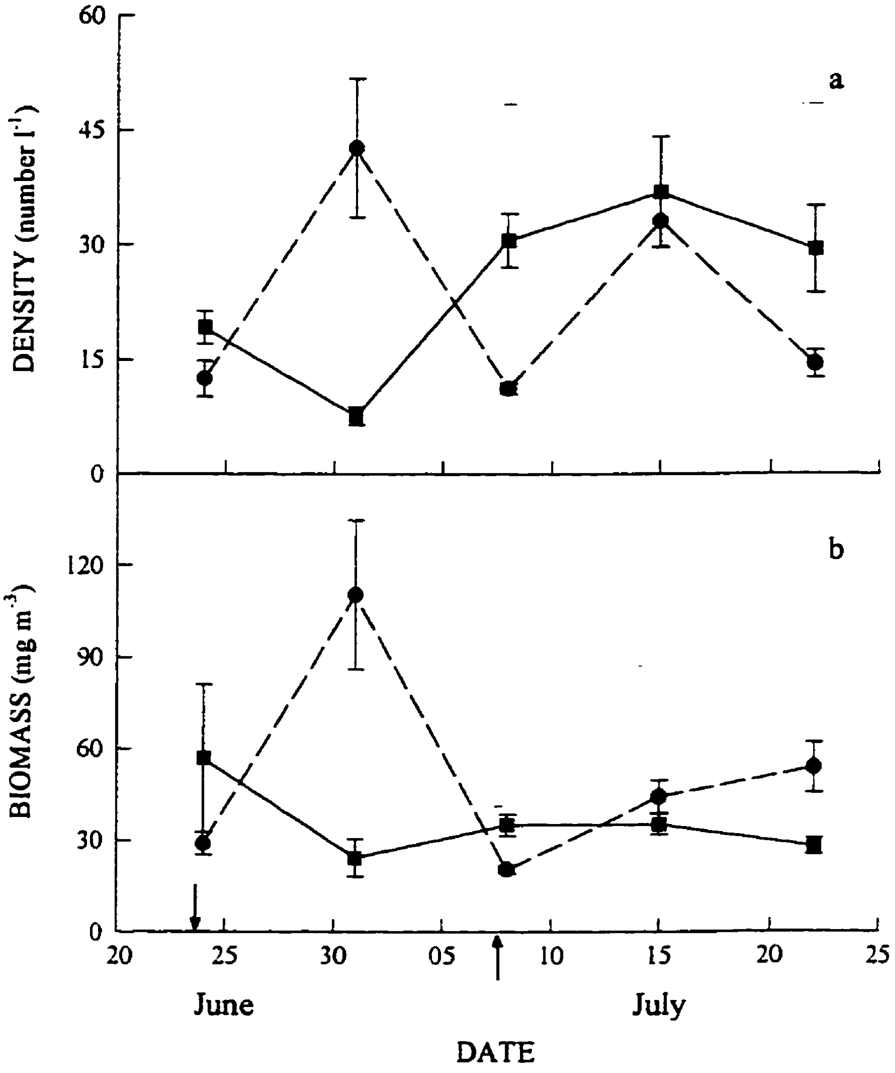

Figure 3.7. The mean (a) density and (b) biomass of zooplankton in exposed (dashed line) and protected (solid line) habitats during the smallmouth bass nesting season in Lake Opeongo, 1993. The downward and upward pointing arrows in (b) indicate the mean date of first-feeding and metamorphosis for the Lake Opeongo smallmouth bass population in 1993, respectively. Weekly zooplankton samples in each site (n = 7) were collected from fixed sites within each habitat. Samples collected during the larval period of bass development were comprised of the first two weekly samples. Values for the juvenile period of development were derived from samples collected in the last three weeks. Total sample size = 70.

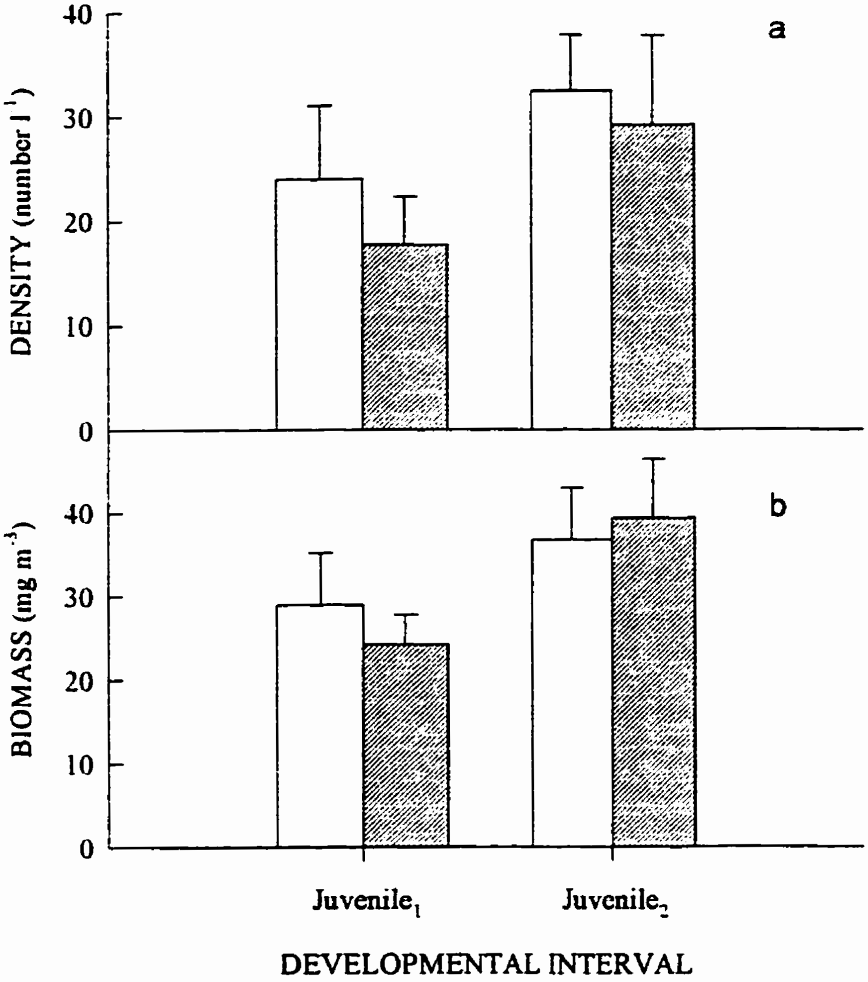

Figure 3.8. Average (a) density (individuals l^{-1}) and (b) biomass (mg m^{-3}) of littoral-zone zooplankton within (open bars) and outside (hatched bars) broods of smallmouth bass in Lake Opeongo, 1993. Samples were collected twice during the juvenile period: Juvenile$_1$ (TL = 18.5 mm) and Juvenile$_2$ (TL = 28.5 mm). Vertical lines above bars indicate +1 SE.

Chapter 4

Relationship of Growth and Mortality of Larval and Juvenile Smallmouth Bass to Prey Concentration and Water Temperature

4.1 Introduction

Year-class strength of fish populations is limited in large part through growth and survival rates during early life history stages (Lasker 1985; Rothschild 1986). It is during these early life history stages that fishes are most vulnerable to the primary causes of mortality: starvation and predation, which may act independently or in combination (Shepherd and Cushing 1980; Sissenwine 1984). The focus on starvation as a primary mechanism limiting survival began with Hjort's (1914) critical period hypothesis, in which he proposed that starvation, resulting from inadequate zooplankton densities at the onset of exogenous feeding, was the primary cause of larval mortality. Some studies have linked mortality rates at first feeding with ambient prey concentrations (Fortier and Leggett 1984; Hewitt, et al. 1985; Theilacker 1986), whereas others (Crecco and Savoy 1987; Taggart and Leggett 1987; McGurk 1993) have found no relationship between larval mortality and prey abundance.

A second starvation hypothesis, the match-mismatch hypothesis (Cushing 1975b), proposes that growth, survival and ultimately, recruitment of larvae depend on the match/mismatch in the production cycle of larvae and their prey. Complimenting the critical period hypothesis, it removes the restriction that food limitation is confined to a particular critical stage of larval development (Leggett and Deblois 1994). Fortier and

Gané (1990) examined growth and survival in spring and fall cohorts of larval herring *Clupea harengus*, and determined that development of the spring larval cohort was matched to the occurrence of appropriate prey. More recently, Fortier et al. (1995) found that the match in timing of prey production and spawning in several species of marine fishes in southeastern Hudson Bay explained both feeding success and growth in larvae. Other field studies have also linked seasonal (Crecco and Savoy 1985; Hovenkamp 1990) and inter-annual (Haldorson, et al. 1989) variations in growth to prey abundance.

A more recent starvation hypothesis, termed the growth-mortality hypothesis (Anderson 1988), integrates the roles of starvation, food limitation and predation. Based on the idea that predation decreases with increasing body size, this hypothesis predicts that larval growth and mortality rates are inversely correlated (Ware 1975; Shepherd and Cushing 1980). Consequently, prey abundance, which plays such an important role in larval growth rates, may ultimately determine survival. A different aspect of the growth-mortality hypothesis has been proposed by Chambers and Leggett (1987) and Houde (1987). These authors suggest that since larval mortality is generally greater than juvenile mortality, the longer an individual remains in the larval period, the lower its probability of survival. This facet of the hypothesis suggests that cumulative mortality through the larval period is directly related to larval period duration, with the ability of larvae to transform into juveniles being determined by various biotic and abiotic factors (Chambers and Leggett 1987; McCormick 1994). Together, these three food limitation hypotheses share the assumption that starvation plays a role either as a direct or indirect source of mortality.

For fishes living in temperate waters, maximizing surplus energy by the end of the first growing season may be an important strategy towards surviving the first winter, as both laboratory (Oliver, et al. 1979; Toneys and Coble 1980) and field (Shuter, et al. 1980; Post and Evans 1989) studies have demonstrated a positive relationship between body size and overwinter survival. For smallmouth bass *Micropterus dolomieu* (hereafter SMB) populations near the northern limit of their distribution, size attained by the end of the first summer and duration of the following winter were important factors determining recruitment (MacLean, et al. 1981). Thus, first-year growth is an important factor in determining the number of offspring that will be recruited into the adult population.

Surprisingly, field studies investigating the importance of prey availability to growth and mortality of YOY SMB are rare. Research by (Emery 1975) suggests that prey availability may limit growth of juvenile SMB in Lake Opeongo. Additionally, consumption rates by juvenile SMB have been found to be positively related to growth rates (Wales 1981). However, prey concentrations were not quantified and no clear relationship could be established between prey abundance, prey consumption and growth rates.

The objectives of this chapter were to examine patterns in growth and mortality in larval and early juvenile SMB to determine if these patterns were related to prey concentrations as predicted by the three starvation hypotheses. I also examined the effects of water temperature on growth and mortality of YOY SMB, owing to the direct effects of temperature on growth (Horning and Pearson 1973; DeAngelis and Coutant 1979; Oliver, et al. 1979) and development (Webster 1948; Shuter, et al. 1980) of YOY SMB, in addition to its indirect role in controlling the duration of the first-year growing season

(Ridgway, et al. 1991; Sabo and Orth 1995). Data were collected in 1988, 1989 and from 1991-1993 on a single population located in central Ontario, Canada. Specifically, I test the following predictions of the three starvation-based hypotheses: (1) since smaller individuals are more susceptible to starvation (Miller, et al. 1988), starvation mortality, resulting from reduced growth rates, will be most intense at first feeding (critical period hypothesis); (2) within a nesting season, growth and mortality of larval SMB will be positively and negatively associated with prey availability respectively (match-mismatch hypothesis); (3) among nesting seasons, growth rates will be reduced and mortality rates will be higher in years experiencing a temporal mismatch between production of SMB larvae and their prey (match-mismatch hypothesis); (4) larval mortality is negatively related to larval growth rates (growth-mortality hypothesis).

In this chapter, I present the results of a fine scale, multi-year field study on a single SMB population. An analysis of abundance and vital rates (development, growth and mortality) of larval and early juvenile SMB is presented to describe how important variables, prey availability and temperature, affect year-class and brood-specific growth and survival. I employ a non-traditional approach in larval fish studies and base the investigation entirely on underwater sampling and observations.

4.2 Methods

4.2.1 Field Methods and Sample Collection

Field data were collected during the summers of 1988, 1989, and 1991-1993 in Jones Bay, Lake Opeongo, Ontario. Methods of collecting YOY SMB and environmental data are described briefly below and in more detail in Chapter 2: General Methods. Shoreline swims to locate nesting male SMB began in late May each year, just prior to initial spawning activity, and continued throughout the SMB reproductive season. Once located, nests were monitored on a daily basis throughout the parental care period of development, providing precise estimates of offspring age, including date of spawning, hatch, first feeding and metamorphosis for all broods. Additionally, I recorded the date on which broods failed or successfully dispersed from nesting territories.

SMB larvae and juveniles were sampled from all broods, beginning at first feeding and at 4 day intervals thereafter. All sampled fish were transferred to vials containing 5% formalin and subsequently measured for total length to the nearest 0.1 mm, using a dissecting microscope fitted with an ocular micrometer. Length measurements were corrected for shrinkage and all results were expressed as fresh lengths.

Brood size estimates were made on alternate days, beginning at first feeding, for all nests in the study area. Brood size estimates were repeated until broods either failed or successfully dispersed from nesting territories. Total abundance-at-age in the study area was determined by summing brood size estimates for all SMB nests. Mean brood size-at-age for all nests in the study area was determined by dividing total abundance-at-age by the number of active nests.

Littoral zone water temperatures were recorded at a fixed site using a continuous recording thermograph throughout each of the SMB reproductive seasons. Mean water temperatures were determined for the spawning interval in each season as well as for the SMB embryonic, larval and juvenile periods of development. Also, using the developmental history of each nest, including date of spawning, hatch, first-feeding, metamorphosis and dispersal, in combination with the mean daily water temperature data recorded in each of the five nesting seasons, I calculated mean brood-specific water temperature for all nests in the study area during the embryonic, larval and juvenile periods of development. Brood-specific data were used to examine relationships between growth and mortality of YOY SMB and water temperature within years. Interannual relationships between growth and mortality of YOY and temperature were examined using mean values for year classes.

Developmental times for embryos, larvae and juveniles were estimated from daily field swims conducted during all five field seasons. Daily shoreline swims of the study site ensured that the spawning time for all nests could be accurately estimated to within 24 hours. To estimate developmental times for early larvae (early larval phase) in each nesting season I sampled larvae (n = 5) daily from 4 nests located adjacent to the study site, beginning on the first day of exogenous feeding. These larvae were returned to the laboratory and maximum length of the yolk sac and total length of larvae were measured using an ocular micrometer and dissecting microscope at 10 x. I considered the yolk-sac phase to be completed when the mean maximum diameter of yolk sacs for individuals within a brood had been reduced to 10% of its original length at first feeding. The length of the yolk-sac phase for a brood was defined as the number of days between first feeding and the day on which the mean maximum length of the yolk sac for individuals within a brood was ≤ to 10% of its original length at first feeding. The length of the late larval phase (post-yolk sac phase) was defined as the number of days between scoring a brood as having metamorphosed and the last day of the yolk-sac phase.

Metamorphosis was operationally defined as the point at which 80% of the individuals within a brood had transformed from larvae to juveniles. The morphological criteria I used for identifying the transition from the larval to juvenile period in SMB, as suggested by Balon (1985; 1990) for other species of fish, included disappearance of the median finfold, presence of all fin rays, presence of scales, and most importantly, a change in body coloration from the black pigmentation characteristic of larvae to a green/brown colour typical of juveniles and adults. Age at metamorphosis for a brood was defined as the number of days between scoring a brood as having metamorphosed and the first day of exogenous feeding. Developmental rate for the larval period was derived from age estimates at metamorphosis and is defined as the reciprocal of age at metamorphosis.

4.2.2 Prey Biomass and Abundance

Twenty litre zooplankton samples were collected from mid-depth at two fixed littoral zone stations, at one or two week intervals, over four SMB nesting seasons. To track seasonal changes in zooplankton abundance, a total of 126, 98, 84 and 98 samples were collected in 1988, 1991, 1992 and 1993 respectively. Following collection, samples were fixed and preserved in 5% formalin (see Chapter 2 for details).

To quantify zooplankton abundance and composition, a minimum of 200 individuals were identified from each sample. Sub-samples of organisms for identification were obtained by mixing zooplankton in a 50-ml graduated cylinder and collecting an integrated sample throughout the water column with a large bore pipette. All organisms in samples and sub-samples were counted, identified and measured for body length and head width or depth). Measurements of body dimensions were used in length-weight regressions to estimate biomass (mg dry weight) (Dumont, et al. 1975; Culver, et al. 1985). I examined the relationships between instantaneous growth and mortality rates of larval SMB and zooplankton biomass.

4.2.3 YOY Growth Estimates

Growth rates of YOY SMB were estimated at two levels:

1) Year-class growth rates: Samples of YOY from individual broods were combined for analysis. The linear regression coefficients of total length-at-age were estimates of year-class growth rates.

2) Brood-specific (family) growth rates: Offspring were sampled from all nests in the study area at regular intervals, beginning at first feeding. The linear regression coefficient of total length-at-age was an estimate of brood-specific growth rate.

Growth rate estimates of SMB were compared within and among years. Within years, I tested for differences in growth rates between developmental periods (larval versus juvenile). I also compared growth-at-age across 4-d growth intervals for larval SMB to determine if growth rates of first feeding larvae were significantly lower than in older larvae. Among years, I tested for significant differences within development periods (larval and juvenile).

Growth rates of YOY were derived from regressions of fish lengths on ages,

$$L_t = a + b(t) \qquad (1)$$

where Lt = total length (mm), a = regression intercept, an estimate of total length at time = 0, t = age in days beginning on the first day of the larval period and b = regression coefficient, used to estimate growth rate (mm d^{-1}). Instantaneous growth rate was calculated as,

$$G = (\log_e Y_2 - \log_e Y_1)/(t_2 - t_1) \qquad (2)$$

where, G = instantaneous growth rate, Y_2 = size (total length) at time 2, Y_1 = size (total length) at time 1 and, t_2 and t_1 = final and initial times.

4.2.4 YOY Mortality Estimates

Mortality rates were calculated at two levels: year-class and brood (family).

Year-class mortality rates: Cohort mortality rates were determined by regressing the decline in abundance over time of total numbers of young fish from all active broods in the study area, allowing comparisons among entire year-classes.

Brood-specific (family) mortality rates: Brood specific mortality rates were derived from regressions of daily brood size estimates throughout the parental care period of development.

Mortality rates of SMB were compared within and among years. Within-year comparisons consisted of testing for differences in mortality rate across developmental periods (larval versus juvenile). I also compared mortality rate estimates across larval phases (early versus late) within years to determine if mortality rates in first-feeding larvae were significantly higher than in older larvae. Among-year comparisons consisted of testing for significant differences within development periods.

Linear regression analysis was used to derive mortality rate estimates. The natural logarithm of abundance was regressed against age (days) using the exponential model,

$$N_t = N_0 e^{-Zt} \tag{3}$$

where, N_t = estimated number of surviving larval or juvenile fish at t days after first feeding (first day of larval period), N_0 = initial number of larvae in a brood at first feeding, Z = slope of the regression and is defined as instantaneous mortality rate for the entire interval and t = duration (days) of the interval. The daily mortality rate (M_d) (percent per day) was calculated as,

$$M_d = (1 - e^{-Z}) \times 100\% \tag{4}$$

Total instantaneous mortality (Z) originated from two sources: i) natural mortality (M) and ii) sampling mortality (S). Thus, instantaneous mortality equalled

$$Z = M + S. \tag{5}$$

I solved for natural mortality by subtracting sampling mortality from total mortality. Cumulative mortality was derived from the product of phase duration (days) and daily instantaneous mortality rate for the early and late larval phases of development.

With respect to mortality estimates, I assumed that broods which disappeared from nesting territories during the larval period experienced 100% mortality. For these broods, mortality rate was derived from brood size estimates extending from date of first feeding to date on which brood size equalled zero. For broods that survived beyond metamorphosis, mortality rates for the larval period were derived from brood size estimates extending from first feeding date to metamorphosis date. Date of metamorphosis for a brood was defined as the date on which 80% of individuals had metamorphosed. Mortality rate estimates for juveniles were derived from brood size estimates beginning at metamorphosis and ending on the last day that juveniles were observed at the nest site. As it was highly unlikely that all juveniles that disappeared from nesting territories during this interval actually died, this method overestimated juvenile mortality rates.

I did not conduct a systematic examination of embryonic mortality; however, daily observation of nests in the study area indicated high apparent losses in all years. Previous studies show that the female size-fecundity relationship is relatively consistent among SMB populations (Hubert 1976; Serns 1984; Mackereth 1995). Moreover, (Mackereth 1995) shows egg counts of SMB nests in Lake Opeongo to be positively associated with length of nesting males; and male size-egg regressions do not differ significantly from female size-fecundity regressions for the same population. Embryo mortality may be calculated as the difference between potential egg production (total female fecundity) and larval abundance at first-feeding (Bouwes and Luecke 1997). This technique has received some criticism as an estimate of egg mortality at the population level (Clady 1975; Dahlberg 1979), but can serve as a very useful technique for estimating embryonic mortality in a sub-population. To estimate the mean number of embryos in SMB nests at spawning in 1992 and 1993 I substituted the average fork lengths of nesting males from the present study into the egg count-male size regression equations of Mackereth (1995):

$$\text{(1992) Embryo\#} = 615\ (\text{male length}) - 9458$$

$$\text{(1993) Embryo\#} = 609\ (\text{male length}) - 8610.$$

I used mean brood size estimates at spawning and first-feeding, together with the number of active nests at each of these sampling times, to estimate percent survival during the embryonic period.

4.2.5 Analysis

I used one-way ANOVA and Tukey multiple comparisons to test for differences among years with regard to the following variables: 1) average size of spawning males; 2) total abundance of SMB offspring at first feeding and metamorphosis; 3) average water temperature during the spawning period; 4) average, brood-specific water temperature during the embryonic, larval and juvenile periods; 5) average zooplankton density and biomass during the larval and juvenile periods of development in SMB; 6) average duration (days) of the embryonic, larval and juvenile period of development in SMB; 7) average total length of SMB offspring at first feeding and metamorphosis and 8) average, brood-specific instantaneous growth rate during the larval and juvenile period of development. All data were $\log_e$ transformed for analysis. For the purposes of analysis, a constant of 5.0 was added to all instantaneous growth estimates prior to logarithmic transformation.

In analyzing age effects on brood-specific growth rates, I used repeated-measures ANOVA's and Tukey multiple comparisons to determine if mean growth rate differed among 4-day growth intervals. Growth interval was the repeated factor and data were $\log_e$ transformed before analysis. Due to declining sample sizes (broods) with age, analyses were restricted to the larval period of development. Bartlett's Test for Homogeneity of Variances and Tukey's multiple comparison were used to determine if variances in brood-specific growth rate of larvae differed among years.

Differences in slopes and intercepts among years for; 1) YOY length-at-age and 2) abundance-at-age, with age as the covariate and 3) brood size at first feeding versus male fork length, with male fork length as the covariate, were tested by ANCOVA. In this type of test, I assessed differences in slopes using a preliminary ANOVA including interaction terms. If differences occurred, Tukey's test (Zar 1984) was used to determine significant differences among slopes. If slopes did not differ significantly, interaction terms were dropped and differences in intercepts were determined by standard ANCOVA.

I correlated relative variation in mean age of larvae at yolk absorption and metamorphosis with mean water temperature to examine the association of water temperature with developmental rate. To assess relative variation in length and age at metamorphosis I correlated mean length with age during the entire larval period. Length and age were converted to growth and developmental rates for the entire larval period and assessed using correlation. Finally, I compared brood-specific variation in mean length and age at metamorphosis among years using a paired t-test.

I explored the association of mortality with water temperature by correlating mean brood-specific instantaneous mortality rate and brood-specific cumulative mortality with mean water temperature for the early and late larval phases of development. To assess the relationship between mortality and growth rates among years I correlated brood-specific mortality rate with brood-specific growth rate.

I used correlation analysis to compare instantaneous growth rates between larval and juvenile periods within years. This comparison tested whether year-classes that grew quickly during the larval period were more likely to grow faster during the juvenile period. Correlation analysis was also used to evaluate year-class instantaneous growth rates of SMB larvae with mean zooplankton biomass in each year. This comparison demonstrated whether zooplankton biomass ultimately affected year-class growth rates of SMB larvae.

Brood-specific mortality distributions were highly skewed (right) in all years. Distributions in some years remained skewed following Log_e transformation, preventing analysis of mean instantaneous mortality rates using ANOVA. Consequently, chi-square contingency tests and Tukey multiple comparisons were used to determine if brood-specific, median instantaneous mortality rate differed within developmental periods (larval and juvenile) among years, between developmental periods within years (larval versus juvenile) and between larval phases (early versus late) within years.

Relationships between mean water temperature and brood-specific growth rates of larval and juvenile SMB were examined by simple linear regression. Similar statistical analyses were made between brood-specific growth rates and brood-specific mortality rates of larvae. Brood-specific growth and mortality rates of SMB larvae were regressed on time (days) between the seasonal peak in prey biomass and first feeding of broods, mean brood-specific water temperatures and variation in brood-specific water temperatures, using multiple regression analysis to detect possible relationships between prey abundance and brood-specific growth and mortality rates. The level of significance for all tests was set at $P < 0.05$. All statistical analyses were conducted using SYSTAT (Wilkinson, et al. 1992).

4.3 Results

4.3.1 Spawning Distribution of Nesting Males

SMB spawned during late May and June, coinciding with rising water temperatures (Fig. 4.1). In each year, spawning peaked when water temperatures rose above 14 °C. The median spawning date for males ranged from 22nd of May in 1991 to 10th of June in 1989. In several years (1988, 1989), secondary spawning peaks were evident, and in 1993 approximately 12% of the nesting males spawned nearly 2 weeks prior to the median spawning date. The duration of the spawning period ranged from 11 days in 1991 to 27 days in 1993 (Table 4.1) and the mean spawning date varied significantly among years ($F_{4, 470} = 172.56$; $p < 0.0005$).

Fork length of nesting males ranged between 22.2 and 45.5 cm and averaged 30.7 cm during the five spawning seasons. Fork length of nesting males averaged 29.8, 29.6, 32.0, 31.6 and 31.4 cm in 1988, 1989, 1991 1992 and 1993, respectively and differed significantly among years. ($F_{4,433} = 5.02$; $p = 0.001$; Fig. 4.2). Tukey's test showed that nesting males in 1988 and 1989 were significantly smaller than those in 1991 and 1992.

4.3.2 YOY Abundance

4.3.2.1 Day 1- Larval Period

The total abundance of first-feeding larvae in the South Section of Jones Bay, based upon individual brood size estimates, is shown in Table 4.2. The total production of first feeding SMB larvae was highest in 1992, lowest in 1991 and intermediate in 1988, 1989 and 1993 (Fig 4.3). Total production of first-feeding larvae was 8 times higher in 1992 than in 1991; however only 2 times as many males nested in 1992 as in 1991. The average production of first-feeding larvae during the 5 years equalled 80,130. Seasonal timing in production of first-feeding larvae varied considerably among years (Fig. 4.3) and mean date on which larvae initiated first feeding differed significantly among years ($F_{4,331} = 294.85$; $p < 0.0005$). Brood size at first-feeding was negatively related to spawning date in 4 of 5 nesting seasons (Fig. 4.4); however, this relationship was generally weak and explained a significant amount of the variation in brood size in only two years (Table 4.3).

Mean brood size at first feeding differed significantly among years ($F_{4,291} = 12.06$, $p < 0.0005$), with values ranging from 495 in 1991 to 1910 in 1992. Tukey's test showed that mean brood size was significantly lower in 1991 than in all other years and that mean brood size was significantly lower in 1989 than in 1992 (Fig. 4.5). Brood sizes varied considerably within nesting seasons, ranging by two orders of magnitude in all years (Table 4.4). The magnitude of variation in mean brood size was similar in 4 of 5 nesting seasons (1988, 89, 92, 93), but was considerably higher in 1991, a year characterized by extremely low brood sizes. Finally, size distributions of broods were skewed to the right in all years, as a result of a relatively few nests containing a large number of offspring.

There was a positive relationship between male size and the number of first-feeding larvae in all years (Fig. 4.6). A linear model accounted for between 12 and 46% of the variation in brood size and the relationship was significant in 4 of 5 years (Table 4.5). Analysis of covariance indicated that the slopes differed significantly.

4.3.2.2 Day 1 - Juvenile Period

The estimated production of juveniles in the South Section of Jones Bay was highest in 1989, lowest in 1991 and intermediate in 1988, 1992 and 1993 (Table 4.2). Production of juveniles was approximately 8.0 times higher in 1989 than in 1991. The mean annual production of juveniles over the five seasons was 30,335, approximately 38% of the initial production of first-feeding larvae. The seasonal timing in production of juveniles differed significantly among years ($F_{4,159} = 246.07$; $p < 0.0005$). The mean date on which larval broods metamorphosed ranged from June 16 in 1991 to July 12 in 1993, a difference of 26 days (Fig 4.7). The temporal production of juveniles in 1988 differed from other years in that most larvae metamorphosed over a short interval of 2 days.

Mean brood number on the first day of the juvenile period differed significantly among years ($F_{4,148} = 5.19$, $p = 0.001$), being highest in 1992 (mean = 1416) and lowest in 1991 (mean = 443). Tukey's test showed that mean brood number was significantly lower in 1991 than values in 1989, 1992 and 1993 (Fig. 4.8). Mean brood number ranged by approximately 2.0 orders of magnitude in all years (Table 4.6). The variability in mean brood number within a year, expressed as the coefficient of variation, was similar in 1988, 1991, 1992 and 1993, but lower in 1991. The coefficient of variation for mean brood number on day-1 of the juvenile period, averaged over the five nesting seasons was 98%, which was considerably higher than the mean value (74%) on day-1 of the larval period. Similar to larval broods at first feeding, mean brood size distributions of recently metamorphosed broods were strongly skewed to the right in all years (Figure 4.8).

4.3.3 Temperature

Mean water temperatures during the SMB spawning period in Lake Opeongo differed significantly among years ($F_{4,103} = 17.79$; $p < 0.0005$). Mean daily temperatures were warmest during the 1988 spawning season and lowest in 1993 (Table 4.7). A continuous recording thermograph indicated that temperatures increased steadily prior to and during the spawning period in 4 of 5 nesting seasons. In 1993 the pattern differed somewhat, as temperatures did not rise until early June, which was well into the spawning season (refer to Fig. 4.1). Variation in mean daily water temperature during the spawning season, expressed as the coefficient of variation, differed considerably among years (Table 4.7). Temperatures were most variable in 1993, least variable in 1989 and intermediate in the remaining three years.

Following spawning, water temperatures continued to rise steadily throughout the SMB reproductive season (Fig. 4.9) and mean water temperatures differed significantly among years during the embryonic ($F_{4,148} = 13.57$; $p < 0.0005$), larval ($F_{4,123} = 20.06$;

$p < 0.0005$) and juvenile ($F_{4,101} = 23.929$; $p < 0.0005$) periods of development (Fig. 4.10). During the embryonic period, water temperatures were coldest in 1993, warmest in 1989 and intermediate during the 1988, 1991 and 1992 reproductive seasons (Table 4.8a). Tukey's test showed that mean water temperatures were significantly lower in 1993 than in other years and that temperatures in 1988 differed significantly from those in 1992. Variation in water temperature during the embryonic period was highest in 1993 and lowest in 1992 and was not correlated with mean temperature. Continuous temperature profiles in 1993 showed that embryos from nests spawned early in the season experienced minimum temperatures between 10 - 11 °C for the first 10 days of their development. The high mortality rate of eggs from early-spawned nests, together with the high incidence of nest abandonment by early spawning males, may reflect the extremely low temperatures that occurred in 1993.

Water temperatures corresponding with the SMB larval and juvenile periods of development were highest in 1989 and lowest in 1992 (Table 4.8b,c). Tukey's test showed that mean water temperature during the larval and juvenile periods was significantly lower in 1992 than in other years. Variation in mean water temperature during the SMB larval and juvenile periods differed considerably among years. Mean water temperature during the larval period was most variable in 1993 and least variable in 1991. In contrast, during the juvenile period, mean water temperature was most variable in 1988 and least variable in 1989.

Brood-specific water temperatures during the early larval phase of development, corresponding with first feeding of larvae, also differed significantly among years

($F_{4,331}$ = 476.96; $p < 0.0005$). Mean brood-specific temperatures during the early larval phase ranged from a low of 17.1 oC in 1992 to a high of 21.9 oC in 1989. Tukey's test showed that mean brood-specific temperatures differed significantly among all 5 years.

4.3.4 Prey Biomass and Abundance

Mean densities of combined zooplankton taxa were significantly different among years during the SMB larval ($F_{3,53}$ = 7.35; $p < 0.0005$) and juvenile ($F_{3,51}$ = 11.21; $p < 0.0005$) periods of development. Mean densities of zooplankton during the SMB larval period were highest in 1991 and lowest in 1993 (Fig. 4.11). Tukey's test showed that the mean density of zooplankton during the SMB larval period was significantly higher in 1991 than in 1992 and 1993 and that the mean density was significantly higher in 1988 than in 1993. During the juvenile period, Tukey's test showed that the mean density of zooplankton was significantly lower in 1992 than in other years. Within years, mean zooplankton density was higher during the larval period of SMB development than during the juvenile period of development in 3 of 4 years (Fig. 4.11).

The mean dry biomass of combined zooplankton taxa differed significantly among years during the SMB larval ($F_{3,53}$ = 13.41; $p < 0.0005$) period (Fig. 4.11). Tukey's test showed that the mean biomass in 1992 was significantly lower than values in the other three seasons and mean biomass was significantly higher in 1991 than in 1993. No significant difference was found between mean biomass of zooplankton during the SMB juvenile period of development ($F_{3,51}$ = 1.89; $p = 0.15$). Mean biomass values during the larval period were highest in 1991 (133 mg m^{-3}) and lowest in 1992 (25.7 mg m^{-3}).

Zooplankton biomass declined seasonally, such that mean values during the juvenile period were approximately 50% below values determined for the larval period in 3 of 4 years.

Seasonal timing in the production of zooplankton in Lake Opeongo varied considerably among years (Fig. 4.12). Zooplankton biomass increased as the season progressed, peaked, and subsequently declined in all years. In 1992 and 1993 zooplankton biomass peaked in late May/early June, 2-3 weeks prior to the production of first-feeding larvae. In 1988 and 1991, however, zooplankton biomass peaked in the end of June, approximately 1-2 weeks following production of first feeding SMB larvae.

Adult cladoceran and copepod nauplii numerically comprised 85-95% of the zooplankton taxa in Lake Opeongo in all four years (Table 4.9). Calanoid copepods were dominated by *Leptodiaptomus minutus* while cyclopoid copepods were dominated by *Diacyclops thomasi*, *Mesocyclops edax* and *Tropocyclops extensus*. The cladocerans showed greater species diversity, but were largely dominated by *Bosmina longirostris* and *Polyphemus pediculus*. The percentage abundance of both copepod nauplii and adult cladocerans during the SMB larval period ranged considerably among years (Fig. 4.13). In 1992 and 1993, when prey production peaked 2-3 weeks prior to the production of first feeding SMB larvae, copepod nauplii comprised 86% and 61% of total zooplankton abundance during the SMB larval period (Fig. 4.13c,d). In contrast, in 1988 and 1991, when the seasonal peak in zooplankton abundance followed the production of first feeding SMB larvae, cladocerans comprised 75% and 93% of the total zooplankton abundance during the SMB larval period (Fig. 4.13a,b). During the SMB juvenile period, copepod nauplii and cladocerans again dominated and were similarly abundant in 3 of the 4 nesting seasons (Fig. 4.13e-h). The exception was 1988, when copepod nauplii comprised 65% of total zooplankton abundance compared to 28% for cladocerans.

The absolute density of copepod nauplii and adult cladocerans varied considerably over the 4 seasons. During the SMB larval period of development, densities of copepod nauplii and adult cladocerans ranged from 3 (1991) to 26 (1992) and from 3 (1992) to 47 (1988) individuals l^{-i}, respectively. Variation in abundance of copepod nauplii and adult cladocerans followed a similar pattern during the juvenile period, with values ranging from 7 (1992) to 29 (1988) and from 6 (1992) to 20 (1993) individuals l^{-1}, respectively.

Despite their high numerical abundance, the contribution of copepod nauplii to total zooplankton biomass was considerably less (Fig. 4.14). During the SMB larval period, copepod nauplii comprised <8% of the total zooplankton biomass in 3 of 4 years (Table 4.10). This pattern also persisted through the SMB juvenile period. Total biomass of copepod nauplii over the 4 seasons ranged from a low of 0.5 (1991) to a high of 7.0 (1992) mg m^{-3} (Table 4.11). Total biomass of zooplankton was dominated by cladocerans in all 4 years, with cladocerans comprising 82 and 79% of the total biomass during the SMB larval and juvenile periods, respectively.

4.3.5 Embryonic, Larval and Early Juvenile Development

Mean duration of embryonic, larval and juvenile periods varied considerably in SMB broods in Lake Opeongo (Fig. 4.15). Water temperatures experienced by individual broods in each of the developmental periods was strongly influenced by the combination of seasonal timing in spawning and variation in mean daily water temperature. Generally, as water temperatures increased, the length of the developmental periods decreased. For broods that survived to metamorphosis, mean length of time that offspring remained with a parental male differed significantly among years ($F_{4,163} = 31.23$; $p < 0.0005$), ranging from 29 d in 1991 to 43 d in 1992 and averaged 35 d over the 5 years.

A one-way ANOVA indicated a significant difference in mean length of the embryonic period among years ($F_{4,348} = 38.53$; $p < 0.0005$). Mean embryonic duration ranged from 13.4 d in 1991 to 16.4 d in 1992. Larval duration also differed significantly among years ($F_{4,173} = 423.78$; $p < 0.0005$), ranging from 8.7 days in 1989 to 17.4 d in 1992 and averaged 12.8 days over the 5 years. Tukey's test showed that mean length of the larval period differed across all years. Juvenile duration, defined here as the time between metamorphosis and brood dispersal, differed significantly among years ($F_{4,159} = 7.23$; $p < 0.0005$), ranging from 3.9 d in 1993 to 9.5 d in 1992.

Time available for first-feeding larvae to find adequate food resources is determined, in part, by time to yolk absorption, which defines the period during which larvae can rely on endogenous energy reserves. The correlation between mean duration of the early larval phase and mean water temperature was significantly negative across spawning seasons (Fig. 4.16a; $r = -0.94$, $p = 0.017$, $n = 5$). The correlation between mean duration of the late larval phase and mean water temperature was also strongly negative but not significant (Fig 4.16b; $r = -0.86$, $p = 0.062$, $n = 5$), but statistical significance was limited by small sample size. Mean total length of larvae was significantly positively correlated with mean age at metamorphosis across years (Fig 4.17a; $r = 0.91$, $p = 0.029$, $n = 5$). This suggested that year-classes that metamorphosed late did so at significantly larger sizes. Brood-specific variation in age at metamorphosis was greater than variation in length at metamorphosis in all years as indicated by the coefficient of variation (Table 4.12). Comparison of mean CV's for length and age during the five spawning seasons showed that age at metamorphosis was significantly more variable than length at metamorphosis (CV (means) = 0.119 and 0.067, respectively; t = 6.216, df = 4, p = 0.003). Inter-annual variation in mean age and length of larvae at metamorphosis was greater than mean variation within years; CV's for mean variability in age and length among years equalled 0.265 and 0.078, respectively. The CV for mean age at metamorphosis among years (0.265) was approximately 122% greater than the mean CV for age within years (0.119) and reflected the wide range in mean age at metamorphosis (9 d in 1991 - 18 d in 1992). In contrast, the CV of mean length among years (0.078) was only 18% higher than the mean CV of length within years (0.066). The correlation between mean instantaneous growth rate and developmental rate was strongly positive but not significant across years (Fig 4.17b; r = 0.80, p = 0.102, n = 5). Thus, year-classes that experienced relatively high growth rates metamorphosed early, but at a smaller mean size.

4.3.6 YOY Length

Brood-specific mean total length of first feeding SMB larvae differed significantly among years ($F_{4,298} = 27.66$; $p < 0.0005$). Mean total length of first-feeding larvae in broods ranged from a low of 9.2 mm in 1991 to a high of 9.6 mm in 1988 and 1992 (Fig. 4.18). Tukey's test showed that total length of larvae at first feeding was significantly lower in 1989 and 1991 than in 1988, 1992 and 1993. Brood-specific mean total length at metamorphosis also differed among years ($F_{4,160} = 48.16$; $p < 0.0005$), ranging from 14.0 mm in 1991 to 17.0 mm in 1992 and averaging 15.9 mm over the five nesting seasons (Fig. 4.19). Tukeys' test showed that mean total length of broods in 1989 and 1991 differed significantly from all other years.

Variation in mean total length of first-feeding larvae, expressed as the coefficient of variation (%), was similar across years, with values ranging from a low of 3.4 % in 1993 to a high of 4.9 % in 1989. Measurements of offspring length at 4 day intervals showed that variation in mean length increased progressively between first feeding and metamorphosis in all years (Table 4.13). Following metamorphosis, variation in mean total length of juveniles decreased. This decline most likely resulted from small sample sizes (broods) during the juvenile period, as most of the variation in length-at-age can be attributed to differences among broods and not within broods (Friesen 1990).

4.3.7 YOY Growth

4.3.7.1 Year-Class Growth Rates

Mean instantaneous growth rates of larvae varied considerably among year classes, ranging from 0.032 (0.39 mm d^{-1}) in 1992 to 0.059 (0.69 mm d^{-1}) in 1989 and averaging 0.044 (0.54 mm d^{-1}) over the five spawning seasons (Table 4.14). Linear models provided the best fit to the length-age regressions in all years, and age alone explained from 85 to 92% of the variance in body length (Fig. 4.20). Analysis of covariance (ANCOVA), with year as treatment and larval length as the covariate, showed a significant difference among regression coefficients for the five regression lines ($p < 0.0005$).

During the SMB juvenile period, mean instantaneous growth rates ranged from 0.032 (0.68 mm d^{-1}) in 1992 to 0.080 (1.66 mm d^{-1}) in 1989, and averaged 0.058 (1.16 mm d^{-1}) over the five years (Table 4.14). Following metamorphosis, instantaneous growth rates increased in all years, with the exception of 1992, when growth rates remained relatively constant throughout the larval and early juvenile periods. Age explained 83 to 94% of the variance in body length during the juvenile period and linear models provided the best fit to the length-age regressions in all years, with the exception of 1992, where a second order polynomial model provided a better fit (Fig. 4.21). Over the 5 year study, mean instantaneous growth rates of larvae and juveniles were positively correlated ($r = 0.94$; Fig. 4.22).

Growth rates were determined at 4-day intervals between first feeding and brood dispersal for all 5 year-classes. Instantaneous growth rates, as reflected by the regression coefficients (b) in the linear models, were lowest at first feeding in all 5 year-classes, when larvae were switching from endogenous to exogenous food resources (Table 4.15). Growth rates generally increased with age, peaking at or near the time of metamorphosis in each season. An exception occurred in 1992, where growth rates remained relatively constant throughout the parental care period of development.

4.3.7.2 Brood-Specific Larval Growth

Brood-specific larval growth rate differed significantly among years ($F_{4,243} = 91.73$; $p < 0.0005$). Mean growth rates ranged from a low of 0.32 mm d^{-1} in 1992 to a high of 0.74 mm d^{-1} in 1989 (Fig. 4.23). Over the five seasons, growth rates of larval broods averaged 0.56 mm d^{-1}. Differences in mean growth rate are partly explained by different temperature regimes among years. For instance, mean brood-specific growth rate of larvae was highest in 1989 and lowest in 1992, years that experienced the highest and lowest mean water temperatures, respectively. However, much of the variation in larval growth rates among years was not explained by differences in temperature regimes. For example, Tukey's test showed that mean brood-specific growth rates differed significantly in 1991 and 1993, while mean brood-specific temperatures were identical (20 °C).

Brood-specific growth rates during the SMB larvae period were highly variable within years (Table 4.16). Maximum brood-specific growth rates were 50, 75, 114, 62 and 39% higher than average rates in 1988, 1989, 1991, 1992 and 1993, respectively. Growth rates were most variable in 1989, with instantaneous growth rates ranging between 0.031 - 0.097 (0.32 - 1.30 mm d^{-1}). Variability in instantaneous growth rate was 2 times higher in 1989 than in the other 4 years. Bartlett's test for homogeneity of variances indicated that variance in instantaneous growth rate differed significantly among years ($B_c = 96.99$; $X^2_{0.05,4} = 9.488$; $p < 0.0005$). Tukey's test indicated that the variance in instantaneous growth rate in 1989 was significantly higher than in other years.

Brood-specific growth rates were regressed against brood-specific mean water temperatures in each year. The relationships are shown in Figure 4.24 and the regression equations are listed in Table 4.17. Brood-specific growth rates were positively associated with brood-specific water temperatures during the larval period in 4 of 5 years. The slope of the regression line describing these relationships differed significantly from zero in only 3 years and mean water temperature explained > 15% of the variation in mean growth rate of SMB larvae in only 2 years.

The slope of the regression line describing the relationship between growth rate and water temperature differed among years, owing to the negative relationship between water temperature and larval growth rates in 1988. The negative relationship between brood-specific growth rate and water temperature in 1988 resulted, in part, from extremely low growth rates in a small number of broods spawned late in the season. Removal of these nests from the analysis resulted in a positive, but non-significant ($p = 0.441$) relationship between growth rate and water temperature in 1988. A test for similarity of slopes among the four nesting seasons having a positive relationship between growth rate and water temperature also showed that the slopes differed among years ($F_{4,187} = 13.56$; $p = 0.001$). Thus, the relationship between growth rate and temperature varied across nesting seasons, and no single regression equation describing growth, with respect to temperature, could be constructed.

Larval growth rates were positively associated with spawning date in most years and likely reflected the seasonal increase in littoral zone water temperature. Lack of a strong relationship between larval growth rates and temperature likely resulted from low variability in brood-specific temperatures within nesting seasons. For example, mean brood-specific water temperature varied by ≤ 2 °C for 75% of all broods during the larval period in 1989 and 1993, while mean brood-specific water temperatures varied by ≤ 1 °C for 75% of all broods in 1988 and 1992. Brood-specific water temperature was least variable in 1991, when mean temperatures ranged by < 1 °C for all larval broods. Interestingly, brood-specific water temperatures were most variable in the 3 years in which significant relationships between larval growth rates and water temperature were found.

4.3.7.3 Brood-Specific Juvenile Growth

Brood-specific growth rates of juvenile SMB differed significantly among years ($F_{4,97} = 47.28$; $p < 0.0005$). Instantaneous growth rate ranged from 0.034 (0.68 mm d^{-1}) in 1992 to 0.089 (1.73 mm d^{-1}) in 1989 (Fig. 4.25). Over the five nesting seasons, brood-specific instantaneous growth rate averaged 0.064 (1.25 mm d^{-1}) during the juvenile period. Tukey's test showed that mean growth rate in juvenile broods was significantly higher in 1989 than in other years, while mean growth rate was significantly lower in 1993 than in other years. The relative magnitude in mean growth rate among years in the juvenile period was very similar to the pattern observed in the larval period.

Inter-annual variation in mean growth rate of juveniles was strongly associated with mean water temperaturse. In 1989, juvenile broods experienced the highest mean temperatures and also had the highest instantaneous growth rates, averaging 0.089 (1.73 mm d^{-1}; Table 4.18). In contrast, brood-specific water temperature averaged 18.6 °C in 1992, nearly 3 °C lower than in 1989. Mean instantaneous growth rate in juvenile broods was 0.034 (0.68 mm d^{-1}) in 1992, only 38% of the value recorded for broods in 1989.

Similar to the larval period, the relationship between juvenile brood-specific growth rate and water temperature was not as strong within years as among years. Although brood-specific growth rate was positively associated with brood-specific mean water temperature in 4 of 5 years, the slope of the regression line describing this relationship differed significantly from zero only in 1988 and 1989 (Table 4.19). Slopes of the regression lines differed among years, thus no single regression equation describing growth with respect to water temperature could be constructed for all years.

4.3.7.4 Variability in Brood Growth Rates at 4-day Growth Intervals

Growth patterns in SMB broods were examined at 4-day intervals, beginning at first feeding. Brood-specific growth rates were lowest in the first 4-day growth interval in all years, when larvae switched from endogenous to exogenous food resources (Figs. 4.26, 4.27). Mean growth rate for the 4-day growth intervals increased between first feeding and metamorphosis in 4 of the 5 nesting seasons. Brood-specific growth rates remained relatively stable throughout the larval and early juvenile periods in 1992, a year characterized by unseasonably low water temperatures. Instantaneous growth rates were highest at or near the point of metamorphosis in all years. Following metamorphosis, instantaneous growth rates declined or remained relatively stable.

A one-way repeated measures ANOVA showed that brood-specific instantaneous growth rates, determined for successive 4-day growth intervals, differed significantly in all years (Table 4.20). Post-hoc multiple contrasts showed that mean growth rates in the first 4-day growth interval was significantly lower than growth rates in subsequent intervals in all years. Instantaneous growth rates during the first 4-day growth interval of the juvenile period were 107, 79, 67, 77 and 90% higher than those for the first 4-day growth interval of the larval period in 1988, 1989, 1991, 1992 and 1993, respectively.

4.3.7.5 Smallmouth Bass Growth in Relation to Food Availability & Temperature

Multiple regression analyses revealed that timing between the production of SMB larvae and peak prey biomass levels explained little of the seasonal variation in brood-specific growth rates. In 1988 and 1992, timing between production of first-feeding broods and peak prey biomass levels explained none of the variation in brood-specific growth rates. In 1991, variation in brood-specific mean water temperature and peak food availability explained 33% of the variation in brood-specific growth rates; however, the temporal match between larval production and peak prey levels explained only 1% of this variation (Table 4.21). In 1993 the full regression model explained 29% of the variation in brood-specific growth rates. There was a moderate negative relationship ($r^2 = 0.11$) between brood-specific growth rates and the temporal match between larval production and peak prey biomass levels in 1993. As production of first-feeding larvae occurred 2 weeks after peak prey production in 1993 (see Fig. 4.12), broods spawned earlier in the season experienced relatively higher growth rates than late-spawned broods.

Prey availability also explained little of the variation in larval growth rates among years. Although mean instantaneous growth rate in SMB larvae was positively correlated with mean zooplankton biomass among years, the relationship was not significant ($r = 0.34$; $n = 4$; $p = 0.66$). Mean instantaneous growth rate in SMB larvae ranged from 0.032 (0.39 mm d^{-1}) in 1992 to 0.051 (0.68 mm d^{-1}) in 1993, while mean zooplankton biomass during the larval period ranged from 26 (1992) to 133 (1991) mg m^{-3}. Lack of a strong relationship between prey abundance and larval growth rates is perhaps best illustrated by comparing the 1991 and 1993 year-classes. Larval growth rates were high in both years, with mean values differing by < 10%. Prey abundance, however, differed dramatically between years, with mean zooplankton biomass approximately 2 times higher in 1991(133 mg m^{-3}) than in 1993 (67 mg m^{-3}). Moreover, water temperatures during the larval period did not differ, averaging 20.4 °C in both years.

In contrast to prey levels, variation in mean water temperature explained much more of the year-to-year variation in larval growth rates. The among-year correlation between average brood-specific growth rate and brood-specific water temperature was strongly positive, but not significant, for both the early larval ($r = 0.75$, $p = 0.143$, $n = 5$; Fig. 4.28a) and late larval ($r = 0.78$, $p = 0.121$, $n = 5$ Fig. 4.28b) phases of development. The strong association of increased growth rates with increasing temperature suggests that growth of SMB larvae may be physiologically constrained as opposed to food-limited.

4.3.8 YOY Mortality

4.3.8.1 Mortality: Year-Class Level

The overall trend in age-specific survival was similar across years (Fig. 4.29). A linear model of mortality provided the best fit to abundance-at-age over the entire parental care period in 4 of 5 year-classes. Instantaneous mortality rate ranged from a low value of 0.11 (10.4% d^{-1}) in 1992 to a high of 0.17 (15.6% d^{-1}) in 1989. Analysis of covariance (ANCOVA), with year as the treatment and age as the covariate, showed a marginally significant difference among regression coefficients for the five regression lines ($p = 0.05$).

The relationship between abundance and age followed a similar pattern each year (Fig. 4.29). Abundance estimates began below the regression line, crossed above the line and then fell below the regression line again prior to brood dispersal. The point at which abundance estimates cross above the regression lines corresponded closely with the timing of metamorphosis in each year, suggesting that mortality rates at the year-class level may be lowest near the end of the larval period. Following metamorphosis, abundance estimates fell below the regression line, suggesting higher mortality rates in juvenile SMB.

Survival of embryos equalled 13.4 and 16.4% in 1992 and 1993, respectively. Year-class instantaneous mortality rates during the embryonic period equalled 0.129 (12.1% d^{-1}) in 1992 and 0.134 (12.5% d^{-1}) in 1993, approximately 2 times higher than larval mortality rates.

During the larval period, year-class instantaneous mortality rates varied considerably among years, ranging from a low of 0.067 (6.5% d^{-1}) in 1989 to a high of 0.102 (9.7% d^{-1}) in 1991 and averaging 0.081 (7.9% d^{-1}) over the five years (Table 4.22). Instantaneous mortality rate also varied among years in both the early and late larval phases of development. In the early larval phase, instantaneous mortality rates were highest in 1988 ($Z = 0.109$; 10.3% d^{-1}) and 1992 ($Z = 0.107$; 10.1% d^{-1}), with values approximately 2.3 times higher than in 1993 ($Z = 0.047$; 4.6% d^{-1}). The instantaneous mortality rate was less variable among years during the late larval phase of development, ranging from 0.063 (6.2% d^{-1}) in 1988 to 0.095 (9.1% d^{-1}) in 1991. Thus, not only did instantaneous mortality differ among years during each of the larval phases, but the relative magnitude of mortality among years differed between the two phases. For example, while the 1988 year-class experienced the highest mortality rate during the early larval phase, it also experienced the lowest mortality rate during the late larval phase.

In 3 of 5 years, year-class mortality rates of larvae during the early larval phase exceeded values for larvae during the late larval phase, however, mean daily mortality rate over the 5 years differed by < 1% between the two larval phases.

4.3.8.2 Brood-Specific Mortality

Mean instantaneous mortality rates in SMB larvae ranged from 0.44 (28% d^{-1}) in 1993 to 0.91 (40.3% d^{-1}) in 1988 and averaged 0.74 (33.8% d^{-1}) over the 5 years (Table 4.23). Brood-specific mortality rates were highly variable in all years, ranging between 0 - 100% d^{-1} in all years. Mortality distributions were strongly skewed to the right, which indicated that a small percentage of broods experienced high mortality each season (Fig's. 4.30, 4.31). The skewed nature of the mortality distributions prevented testing of mean instantaneous mortality rates among years; however, chi-square analysis revealed that brood-specific median instantaneous mortality rate differed significantly among years during the larval period ($X^2 = 12.89$; $p < 0.0005$). Median instantaneous mortality rates ranged from 0.02 (2.3 % d^{-1}) in 1989 to 0.50 (39.2% d^{-1}) in 1988 and averaged 0.28 (24.5% d^{-1}) over the 5 seasons. Median brood-specific mortality rates were exceptionally low in 1989, being more than an order of magnitude below values in other years.

The magnitude of brood-specific and year-class level mortality rates differed considerably in all years (Fig. 4.32). Mean and median brood-specific instantaneous mortality rates were approximately 10 and 5 times higher than year-class values, respectively, with the exception of 1989, when the median brood-specific mortality rate was very similar to the mortality rate for the year-class. The discrepancy in the magnitude of mortality rates between year-class and brood-specific levels stemmed from the highly skewed distribution of mortality rates at the brood level.

Brood-specific mortality rates were examined independently in the early and late larval phases of SMB development. During the early larval phase, mean instantaneous mortality rate ranged from a low of 0.241 in 1993 to a high of 0.741 in 1991, averaging 0.16 over the 5 years (Table 4.24). During the late larval phase mean instantaneous mortality rate ranged from a low of 0.04 in 1989 to a high of 0.19 in 1988 and averaged 0.11 over the five spawning seasons. Mortality distributions were skewed to the right during both larval phases in all years (Fig. 4.33).

Chi-square analysis revealed that median instantaneous mortality rate differed significantly among years in both the early ($X^2 = 33.87$; $p < 0.0005$) and late ($X^2 = 25.65$; $p < 0.0005$) larval phases. In the early larval phase, median instantaneous mortality rates ranged from a low of 0.013 (1.3% d^{-1}) in 1989 to a high of 0.191 (17.3% d^{-1}) in 1991 and averaged 0.042 (4.1% d^{-1}) over the 5 years (Table 4.24). Thus, the median instantaneous mortality rate in 1991 was approximately 15 times higher than in 1989. During the late larval phase, median instantaneous mortality rate ranged from a low of 0.011 (1.1% d^{-1}) in 1989 to a high of 0.352 (29.6% d^{-1}) in 1992 and averaged 0.106 (10.1% d^{-1}) over the 5 years. The median instantaneous mortality rate during the late larval phase in 1992 was approximately 32 times higher than in 1989. Although the median mortality rate remained extremely low during both the early and late larval phases in 1989, the relative magnitude in median mortality rate among the 4 remaining years differed between the early and late larval phases (Table 4.24).

Brood-specific median instantaneous mortality rate differed significantly between the early and late larval phases in 2 of 5 years (Table 4.25). In the two years where significant differences occurred (1988, 1993), median mortality rate was higher in the late larval phase. Thus, with respect to median mortality rate, no evidence of a critical period was evident in any of the 5 spawning seasons. The magnitude of difference in the median instantaneous mortality rate between the larval phases differed considerably among years, ranging from 0.2% in 1989 to 21.2% in 1993. Over the 5 years, the median instantaneous mortality rate was 6% higher in the late larval phase than in the early larval phase.

4.3.8.3 Juvenile Brood Mortality

Brood-specific mean instantaneous mortality rate during the early juvenile period was highly variable among years, ranging from 0.13 (10.9% d^{-1}) in 1989 to 0.36 (23.9% d^{-1}) in 1988 and averaged 0.21 (16% d^{-1}) over the 5 spawning seasons (Table 4.26). Mean instantaneous mortality rate in juvenile broods was 60, 83, 76, 70 and 48% lower than in larval broods in 1988, 1989, 1991, 1992 and 1993 respectively. As in larval broods, juvenile brood-specific mortality rates were highly variable within years, with mortality distributions strongly skewed to the right in all years (Figure 4.34).

Chi-square analysis showed that median instantaneous mortality rate in juvenile broods differed significantly among years ($X^2 = 14.06$; $0.005 < p < 0.01$). Median instantaneous mortality rate ranged from a low of 0.05 (4.5% d^{-1}) in 1989 to a high of 0.18 (16.8% d^{-1}) in 1988 and averaged 0.10 (9.7% d^{-1}) over the 5 years. Within years, median instantaneous mortality rate was lower in juvenile broods than in larval broods in 4 of 5 years. The exception was 1989, when mortality rates remained low throughout the parental care period. Chi-square analysis showed that median mortality rates differed significantly between juvenile and larval broods only in 1992 (Table 4.27).

4.3.8.4 Smallmouth Bass Mortality in Relation to Food Availability & Temperature

The regression model used to analyze the importance in timing between production of first-feeding SMB larvae and date of peak prey biomass and water temperature explained a significant amount of the seasonal variation in brood-specific mortality rates in SMB in all 4 years. In 3 of 4 years, the model explained over 50% of the seasonal variation in brood-specific mortality (Table 4.28). However, timing between production of SMB larvae and peak prey biomass levels explained only 4% (1991), 7% (1992), 13% (1988) and 16% (1993) of the variation in brood-specific mortality rate.

For years in which first-feeding larvae were produced prior to the peak seasonal production of zooplankton (1988, 1991), brood-specific mortality rates were negatively related to time between production of first-feeding larvae and date of peak prey biomass levels. This is indicated by the negative partial correlation coefficients for the independent variable 'time' in the regression models for 1988 and 1991 (Table 4.28). Thus mortality rates were highest in broods that initiated first feeding nearest to the date of peak prey production (latest in the season). In contrast, in those years in which first-feeding larvae were produced after the seasonal peak in prey production (1992, 1993), brood-specific mortality rates were positively related to time between production of first-feeding larvae and date of peak prey biomass levels. Broods that initiated first-feeding nearest to the date of peak prey biomass in 1992 and 1993 experienced lower mortality rates, on average, than broods which initiated feeding later in the season. To summarize, the sign of the relationship between mortality of SMB larvae and the timing of production of first-feeding SMB larvae and their prey changed among years, depending on whether larvae were produced prior to or after the peak production of zooplankton. Importantly, these results also indicated that regardless of whether first-feeding larvae were produced prior to (1988, 1991) or following (1992, 1993) the peak production of zooplankton, mortality rates increased seasonally in all years.

Timing between production of SMB larvae and date of peak prey biomass explained only a moderate amount of the seasonal variation in brood-specific growth rates in SMB, but the relationship may be spurious because the regression coefficient for time (days) between production of SMB larvae and date of peak prey biomass was negative in 1988 and 1991, indicating that larval mortality rates were highest when zooplankton biomass was highest. Moreover, mean water temperature and variation in mean water temperature, the remaining independent variables, contributed significantly to the multiple regression model in 3 of 4 years.

Mean brood-specific mortality rate of early larvae was moderately positively associated with mean water temperature among years ($r = 0.56$, $p = 0.33$, $n = 5$) (Fig. 4.35a). However, as a result of the strong negative effect of temperature on developmental rate mean cumulative mortality rate was negatively associated with water temperature among years during the early larval phase of development ($r = -0.43$, $p = 0.47$, $n = 5$) (Fig. 4.35b). In contrast to the early larval phase, mean brood-specific mortality rate was significantly negatively associated with mean water temperature among years during the late larval phase of development ($r = 0.99$, $p = 0.001$, $n = 5$) (Fig. 4.36a). Due to the strong negative relationship of developmental time and mortality rate with temperature, cumulative mortality rate of late larvae showed a significant negative relationship with temperature among years ($r = -0.98$, $p = 0.003$, $n = 5$) (Fig. 4.36b). Due to the influence of temperature on developmental rate, cumulative mortality was positively associated with phase duration during both the early larval ($r = 0.28$. $p = 0.64$, $n = 5$; Fig. 4.37a) and late larval phases ($r = 0.93$, $p = 0.022$, $n = 5$; Fig. 4.37b) of development.

4.3.9 Relationship Between Mortality and Growth

Brood-specific instantaneous mortality rates were negatively related to brood-specific instantaneous growth rates in SMB within years (Fig. 4.38). Linear slopes of the regression lines describing these relationships were significant in 3 of the 5 spawning seasons (Table 4.29). Lack of a strong relationship between mortality rate and growth rate in 1989 ($R^2 = 0.07$) likely resulted from the highly skewed mortality distribution. Extremely high mortality rates in a small number of broods contributed to the high variation in brood-specific mortality rate in 1989. However, mortality rates differed little among the remainder of the broods in 1989.

The relationship between growth and mortality showed a similar pattern among years. At the year-class level, the correlation between mean instantaneous mortality and growth rate for the full larval period was negative, but insignificant ($r = 0.49$, $p = 0.40$, $n = 5$; Fig. 4.39a). Similarly, at the brood level, the correlation between median brood-specific instantaneous mortality and growth rate was negative, but insignificant ($r = 0.84$, $p = 0.07$, $n = 5$; Fig. 4.39b).

4.4 Discussion

4.4.1 Food Limitation, YOY Growth and Mortality

This study demonstrated significant inter-annual variation in the mean spawning date of SMB within a temperate lake. Spawning occurred from late May through late June at mean daily temperatures ranging from 11.5 to 21 °C, consistent with earlier studies on SMB in rivers (Graham and Orth 1986; Lukas and Orth 1995) and lakes (Turner and MacCrimmon 1970; Ridley 1978; Shuter, et al. 1980). Both the onset and the duration of spawning activity appeared to be regulated by water temperature. Previous studies demonstrate that much of the variation in spawning time of SMB in lentic environments is associated with two important aspects of water temperature; average temperature and the rate of increase in water temperature (Shuter, et al. 1980; Vogele 1981; Ridgway, et al. 1991). The early mean spawning date in 1991 was associated with a rapid rise in spring water temperatures. As a consequence, spawning activity in 1991 was essentially completed prior to the date of onset of spawning in any other year. Male size was negatively related to spawning date in all years, consistent with previous studies on the same population (Ridgway, et al. 1991; Ridgway and Friesen 1992).

The existence of seasonal and inter-annual variability in spawning time may have important ecological implications for SMB population dynamics. A key assumption of the match-mismatch hypothesis is that the seasonal timing of spawning has evolved so as to synchronize the annual production of offspring with maximum annual availability of their prey (Cushing 1969). Results of my study did not indicate a consistent reproductive strategy in relation to the availability of YOY prey. First-feeding larvae were produced both prior to (1988, 1991) and following (1992, 1993) the date of peak zooplankton production. The production of first-feeding larvae coincidental with peak prey levels has been termed a 'synchronous' strategy (Sherman, et al. 1984) and has been reported in numerous marine species (Drolet, et al. 1991; McGurk, et al. 1993; Ponton, et al. 1993). In herring, synchronous production of larvae and their prey was noted in the spring cohort but not in the fall cohort (Fortier and Gagne 1990). The close match between the production of first-feeding larvae and their food in 1988 and 1991 suggested a synchronous spawning strategy. In contrast, the production of first-feeding larvae following the date of peak zooplankton production (1992, 1993) did not support the assumption of larvae-prey synchrony. The low warming rate of water in Lake Opeongo prior to spawning, together with extremely low temperatures during the embryonic period, contributed to the seasonal delay in production of first-feeding larvae in 1992 and 1993.

A second assumption of the match-mismatch hypothesis states that the timing of larval production should be relatively invariant among years, in contrast to prey production, which may show considerable year-to-year variability (Cushing 1969). The timing of larval production appeared remarkably constant in 4 of 5 years, consistent with this second assumption of the match-mismatch hypothesis. The mean date of spawning occurred significantly earlier in the season in 1991 than it did in other years. Consequently, the mean date of production of first-feeding larvae and the mean date of peak prey production in Lake Opeongo both varied by approximately 3 weeks over the entire duration of the study. Although larval production coincided with the seasonal increase in water temperatures, results of my study did not fully support this second assumption of the match-mismatch hypothesis.

Variability about the mean spawning date was high in 4 of 5 years, and may have important implications for growth and survival of YOY SMB. Given the seasonal increase in water temperature in Lake Opeongo, YOY from nests spawned earlier in the year generally experienced lower brood-specific temperatures throughout development. Low temperatures may negatively impact survival of YOY SMB in several ways. Previous research has shown that low temperatures are associated with a higher incidence of nest desertion in spawning males, leaving offspring vulnerable to predation, siltation and spread of fungus (Coutant 1975; Shuter, et al. 1980). This indirect effect of water temperature on YOY survival was most apparent in 1992, when cold temperatures persisted for several weeks following initiation of the spawning season, resulting in high nest failure among early-spawning males. Low temperature may also affect YOY survival directly, by reducing growth and developmental rates and thereby increasing the duration of the larval period (Chambers and Leggett 1987). Results of the present study showed that larval growth rates were positively associated with temperature in most years, and that larval growth rates were positively associated with developmental rates among years. It has been suggested that slow growth during the larval period may lead to higher cumulative mortality due to predation (Chambers and Leggett 1987; Pepin 1991; Rice, et al. 1993).

There are also potential benefits associated with early spawning for SMB offspring. With regard to predation risk, shoreline transect swims of Jones Bay showed that: 1) the abundance of potential predators increased seasonally and 2) the abundance of potential predators in the exposed habitat was extremely low relative to the protected habitat (unpublished data). Thus, offspring raised early in the season in exposed habitat may have experienced lower predation risk than young raised later in the season in protected habitat. Bollens et al. (1992) suggests that early spawning in fishes in temperate coastal waters may be governed by seasonal increases in YOY predators. Hatching early in the season may also allow SMB larvae from early-spawned nests to shift from zooplanktivory to benthivory earlier in the season. Because survivorship of YOY SMB is strongly size dependent, particularly through the first winter (Shuter, et al. 1980; MacLean, et al. 1981), the timing of the diet shift may be critical in determining survival and recruitment rates. In largemouth bass, seasonal timing of spawning and larval growth rates both play a critical role in the timing of the shift to piscivory in juveniles and in survival during the first winter of life (Miller and Storck 1984; Olson 1996).

The mismatch between timing of production of first-feeding larvae and peak prey abundance in 2 of 4 years suggested that a match or mismatch of larvae and their prey may not be the only factor regulating the spawning behaviour of SMB in Lake Opeongo. Indeed, for SMB populations near the northern limit of their range, the seasonal timing of spawning has been shown to be constrained by the energy stores of nesting males (Ridgway, et al. 1991). The strong positive relation between total length and age of YOY SMB in my study indicated that initial length advantages resulting from earlier spawning persisted through to dispersal, regardless of the degree of match or mismatch in the production of SMB larvae and their prey. Previous studies of largemouth bass also show that initial length advantages of individuals from early-spawned nests persist throughout the first growing season (Keast and Eadie 1985; Goodgame and Miranda 1993). Failure of my data to meet two important assumptions of the match-mismatch hypothesis, together with the strong linear relation between length and age in all years, suggested that a match or mismatch of first-feeding SMB larvae with their prey may be of secondary importance in determining the spawning strategy of SMB.

Critical Period Hypothesis

Brood-specific growth and mortality rates of larvae varied considerably within and among years; however, results of this study did not support Hjort's (1914) critical period hypothesis that prey availability coinciding with the production of first-feeding larvae contributes significantly to growth and survival of larval fish. During this multi-year field study, I was unable to detect a critical period of high mortality associated with the onset of first-feeding. Although the production of SMB larvae was associated with the seasonal rise in prey concentration in all years, production of first-feeding larvae and their prey were never precisely matched. First-feeding larvae were produced either before (match years - 1988, 1991) or just after (mismatch years - 1992, 1993) the peak date of prey production. Mean and median brood-specific growth rates were inconsistently associated with prey concentration across years. The strong effect of temperature on larval growth rates may have obscured effects of food-limitation on larval growth. Repeated measures analysis of growth at consecutive 4-d intervals showed that brood-specific instantaneous growth rates of early larvae were consistently lower than those of older larvae. These results suggested that factors other than prey concentration alone were influencing growth rates of early larvae. Lower temperatures during the early larval phase of development, due to the seasonal rise in water temperature, may have contributed to the lower growth rates of early larvae. Alternatively, the higher growth rates of late larvae may have reflected ontogenetic changes in foraging behaviour, as a fish's ability to locate and capture prey improves markedly and rapidly during ontogeny (Blaxter 1986; Noakes and Godin 1988; Browman and O'Brien 1992; Wanzenböck 1992).

Median brood-specific instantaneous mortality rates of early larvae ranged by an order of magnitude among years. However, inter-annual variability in mortality of early larvae was not related to prey abundance. With the exception of 1991, annual brood-specific mortality rates of early larvae showed a negative relation with mean annual water temperatures. Mortality rates of early larvae were lowest in warm calm years (1989, 1993) and highest in cold (1992) or windy (1988) years.

Importantly, my results indicated that median brood-specific mortality rates of early larvae did not exceed those of late larvae in all years. Thus, low growth rates of early larvae did not translate into higher mortality rates as predicted by the critical period hypothesis. My results are consistent with those of Taggart and Leggett (1987) who found no relation between mortality of larval capelin *Mallotus villosus* and prey abundance. Similarly, Johnson and Mathias (1993) were unable to detect a critical period of high starvation in pond-reared larval walleye *Stizostedion vitreum* at the onset of first-feeding. Fortier and Leggett (1984) found that mortality of first-feeding capelin larvae was related to prey abundance, although the magnitude of the effect is small.

Several factors may have contributed to the low mortality rates of early larvae. First, death from starvation was unlikely, as brood-specific growth rates of larvae were only weakly related with prey abundance in any year. Second, variability in YOY TL was extremely low during the early larval phase of development. The effect of size-selective mortality, assuming it was operating, may not have been apparent during the early larval phase of development. Variability in length increased with age, and the effects of size selective mortality may not have been apparent until the late larval phase of development, as observed at the individual-level in YOY yellow perch (Post and Prankevicius 1987). Third, the volume of water occupied by broods and the mean swimming speed of larvae (see Chapter 3) were both significantly lower for early larvae than for older larvae. In other species, vulnerability to predation during early life phases may be reduced because of their low visibility and/or low motility (Folkvord and Hunter 1986; Litvak and Leggett 1992; Pepin, et al. 1992; Bertram and Leggett 1994). That larger and faster growing larvae experienced higher mortality rates was consistent with more recent studies, which propose that vulnerability of larvae to predators should follow a dome-shaped function (Bailey and Houde 1989; Fuiman and Margurran 1994; Paradis, et al. 1996). My results are also consistent with previous experiments that show predation mortality for early larvae to be less than (Litvak and Leggett 1992; Pepin, et al. 1992) or equal to (Bertram and Leggett 1994) that of older larvae. Finally, the low mortality rates for early larvae may have resulted from changes in parental effort of guarding males, as previous studies show a decline in parental defence behaviour of nesting male SMB following first-feeding of larvae (Ridgway 1986; Ridgway 1989; Mackereth 1995).

Match-Mismatch Hypothesis

The results of this study did not support the basic predictions of the match-mismatch hypothesis as related to growth and survival of SMB larvae. The match-mismatch hypothesis predicts good growth and survival of larvae in years of match in the peak production of larval fish and their prey. Growth rates of larval SMB were generally inconsistent with the prediction that inter-annual growth rates will be higher in years of larval fish-prey match than in years of mismatch. For instance, the mean brood-specific growth rate of larvae was higher in 1993 (mismatch year) than in 1989 and 1991 (match years). The higher mean larval growth rate in 1993 could not be attributed to temperature effects, as mean brood-specific temperatures during the larval period did not differ significantly among the three years. In 1992, low larval growth rates were associated with extremely low prey concentrations. However, mean brood-specific water temperature during the larval period in 1992 was significantly lower than mean temperatures in the other 4 years. Temperature is often the main factor regulating larval fish growth (Houde 1989), and the positive relation between mean annual larval growth rates and mean annual prey abundance was likely due to the strong positive correlation between larval growth rates and temperature. Previous field studies have associated inter-annual variation in YOY fish growth with prey abundance (Haldorson, et al. 1989; Karakiri, et al. 1989; Bailey, et al. 1995; Fortier, et al. 1995; McGovern and Olney 1996). Other studies (Butler 1989; McGurk, et al. 1992) found inter-annual variation in larval growth rates to be unrelated to prey concentrations.

The match-mismatch hypothesis also predicts that variation in larval growth rates within a growing season is a function of the temporal match between larvae and peak prey abundance (Cushing 1990). Regression analysis showed that seasonal variability in brood-specific growth rates was not related to the timing of peak prey production in 1988, 1991 and 1992. In 1988 and 1991, production of SMB larvae and their prey was closely synchronized. Under such favourable prey concentrations, the likelihood of food limitation would have been greatly reduced. In 1992 and 1993 production of first-feeding larvae followed the seasonal peak in prey abundance. Prey concentrations during the SMB larval period were extremely low in both years, but values did not differ significantly from one another. However, mean growth rates of larvae in 1992 and 1993 differed significantly, as the mean growth rate of larvae in 1993 was nearly twice as high as that for larvae in 1992. Given the temperature constrained growth and developmental rates of SMB larvae in 1992, the absence of any effect of prey concentration on brood-specific growth was not surprising. Prey concentration may not have been the most important factor limiting larval growth in 1992. In 1993, SMB larvae grew at very high rates despite low prey concentrations and the temporal match between larval production and peak prey abundance explained 11% of the variation in brood-specific growth rates. My results contrast with those of Emery (1975) who proposed that first-year growth of Lake Opeongo SMB is limited by food availability. Recent studies of American shad in the Connecticut River (Crecco and Savoy 1985) and larval plaice *Pleuronectes platessa* in the North Sea (Hovenkamp 1990) have clearly linked seasonal variations in growth rates with prey concentration. In contrast, differences in cohort-specific growth rates of Pacific herring *Clupea pallasi* larvae were not related to prey abundance (McGurk, et al. 1993).

Inter-annual differences in brood-specific mortality rates of SMB larvae were not related to the availability of prey abundance. For example, in years of larvae-prey match (1988, 1991) brood-specific mortality rates were greater than or equal to those in years of larvae-prey mismatch (1992, 1993). In contrast, Bailey et al.(1995) found that inter-annual variability in prey abundance at the time of maximum production of first-feeding walleye pollock *Theragra chalcogramma* larvae was the most important factor in larval mortality rates. Similarly, inter-annual differences in the feeding success of fish larvae in Hudson Bay, Canada, was related to the availability of prey abundance, also consistent with the match-mismatch hypothesis (Fortier, et al. 1995).

Results of this study showed that variability in brood-specific mortality rates of larvae within years was weakly influenced by the temporal overlap between larvae and their prey, as predicted by the match-mismatch hypothesis. In years of larvae-prey match (1988, 1991), first-feeding larvae were produced 1-3 wks prior to the seasonal peak in prey abundance. The negative partial correlation coefficients in the regression models for the two larvae-prey match years indicated that broods spawned earliest in the season experienced the lowest mortality rates. In the years of larvae-prey mismatch (1992, 1993), when larvae were produced following the occurrence of the seasonal peak in prey abundance, positive partial correlation coefficients in the regression models again indicated that broods spawned earlier in the year experienced lower mortality rates. Regardless of the synchronism between the seasonal occurrence of SMB larvae and their prey, broods spawned earlier in the year experienced slightly lower mortality rates. For the 4 years in which prey abundance was measured, spawning date explained 13, 4, 7 and 16% of the variation in brood-specific mortality rate. Interestingly, the contribution of spawning date to variation in brood-specific mortality rate was lowest in 1991 (4%) when spawning period duration was shortest. This result is consistent with Mertz and Myers (1994) suggestion that variability in spawning duration of Atlantic cod can affect the extent of overlap between larvae and their prey, and thereby affect recruitment dynamics.

Results of previous field studies have both confirmed and rejected the importance of intra-annual variability in prey abundance to larval fish mortality. Fortier and Gagne (1990) show survival in spring-spawned herring larvae *Clupea harengus* produced several weeks prior to the peak in plankton production to be higher than that of autumn-spawned larvae which are produced in conditions of declining prey concentration. In contrast, mortality rates of Pacific herring cohorts show no relation to seasonal patterns in prey abundance (McGurk, et al. 1993).

Although the match-mismatch hypothesis assumes that spawning strategies in fish have evolved to synchronize annual production of fish larvae and their prey, others (Bollens, et al. 1992) suggest that early spawning strategies in some species may function to minimize predation risk of their offspring to potential predators. There was a substantial seasonal increase in the abundance of potential fish predators of SMB larvae in the littoral zone of Lake Opeongo (unpubl. data). Thus, avoidance of piscivorous predators that may feed on their offspring may be another constraint that influences the timing of spawning in SMB. Initiating exogenous feeding early may not only allow larvae of early spawners to maximize growth during the first year of life, but it may also reduce their risk of predation during the first few months of life.

Growth-Mortality Hypothesis

Importantly, results of this study clearly demonstrated that brood-specific growth rates of larval and juvenile SMB were highly variable and contributed importantly to YOY survival in some years. The negative relationship between brood-specific growth and mortality rates suggested that the probability of surviving through to the juvenile period of development was higher for individuals from faster-growing broods. My results contrast with those of Sabo and Orth (1996) who used otolith analysis to show that individual SMB that survived to become juveniles were not statistically larger as larvae than the average-sized larvae in the population. However, my results are consistent with earlier reviews of the larval fish literature that show that survival of cohorts tend to be positively related to growth rates during the early stages (Anderson 1988) and that body size is important to larval survival (Miller, et al. 1988). Previous studies have also shown that faster-growing larvae may be favoured over slower-growing individuals (Rosenberg and Haugen 1982; Post and Prankevicius 1987; Rice, et al. 1987; Rice, et al. 1993). Other field studies have shown a negative relation between larval mortality and growth rates at the cohort level (Graham and Townsend 1985). Furthermore, if size-dependent mortality is operational, small changes in growth rate can have a large impact on larval survival (Houde 1987). Rice et al. (1993), using an individual-based simulation model, demonstrate how changes in the mean and variance of growth rates of individual larvae interact with size-dependent mortality to affect both the number and characteristics of survivors.

Inter-annual brood-specific growth and mortality rates of larvae were also negatively correlated. Survival rates have been shown to be highest for the fastest growing year classes in striped bass *Morone saxatilis* (Rutherford 1992). Since year-class growth rates were positively related to mean annual temperatures, larval period durations were also shorter for the faster growing year classes. Thus, larvae from faster-growing year classes were not only exposed to predation for a shorter period of time, but they may also have been less vulnerable to predation during the larval period because of size-based mortality. Together these effects could produce substantial differences in cumulative mortality of larvae among year classes. The size-dependent pattern of mortality rates in my study provided support for the growth-mortality hypothesis, although evidence to suggest food-limitation as the principle cause of mortality was not apparent.

4.4.2 YOY Production

Mean Brood Size

Production of first-feeding larvae in Lake Opeongo varied considerably, both within and among years. Mean brood size of first-feeding larvae differed significantly among years, ranging from a low of 498 larvae per nest in 1991 to a high of 1970 in 1993 and showed a moderate positive association with spawning stock abundance. Estimates of mean brood size fell within the range of values reported for other SMB populations (Neves 1975, x = 3943); (Raffetto and Baylis 1990, x = 482-1699); (Lukas and Orth

1995, x = 608), however, the 4-fold difference in mean productivity across years was larger than previously reported. Brood sizes were also highly variable within nesting seasons, ranging by two orders of magnitude in all years (1988, 45-3050; 1989, 10-3330; 1991, 26-1800; 1992, 17-5900; 1993, 28-5000). Ranges reported in earlier studies are generally lower and narrower than values measured in the present study (Pfieger 1966, 1651-3952; Clady 1975, 103-2608; Neves 1975, 451-7856; Lukas and Orth 1995, 98-1802). Results of this study also showed that brood size distributions were consistently skewed right, indicating that a small percentage of nests produced a large proportion of first-feeding larvae in each reproductive season. This is the first long-term field study that has determined brood size distributions of first-feeding SMB larvae, although Lukas and Orth (1995), studying reproductive success of SMB in the North Anna River, Virginia, observed that a small number (13%) of large males accounted for 31% of the total production of first-feeding larvae.

Brood size of first-feeding larvae was positively associated with male length in all years, consistent with previous studies (Neves 1975; Wiegmann, et al. 1992; Lukas and Orth 1995). Other studies have demonstrated a positive relation between female size and fecundity in SMB (Clady 1975; Hubert 1976; Vogele 1981; Serns 1984) including the Lake Opeongo population (Mackereth 1995). Earlier research on the reproductive behaviour of SMB in Lake Opeongo shows a consistent pattern of large males preceding small males in establishing nests, and has outlined bioenergetic hypotheses to account for the pattern (Ridgway, et al. 1991). By nesting earlier in the season, large males are more likely to mate with larger females, that are also able to spawn earlier in the season than smaller females (Ridgway, et al. 1991), thereby obtaining more eggs.

Male size explained much of the variation in brood size within years; however, it did not explain the 4-fold difference in mean brood size among years. For instance, the mean size of nesting males was highest in 1991, in a year that was also unique in having the smallest mean larval brood sizes. It is unlikely that the low brood sizes of first-feeding larvae in 1991 resulted from high embryonic mortality rates, as brood sizes at spawning were also extremely low (pers. obs.). Several studies on SMB report high inter-annual variability in total egg production (Clady 1975; Serns 1984), but provide no estimate of variability in mean fecundity of females among years. Inter-annual variation in mean fecundity has been reported for other species in the field, including plaice *Pleuronectes platessa* (Bagenal 1969), lake trout, *Salvelinus namaycush* (Martin 1970), bay anchovy *Anchoa mitchilli* (Zastrow, et al. 1991) and weakfish *Cynoscion regalis* (Lowerre-Barbieri and Chittenden 1996). Although it is generally accepted that food availability is of prime importance in determining the reproductive potential of different species, much of the field evidence is circumstantial, owing to the difficulties of separating out the effects of other environmental variables on fecundity. Laboratory experiments demonstrate a more direct effect of nutrition on fecundity in fishes (Wootton 1977; Springate, et al. 1985; Kjesbu, et al. 1996). Results of the present study suggest that variable fecundity may be an important component of SMB population dynamics. Further work is required to assess the effects of variable egg production on SMB population dynamics.

Fecundity, or initial egg number, may also have affected production of YOY SMB indirectly, through its influence on parental care behaviour in guarding males. Despite what appeared to be ideal weather conditions for nesting in 1991, the percentage of nests producing larvae was 40 to 50% below that of other years. Maximizing one's lifetime reproductive success is a function of a tradeoff between current and future reproduction (Sargent and Gross 1986). The parental effort of male SMB should be in response to the value of both the current brood and future reproductive expectations. Parental fish are able to adjust their level of behaviour in direct response to brood number (Ridgway 1989; Sabat 1994), which may include the decision to abandon their nests.

The early spawning season in 1991 may also have contributed to the low production of larvae in 1991. Ridgway et al. (1991) show that male body size acts as a constraint on the seasonal timing of reproduction in SMB. Due to the higher relative energy debt incurred during the winter, smaller males must allocate energy to growth prior to spawning The mean date of spawning in 1991 occurred 2 to 3 wks earlier than it did in other years. Consequently, smaller males may not have had adequate time between ice-out and spawning to acquire sufficient energy reserves to meet their reproductive needs.

In addition to the size and condition of spawning adults, production of first-feeding larvae has been shown to be influenced by factors that influence within-nest survivorship. Low productivity resulting from displacement of embryos and first-feeding larvae due to turbulence from wave action has been associated with high flow rates in streams (Winemiller and Taylor 1982; Simonson and Swenson 1990; Lukas and Orth 1995) and strong offshore winds in lakes (Coutant 1975; Goff 1985). Displaced offspring or offspring abandoned by males are also more likely to be consumed by predators (Pfieger 1975). In northern lakes, spawning may be interrupted when offshore winds produce upwellings that bring cold, hypolimnetic water into littoral-zone spawning areas (Shuter, et al. 1980). Episodic drops in water temperature are associated with high rates of nest abandonment in guarding males (Shuter, et al. 1980; Vogele 1981; Graham and Orth 1986) and increased egg mortality (Kerr 1966; MacLean, et al. 1981). In 1988, 13 (25%) nests in the study area failed following two days of high winds. Broods abandoned by males during the embryonic and larval periods in the present study were absent, and presumed dead, within 24 h of abandonment. Neves (1975) observed similar results after permanently removing SMB males from broods in a small lake.

Production of larvae has been shown to be higher in nests composed of larger substrate in SMB (Goff 1986; Wiegmann, et al. 1992) and bluegill *Lepomis macrochirus*, a related centrarchid (Bain and Helfrich 1983). Larger substrate offers greater protection for offspring exposed to high offshore winds (Goff 1986) and better protection from predators (Bain and Helfrich 1983; Walters and Wilson 1996). In Jones Bay, nesting habitat situated in the leeward side of islands, or otherwise protected from prevailing northwesterly winds, consisted of sand, silt, low-growing vegetation, or some combination of these substrates and appeared to offer young SMB little protection from predators, relative to the coarse gravel and large boulders that characterized the wind-swept habitat. Large early-nesting males consistently established territories in the wind-swept exposed habitat, in contrast with smaller late-nesting males that tended to establish nests in the protected habitat.

Total YOY Abundance

Results of this study showed that 82, 79, 77, 75 and 47% of SMB nests produced larvae in 1993, 1989, 1992, 1988 and 1991, respectively. The high inter-annual variability in percentage of nests producing first-feeding larvae is consistent with previous studies of SMB in lakes (Goff 1986; Ridgway and Friesen 1992). These authors show that years of low nesting success are characterized by cold and windy conditions, whereas calm, warm conditions result in high nesting success. Nest success during the embryonic period was not strongly associated with water temperature, as the percentage of nests that successfully produced first-feeding larvae was highest in the coldest year (1993; 15.5 °C) and lowest in one of the warmest years 1991 (19.0 °C). Thus, cold water temperature alone may not necessarily result in low nest success. High winds and low temperatures appear to be highly correlated, and further studies are needed to determine both the relative and the interactive effects of these variables on survival of SMB embryos.

Although a high percentage of nests successfully produced first-feeding larvae, the percentage of embryos surviving to become larvae was much lower. For example, in 1992 and 1993, 77 and 82% of the nests produced larvae; however, based on initial egg counts of SMB nests in Jones Bay (Mackereth 1995) and brood size estimates of first-feeding larvae in this study, only 16.4 and 13.4% of the eggs initially deposited in nests survived to become larvae in 1992 and 1993, respectively. Earlier studies show embryo survival of SMB in temperate lakes of similar latitude to Lake Opeongo to range between 25 and 30% (Latta 1963; Clady 1975). Although factors affecting embryo mortality in fishes have not been given a great deal of consideration (Bailey and Houde 1989), the apparent high mortality rates of SMB embryos in this study are not unlike those of other freshwater species that deposit demersal eggs (Forney 1976; Dahlberg 1979; Bouwes and Luecke 1997).

Lukas and Orth (1995) show a seasonal increase in the total production of first-feeding SMB larvae in a stream. These authors propose that higher temperatures reduce developmental times of embryos from late-spawned nests; shorter developmental times, in turn, result in lower cumulative mortality of eggs from fungus. In contrast to Lukas and Orth's (1995) observation, the seasonal pattern of larval production in Lake Opeongo was highly variable; frequency distributions of first-feeding larval abundance plotted against calender date showed distributions to be normal (1993), bimodal (1989, 1992) and skewed (1988). The seasonal pattern of larval production in Lake Opeongo was strongly related to the shape of the spawning date distributions of males. Thus, year classes characterized by bimodal spawning distributions tended to produce first-feeding larval distributions of similar shape. The seasonal pattern of large males receiving eggs prior to smaller males (Ridgway, et al. 1991), together with the positive relation between embryo number (hatched eggs) and male size (Ridgway and Friesen 1992) may also contribute to the seasonal pattern of larval production in Lake Opeongo. Given these relationships, egg numbers in nests would be expected to decline seasonally. A more comprehensive analysis is needed to determine how variability in spawning distribution, initial egg numbers and embryonic mortality operate to regulate the seasonal production of SMB larvae.

Although mortality rates differed significantly among years, the ranking of year-classes with respect to total production remained relatively unchanged between first-feeding and dispersal of juveniles from the natal sites. Year-classes with high initial larval abundances (1989, 1992, 1993) experienced lower mortality rates than year-classes with lower initial abundances. The positive relation between larval and juvenile abundance is the first conclusive evidence that early production patterns in juvenile SMB may be determined by larval supply. As such, this finding has important implications for the study of recruitment patterns in SMB. Previous research (Ridgway and Friesen 1992) shows that inter-annual variation in year-class strength, especially the appearance of strong year-classes at first reproduction, is maintained in age-structures throughout adult life. The strong relation between larval and juvenile abundance in the present study, and the maintenance of strong adult year-classes following first reproduction (Ridgway and Friesen 1992), together suggest that much of the variability in year-class strength of SMB may occur during either the embryonic period and/or later in the juvenile period.

Results of the present study contrast with those of previous studies demonstrating density-dependent mortality in larval fish (Welker, et al. 1994; Michaletz 1997). DeAngelis et al. (1993), modelling growth and survival in first-year SMB, suggest that high initial densities of SMB larvae may result in massive die-offs of YOY, due to resource depression. Although zooplankton densities declined seasonally in Lake Opeongo, there was no clear evidence that these patterns were related to YOY densities, as declines in zooplankton density began prior to the production of first-feeding larvae in two of four years. Given that survival of YOY SMB through the first winter of life is strongly size dependent (Shuter, et al. 1980), the density-dependent mechanism of population regulation in first-year SMB (DeAngelis, et al. 1993) is very persuasive.

As most fish populations neither go extinct or increase to infinity, density-dependent regulation is believed to exist (Rothschild 1986). However, evidence for density-dependence has been demonstrated in few populations (Shepherd and Cushing 1990) and the lack of evidence for density-dependence during the larval period has been attributed to low spawning biomass (Shepherd and Cushing 1980; Shepherd and Cushing 1990). The number of spawning males in Jones Bay, Lake Opeongo, in 1989 exceeded the previous historical record for spawning males by approximately 25 to 30% (Ridgway 1986); yet growth and survival of larvae remained significantly higher than those in the other four field seasons. Lack of evidence for density-dependent growth and survival in 1989 suggests that larval spawning biomass and larval densities in Lake Opeongo may simply be too low for density-dependent mechanisms to operate.

It is possible that density-dependent regulation of SMB populations could occur in other developmental periods or phases. Population regulation in YOY SMB potentially could occur through density-dependent mechanisms as proposed by DeAngelis et al. (1993) in post-metamorphic juveniles. I propose that a likely point in time for such a mechanism to operate may correspond with the ontogenetic diet shift from zooplanktivory to benthivory following dispersal of juveniles from natal areas. The timing of the diet shift from invertebrates to piscivory in first-year juvenile largemouth bass appears to be critical to first-year survival in largemouth bass (Olson 1996).

Production estimates of first-feeding larvae in Lake Opeongo fell within the range of values previously reported (Neves 1975; Wiegmann, et al. 1992; Lukas and Orth 1995). However, comparisons must be made cautiously, as methods used to estimate production have not been standardized. Wiegmann et al. (1992) and Lukas and Orth (1995) base their estimates of first-feeding larval abundance on embryo counts in the nest, made just prior to the time of embryo-larval transformation. Using a suction device to collect embryos from the nest, Wiegmann et al. (1992) determine the number of embryos in each sampled nest volumetrically. Lukas and Orth (1995) also collect embryos by suction, but base their estimates on counts using enlarged projections of photographs taken of the brood (Noltie 1986). By placing enclosures over nests during the 'black fry stage', Neves (1975) collected and counted free-swimming larvae that emerged from nests. Neves' (1975) method may overestimate brood sizes, as mortality factors external to the nest may have been prevented from operating while enclosures remained over nests.

4.4.3 YOY Development

Environmental variables typically display pronounced seasonal patterns on a time scale that encompasses the early developmental periods of fishes in temperate lakes. In Lake Opeongo, mean temperatures varied significantly among developmental periods within years and between similar developmental periods among years. The seasonal rise in water temperature together with the stochastic nature of temperature fluctuations resulted in substantial variation in brood-specific water temperatures within and among developmental periods. Temperature is known to be an important environmental factor affecting early developmental rates of fishes (Youson 1988; Pepin 1991; Miller, et al. 1995; Pepin 1997). Not surprisingly, the timing of first-feeding and metamorphosis varied substantially among broods, both within and among years. The timing of first-feeding and metamorphosis in SMB may be critical to first-year survival, not only because food resources and predator abundance varied seasonally in Lake Opeongo, but also because survival through the first winter of life is strongly size dependent (Shuter, et al. 1980; MacLean, et al. 1981). The timing of first-feeding and metamorphosis is an important component of Hjort's (1914) critical period hypothesis and Cushing's (1975a) match-mismatch hypothesis. Results of this research show how the timing of first-feeding and metamorphosis are affected by temperature-induced changes in developmental rates during the embryonic and larval periods of development.

Results of this study showed that duration of the embryonic period varied substantially, both within and among years. Within years, the duration of the hatch-to-first-feeding phase of embryonic development was consistently longer than the spawn-to-hatch phase of development. Spawn-to-hatch times for broods ranged from 4 to 8 d, similar to values determined for SMB in the laboratory (Webster 1948; Kerr 1966) and field (Shuter, et al. 1980) at similar temperatures. Hatch-to-first-feeding times ranged from 4 to 12 d, somewhat higher than those reported by Shuter et al. (1980). Embryonic period duration differed significantly among years, owing to the large variation in mean annual water temperature. During the embryonic period daily temperatures ranged from a low of 10.8 °C to a high of 23.8 °C, with mean annual temperatures ranging from 15.5 (1993) to 19.2 °C (1988). Inter-annual variability in mean phase duration was much greater during the hatch-to-first-feeding phase than during the spawn-to-hatch phase of embryonic development. Thus, variation in development rates following hatch likely contributed to the significant difference in mean embryonic period duration among years.

The mean duration of the larval period also differed significantly among years. Inter-annual variability in mean period duration was greater for the larval period than for the embryonic period, although inter-annual variability in mean water temperature did not increase. However, due to the seasonal increase of temperature in Lake Opeongo, mean temperatures increased from 17.7 °C during the embryonic period to 21.1 °C during the larval period of development. Optimal growth temperature for larval and juvenile SMB ranges between 26 and 29 °C (Peek 1965; Horning and Pearson 1973). Growth and development of embryos and larvae occurred at temperatures well below the optimum, where the rate of energy assimilation is expected to be an exponentially increasing function of temperature (Kitchell, et al. 1977). As larvae were growing at temperatures closer to their optimum than were embryos, the rate of energy assimilation per unit increase in temperature would be expected to be higher for larvae. Assuming growth rates were positively related to assimilation rates and given the positive relation between growth and developmental rates of larvae in this study, developmental rates of larvae may also have been much more responsive to changes in temperature within the range of temperatures experienced by larvae.

Size and Age at First-Feeding and Metamorphosis

Results of this study showed that mean variation in age at metamorphosis was significantly greater than mean variation in length at metamorphosis within years. Comparisons among years revealed a similar pattern, with variation in mean age much higher than variation in mean length (by a factor of 3.4). Also, mean length and age and mean growth and developmental rate of larval SMB were positively correlated among years. This author is unaware of any previous investigations that have reported on the variation and correlation between size and age of larvae within and among years for a freshwater species under natural conditions. However, my results are in general agreement with previous studies of marine species in both laboratory (Policansky 1982; Chambers and Leggett 1987) and natural settings (Victor 1986). Policansky (1982), working on starry flounder *Platichthys stellatus*, Chambers and Leggett (1987) studying winter flounder *Pseudopleuronectes americanus, and* Victor (1986) investigating bluehead wrasse *Thalassoma bifasciatum*, show length at metamorphosis to be less variable than age at metamorphosis for individuals. Coefficient of variations (CV's) for length and age at metamorphosis for winter flounder averaged 0.051 and 0.123 (Chambers and Leggett 1987) and compare closely to the 5-year mean CV's for length (0.066) and age (0.119) in the present study. Chambers and Leggett (1987), using Victor's (1986) data, calculated the CV's for length and age of wrasses at metamorphosis to be 0.063 and 0.120, respectively. The similarity between the CV's for age and length at metamorphosis in the present study and those for winter flounder and bluehead wrasse is intriguing, given that these fish are not closely related and that data were derived from laboratory and field settings. Moreover, unlike these earlier studies, data from the present study were not sizes and ages of individuals, but instead reflected annual and inter-annual averages for broods of larval SMB. Given the heterogeneous conditions in Lake Opeongo, I anticipated that the variation in age and length of recently metamorphosed juveniles in Lake Opeongo would be larger than that determined for other species under laboratory conditions. It is likely that some of the variation in age and length that occured at the individual-level may not have been detected as a consequence of assessing variation at the brood-level.

Mean length and age of YOY SMB at metamorphosis were positively correlated among years, consistent with previous studies on other species of fish in the laboratory (Chambers and Leggett 1987) and field (Victor 1986). Others have found the correlation to be non-significant or negative (Policansky 1982). Also, the positive correlation between mean annual growth and developmental rate for larval SMB is consistent with that reported for a number of marine species (Chambers and Leggett 1987, for a review). My results suggested that although age and size both influenced the timing of metamorphosis in SMB, the influence of size was much stronger. This was supported by the high variability in mean age at metamorphosis compared to the lower variation in mean size at metamorphosis. Quantifying these patterns in the field is an important step in understanding the underlying relationships between development, growth and environmental variability.

4.4.4 Temperature, Growth and Mortality

Results of this study showed substantial intra-annual variation in brood-specific size (TL) of first-feeding larvae and recently metamorphosed juveniles. Total length of first-feeding larvae and juveniles also differed significantly among years. Variability in length increased with age, consistent with previous research on this same population (Friesen 1990). Friesen (1990) also shows that much of the variation in length-at-age occurs among broods and not within broods.

Water temperature is often the principle factor influencing larval fish growth (Houde 1989), including SMB (Shuter, et al. 1980). Growth rate of YOY SMB increases between 15-25 °C (Horning and Pearson 1973) with maximum growth rate occurring between 26-29 °C (Peek 1965; Horning and Pearson 1973; DeAngelis and Coutant 1979). Given the inverse relationship between brood-specific growth and mortality rate, the sub-optimal and seasonally increasing water temperatures in Lake Opeongo and the positive relation between YOY growth and temperature, I anticipated that brood-specific mortality rates of SMB larvae would decline seasonally. However, brood-specific mortality rates did not fit this pattern in any year. Rather, brood-specific mortality rate tended to be lowest for broods that initiated first-feeding earliest in the season. That mortality rates did not decline seasonally may have stemmed, in part, from the low variation in brood-specific temperatures within years. Although brood-specific growth rates were positively associated with temperature in 4 of 5 years, the relationships were generally weak. During the five field seasons, water temperature explained a maximum of 56% of the intra-annual variation in brood-specific growth rate, leaving a considerable amount the variation unexplained. Previous studies have demonstrated a positive linear relationship between temperature and larval growth rates for YOY juvenile SMB under laboratory (Rowan 1962; Peek 1965; DeAngelis and Coutant 1979) and field (Shuter, et al. 1980) conditions. Sabo and Orth (1995) found that growth rates of first-year juvenile SMB were not correlated with temperature in a year with nearly optimal temperatures, but were positively related to water temperature in a colder year. Similar to my results, these authors found that inter-annual differences in growth rate were strongly related to mean annual temperature.

The critical role of temperature, particularly its potential to cause high embryonic mortalities and its effect on growth and survival has been identified in earlier research on SMB. For example, several studies demonstrate a positive correlation between specific temperature indices and year-class strength (Fry and Watt 1957; Forney 1972). Laboratory and field experiments show that YOY SMB are particularly susceptible to water temperature fluctuations soon after fertilization (MacLean, et al. 1981, for a review). Shuter et al. (1980) developed a model to assess the relations between growth and survival of post-dispersal juvenile SMB in Lake Opeongo and found that growth rates were below laboratory-derived predicted values of Rowan (1962). Shuter et al. (1980) suggest that factors in addition to temperature may control growth rates of YOY SMB in Lake Opeongo. What was equally intriguing about Shuter et al.'s (1980) growth rate-temperature regression for YOY juveniles in Lake Opeongo was the high variability in individual growth rates for a given temperature, relative to the low variability observed by Peek (1965) under laboratory conditions. Individual growth rates of juveniles in Lake Opeongo varied by as much as an order of magnitude at a given temperature. In my study, brood-specific growth rates also showed high intra-annual variability over a relatively narrow temperature range, although the magnitude of variation was lower than that reported among individual juveniles by Shuter et al. (1980). My results confirmed the prominence of temperature to YOY growth rates in SMB; however, the high variability in brood-specific growth rates suggested that other unidentified factors were also important.

Previous research has shown that small reductions in larval growth rate may cause survival to decline simply by prolonging the period of vulnerability to mortality (Chambers and Leggett 1987; Pepin 1990; Michaletz 1997). Consequently, any factor that strongly affects period duration may exert a strong influence on year-class strength (Houde 1987; Pepin and Myers 1991). My results showed that temperature affected survival and production of first-feeding larvae and juveniles through its positive influence on growth and developmental rates. For instance, the percentage of first-feeding larvae that survived to become juveniles each year was strongly associated with mean annual growth and developmental rates. In 1992, when water temperatures were very cold, decreased growth rates of YOY allowed mortality factors to act longer, causing broods to experience higher cumulative mortality rates. Interestingly, year-classes differed in their ranking with regard to cumulative mortality and mean instantaneous mortality rates (I did not analyze this formally). This finding has important implications for SMB population dynamics and suggests that in addition to mortality rate estimates, accurate predictions of year-class success may also require estimates of YOY growth and period durations.

Despite the high intra-seasonal and inter-annual variability in brood-specific mortality rates, I was unable to demonstrate that mortality rates were linked to food availability. Either mortality rates of YOY SMB were not strongly affected by prey availability or I was unable to detect it. For instance, the effects of small-scale spatial and temporal variation in prey availability may not have been resolved in my study. The prey conditions I measured (average density and biomass) may not have been those experienced by YOY SMB because prey availability changed over periods of time shorter than 1-week. If food availability is largely a function of small-scale local turbulence, then my coarsegrained (ie. average density) measures of zooplankton abundance would not have reflected a proper measure of food availability. Also, the cause of mortality may have been predation or some other unidentified source. Taggart and Leggett (1987) made the important distinction that relationships between fish larvae and their predators often are noticeable because they are instantaneous, while effects of prey densities on nutritional condition and growth of larvae are less obvious, as they are cumulative over time.

Conclusions

Earlier research on first-year growth and survival in fishes focused largely on the early larval phase where mortality rates were presumed to be the highest (May 1974). My results support a growing body of work that suggests that variability in growth and mortality during the late larval phase and juvenile period of development may be more important in determining year-class strength than that during the early larval phase of development (Leggett and Deblois 1994), and that such effects may be mediated through the negative relation between mortality and growth rates (Anderson 1988). My results did not support a major link between food-abundance at first-feeding and growth and mortality of larvae and therefore offered no support for Hjort's (1914) critical period hypothesis. Although production of YOY SMB coincided with the seasonal warming of littoral-zone water masses and the development of food resources, the hypothesis that growth and mortality are regulated by the degree of match or mismatch in the production of larvae and their prey was not strongly supported. Therefore, this study offers only partial support for Cushing's (1975a; 1990) match-mismatch hypothesis.

I believe that early juvenile production was essentially set by the abundance of first-feeding larvae, as the relative production of first-feeding larvae and recently metamorphosed juveniles were strongly correlated in Lake Opeongo. Temperature also had a strong influence on year-class success, as mean larval growth, mortality and development rates all showed strong positive correlations with temperature. The effect of temperature on intra-annual brood-specific growth and mortality was much weaker, and likely stemmed from the low variability in brood-specific temperatures. Examination of year-class and brood-specific growth and survival among developmental periods and phases within years and within developmental periods and phases among years has provided a clearer picture of the processes influencing early life history dynamics of SMB.

I conclude that growth and mortality of larval and early juvenile SMB were not food- limited. The SMB population in Lake Opeongo may be an example of a low-density population whose dynamics are not constrained by food, but by other factors such as predation. In the following chapter, I employ in situ enclosures to further investigate the effects of prey availability on growth and survival of YOY SMB. Under these semi-controlled conditions I examine the effects of larval stocking density and supplemental feeding on YOY growth and mortality.

Table 4.1. Summary statistics of seasonal timing in spawning by male smallmouth bass in Lake Opeongo, Ontario. Sample size (N) refers to the number of nests which received eggs in each spawning season. Julian date 152 = 1 June.

		Julian Date of Spawning		
Year	N	Mean	±S.D.	Range
1988	112	155.9	5.88	23
1989	123	163.4	6.20	20
1991	72	143.5	2.75	11
1992	92	159.9	5.14	22
1993	76	160.9	5.84	27

Table 4.2. Summary of smallmouth bass larval and juvenile abundances in Jones Bay, Lake Opeongo. Embry refers to the embryonic period. Spawning = time of egg deposition, First Feeding = first day of larval period, Metamorphosis = first day of juvenile period and, Median Day refers to the median time (days) that offspring remained within the territory of the guarding male beyond metamorphosis for all nests within a given spawning season. Nests = number of active nests and YOY# = total number of offspring in all active nests.

Year	Developmental Period						
	Embry	Larval		Juvenile			
	Spawning	First Feeding		Metamorphosis		Median Day	
	Nests	Nests	YOY#	Nests	YOY#	Nests	YOY#
1988	63	47	59,720	19	13,310	8	6,560
1989	123	97	110,124	54	60,177	39	36,870
1991	72	34	16,968	17	7,535	14	4,830
1992	92	71	135,600	28	39,646	16	21,940
1993	76	62	97,273	28	31,003	10	9,600

Table 4.3. Regression equations relating brood size (number of offspring in a brood) to first feeding date (expressed as Julian date) for nesting male smallmouth bass in Lake Opeongo. First-feeding signifies the initiation of the larval period. Sample sizes (N) represent the number of nests that successfully reached the larval period of development. Asterisk indicates a significant ($p < 0.05$) relationship between brood size and julian date.

Year	N	r^2	F	P	Regression Model
1988	73	0.21	14.70	0.001*	Brood size = -85.3(date) + 15796
1989	97	0.03	3.02	0.085	Brood size = -50.4(date) + 10100
1991	34	0.04	1.21	0.280	Brood size = -37.4(date) + 6273
1992	71	0.16	12.71	0.001*	Brood size = -109.8(date) + 21077
1993	62	0.00	0.00	0.965	Brood size = 2.6(date) + 1116

Table 4.4. Summary statistics of brood size for first-feeding smallmouth bass in Lake Opeongo. N = number of active nests, Min = minimum brood size estimate, Max = maximum brood size estimate and CV= coefficient of variation, expressed as percentage. Note: first feeding signifies the first day of the larval period.

	Brood Size						
Year	N	Min	Max	Range	Mean	SD	CV (%)
1988	68	45	3050	2535	1230	747	61.0
1989	97	10	3300	3290	1135	828	73.0
1991	34	26	1800	1774	495	496	99.4
1992	71	17	5900	5883	1910	1255	65.8
1993	62	28	5000	4972	1570	1128	71.9

Table 4.5. Regression equations relating brood size at first-feeding to male fork length (cm) for nesting smallmouth bass in Lake Opeongo. Sample sizes (N) represent the number of nests receiving eggs in each year. Asterisk indicates a significant ($p < 0.05$) relationship between brood number and male length.

Year	N	r^2	F	P	Regression Model
1988	73	0.46	38.70	0.001*	Brood number = 105.2(FL) - 2038
1989	95	0.20	23.16	0.001*	Brood number = 97.2(FL) - 1723
1991	34	0.09	3.25	0.081	Brood number = 33.5(FL) - 598
1992	71	0.16	13.14	0.001*	Brood number = 118.1(FL) - 1857
1993	60	0.12	7.76	0.007*	Brood number = 70.6(FL) - 627

Table 4.6. Summary statistics of brood size at metamorphosis. N = number of active nests, Min = minimum brood size estimate, Max = maximum brood size estimate and CV= coefficient of variation, expressed as percentage.

	Brood Size						
Year	N	Min	Max	Range	Mean	SD	CV (%)
1988	26	44	2600	2556	586	879	103
1989	54	10	3150	3140	1114	819	74
1991	17	12	1540	1528	443	494	112
1992	33	30	5250	5220	1416	1308	92
1993	28	76	4700	4625	1107	1232	111

Table 4.7. Annual variation in mean water temperature during the smallmouth bass spawning season in Lake Opeongo during five nesting seasons. Days = duration of the spawning season in each reproductive season.

Year	Days	Daily Temperature				
		Min	Max	Mean	±SD	CV (%)
1988	24	15.6	20.6	18.5	1.48	8.0
1989	21	15.2	17.7	16.5	0.78	4.7
1991	12	15.4	21.0	17.8	1.82	10.2
1992	23	12.2	19.4	16.2	2.28	14.1
1993	28	10.8	19.1	14.1	2.70	19.2

Table 4.8. Annual variation in mean water temperature during the (a) embryonic, (b) larval and (c) juvenile periods of smallmouth bass development in Lake Opeongo during 5 reproductive seasons. Days = duration of a developmental period within each reproductive season.

4.8a Embryonic Period

Year	Days	Daily Temperature				
		Min	Max	Mean	±SD	CV (%)
1988	35	15.6	21.9	19.2	1.63	8.5
1989	29	15.2	23.8	17.9	2.56	14.3
1991	22	15.4	21.5	19.0	1.96	10.3
1992	27	14.6	19.4	17.2	1.31	7.6
1993	40	10.8	20.5	15.5	3.25	21.0

4.8b Larval Period

Year	Days	Min	Max	Mean	±SD	CV (%)
1988	27	18.0	25.8	20.9	2.02	9.7
1989	21	17.0	23.8	21.3	2.18	10.2
1991	18	18.7	22.0	20.4	0.97	4.8
1992	34	15.0	20.0	17.6	1.33	7.6
1993	28	16.7	24.1	20.4	2.27	11.1

4.8c Juvenile Period

Year	Days	Min	Max	Mean	±SD	CV (%)
1988	20	18.0	25.8	22.3	2.74	12.3
1989	17	21.2	23.3	22.5	0.55	2.4
1991	14	18.7	22.4	21.0	1.15	5.5
1992	35	15.8	22.4	18.9	1.56	8.3
1993	20	20.5	24.1	22.4	1.08	4.8

Table 4.9. Copepod nauplii and cladoceran crustaceans presented as percentage density and biomass of total littoral-zone zooplankton in Lake Opeongo during the smallmouth bass larval and juvneile periods of development in 1988, 1991, 1992 and 1993. Estimates for density and biomass were determined from samples collected at weekly intervals during the larval and juvenile periods.

Year	Major Zooplankton Taxa							
	Copepod Nauplii				Cladocera			
	Larval Period		Juvenile Period		Larval Period		Juvenile Period	
	Den%	Bio%	Den%	Bio%	Den%	Bio%	Den%	Bio%
1988	18	2	65	17	75	85	28	70
1991	3	1	58	6	93	95	36	84
1992	86	27	46	3	9	61	36	83
1993	61	7	33	4	29	85	56	81

Table 4.10. Descriptive statistics of density (number/litre) estimates for the major zooplankton taxa collected in Lake Opeongo during the smallmouth bass reproductive season. Estimates correspond with the timing of smallmouth bass larval and juvenile periods of development. Larval refers to the smallmouth bass larval period of development; juvenile refers to the smallmouth bass juvenile period of development. Ave = mean number of individuals per litre.

	Zooplankton Taxa															
	Copepod Nauplii				Adult Copepods & Copepodites				Cladocera				Total Zooplankton Taxa			
Yr	Larval		Juvenile		Larval		Juvenile		Larval		Juvenile		Larval		Juvenile	
	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE
1988	11.2	2.3	28.9	4.1	4.5	0.9	3.0	0.4	46.6	15.2	12.4	4.1	62.3	14.6	44.3	7.5
1991	2.6	0.3	24.6	4.2	3.5	0.5	2.4	0.3	75.2	13.5	15.2	2.7	81.1	14.2	42.2	3.8
1992	25.7	6.1	7.2	1.6	1.7	0.2	2.8	0.4	2.6	0.5	5.6	0.4	30.0	6.2	15.6	2.3
1993	15.2	6.0	11.7	3.6	2.7	0.4	3.7	0.6	7.2	1.2	19.6	2.4	25.1	6.5	35.0	3.9

Table 4.11. Descriptive statistics of biomass (mg/m^3) estimates for the major zooplankton taxa collected in Lake Opeongo during the smallmouth bass reproductive season. Estimates correspond with the timing of smallmouth bass larval and juvenile periods of development. Larval refers to the smallmouth bass larval period of development; juvenile refers to the smallmouth bass juvenile period of development. Ave. = mean number of individuals per litre.

	Zooplankton Taxa															
	Copepod Nauplii				Adult Copepods & Copepodites				Cladocera				Total Zooplankton Taxa			
Yr	Larval		Juvenile		Larval		Juvenile		Larval		Juvenile		Larval		Juvenile	
	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE	Ave.	SE
1988	1.9	0.4	7.3	1.3	8.2	1.6	5.6	1.1	81.5	21.7	29.6	6.7	91.6	21.3	42.7	7.6
1991	0.5	0.1	3.8	0.6	6.8	1.1	5.5	1.0	126	12.4	49.7	9.1	133	13.3	59.0	10.2
1992	7.0	1.7	1.3	0.3	3.1	0.5	5.0	0.7	15.6	3.9	31.3	5.3	25.7	4.7	37.6	4.8
1993	4.5	1.7	1.6	0.3	5.7	1.2	6.1	1.0	57.1	15.9	32.0	3.3	67.3	16.9	39.7	3.3

Table 4.12. Summary statistics for brood-specific age and length at metamorphosis for the Lake Opeongo smallmouth bass population during five nesting seasons. Average values are presented for each year-class. N = number of broods, CV = coefficient of variation.

		Age at Metamorphosis (days)			Size at Metamorphosis (total length; mm)		
Year	N	Mean	SD	CV[1]	Mean	SD	CV
1988	26	15.5	1.76	0.114	16.5	1.24	0.076
1989	54	9.2	1.19	0.129	14.8	1.05	0.069
1991	17	11.0	1.60	0.145	14.2	0.88	0.062
1992	33	18.3	1.85	0.101	17.1	0.99	0.058
1993	28	13.9	1.49	0.107	16.3	1.10	0.067

Table 4.13. Descriptive statistics of YOY total length (mm) for smallmouth bass in Lake Opeongo during five nesting seasons. Samples were collected at 4-d intervals beginning at first-feeding and continued throughout the larval (Lar) and early juvenile (Juv) periods of development. Devel Period = developmental period of offspring and Day = time (days) post-first feeding. Coefficient of variation (CV) is expressed as percentage.

				Total Length				
Year	Devel Period	Day	N	Mean	Min	Max	Range	CV (%)
1988	Lar	1	539	9.63	8.53	10.96	2.44	4.3
	Lar	5	385	10.81	9.57	12.38	2.81	5.7
	Lar	9	313	12.90	11.01	14.81	3.80	6.6
	Lar	13	274	14.63	12.39	17.57	5.18	7.1
	Juv	17	241	16.60	13.92	19.85	5.93	7.5
	Juv	21	144	20.74	16.70	25.31	8.60	9.7
	Juv	25	42	25.85	21.95	28.35	6.41	7.5
	Juv	29	15	29.48	27.62	32.45	4.83	4.7
1989	Lar	1	692	9.24	8.08	10.84	2.75	4.9
	Lar	5	558	11.45	9.29	13.59	4.30	7.3
	Lar/Juv	9	416	14.86	12.21	17.54	5.33	7.8
	Juv	13	383	22.22	18.48	24.26	5.78	5.4
	Juv	17	154	28.39	23.84	31.87	8.03	6.9
	Juv	21	27	32.84	29.65	36.65	7.00	6.6
1991	Lar	1	155	9.15	7.96	10.12	2.16	3.6
	Lar	5	159	10.59	9.32	12.16	2.84	5.9
	Lar	9	145	13.00	10.75	15.26	4.51	7.5
	Juv	13	35	16.52	14.09	18.64	4.55	6.7
	Juv	17	13	21.07	18.48	22.91	4.43	5.8

Table 4.13 (continued)

Year	Devel Period	Day	N	Total Length Mean	Min	Max	Range	CV (%)
1992	Lar	1	532	9.57	8.66	10.94	2.28	3.5
	Lar	5	425	10.46	9.00	11.85	2.85	5.4
	Lar	9	369	11.91	10.25	13.46	3.21	5.7
	Lar	13	317	13.99	11.73	16.22	4.49	5.6
	Lar	17	306	16.03	13.22	18.23	5.01	6.7
	Juv	21	230	18.61	15.82	21.15	5.34	7.1
	Juv	25	169	20.60	17.85	24.19	6.34	7.3
	Juv	29	135	23.49	20.34	26.41	6.07	5.8
	Juv	33	34	27.38	25.31	30.41	5.09	4.4
	Juv	37	37	31.42	28.40	34.86	6.46	5.5
1993	Lar	1	589	9.44	8.43	10.94	2.51	3.4
	Lar	5	554	11.27	9.34	13.44	4.10	6.7
	Lar	9	515	13.68	11.28	16.41	5.13	7.1
	Lar	13	457	17.57	13.90	20.96	7.06	8.6
	Juv	17	296	23.15	19.05	26.78	7.72	7.5
	Juv	21	78	29.35	25.57	33.50	7.93	6.1

Table 4.14. Year-class specific growth rates of YOY smallmouth bass in Lake Opeongo during the larval and juvenile periods of development. N = sample size; AGR = absolute growth rate (mm d^{-1}) and IGR = instantaneous growth rate.

Year	Developmental Period					
	Larval			Juvenile		
	N	AGR	IGR	N	AGR	IGR
1988	1294	0.437	0.035	440	1.097	0.052
1989	1522	0.689	0.059	763	1.657	0.080
1991	459	0.479	0.043	209	0.955	0.060
1992	1425	0.398	0.032	697	0.682	0.032
1993	1324	0.677	0.051	568	1.429	0.064

Table 4.15. Regressions of total length (mm) on age (days) for YOY smallmouth bass in Lake Opeongo during five spawning seasons. Regression equations are derived for 4-day intervals, beginning at first-feeding. The regression coefficients of the growth equations are the instantaneous growth rates.

Year	Interval	Days	N	Regression Model	r^2
1988	1	1-5	924	$\mathrm{Log}_e(\mathrm{TL}) = 2.235 + 0.030(\mathrm{Age})$	0.60
	2	5-9	698	$\mathrm{Log}_e(\mathrm{TL}) = 2.162 + 0.043(\mathrm{Age})$	0.70
	3	9-13	587	$\mathrm{Log}_e(\mathrm{TL}) = 2.263 + 0.032(\mathrm{Age})$	0.53
	4	13-17	515	$\mathrm{Log}_e(\mathrm{TL}) = 2.261 + 0.032(\mathrm{Age})$	0.45
	5	17-21	385	$\mathrm{Log}_e(\mathrm{TL}) = 1.868 + 0.055(\mathrm{Age})$	0.62
	6	21-25	186	$\mathrm{Log}_e(\mathrm{TL}) = 1.845 + 0.056(\mathrm{Age})$	0.52
	7	25-29	57	$\mathrm{Log}_e(\mathrm{TL}) = 2.270 + 0.038(\mathrm{Age})$	0.55
1989	1	1-5	1250	$\mathrm{Log}_e(\mathrm{TL}) = 2.169 + 0.053(\mathrm{Age})$	0.76
	2	5-9	974	$\mathrm{Log}_e(\mathrm{TL}) = 2.111 + 0.065(\mathrm{Age})$	0.75
	3	9-13	799	$\mathrm{Log}_e(\mathrm{TL}) = 1.791 + 0.101(\mathrm{Age})$	0.90
	4	13-17	537	$\mathrm{Log}_e(\mathrm{TL}) = 2.307 + 0.061(\mathrm{Age})$	0.78
	5	17-21	181	$\mathrm{Log}_e(\mathrm{TL}) = 2.713 + 0.037(\mathrm{Age})$	0.42
1991	1	1-5	314	$\mathrm{Log}_e(\mathrm{TL}) = 2.177 + 0.036(\mathrm{Age})$	0.69
	2	5-9	304	$\mathrm{Log}_e(\mathrm{TL}) = 2.103 + 0.051(\mathrm{Age})$	0.70
	3	9-13	180	$\mathrm{Log}_e(\mathrm{TL}) = 2.050 + 0.057(\mathrm{Age})$	0.62
	4	13-17	48	$\mathrm{Log}_e(\mathrm{TL}) = 1.934 + 0.065(\mathrm{Age})$	0.73

Table 4.15 (continued)

Year	Interval	Days	N	Regression Model	r^2
1992	1	1-5	957	$\text{Log}_e(\text{TL}) = 2.236 + 0.022(\text{Age})$	0.50
	2	5-9	794	$\text{Log}_e(\text{TL}) = 2.185 + 0.032(\text{Age})$	0.57
	3	9-13	686	$\text{Log}_e(\text{TL}) = 2.115 + 0.040(\text{Age})$	0.67
	4	13-17	623	$\text{Log}_e(\text{TL}) = 2.195 + 0.034(\text{Age})$	0.55
	5	17-21	536	$\text{Log}_e(\text{TL}) = 2.140 + 0.037(\text{Age})$	0.54
	6	21-25	399	$\text{Log}_e(\text{TL}) = 2.372 + 0.026(\text{Age})$	0.35
	7	25-29	304	$\text{Log}_e(\text{TL}) = 2.154 + 0.035(\text{Age})$	0.54
	8	29-33	169	$\text{Log}_e(\text{TL}) = 2.039 + 0.038(\text{Age})$	0.55
	9	33-37	71	$\text{Log}_e(\text{TL}) = 2.177 + 0.034(\text{Age})$	0.66
1993	1	1-5	1143	$\text{Log}_e(\text{TL}) = 2.200 + 0.044(\text{Age})$	0.73
	2	5-9	1069	$\text{Log}_e(\text{TL}) = 2.171 + 0.049(\text{Age})$	0.64
	3	9-13	972	$\text{Log}_e(\text{TL}) = 2.039 + 0.063(\text{Age})$	0.72
	4	13-17	753	$\text{Log}_e(\text{TL}) = 1.973 + 0.069(\text{Age})$	0.62
	5	17-21	374	$\text{Log}_e(\text{TL}) = 2.128 + 0.059(\text{Age})$	0.61
	6	21-25	109	$\text{Log}_e(\text{TL}) = 2.402 + 0.046(\text{Age})$	0.32

Table 4.16. Summary statistics of absolute (mm d^{-1}) and instantaneous brood-specific growth rates for smallmouth bass larvae in Lake Opeongo. N refers to sample size (broods) and Combined refers to mean values for the five nesting seasons.

		Brood-specific Growth Rates									
Year	N	Absolute Growth Rate (mm d^{-1})					Instantaneous Growth Rate (Z)				
		Mean	SD	Min	Max	Range	Mean	SD	Min	Max	Range
1988	74	0.40	0.09	0.18	0.60	0.42	0.033	0.007	0.019	0.052	0.033
1989	89	0.74	0.25	0.32	1.30	0.98	0.063	0.018	0.031	0.097	0.066
1991	29	0.48	0.17	0.28	1.03	0.75	0.040	0.009	0.027	0.058	0.031
1992	72	0.32	0.12	0.03	0.52	0.49	0.027	0.009	0.003	0.038	0.035
1993	61	0.70	0.19	0.24	1.00	0.76	0.053	0.008	0.024	0.065	0.041
Combined	325	0.56	0.26	0.03	1.30	1.27	0.045	0.019	0.003	0.097	0.094

Table 4.17. Regression equations of brood-specific growth rate (mm d^{-1}) on brood-specific water temperature (°C) for smallmouth bass larvae in Lake Opeongo. Sample size (N) indicates the number of broods for which growth and temperature estimates were obtained in each season. Asterisk indicates a significant ($p < 0.05$) relationship between growth rate and mean water temperature.

Year	N	r^2	F	P	Regression Model
1988	45	0.15	7.78	0.008*	Growth rate = 2.126 - 0.085(H_2O temp)
1989	65	0.36	35.20	0.001*	Growth rate = -9.462 + 0.467(H_2O temp)
1991	20	0.05	0.98	0.336	Growth rate = -3.524 + 0.197(H_2O temp)
1992	55	0.02	0.87	0.356	Growth rate = -0.521 + 0.049(H_2O temp)
1993	55	0.56	66.68	0.001*	Growth rate = -2.226 + 0.146(H_2O temp)

Table 4.18. Summary statistics of absolute (mm d^{-1}) and instantaneous brood-specific growth rates for juvenile smallmouth bass in Lake Opeongo. N refers to sample size (broods) and Combined refers to the mean values for the five nesting seasons.

		Brood Growth Rates									
Year	N	Absolute Growth Rate (mm d^{-1})					Instantaneous Growth Rate (Z)				
		Mean	SD	Min	Max	Range	Mean	SD	Min	Max	Range
1988	30	1.12	0.36	0.52	1.69	1.17	0.056	0.016	0.029	0.082	0.053
1989	50	1.73	0.34	0.89	2.63	1.74	0.089	0.020	0.047	0.136	0.089
1991	17	0.84	0.19	0.60	1.17	0.57	0.062	0.014	0.043	0.089	0.046
1992	34	0.68	0.21	0.19	1.01	0.82	0.034	0.010	0.011	0.058	0.047
1993	21	1.46	0.18	1.23	1.76	0.53	0.056	0.008	0.045	0.071	0.026
Combined	152	1.25	0.53	0.19	2.63	2.44	0.064	0.027	0.011	0.136	0.125

Table 4.19. Regression equations of brood-specific growth rate (mm d^{-1}) on brood-specific water temperature (°C) for juvenile smallmouth bass in Lake Opeongo. Sample size (N) indicates the number of broods for which growth and temperature estimates were obtained in each season. Asterisk indicates a significant ($p < 0.05$) relationship between growth rate and mean water temperature.

Year	N	r^2	F	P	Regression Model
1988	16	0.59	19.79	0.001*	Growth rate = -4.24 + 0.24(H_2O temp)
1989	37	0.18	7.43	0.010*	Growth rate = 27.78 + 1.30(H_2O temp)
1991	10	0.04	0.31	0.591	Growth rate = -0.96 + 0.09(H_2O temp)
1992	24	0.13	3.31	0.083	Growth rate = -0.75 + 0.08(H_2O temp)
1993	9	0.04	0.27	0.267	Growth rate = 3.81 - 0.11(H_2O temp)

Table 4.20. Results of one-way repeated measures ANOVA to detect differences in instantaneous growth in YOY smallmouth bass during 4-day growth intervals, beginning at first feeding. Pairwise differences in means are shown for intervals that differed significantly at the $p < 0.05$ level of significance.

	ANOVA			
Year	Source	df	F	P
1988	Growth interval	4	12.35	< 0.0005*
	Error	52		

Contrasts

Source	df	F	P
Interval 1 - Interval 2	1	10.61	0.006*
Interval 1 - Interval 5	1	66.71	< 0.0005*
Interval 2 - Interval 3	1	19.01	0.001*
Interval 2 - Interval 5	1	6.04	0.029*
Interval 3 - Interval 5	1	26.79	< 0.0005*
Interval 4 - Interval 5	1	21.40	< 0.0005*
Error	13	21.40	< 0.0005*

Year	Source	df	F	P
1989	Growth interval	3	37.08	< 0.0005*
	Error	36		

Contrasts

Source	df	F	P
Interval 1 - Interval 2	1	6.40	0.026*
Interval 1 - Interval 3	1	87.65	< 0.0005*
Interval 2 - Interval 3	1	25.78	< 0.0005*
Interval 3 - Interval 4	1	97.29	< 0.0005*
Error	12		

Table 4.20 (continued)

Year	Source	df	F	P
1991	Growth interval	2	14.89	< 0.0005*
	Error	20		

Contrasts

Source	df	F	P
Interval 1 - Interval 2	1	20.44	0.001*
Interval 1 - Interval 3	1	19.22	0.001*
Error	10		

Year	Source	df	F	P
1992	Growth interval	4	5.87	< 0.0005*
	Error	88		

Contrasts

Source	df	F	P
Interval 1 - Interval 2	1	6.00	0.023*
Interval 1 - Interval 3	1	14.68	0.001*
Interval 1 - Interval 4	1	17.54	< 0.0005*
Interval 1 - Interval 5	1	34.59	< 0.0005*
Error	22		

Year	Source	df	F	P
1993	Growth interval	3	31.19	< 0.0005*
	Error	66		

Contrasts

Source	df	F	P
Interval 1 - Interval 2	1	9.62	0.005*
Interval 1 - Interval 3	1	32.61	< 0.0005*
Interval 1 - Interval 4	1	80.16	< 0.0005*
Interval 2 - Interval 3	1	15.09	0.001*
Interval 2 - Interval 4	1	59.39	< 0.0005*
Interval 3 - Interval 4	1	6.04	0.022*
Error	22		

Table 4.21. Regression statistics to determine the importance of prey abundance to brood-specific growth rate of smallmouth bass larvae in Lake Opeongo. Regression statistics include sample size (n = broods), F statistic, probability (P) based on the F statistic, the coefficient of determination (r^2), and the partial correlation coefficients. Independent variables in the multiple regression model included; 1) temporal match (days) between production of first-feeding smallmouth bass larvae and date of peak prey biomass, 2) mean water temperatue and 3) variation in mean water temperature. Results are shown for only those years in which the temporal match between production of first-feeding larvae and date of peak prey biomass comprised a significant component of the model.

Year	n	Independent Variables	F	P	r^2	Partial Corr Coeff
1991	21		4.22	0.032	0.33	
		days			0.01	0.50
		temp sd			0.32	0.57
1993	58		6.62	0.001	0.29	
		days			0.11	-0.48
		temp ave			0.14	0.40
		temp sd			0.04	-0.45

Table 4.22. Age-specific mortality rate of larval smallmouth bass for the entire larval period ($Larval_e$), the early larval phase ($Larval_y$) and the late larval phase ($Larval_l$) in Lake Opeongo during 5 spawning seasons. Age interval = age (days) post-first feeding; Length Interval = mean total length of larvae at beginning and end of age interval; Z = instantaneous mortality; M = daily mortality; No = initial number of larvae at beginning of age interval; Nt = number of larvae at end of length interval.

Year	Developmental Stage	Age Interval (days)	Length Interval (mm-TL)	Z	M (%/d)	Equation $\log_e N_t = N_o e^{-Zt}$
1988	$larval_e$	1-17	9.6-16.6	0.089	8.5	$85,562\ e^{-0.089t}$
1989	$larval_e$	1-9	9.2-14.9	0.067	6.5	$119,133\ e^{-0.067t}$
1991	$larval_e$	1-11	9.2-14.8	0.102	9.7	$19,034\ e^{-0.102t}$
1992	$larval_e$	1-19	9.6-17.3	0.075	7.2	$142.914\ e^{-0.075t}$
1993	$larval_e$	1-16	9.4-17.6	0.071	7.4	$111.190\ e^{-0.071t}$
1988	$larval_y$	1-5	9.6-10.8	0.109	10.3	$59,720\ e^{-0.109t}$
1989	$larval_y$	1-5	9.2-11.5	0.053	5.1	$110,130e^{-0.053t}$
1991	$larval_y$	1-5	9.2-10.6	0.102	9.7	$16.970\ e^{-0.012t}$
1992	$larval_y$	1-5	9.6-10.5	0.107	10.1	$135.600\ e^{-0.107t}$
1993	$larval_y$	1-5	9.4-11.3	0.047	4.6	$97.270\ e^{-0.047t}$
1988	$larval_l$	5-17	10.8-16.6	0.063	6.1	$70.034\ e^{-0.063t}$
1989	$larval_l$	5-9	11.5-14.9	0.075	7.2	$128,927\ e^{-0.075t}$
1991	$larval_l$	5-11	10.6-14.8	0.095	9.1	$19.555\ e^{-0.095t}$
1992	$larval_l$	5-19	10.5-17.3	0.073	7.0	$139,525\ e^{-0.073t}$
1993	$larval_l$	5-16	11.3-17.6	0.079	8.2	$123.007\ e^{-0.079t}$

Table 4.23. Descriptive statistics of brood-specific mortality for larval smallmouth bass in Lake Opeongo. Sample size (n) refers to number of broods and Comb[1] indicates average values for the 5 spawning seasons.

		Mortality							
Year	n	Instantaneous (Z)				Daily (% d^{-1})			
		Mean	Median	SD	CV	Mean	Median	SD	CV
1988	74	0.91	0.50	1.33	1.46	40.3	39.2	32.23	0.80
1989	97	0.80	0.02	1.49	1.88	28.2	2.3	36.98	1.31
1991	34	0.76	0.35	0.87	1.16	39.1	29.3	32.58	0.83
1992	73	0.73	0.38	0.99	1.36	37.2	31.5	31.28	0.84
1993	62	0.44	0.30	0.58	1.31	28.0	25.9	25.98	0.93
Comb[1]	340	0.74	0.28	1.17	1.59	33.8	24.5	32.76	0.97

Table 4.24. Summary statistics of brood-specific mortality rates for smallmouth bass during the early and late larval phases of development in Lake Opeongo. Z = instantaneous mortality ; M = daily mortality; n = sample size (broods) and Combined[1] refers to average values for the 5 spawning seasons.

	Early Larval Phase					Late Larval Phase				
Year	n	Z		M (% day^{-1})		n	Z		M (% day^{-1})	
		Mean	Median	Mean	Median		Mean	Median	Mean	Median
1988	74	0.741	0.057	27.9	5.5	56	0.607	0.289	34.0	25.1
1989	97	0.681	0.013	20.7	1.3	77	0.524	0.011	18.8	1.1
1991	34	0.688	0.191	34.4	17.3	25	0.585	0.098	28.7	9.3
1992	72	0.516	0.096	23.6	9.2	60	1.016	0.352	38.5	29.6
1993	62	0.241	0.028	13.6	2.8	55	0.568	0.274	30.8	24.0
Combined[1]	339	0.579	0.042	23.0	4.1	273	0.664	0.106	29.6	10.1

Table 4.25. Results of chi-square analysis to test for differences between median brood-specific instananeous mortality rates for larval smallmouth bass during the early and late larval phases of development. $X^2_{0.05,1}$ = critical chi-square value; X^2_c = calculated chi-square value. Asterisk (*) indicates a significant difference.

Year	$X^2_{0.05,1}$	X^2_c	P
1988	3.841	4.681	$0.025 < P < 0.05$*
1989	3.841	0.464	$0.25 < P < 0.50$
1991	3.841	0.888	$0.25 < P < 0.50$
1992	3.841	3.697	$0.05 < P < 0.10$
1993	3.841	11.706	$P < 0.0005$*

Table 4.26. Descriptive statistics of brood-specific mortality estimates for juvenile smallmouth bass in Lake Opeongo. Sample size (n) refers to number of broods and Comb[1] indicates average values over the 5 spawning seasons.

		Mortality							
Year	n	Instantaneous (Z)				Daily (% d^{-1})			
		Mean	Median	SD	CV	Mean	Median	SD	CV
1988	24	0.36	0.18	0.56	1.54	23.9	16.8	21.90	0.92
1989	52	0.13	0.05	0.19	1.44	10.9	4.5	14.37	1.32
1991	17	0.18	0.11	0.22	1.23	14.6	10.2	14.62	1.00
1992	27	0.22	0.10	0.27	1.21	17.5	9.3	17.78	1.01
1993	24	0.23	0.17	0.26	1.15	18.1	15.9	16.79	0.93
Comb[1]	144	0.21	0.10	0.32	1.51	16.0	9.7	17.29	1.08

Table 4.27. Results of chi-square analyses to test for differences between median brood-specific instananeous mortality rates for juvenile and larval smallmouth bass in Lake Opeongo. $X^2_{0.05,1}$ = critical chi-square value; X^2_c = calculated chi-square value. Asterisk (*) indicates a significant difference.

Year	$X^2_{0.05,1}$	X^2_c	P
1988	3.841	0.969	$0.25 < P < 0.50$
1989	3.841	0.124	$0.50 < P < 0.75$
1991	3.841	3.541	$0.05 < P < 0.10$
1992	3.841	9.597	$0.001 < P < 0.005$*
1993	3.841	0.520	$0.25 < P < 0.50$

Table 4.28. Regression statistics to determine the importance of prey abundance to brood-specific mortality rates for smallmouth bass larvae in Lake Opeongo. Regression statistics include sample size (n = broods), F statistic, probability (P) based on the F statistic, the coefficient of determination (r^2), and partial correlation coefficients. Independent variables in the multiple regression model include; 1) temporal match (days) between production of first-feeding smallmouth bass larvae and date of peak prey biomass, 2) mean water temperatue and 3) variation in mean water temperature.

Year	n	Independent Variables	F	P	R^2	Partial Corr Coeff
1988	65		28.34	< 0.0005	0.58	
		days			0.13	-0.618
		temp ave			0.12	0.684
		temp sd			0.33	0.664
1991	32		26.69	< 0.0005	0.74	
		days			0.04	-0.654
		temp ave			0.16	-0.363
		temp sd			0.54	-0.820
1992	72	days	4.83	0.03	0.07	0.254
1993	58		59.84	< 0.0005	0.77	
		days			0.16	0.555
		temp ave			0.46	-0.837
		temp sd			0.15	-0.624

Table 4.29. Regression equations relating mean instantaneous mortality to mean instantaneous growth in smallmouth bass broods during the larval period of development in Lake Opeongo. Sample size (n) indicates the number of broods for which mortality and growth estimates were obtained; IMR = instantaneous mortality rate and IGR = instantaneous growth rate. Asterisk indicates a significant ($p < 0.05$) negative linear relationship between instantaneous growth and mortality rate.

Year	n	r^2	F	P	Regression Model
1988	44	0.12	3.92	0.054	$IMR_{88} = -14.60 + 0.81(IGR_{88})$
1989	58	0.07	3.90	0.053	$IMR_{89} = -4.66 + 0.39(IGR_{89})$
1991	20	0.46	15.12	0.001*	$IMR_{91} = -17.30 + 0.91(IGR_{91})$
1992	55	0.48	48.49	0.001*	$IMR_{92} = -29.83 + 1.17(IGR_{92})$
1993	56	0.56	68.14	0.001*	$IMR_{93} = -26.97 + 2.81(IGR_{93})$

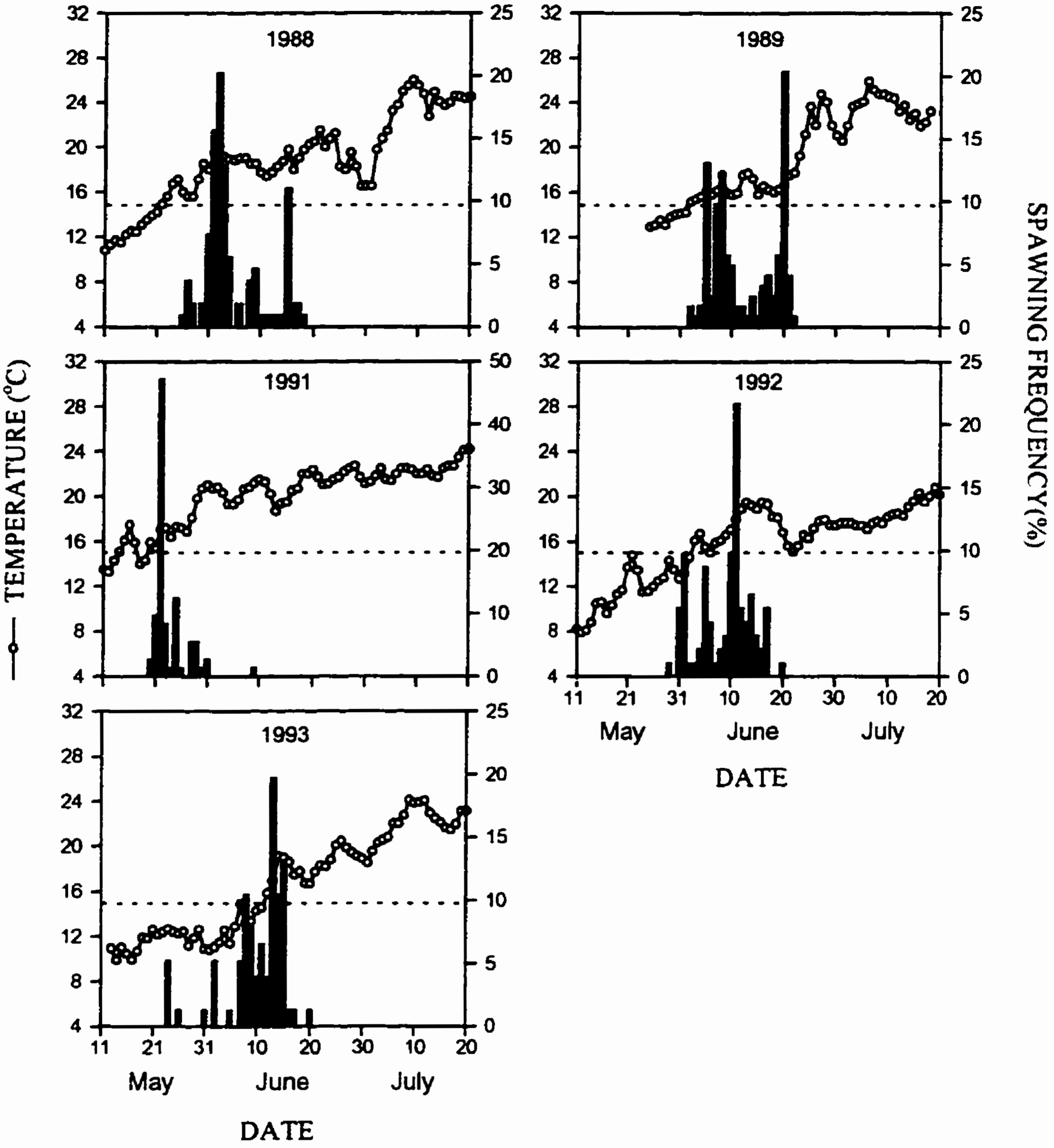

Figure 4.1. Mean daily water temperature (dotted line) and percent spawning frequency (solid bars) of male smallmouth bass in Lake Opeongo during 5 spawning seasons. The dashed horizontal line indicates the 15 °C critical low temperature below which high mortality of smallmouth bass embryos may occur.

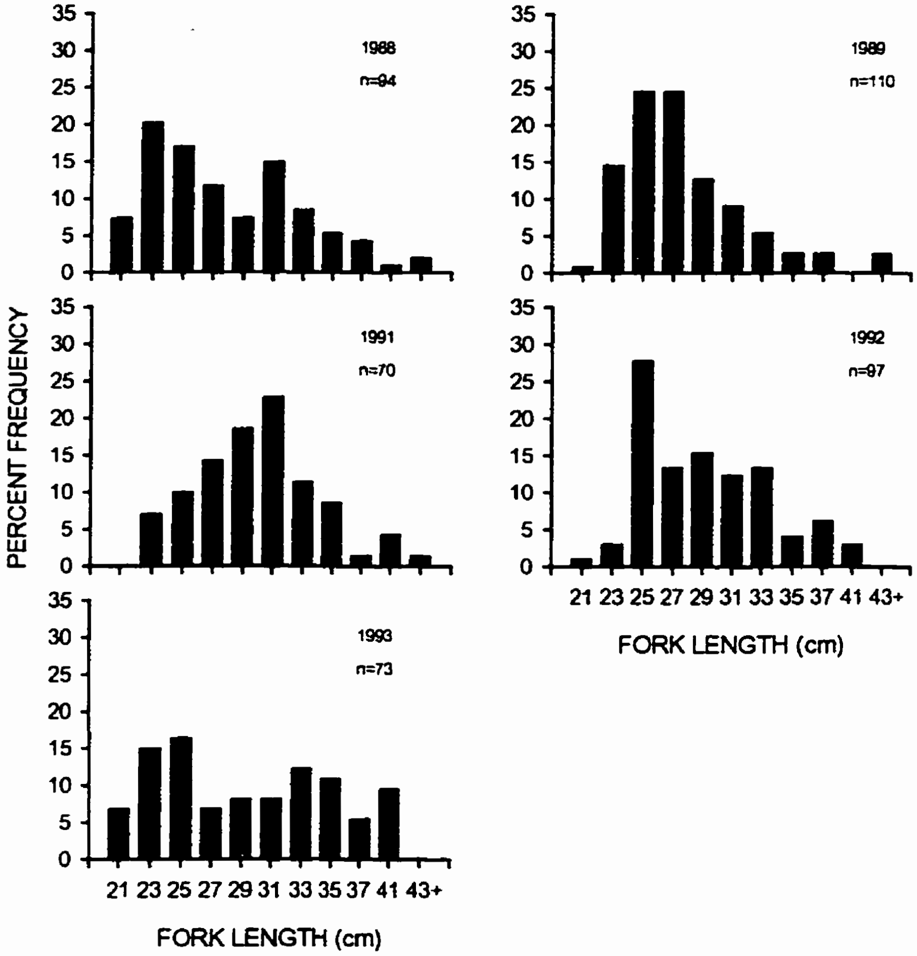

Figure 4.2. Size distribution of nesting male smallmouth bass in Jones Bay, Lake Opeongo during five spawning seasons. Size distributions are divided into 2 cm intervals with midpoint of each interval shown.

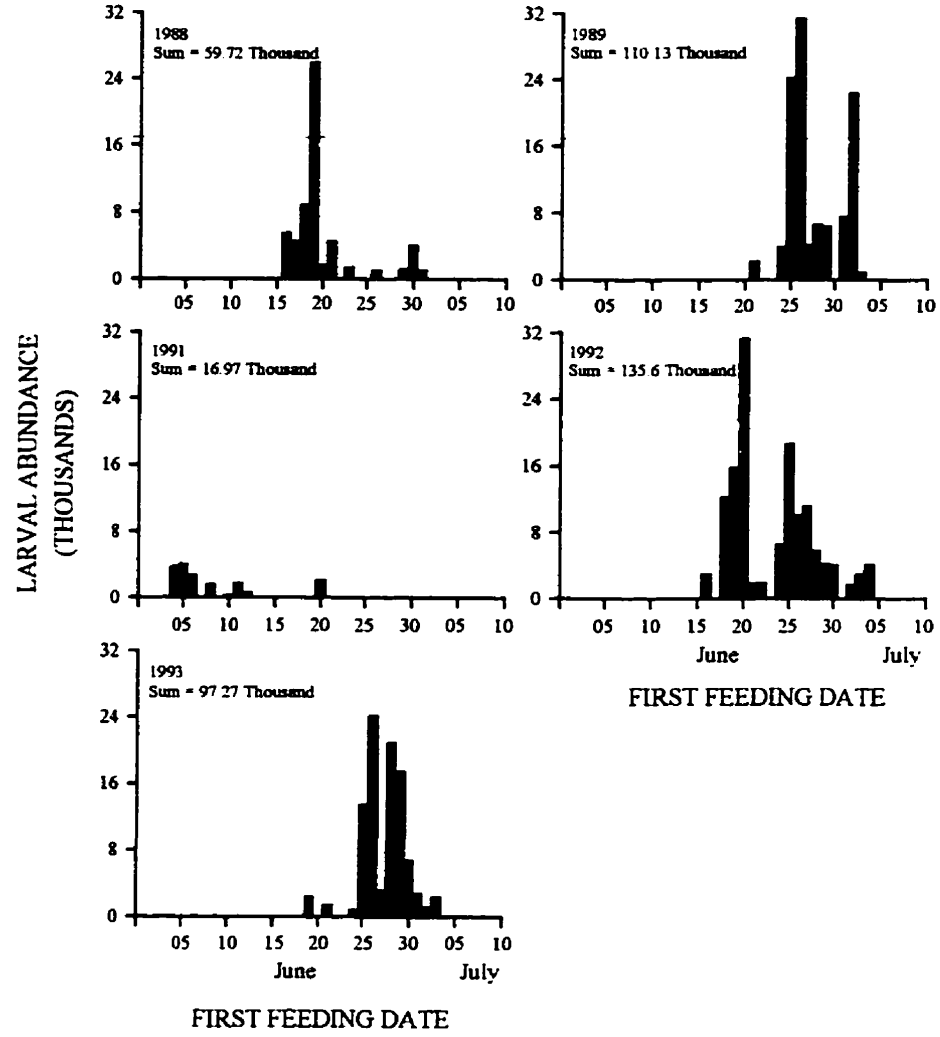

Figure 4.3. Relationship between estimated total production of first-feeding smallmouth bass larvae and date on which larvae initiated first-feeding in Jones Bay, Lake Opeongo during 5 spawning seasons. Total number of first feeding larvae produced each year (sum) is presented in the figures.

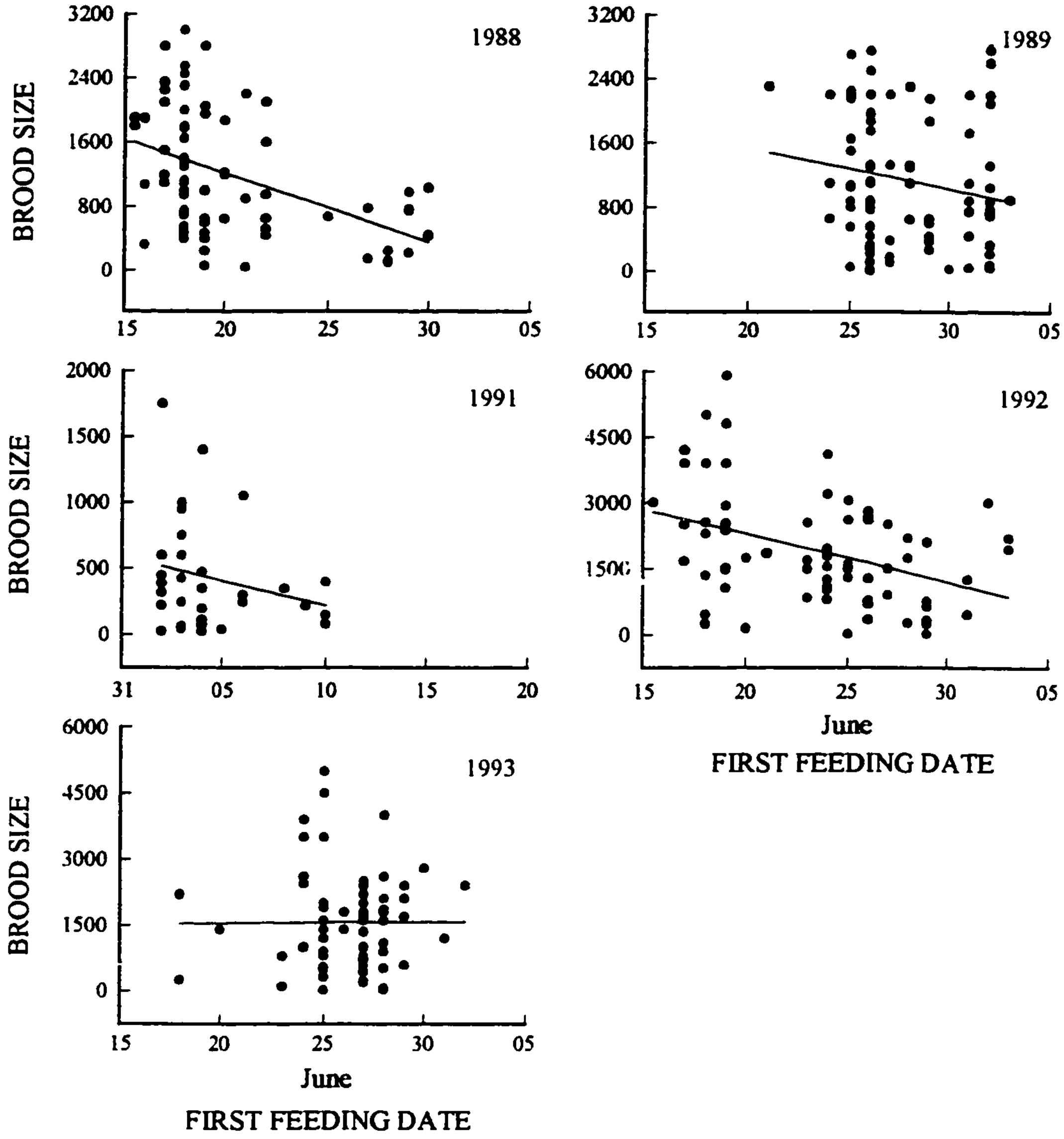

Figure 4.4. Relationship between date of first feeding and brood size (number of offspring in a brood) for larval smallmouth bass in Lake Opeongo during 5 spawning seasons. See Table 4.3 for regression equations and sample sizes.

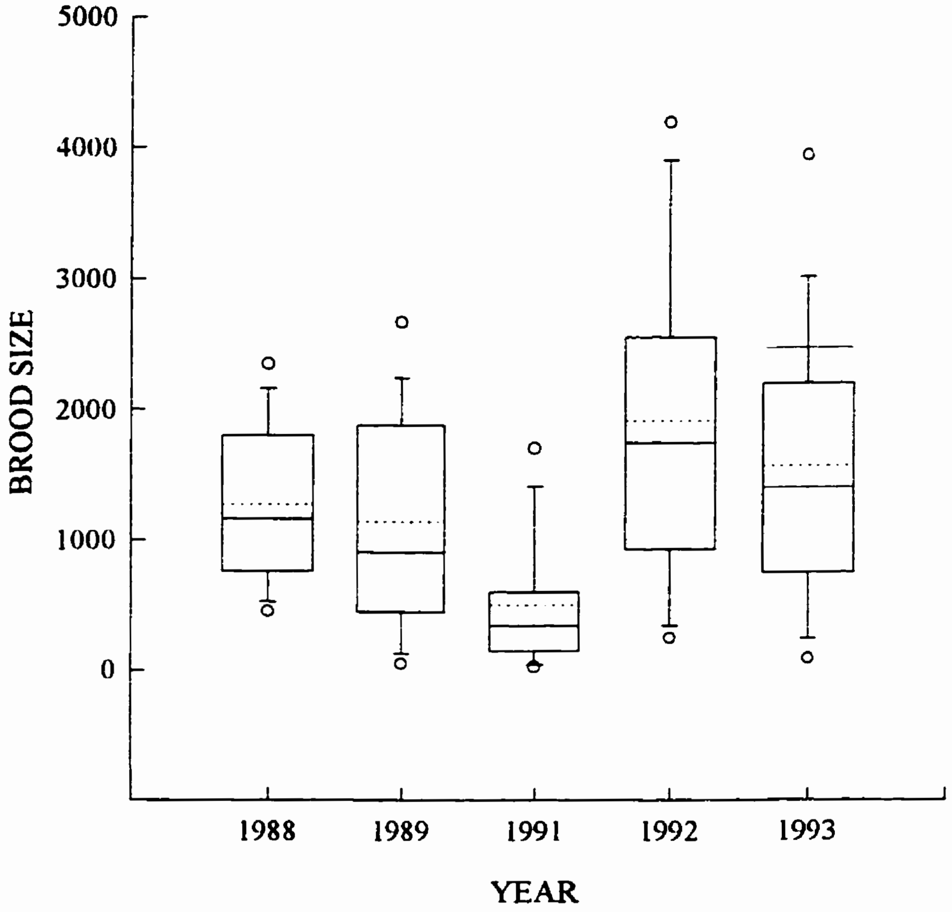

Figure 4.5. Box plots showing median (solid horizontal line inside box), mean (dashed horizontal line inside box), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) of brood size estimates in first-feeding smallmouth bass broods in Lake Opeongo during five reproductive seasons. Sample sizes are presented in Table 4.3.

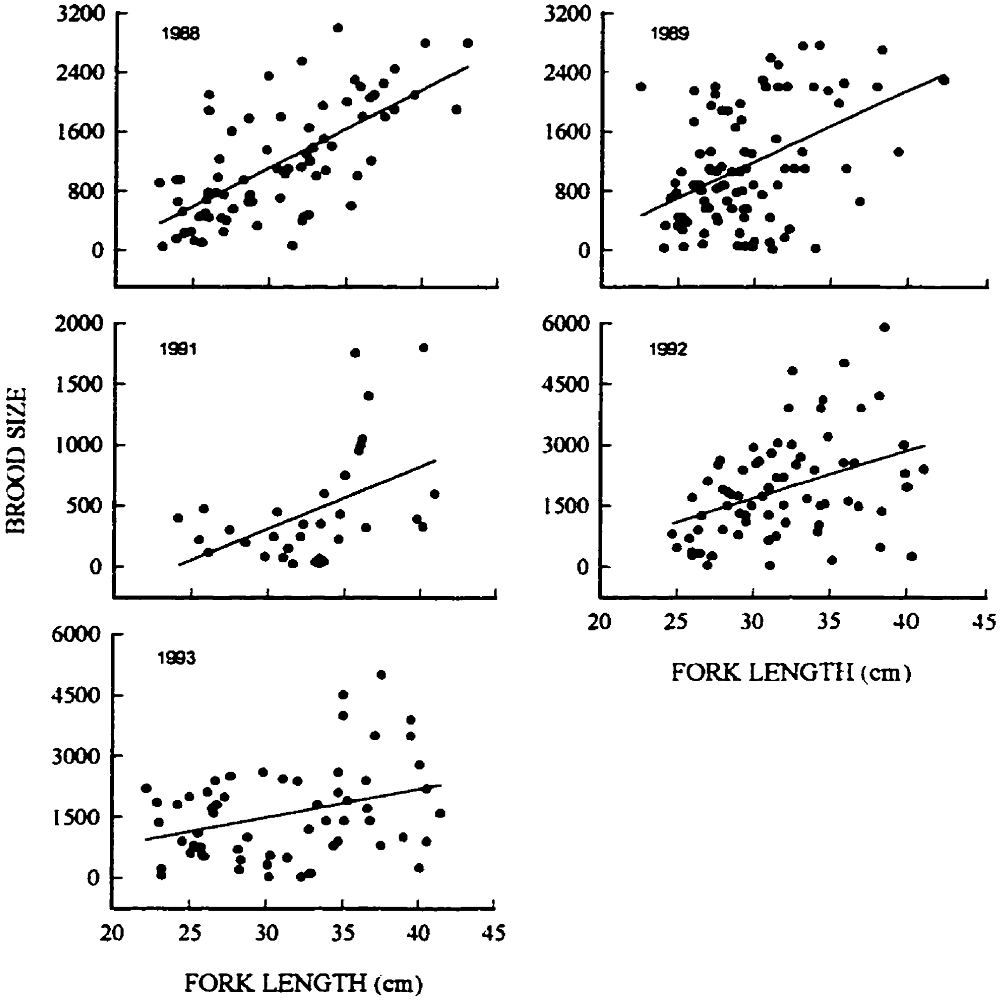

Figure 4.6. The relationship between size (fork length) of nesting males and brood size (total number of offspring in nest) at first-feeding for larval smallmouth bass during five spawning seasons. Regression equations and sample sizes are presented in Table 4.5.

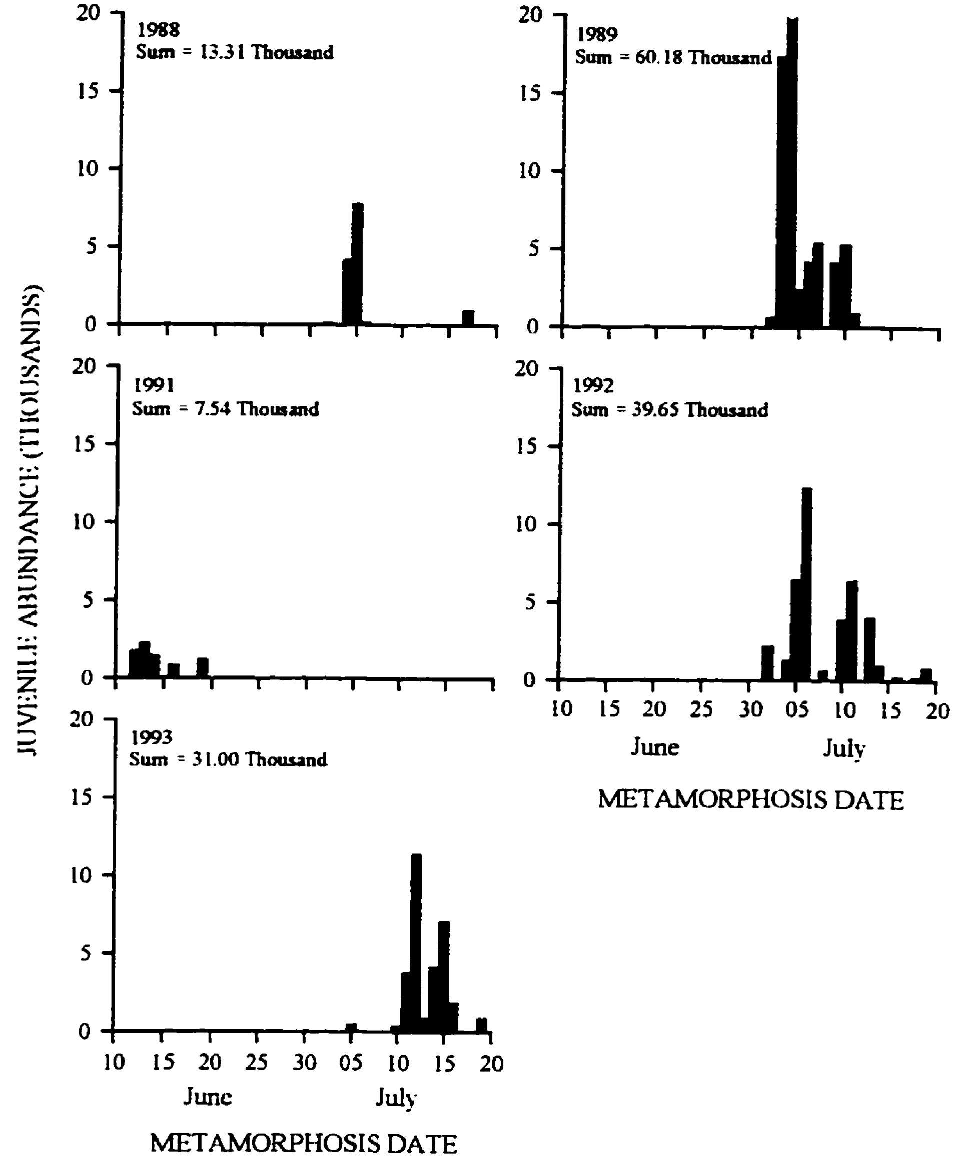

Figure 4.7. Seasonal production of juvenile smallmouth bass in Jones Bay, Lake Opeongo during 5 spawning seasons. Total number of juvenile smallmouth bass produced each year (sum) is presented in the figures.

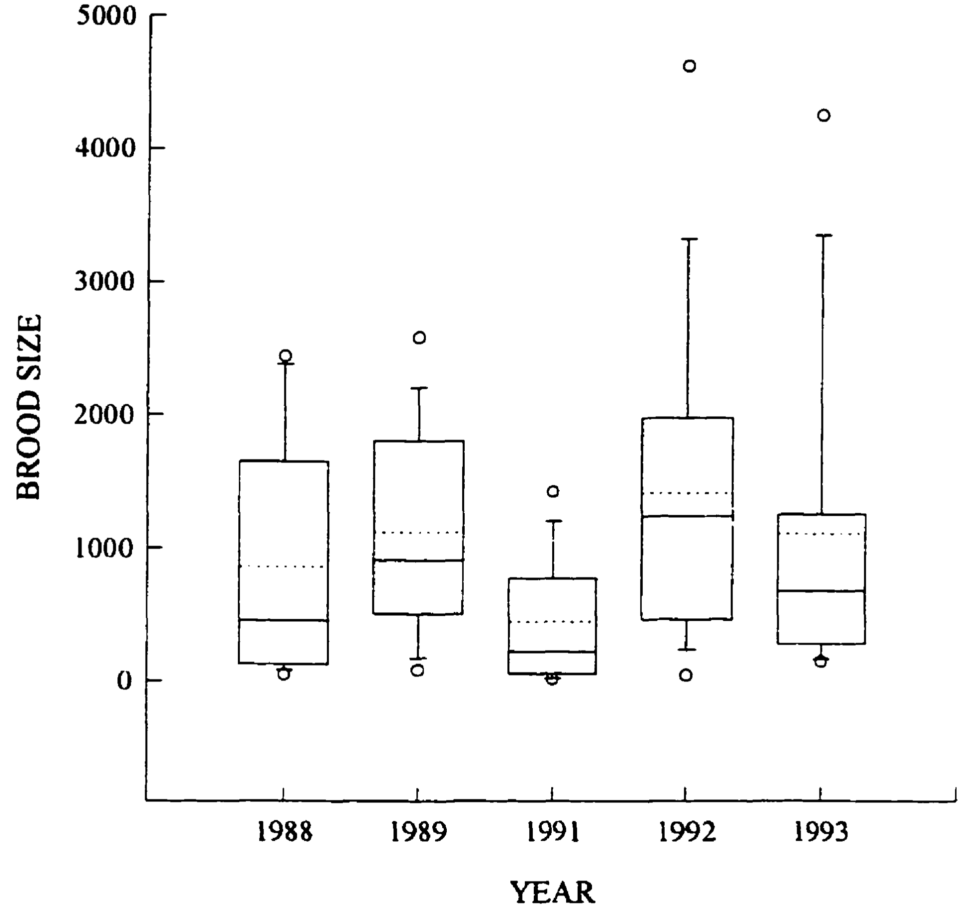

Figure 4.8. Box plots showing median (solid horizontal line inside box), mean (dashed horizontal line inside box), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) of brood size estimates for smallmouth bass broods at metamorphosis. Sample sizes are shown in Table 4.5.

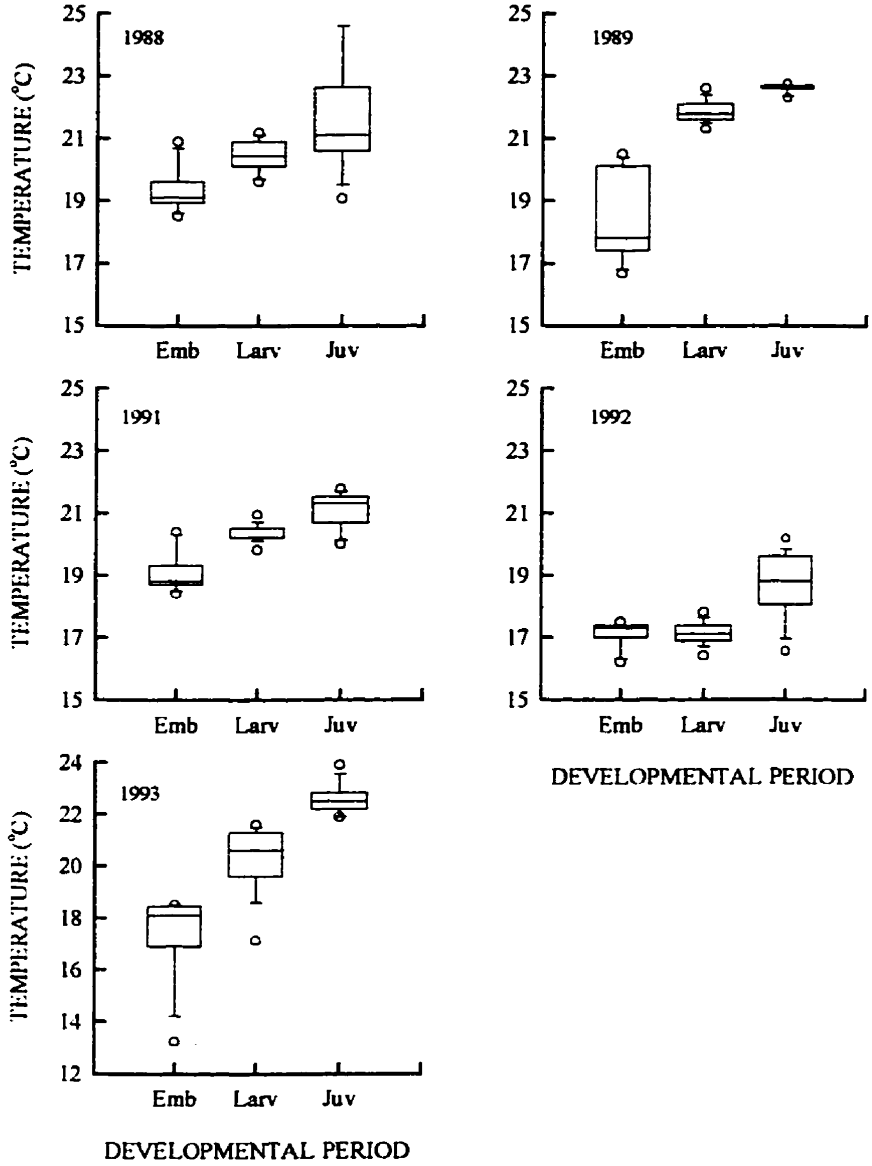

Figure 4.9. Box plots of brood-specific water temperatures for smallmouth bass during the embryonic (Emb), Larval (Larv) and juvenile (Juv) period of development in Lake Opeongo during 5 spawning seasons. Box plots show median (solid horizontal line inside box), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) of water temperature.

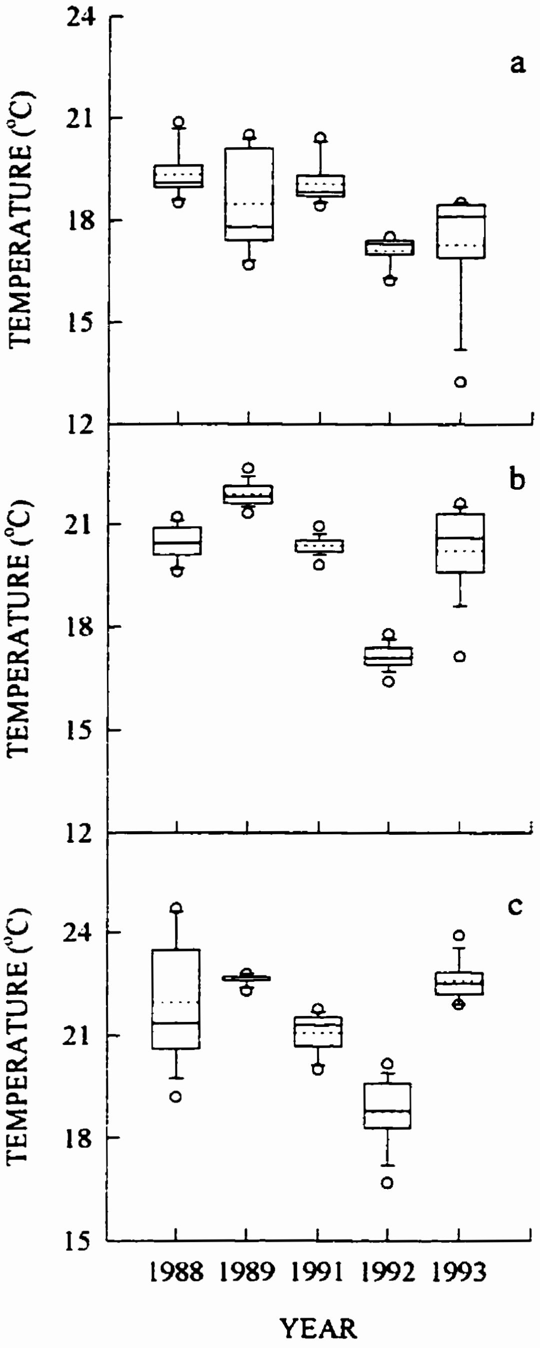

Figure 4.10. Box plots showing mean (dashed horizonal line inside box), median (solid horizontal line inside box), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) of brood-specific water temperatures experienced by smallmouth bass during the (a) embryonic, (b) larval and (c) juvenile period during five spawning seasons.

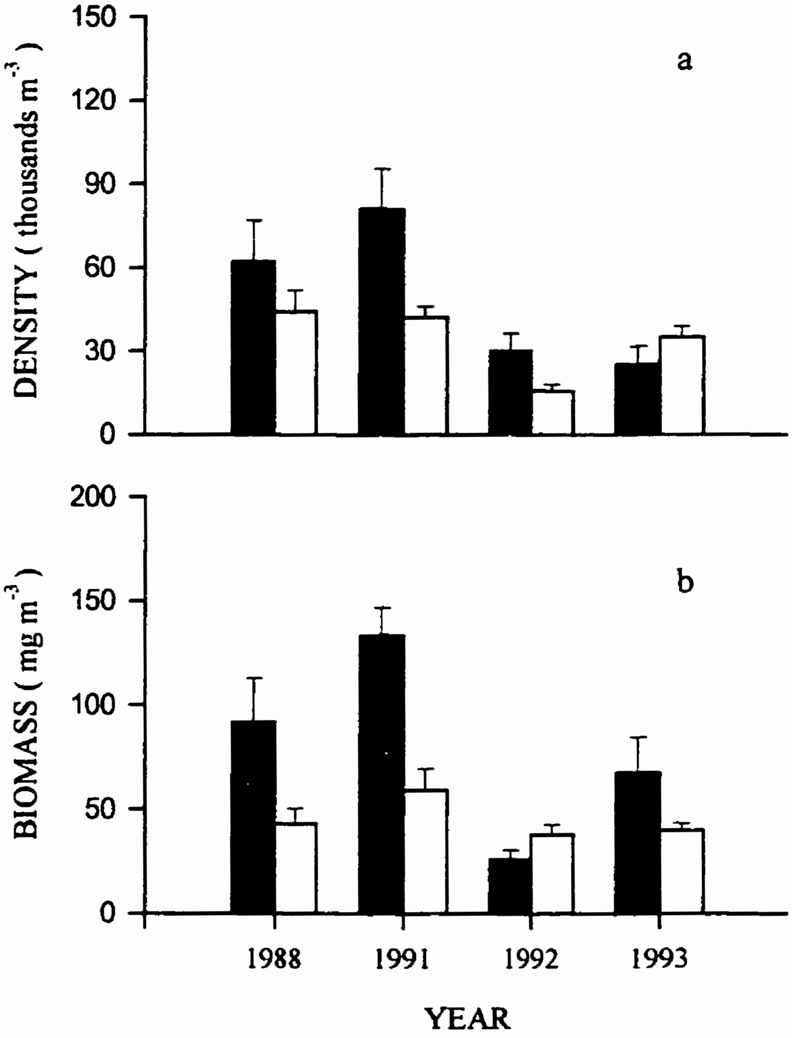

Figure 4.11. Mean (a) density (individuals m^{-3}) and (b) dry weight biomass (mg m^{-3}) of littoral-zone zooplankton in Lake Opeongo in 1988, 1991, 1992 and 1993. Sampling times corresponded with the larval (solid bars) and juvenile (open bars) periods of development in smallmouth bass. Error bars indicate +SE. Total sample size (n) = 140.

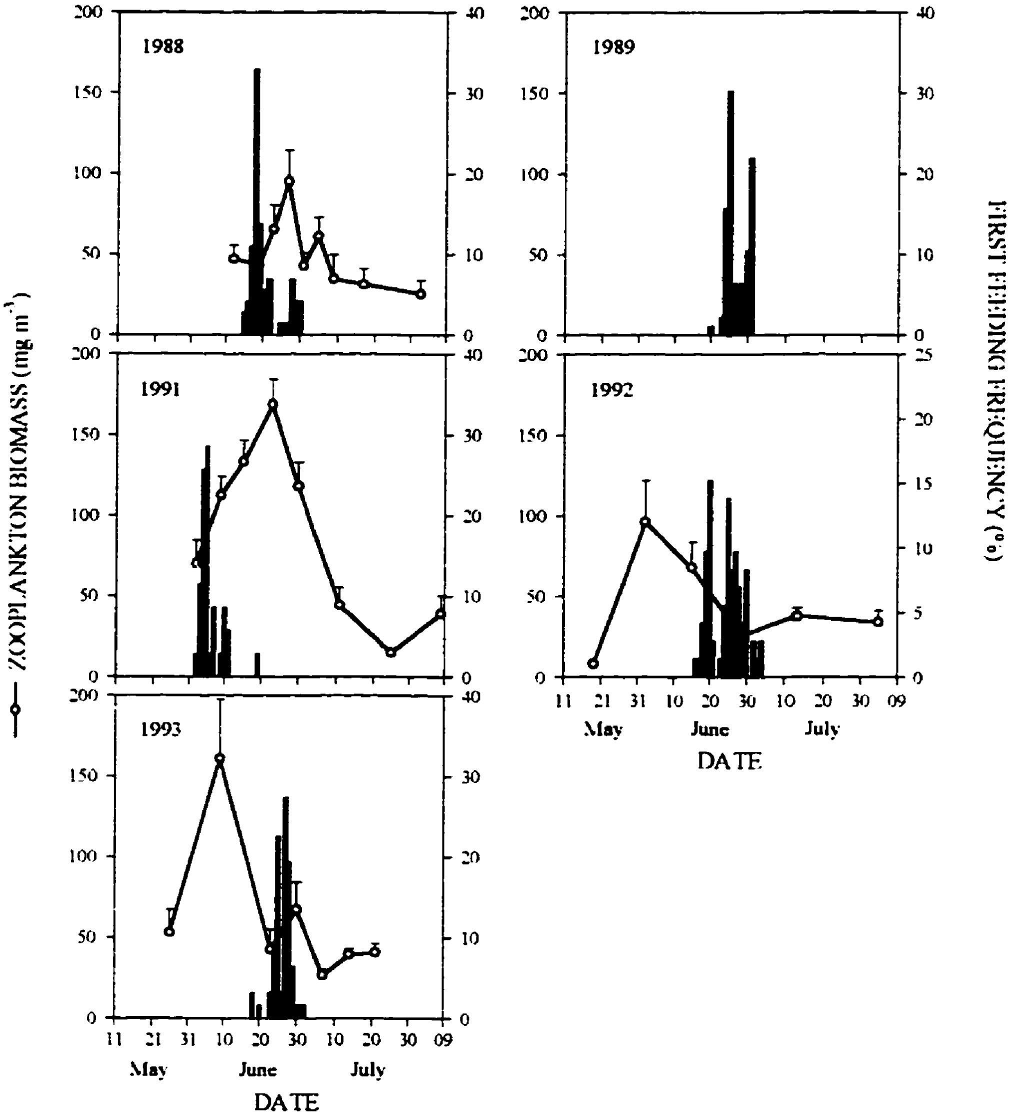

Figure 4.12. Seasonal patterns in biomass of littoral-zone zooplankton (solid line) in 1988, 1991, 1992 and 1993 and percent frequency of first-feeding smallmouth bass larvae (solid bar) during five nesting seasons in Lake Opeongo. Zooplankton biomass was estimated from weekly and biweekly samples collected at fixed stations.

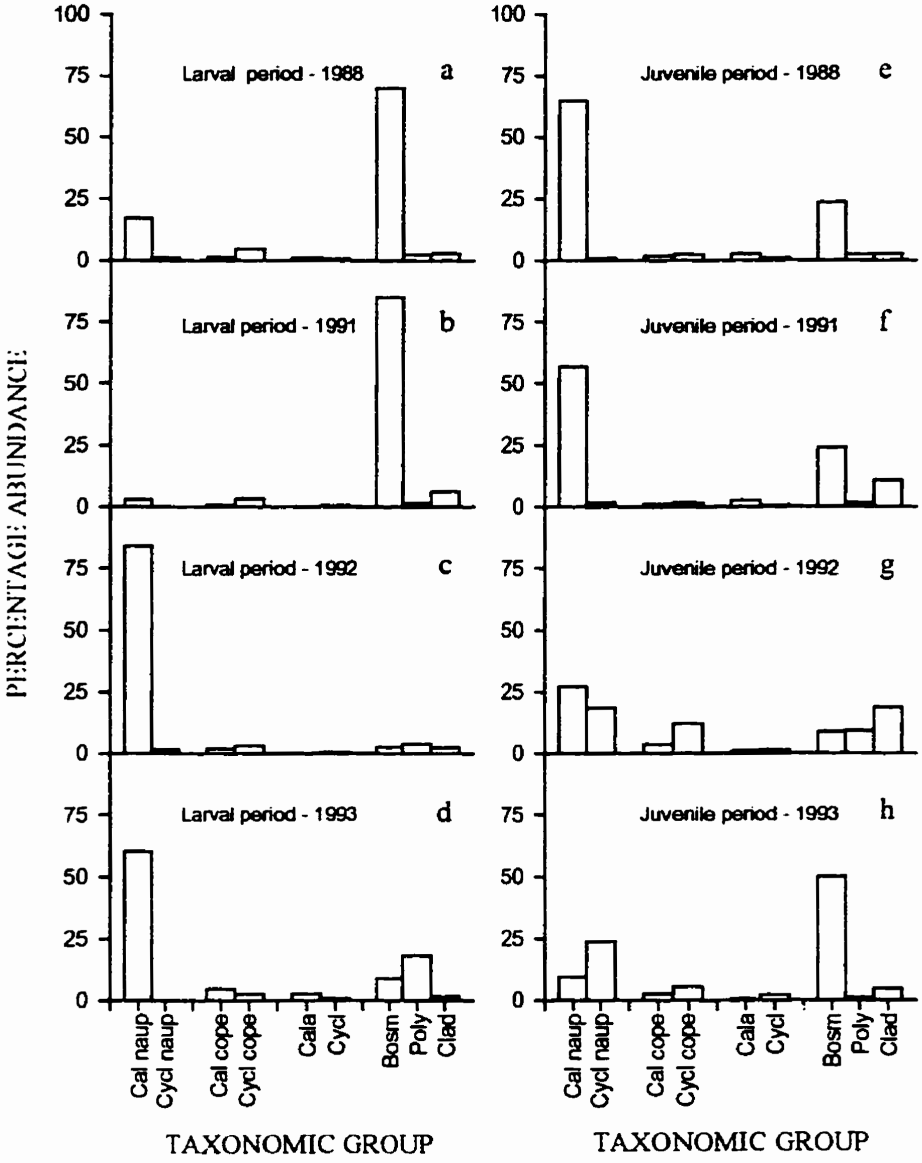

Figure 4.13. Percentage abundance of major taxonomic groups of littoral-zone zooplankton in Lake Opeongo in 1988, 1991, 1992 and 1993. Samples were collected during the smallmouth bass larval (a-d) and juvenile (e-h) period of development. Abbreviations: Cal naup = Calanoid nauplii; Cycl naup = cyclopoid nauplii; Cal cope = calanoid copepodid; Cycl cope = cyclopoid copepodid; Cala = calanoid copepods; cycl = cyclopoid copepods; Bosm = *Bosmina longirostris*; Poly = *Polyphemus pediculus* and Clad = other cladoceran species.

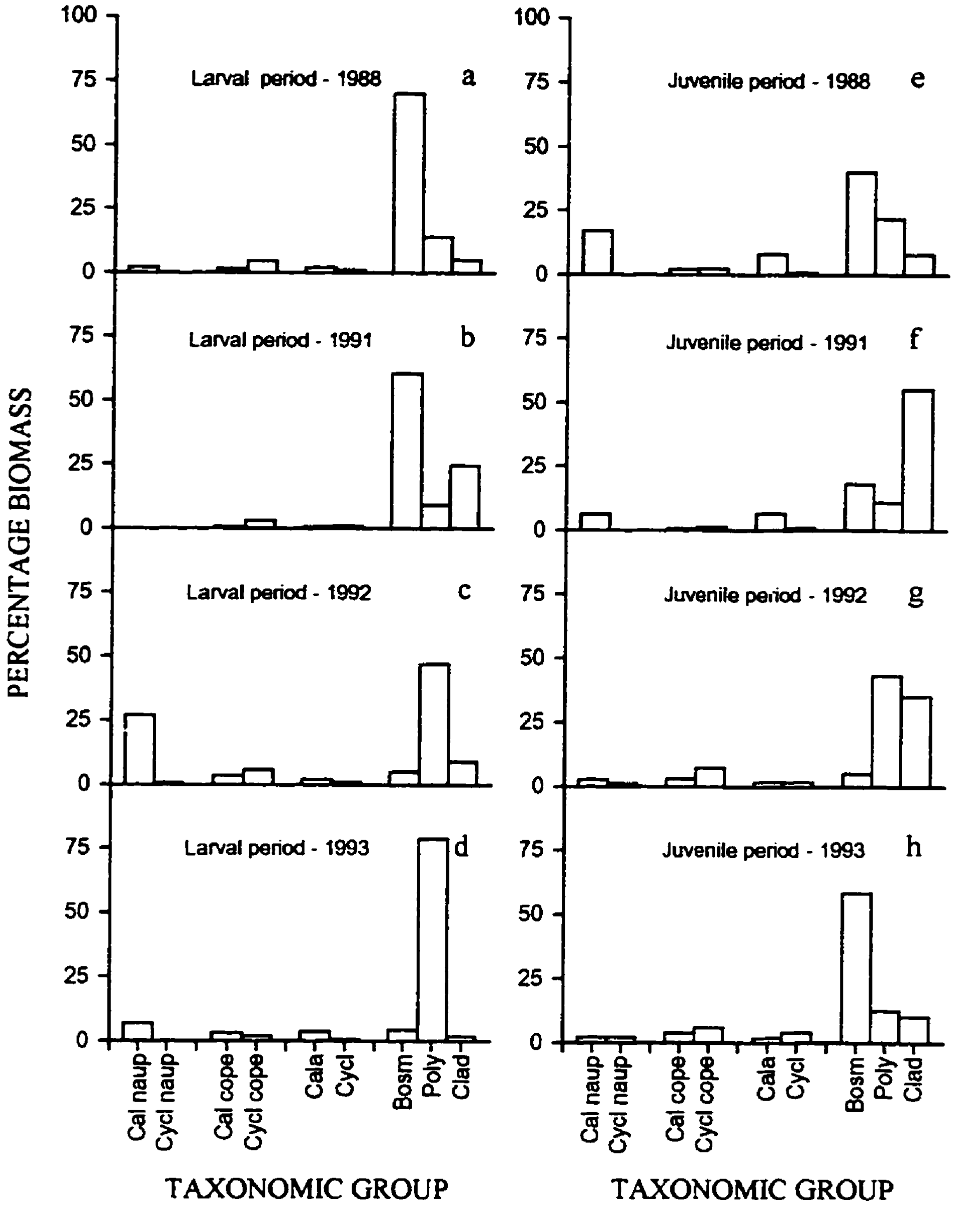

Figure 4.14. Percentage biomass of major taxonomic groups of littoral-zone zooplankton in Lake Opeongo in 1988, 1991, 1992 and 1993. Zooplankton was collected during the smallmouth bass larval (a-d) and juvenile (e-h) periods of development. See Fig. 4.13 for description of taxonomic abbreviations.

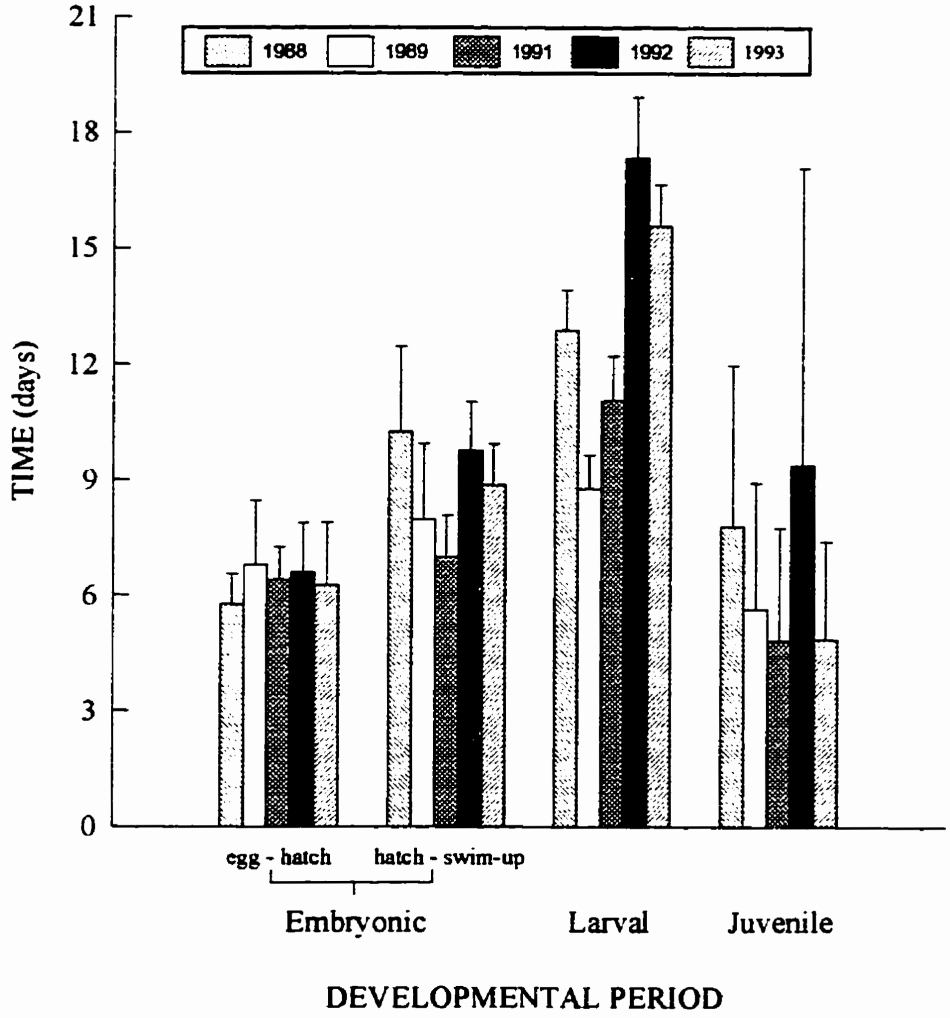

Figure 4.15. Mean (+ SD) duration of embryonic, larval and juvenile developmental periods of smallmouth bass in Lake Opeongo during five nesting seasons. Note, for the purposes of this study the duration of the juvenile period extends from metamorphosis to brood dispersal.

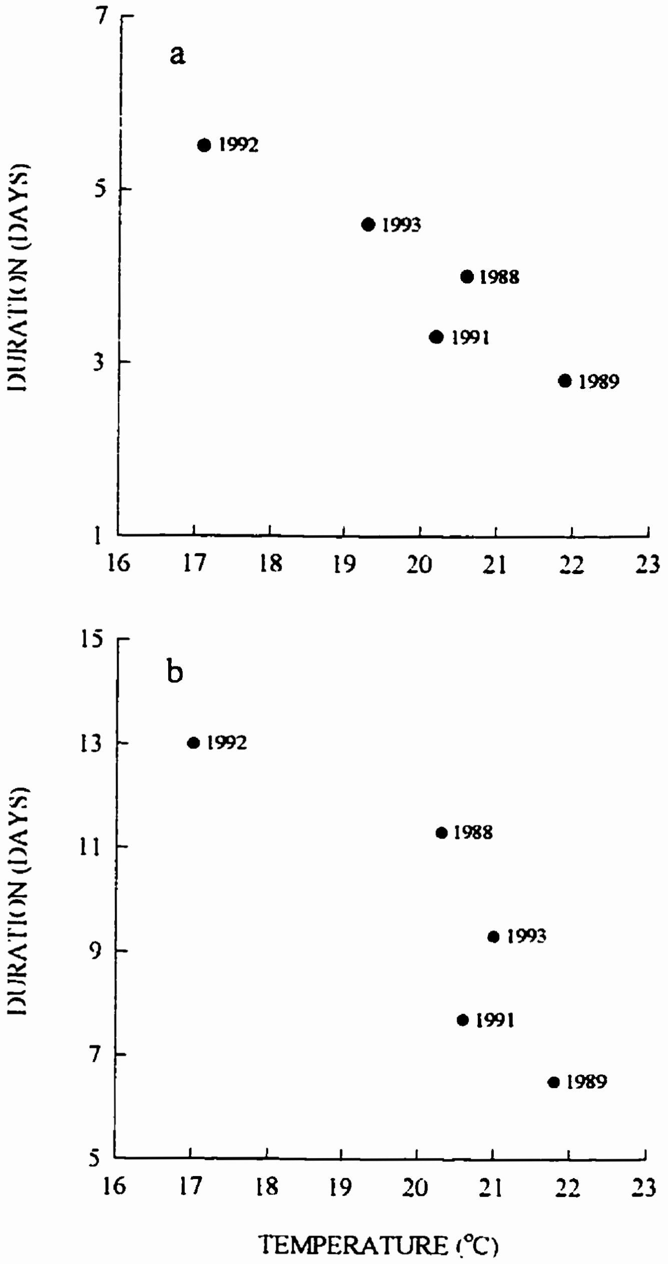

Figure 4.16. Duration (days) of the (a) early larval phase and (b) late larval phase plotted in relation to average water temperature.

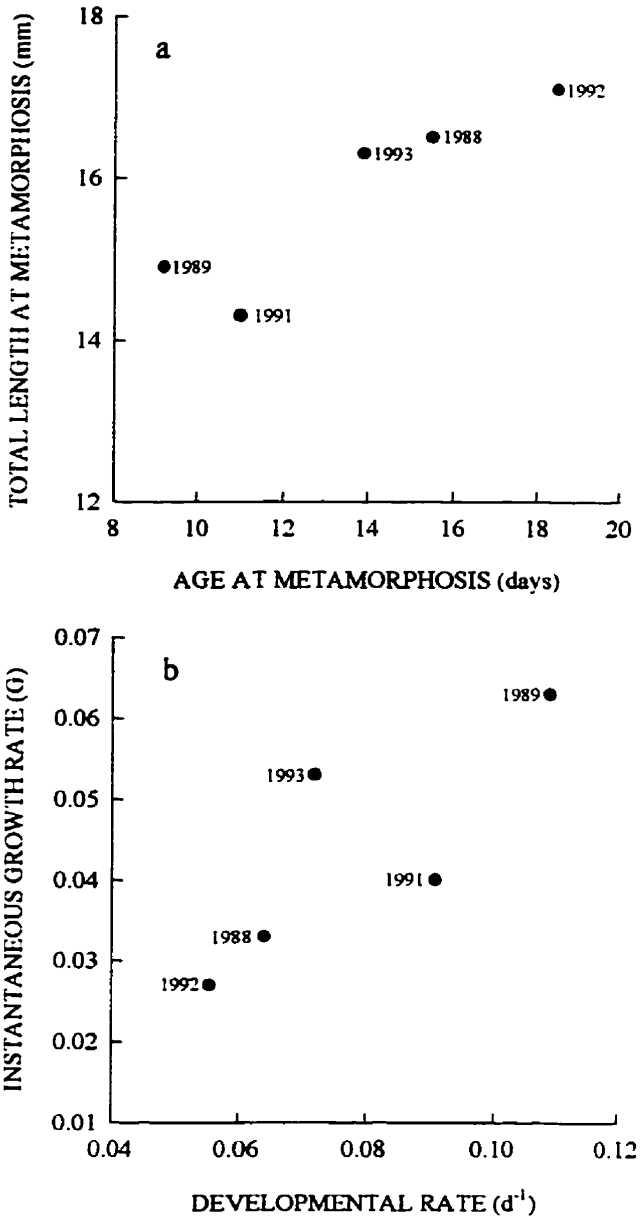

Figure 4.17. (a) Mean total length at metamorphosis plotted against mean age at metamorphosis. Each symbol in plot represents the mean length and age for all broods within a given year-class. (b) Mean instantaneous growth rate plotted against mean developmental rate for the full larval period. Developmental rate refers to the reciprocal of age at metamorphosis.

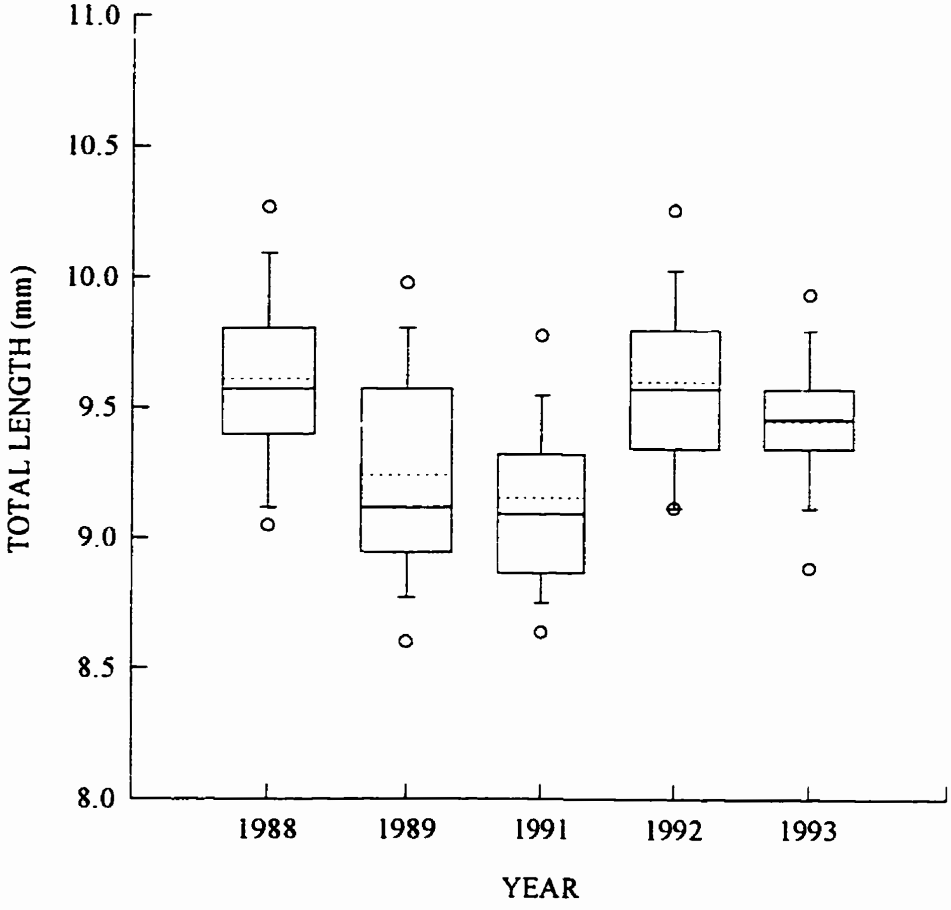

Figure 4.18. Box plots showing mean (dashed horizontal line inside box), median (solid horizontal line inside box), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) of brood-specific total length in first-feeding smallmouth bass larvae in Lake Opeongo. Sample sizes (broods) are presented in Table 4.3).

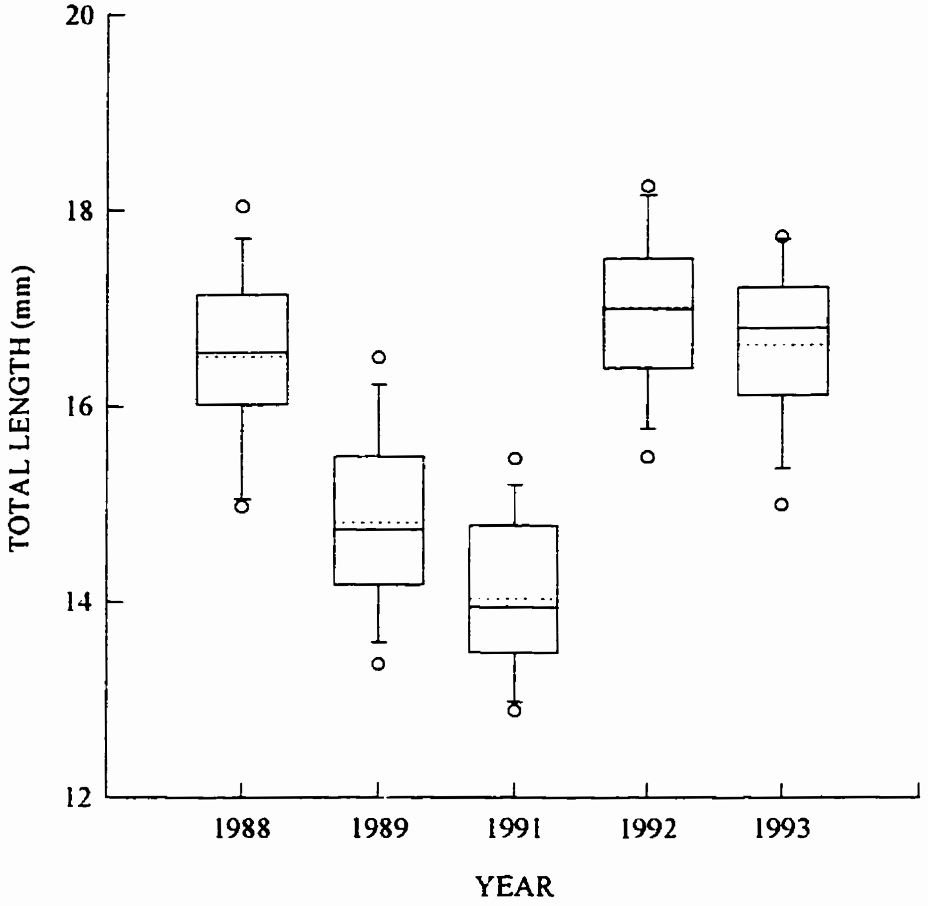

Figure 4.19. Box plots showing mean (dashed horizontal line inside box), median (solid horizontal line inside box), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) of brood-specific total length in juvenile smallmouth bass at metamorphosis. Sample sizes (broods) are presented in Table 4.5.

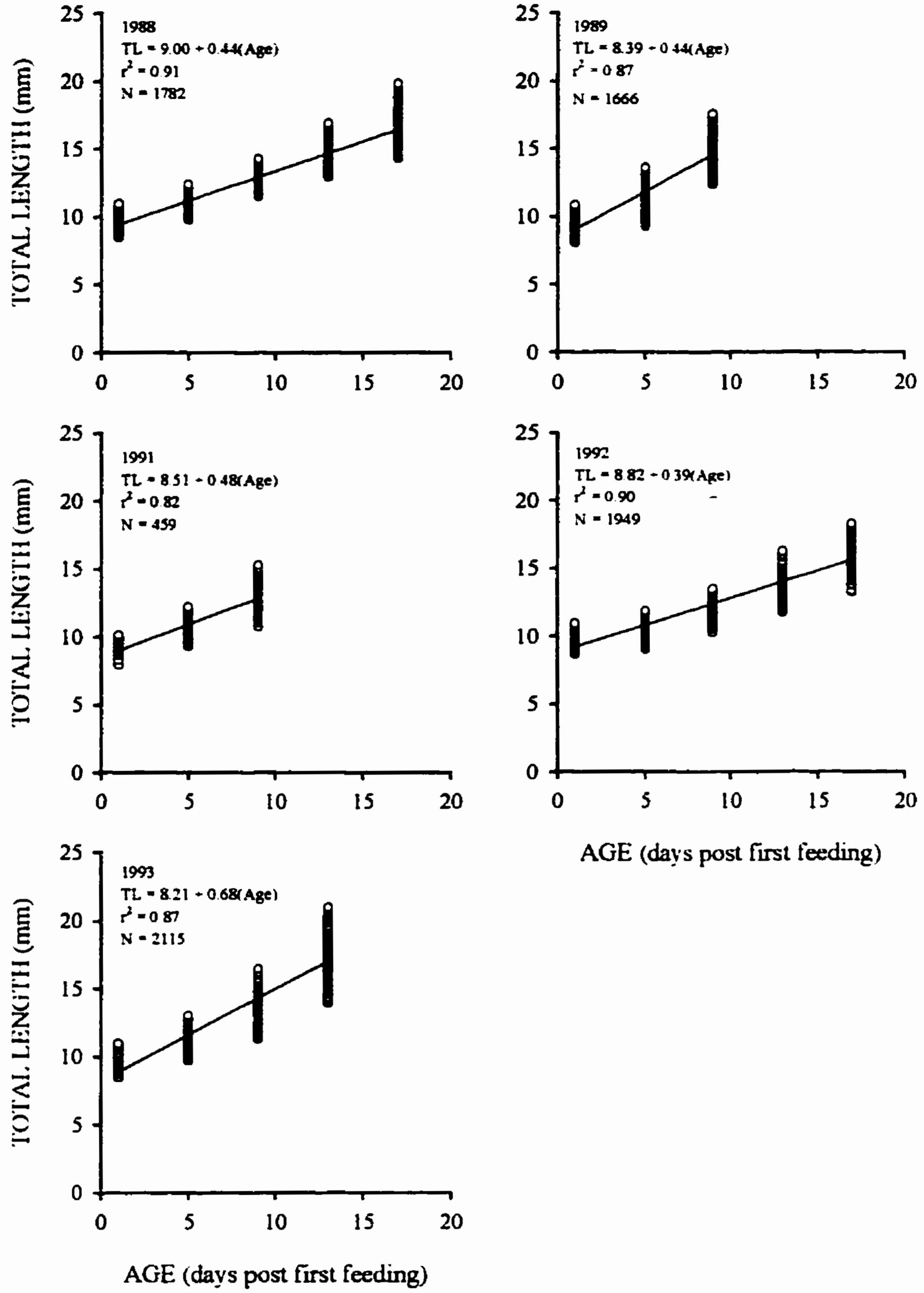

Figure 4.20. Relationship between age (days) and total length (mm) of post-first-feeding larval smallmouth bass in Lake Opeongo during five spawning seasons. Regression coefficients estimate mean growth rates (mm d^{-1}).

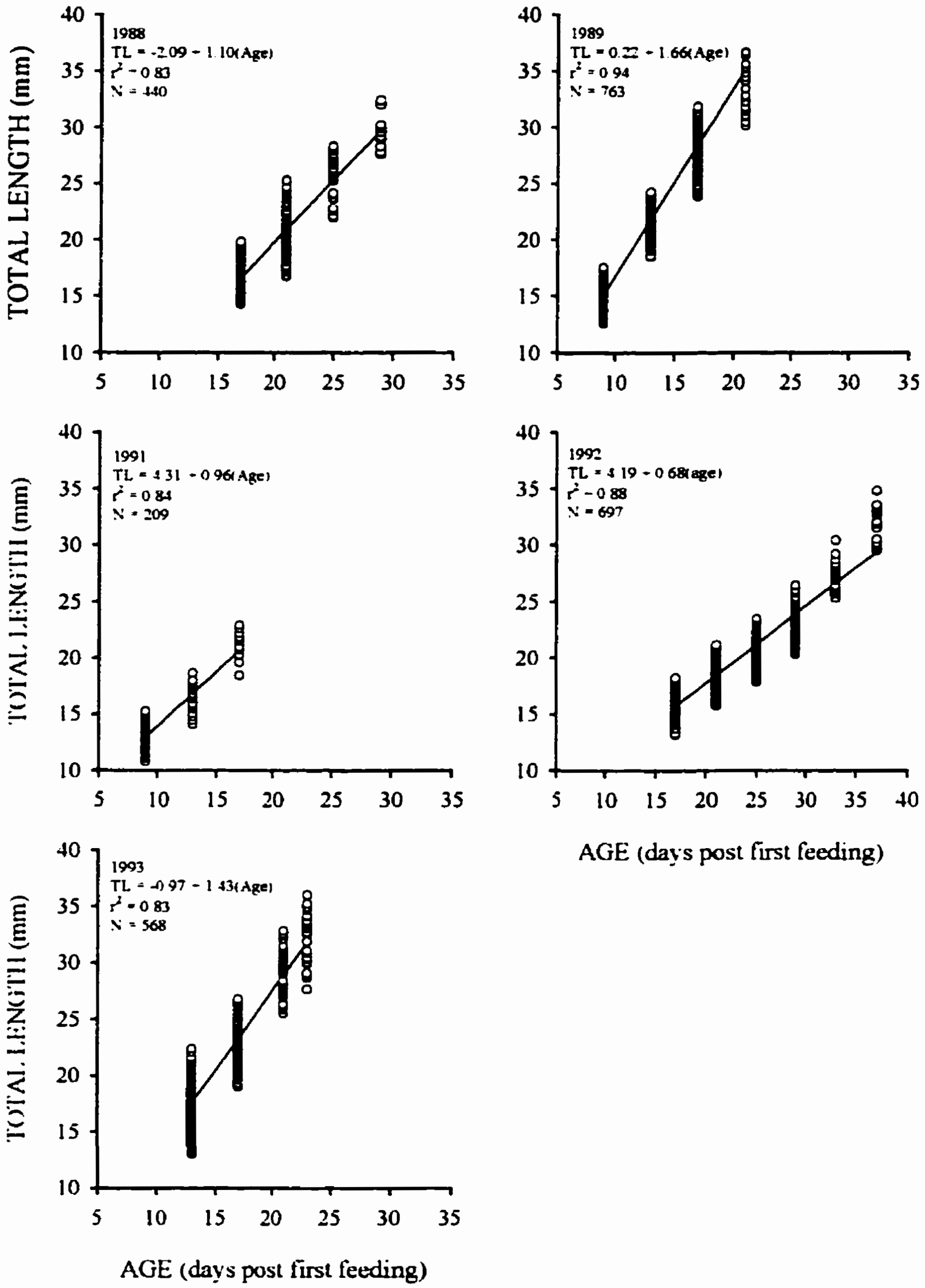

Figure 4.21. Relationship between age (days) and total length (mm) of juvenile smallmouth bass sampled in Lake Opeongo during five spawning seasons. Regression coefficients estimate mean growth rates (mm d^{-1}).

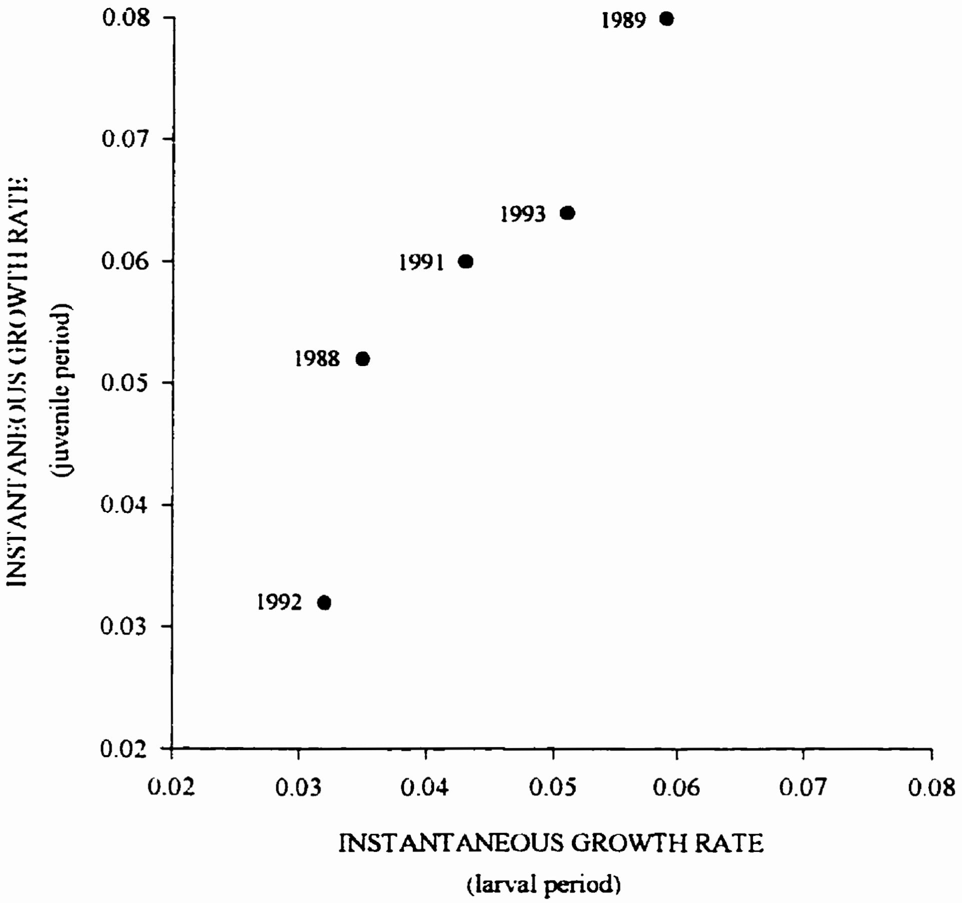

Figure 4.22. Relationship between larval and juvenile instantaneous growth rates for smallmouth bass year-classes in Lake Opeongo.

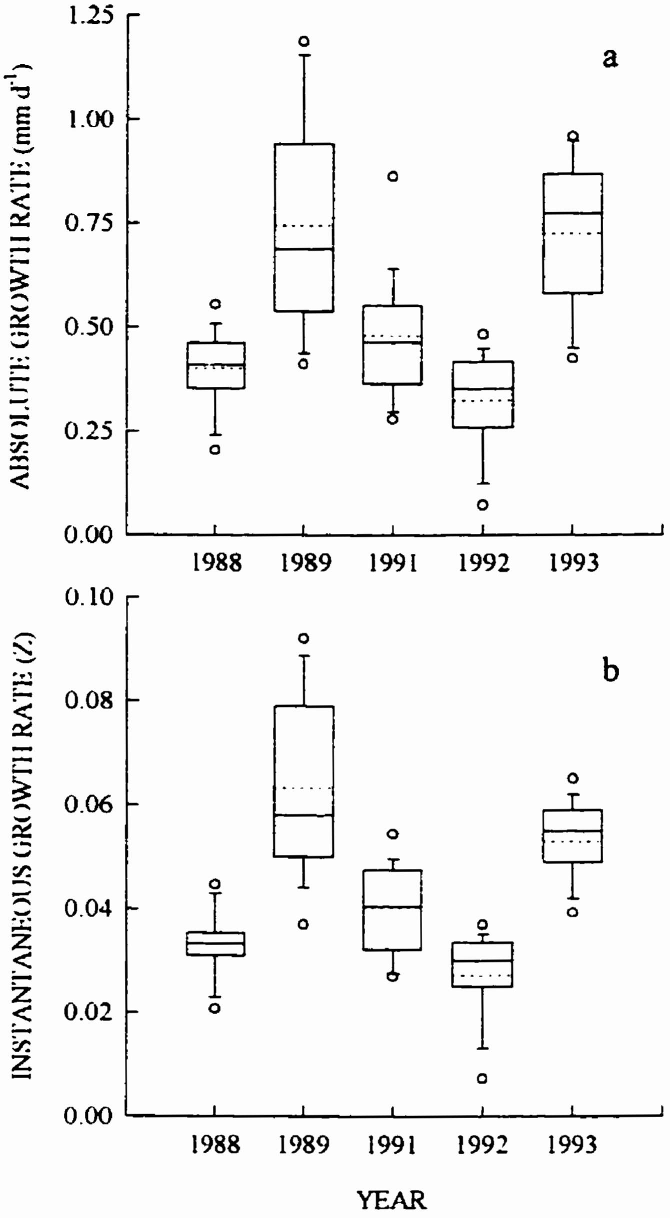

Figure 4.23. Box plots showing mean (dashed horizontal line inside box), median (solid horizontal line inside box), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) for brood-specific (a) absolute and (b) instantaneous growth rates of larval smallmouth bass in Lake Opeongo.

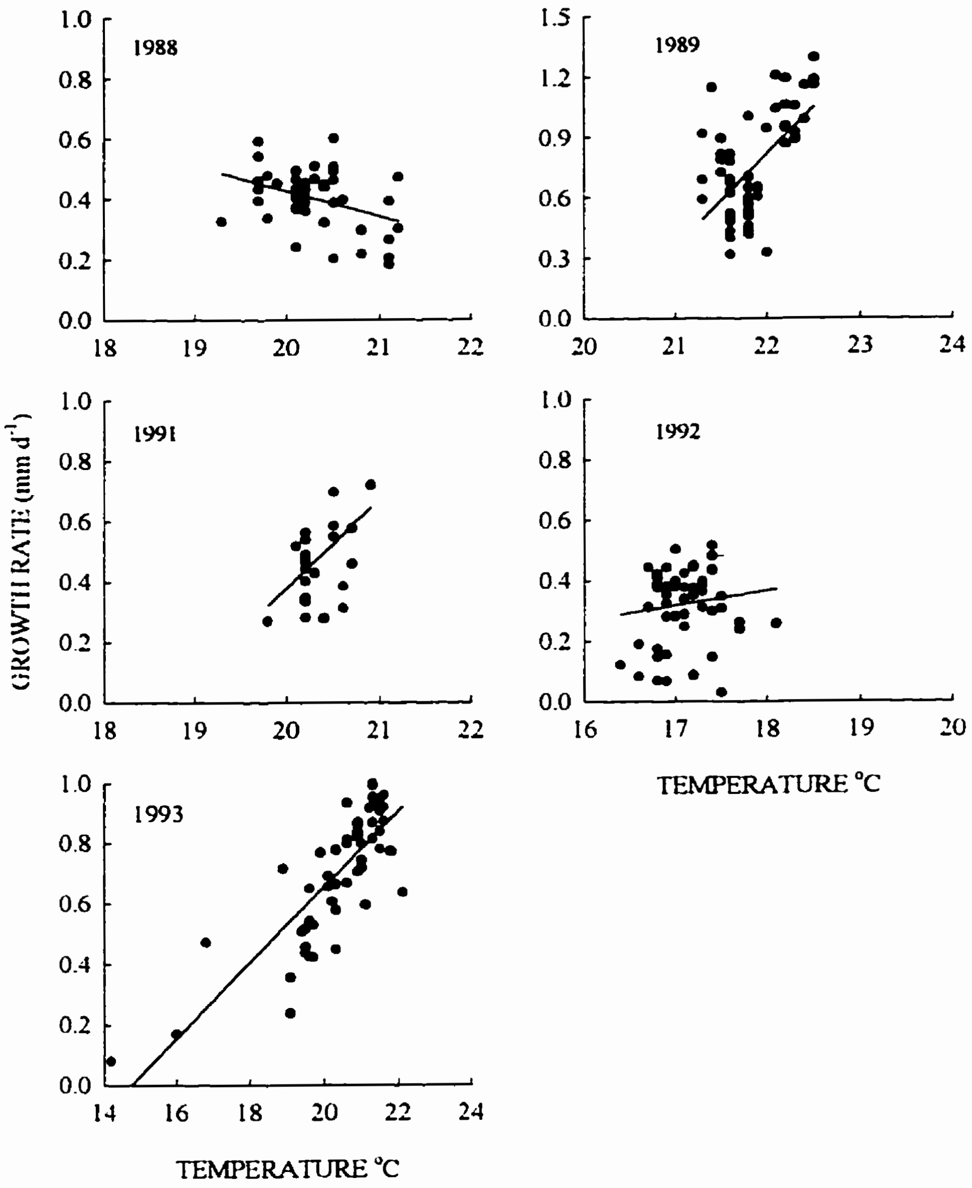

Figure 4.24. Relationship between brood-specific water temperatures and growth rates (mm d^{-1}) for smallmouth bass larvae in Lake Opeongo during five spawning seasons.

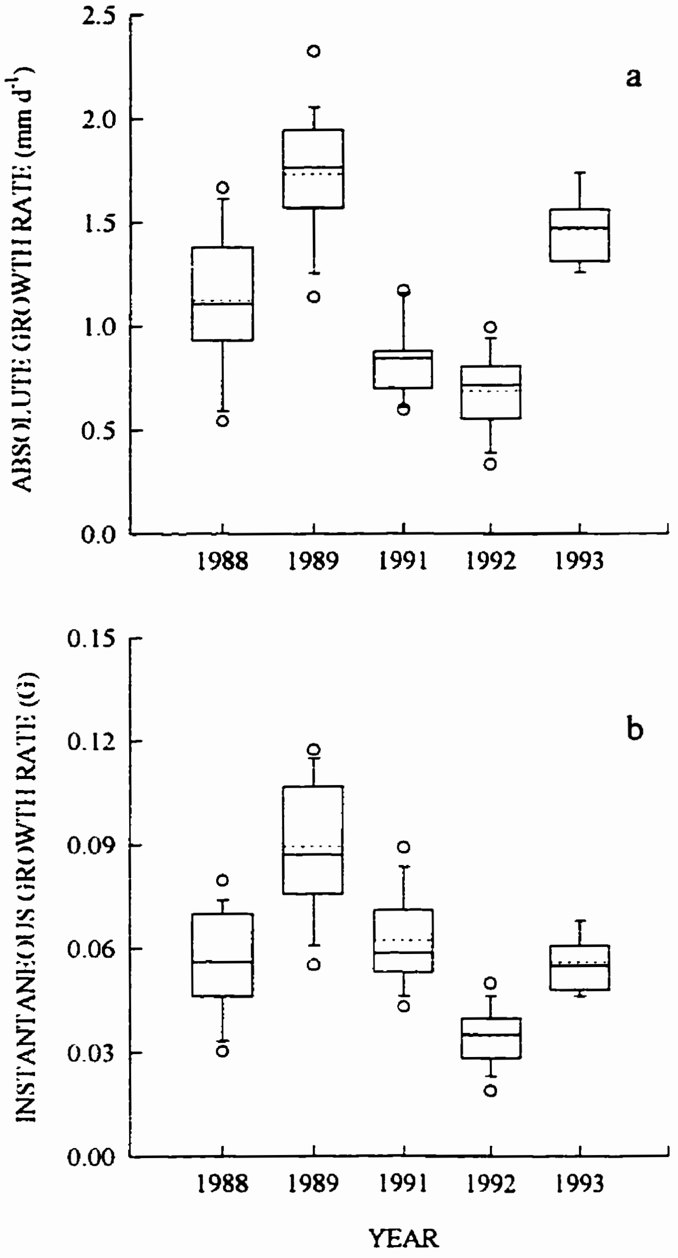

Figure 4.25. Box plots showing mean (dashed horizontal line inside box), median (solid horizontal line inside box), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) of brood-specific (a) absolute and (b) instantaneous growth rates for juvenile smallmouth bass in Lake Opeongo.

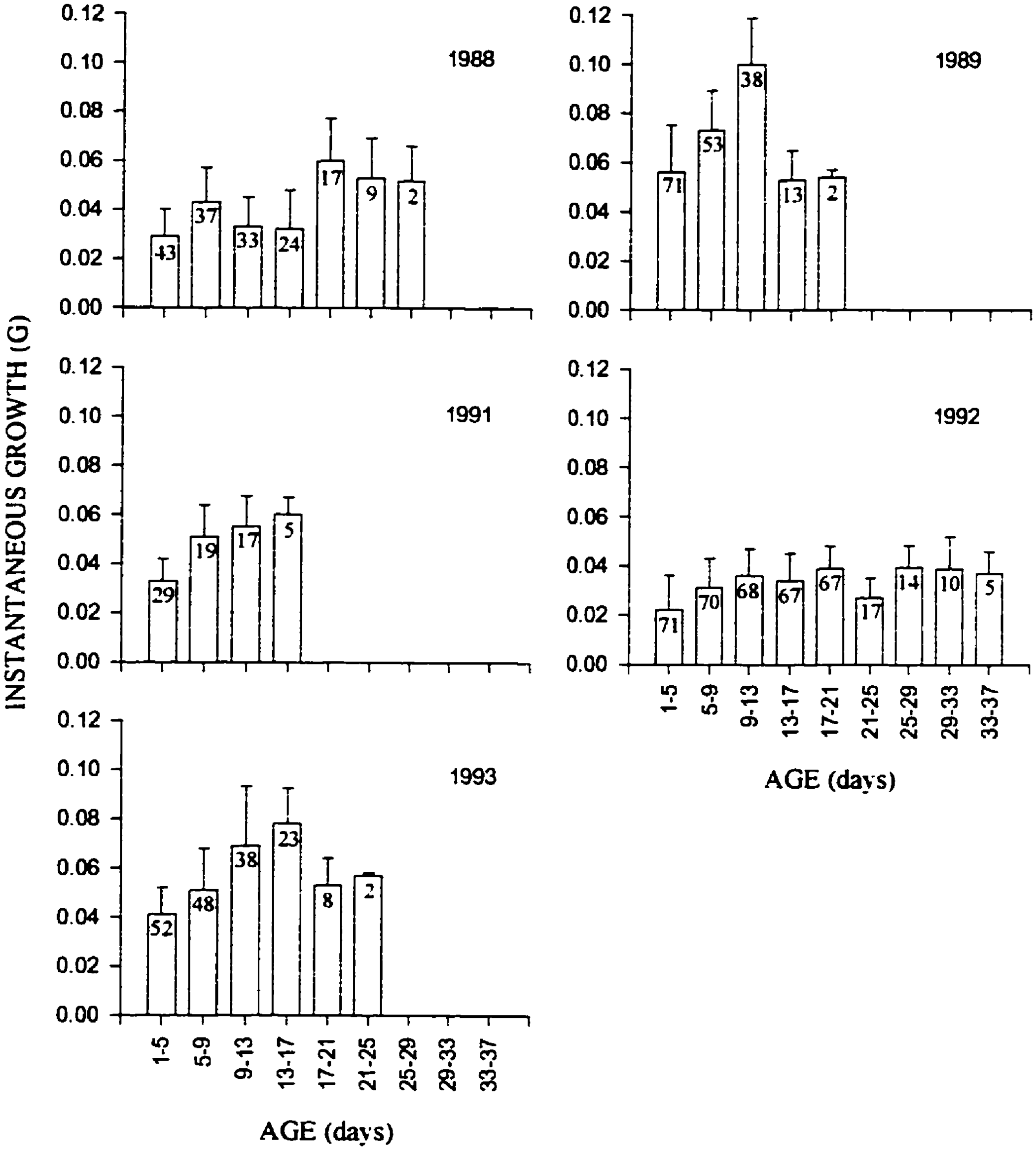

Figure 4.26. Relationship between age (days after first feeding) and mean brood-specific instantaneous growth rates of YOY smallmouth bass during 4-day growth intervals in Lake Opeongo.

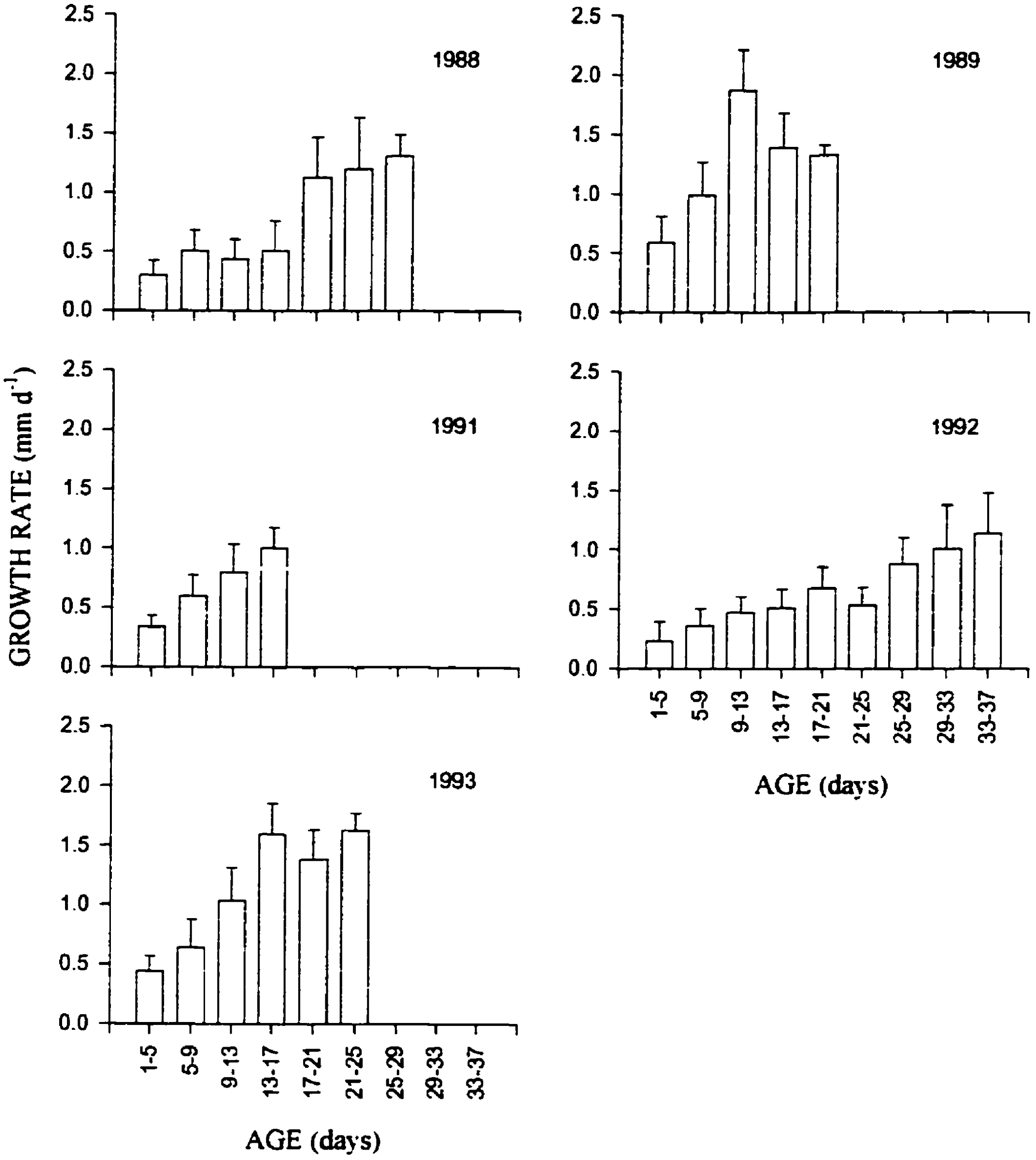

Figure 4.27. Relationship between age (days after first feeding) and mean brood-specific absolute growth rates (mm d^{-1}) of smallmouth bass offspring during 4-day growth intervals in Lake Opeongo.

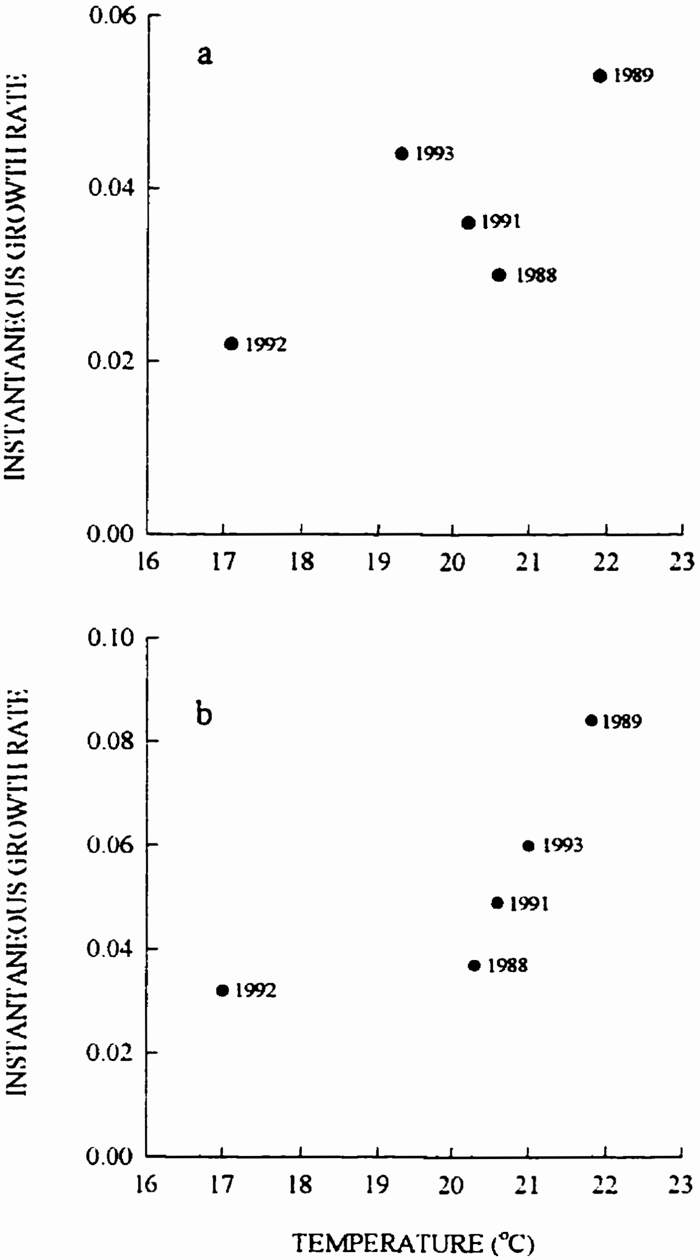

Figure 4.28. Brood-specific daily instantaneous growth rates of smallmouth bass during the (a) early larval and (b) late larval phases of development plotted against mean brood-specific water temperature.

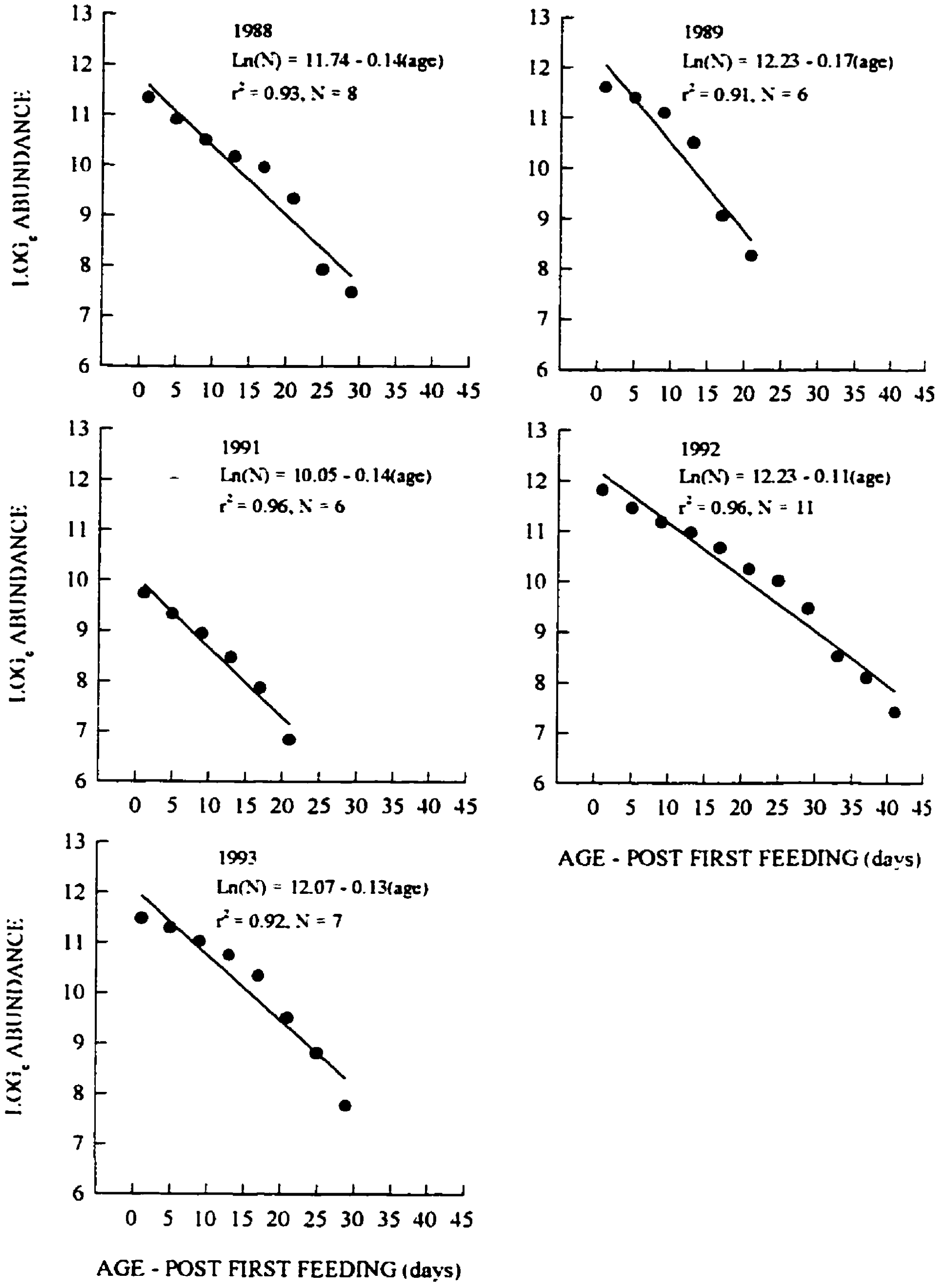

Figure 4.29. Relationship between age (days post-first feeding) and estimated year-class abundance of YOY smallmouth bass in Lake Opeongo during five spawning seasons. Regression coefficients in the models are estimates of the mean instantaneous mortality rate for the year-classes.

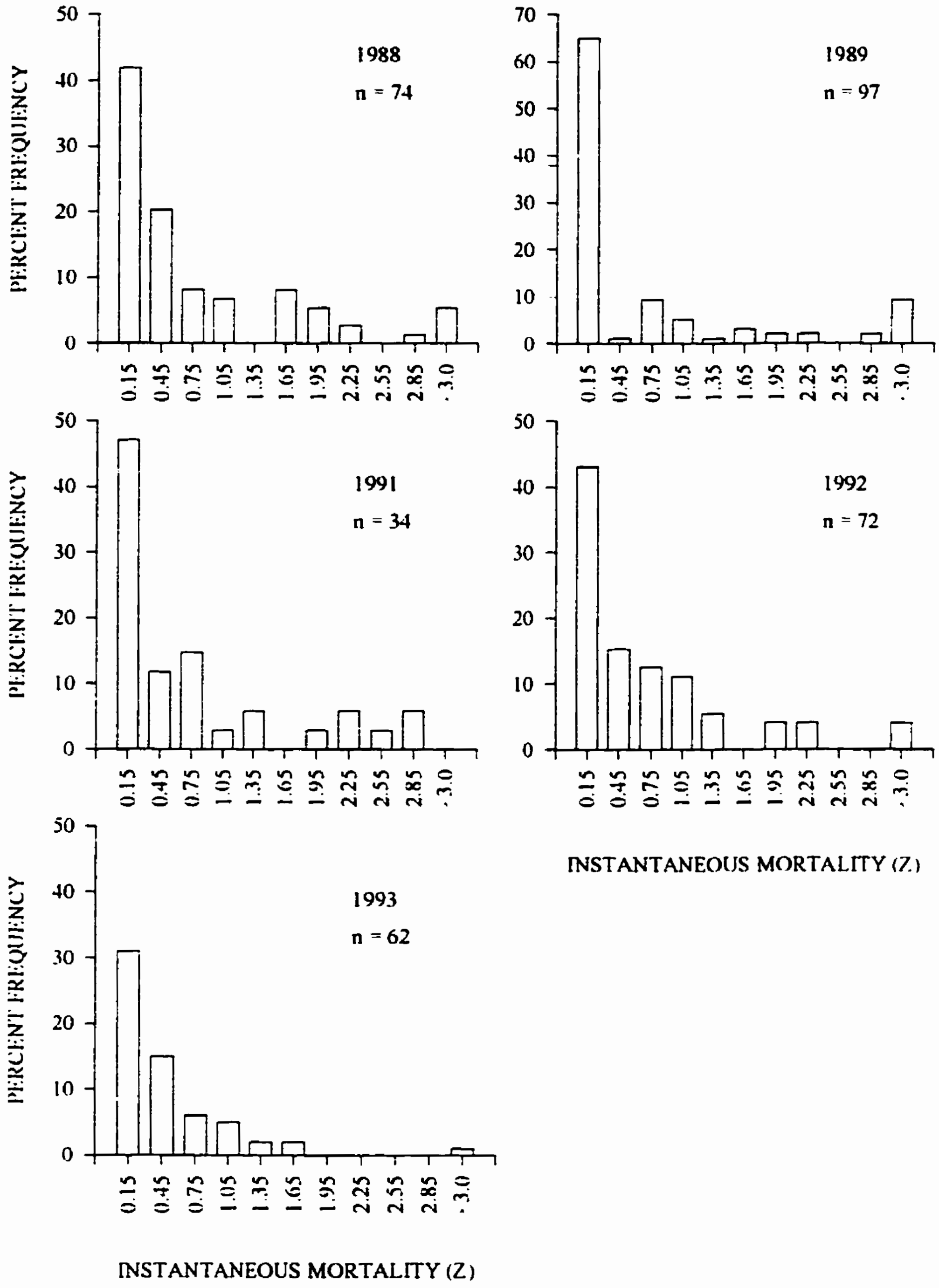

Figure 4.30. Frequency distribution of brood-specific instantaneous mortality rate of smallmouth bass larvae in Lake Opeongo during five spawning seasons. Sample sizes are presented in Table 4.21.

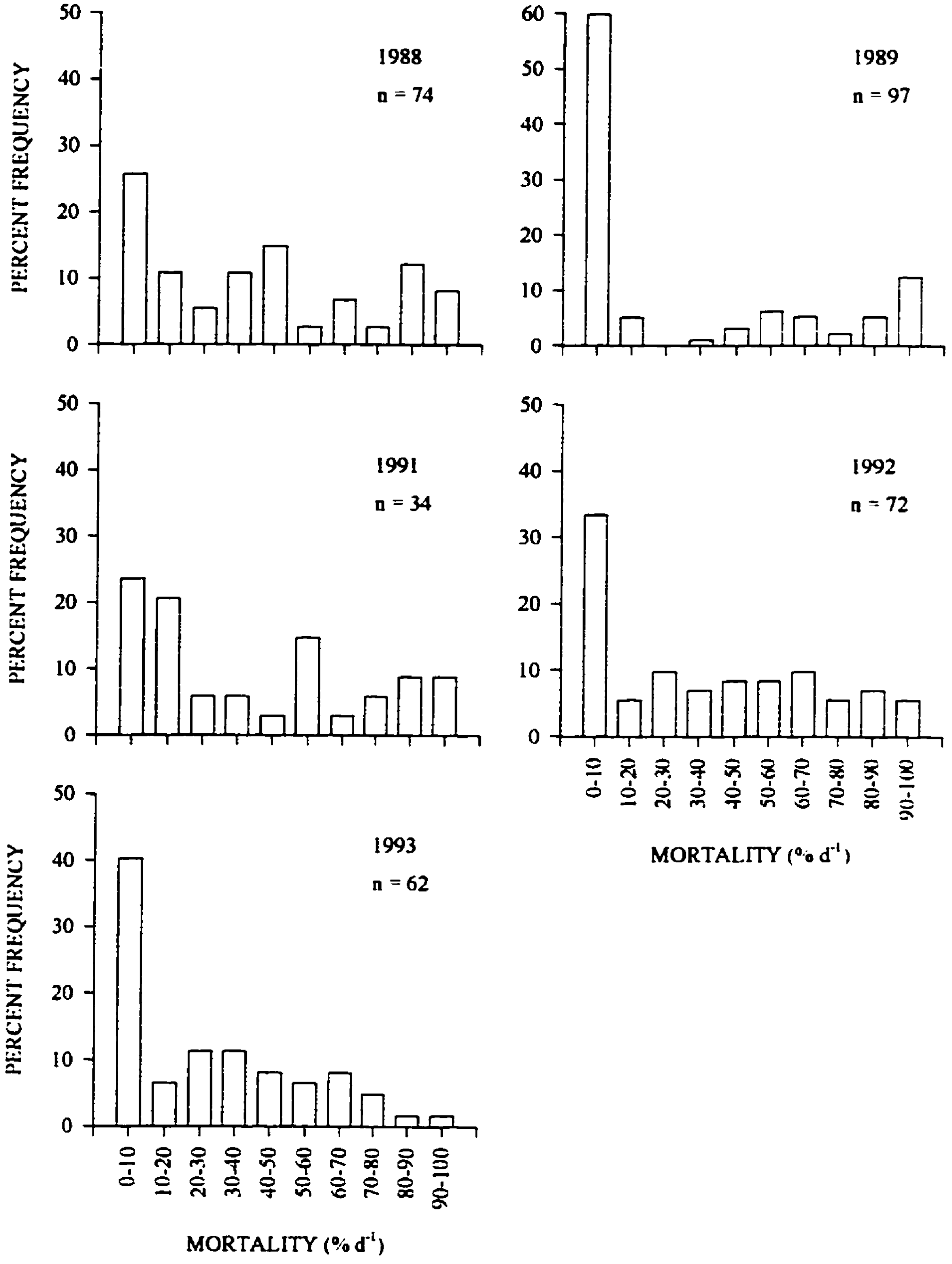

Figure 4.31. Frequency distribution of brood-specific daily mortality rate (% d^{-1}) of smallmouth bass larvae in Lake Opeongo during five spawning seasons. Sample sizes are presented in Table 4.21.

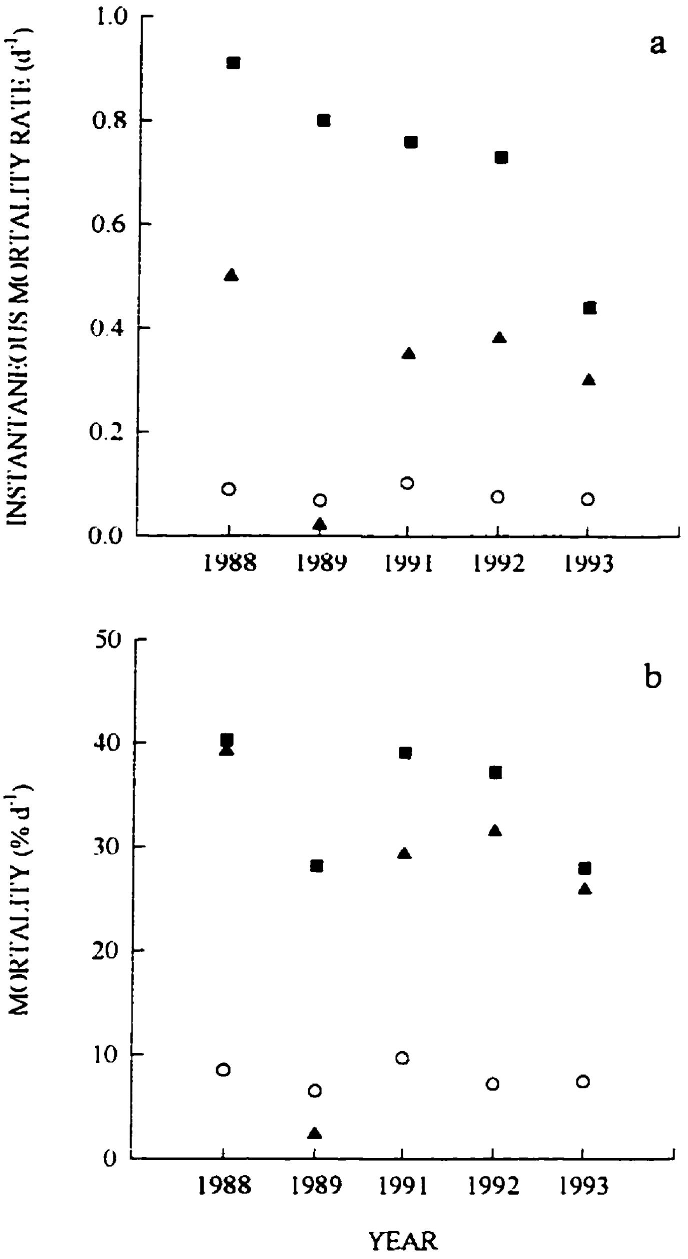

Figure 4.32. (a) Instantaneous (d^{-1}) and (b) daily (% d^{-1}) mortality rates of larval smallmouth bass in Lake Opeongo. Symbols indicate year-class (open circle) and brood-specific mean (solid squares) and median (solid triangles) values.

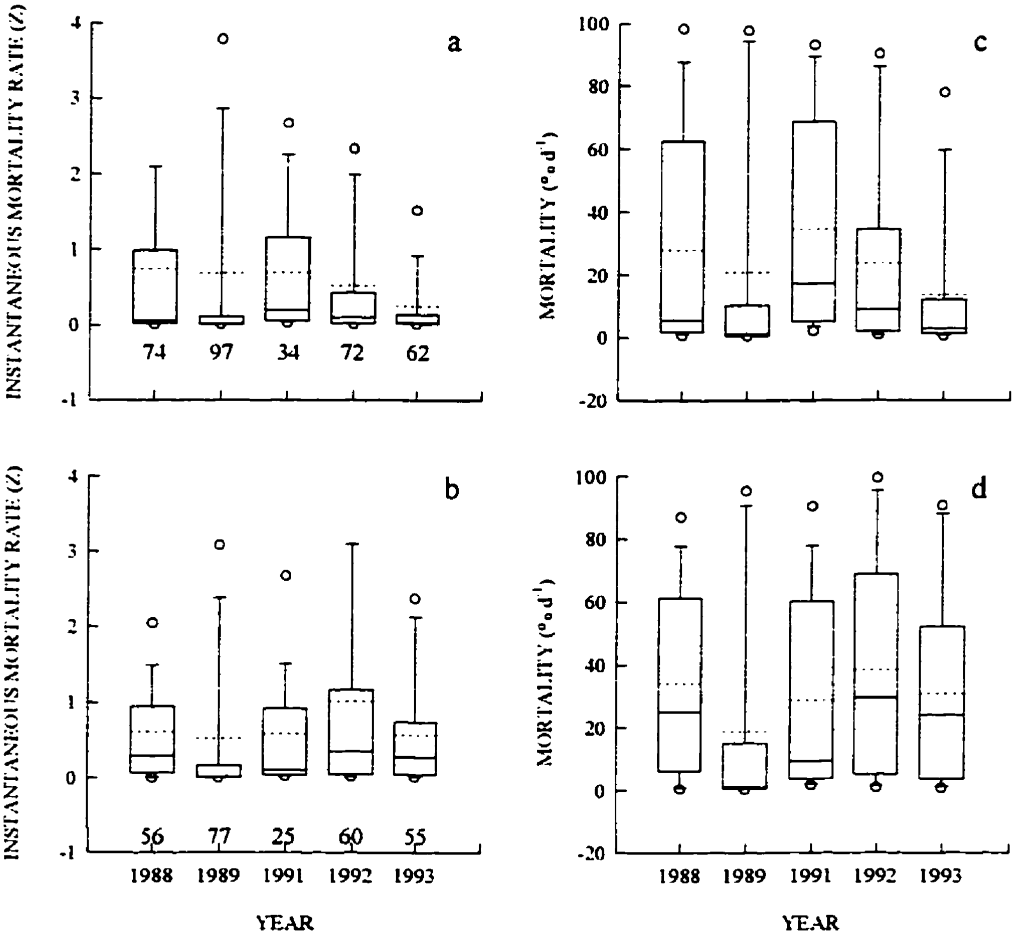

Figure 4.33. Box plots of brood-specific instantaneous and daily (% d^{-1}) mortality rates of smallmouth bass during the (a,c) early larval and (b,d) late larval phases of development. Box plots show mean (dashed horizontal line), median (solid horizontal line), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) of mortality rates.

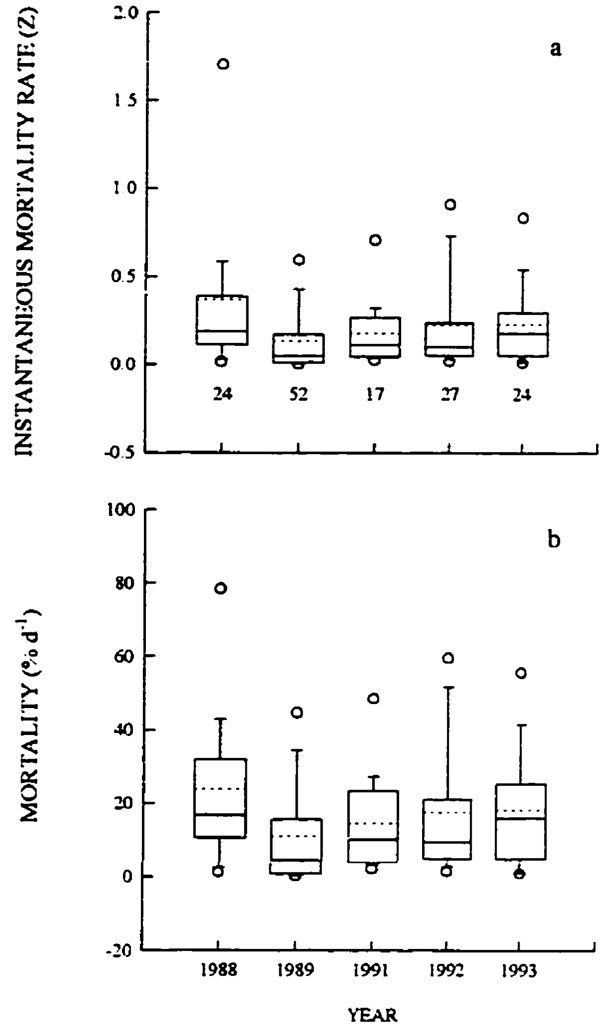

Figure 4.34. Box plots showing mean (dashed horizontal line inside box), median (solid horizontal line inside box), 25th and 75th percentiles (box), 10th and 90th percentiles (capped bars) and 5th and 95th percentiles (symbols) of brood-specific (a) instantaneous and (b) daily (% d^{-1}) mortality rates for juvenile smallmouth bass in Lake Opeongo. Sample sizes (broods) are shown below boxes in (a) above.

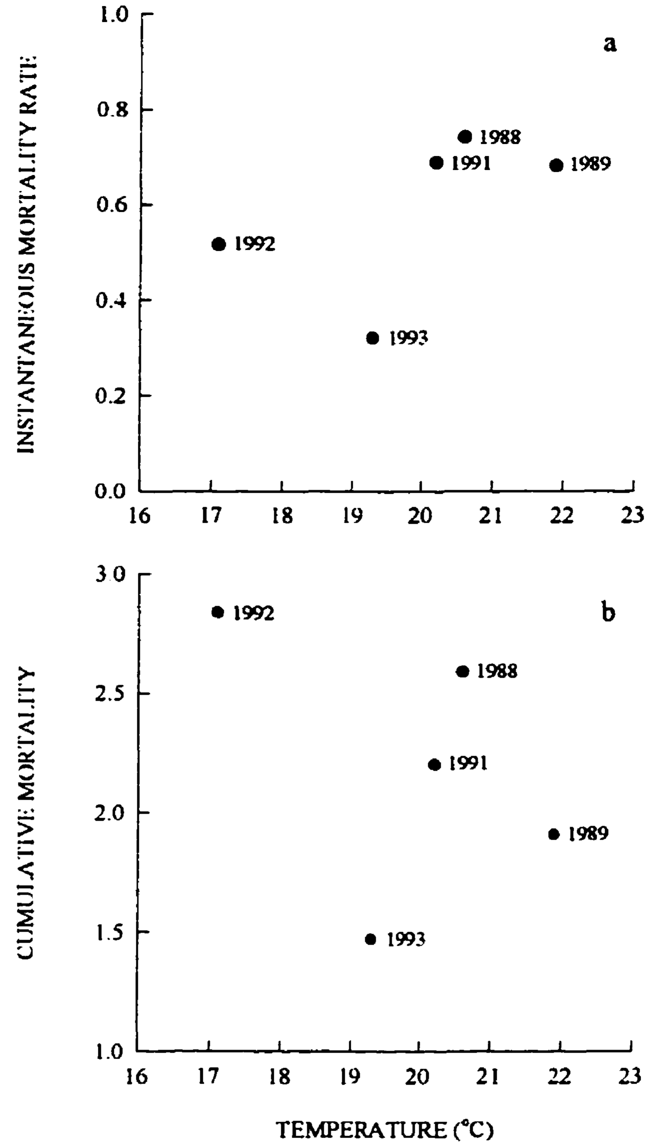

Figure 4.35. (a) Mean brood-specific daily instantaneous mortality rate of yolk-sac larvae plotted in relation to mean brood-specific water temperature. (b) Cumulative brood-specific mortality rate of yolk-sac larvae plotted in relation to mean brood-specific water temperature.

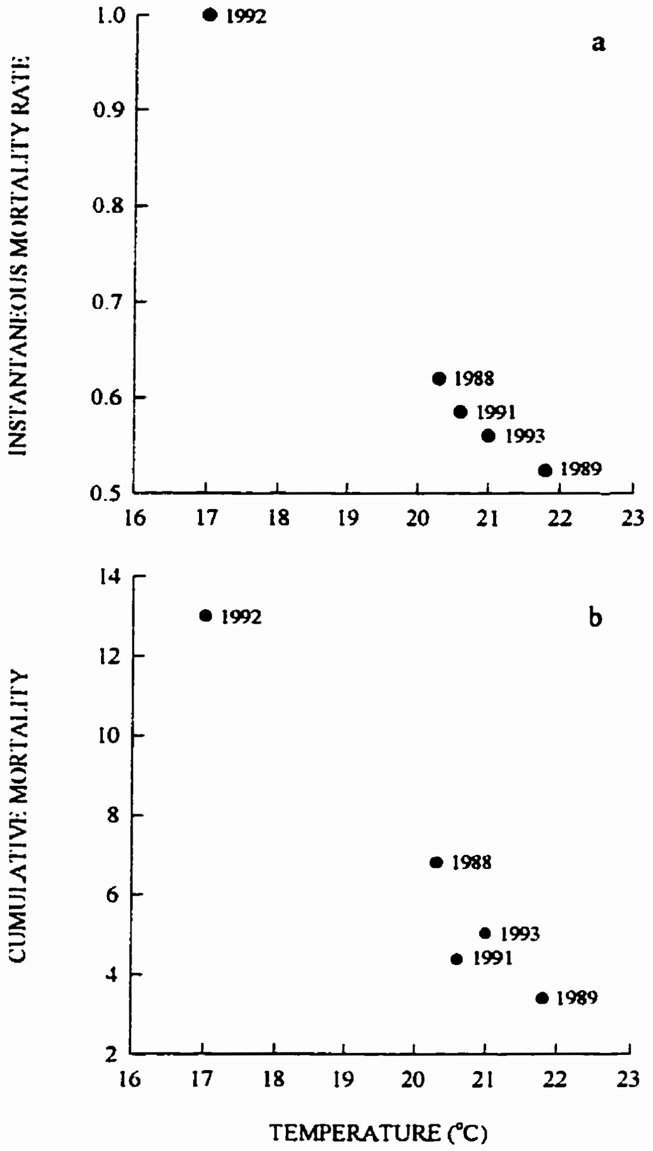

Figure 4.36. (a) Mean brood-specific daily instantaneous mortality rates of post-yolk-sac larvae plotted in relation to mean brood-specific water temperatures. (b) Cumulative brood-specific mortality rates of post-yolk-sac larvae plotted in relation to mean brood-specific water temperature.

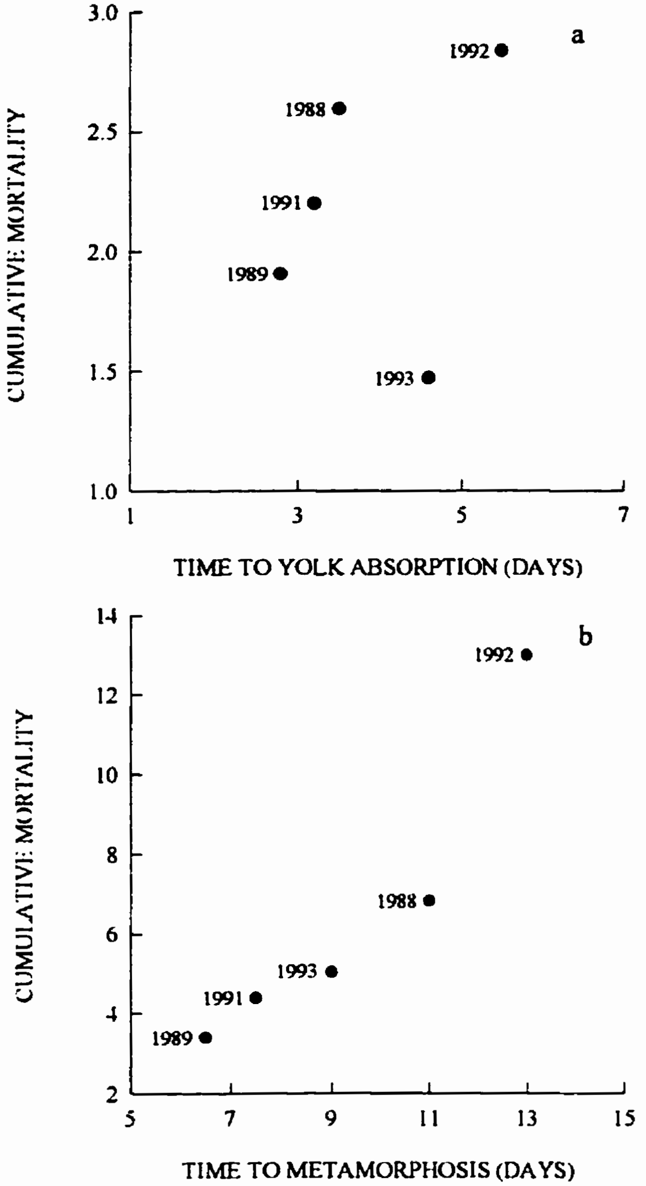

Figure 4.37. (a) Mean brood-specific cumulative instantaneous mortality of yolk-sac larvae plotted against time to yolk absorption. (b) Mean brood-specific cumulative instanttaneous mortality of post-yolk-sac larvae plotted against time to metamorphosis.

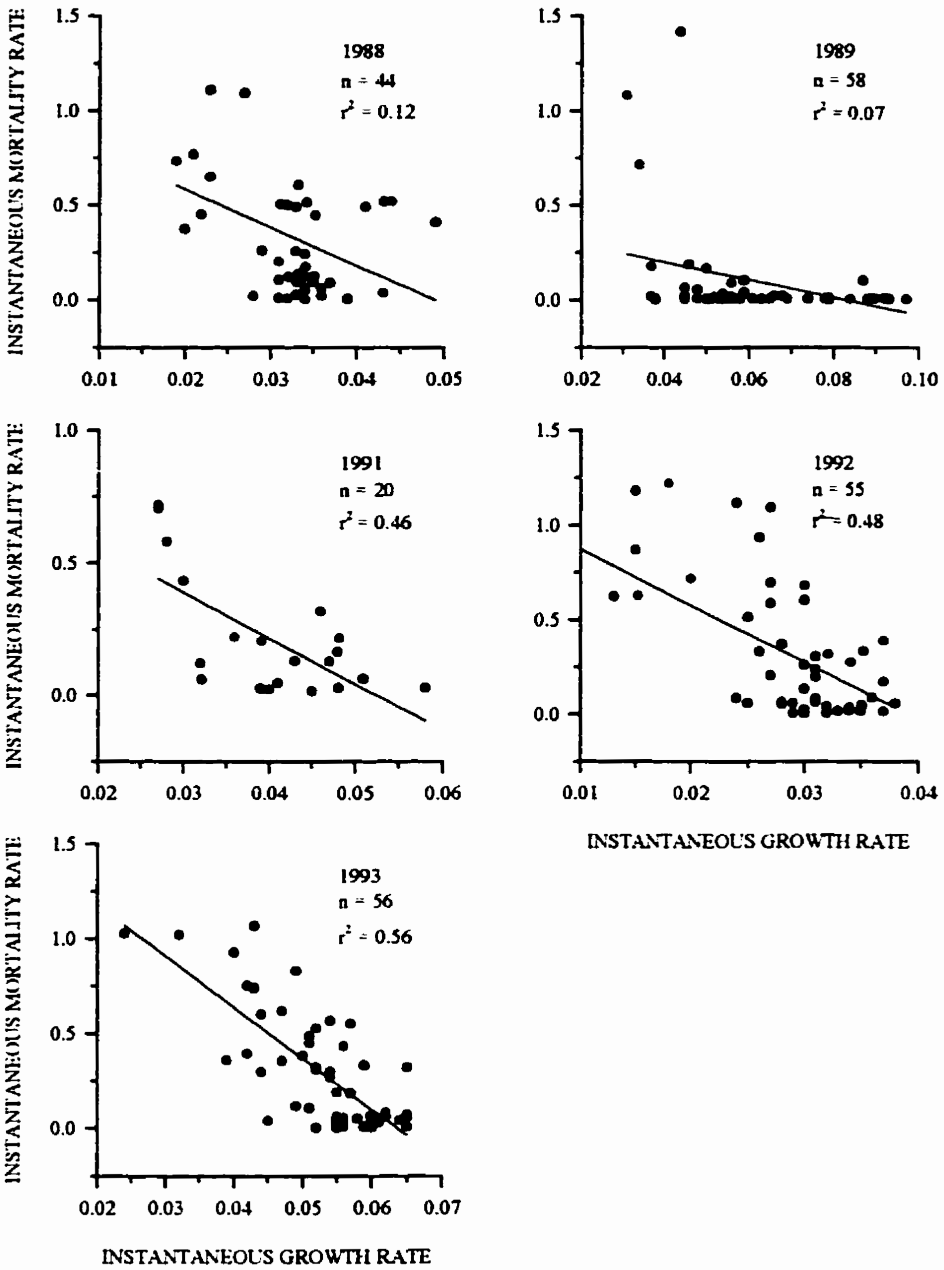

Figure 4.38. Relationship between brood-specific instantaneous growth rates and brood-specific instantaneous mortality rates for smallmouth bass larvae in Lake Opeongo during five spawning seasons. Sample sizes and coefficients of determination for regression equations are presented in figures.

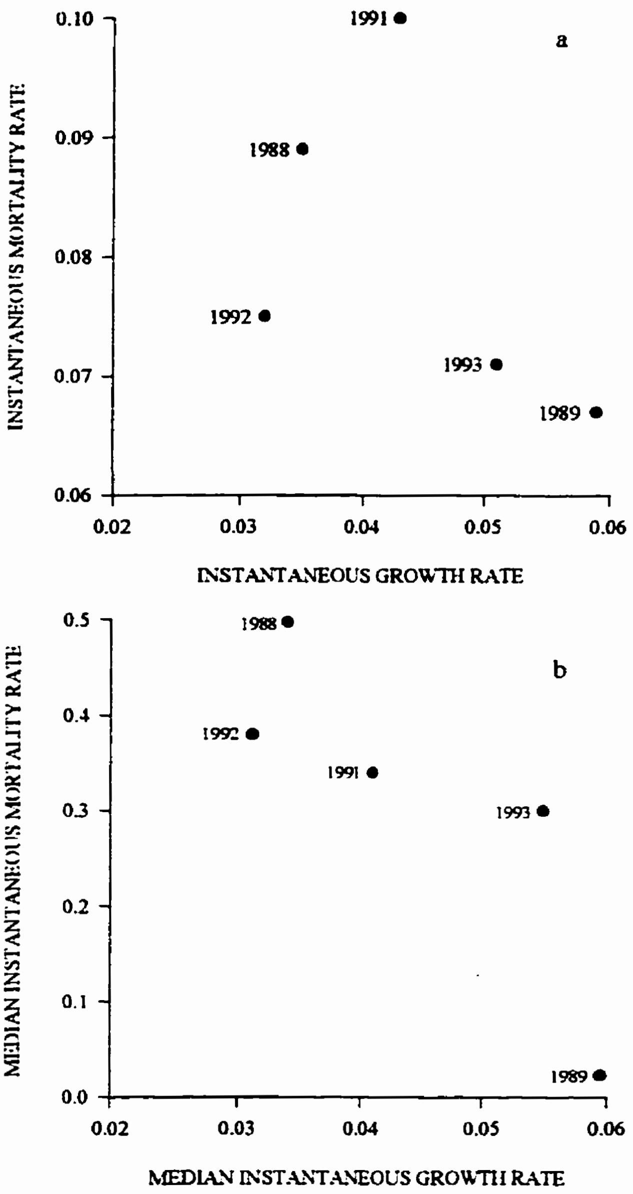

Figure 4.39. (a) Year-class instantaneous mortality rates of larvae plotted in relation to year-class instantaneous growth rates. (b) Median brood-specific instantaneous mortality rates of larvae plotted in relation to median brood-specific instantaneous growth rates.

Chapter 5

Effects of Stocking Density and Prey Abundance on Growth and Survival of Young-of-Year Smallmouth Bass: an Experimental Evaluation Using In Situ Enclosures

5.1 Introduction

Questions of growth, mortality and the effects of food limitation are prominent in studies of young-of-year (YOY) fish ecology. Zooplankton serve as important prey items for young fishes and adequate densities are critical to larval fish growth (Werner and Blaxter 1980; Mills, et al. 1989; Papoulias and Minckley 1992) and survival (Hart and Werner 1987). However, zooplankton densities may vary across habitats or change seasonally (Patalas and Salki 1993). Consequently, although young fishes may experience times when prey is abundant, they may also experience unpredictable episodes of inadequate prey levels. As rapid growth rates favour survival of young fish because mortality decreases with increasing size (McGurk 1986; Miller, et al. 1988; Luecke, et al. 1990) the availability of zooplankton may be an important constraint on growth and survival of young fishes.

In addition to prey availability, population density has also been recognized as a factor that can potentially affect growth and survival of YOY fishes. The first year of life is a crucial portion of the life history of fishes; small fish have the greatest scope for growth and hence the greatest potential for variability in growth (Post and McQueen 1994) and it is during this portion of the life cycle that many of the possible density-dependent mechanisms have been hypothesized to function (Forney 1972; Funk and Fleener 1974). Under limited food resources, high larval density may lead to intra-specific competition for food, which may reduce overall growth rates (Houde 1977; Duffy and Epifanio 1994). Population density may also influence the vulnerability of larvae to predation either directly (McGurk 1986) or indirectly (Houde 1987). Predation rates on early larvae of capelin Mallotus villosus by jellyfish predators were found to be directly related to larval densities (de Lafontaine and Leggett 1989). Indirect effects of population density on predation mortality of larvae may occur when low prey consumption at high population density leads to reduced growth rates and longer period duration (Houde 1987). For a given predation rate, cumulative mortality to the end of the larval period would be positively related to population density of larvae.

Despite the extensive literature on smallmouth bass *Micropterus dolomieu* (hereafter SMB), few studies have investigated the relationship of prey abundance and YOY density to first-year growth and survival. Some studies suggest that growth rates of YOY are related to prey availability (Emery 1975) or quantity of food consumed (Wales 1981). Growth rates of YOY in many temperate lakes appear to be closely related to temperature-predicted values (Shuter, et al. 1980; MacLean, et al. 1981); however, studies of both largemouth *Micropterus salmoides* (Kramer and Smith 1960) and smallmouth (Serns 1982) bass suggest that inter-annual variability in YOY growth rates may be influenced by prey availability. Forney (1972) found a negative correlation between first-year growth of SMB and young perch, *Perca flavescens*, implying interspecific density effects. In contrast, first-year growth of SMB was unrelated to initial YOY densities

(Serns 1982). More recently, modelling investigations of YOY SMB have demonstrated a strong negative feedback loop between YOY density and prey availability, growth and survival (DeAngelis, et al. 1991; DeAngelis, et al. 1993). However, to my knowledge, no empirical studies have experimentally investigated the effects of YOY density and prey abundance on growth and survival of YOY SMB employing in situ enclosures.

Understanding growth and survival patterns of young fish in nature has been difficult because of the large number of physiological, ecological and physical processes that affect growth and survival, and the interactions between these processes (May 1974; Post and McQueen 1994). Numerous laboratory studies have provided valuable information on many aspects of growth and survival in young fishes, nevertheless, there have been serious problems in interpreting laboratory data and linking them with field observations (Houde 1978; de Lafontaine and Leggett 1988). For instance, MacKenzie et al. (1990) show that growth rates of marine larvae in laboratory studies are often higher than values obtained under field conditions, which would suggest food limitation under natural conditions.

In an attempt to overcome these problems, recent experiments have employed in situ enclosures to study growth and mortality of larval fishes in natural settings (Oiestad and Moksness 1981; de Lafontaine and Leggett 1988). In situ enclosures are large enough that young fish may be stocked at natural densities (Ottera 1993), thereby providing results at a scale more relevant to natural conditions (de Lafontaine and Leggett 1987). Moreover, discrepancies in results that often occur between laboratory and field studies can be addressed by employing in situ enclosures (Oiestad 1982; Houde 1987).

The objectives of this chapter were to determine the importance of larval density and prey abundance to first-year growth of SMB. Specifically, I examined the effects of stocking density (1992) and supplemental feeding (1993) on growth and survival of larval and juvenile SMB using in situ enclosures. My experimental designs have removed the effects of potential competitors and predators, and by controlling the initial density of SMB, I have attempted a more direct test of the importance of YOY density and prey abundance on first-year growth and survival. I also compared growth and mortality rates of YOY from Lake Opeongo with those determined for enclosure-held fish. I showed that growth and mortality rates of SMB are highly variable within and among years (see Chapter 4). If the variability in growth and mortality is a function of prey availability I predicted that: (1) growth and survival of YOY would be inversely related to initial larval stocking densities and (2) growth and survival of YOY would be positively related to prey abundance.

5.2 Methods

Stocking density (1992) and food supplementation (1993) experiments were conducted using 2.0 m^3 in situ enclosures situated in Lake Opeongo, Ontario. Enclosures were located in the littoral zone of Jones Bay, Lake Opeongo, at a mean depth of 0.75 m in typical SMB nesting habitat. A continuous recording thermograph, located in the littoral zone at a depth of 1 m, measured water temperatures.

Enclosure Design

Rectangular enclosures, measuring 2 x 1 x 1 m (length x width x height), open on top, and constructed of 2.4 mm white nylon netting, were submerged to a depth of 0.75 m. Enclosures held approximately 1.50 m^3 of water (Fig. 5.1) and were submerged except for 0.25 m, which remained emersed to prevent loss of fish from wash-over of waves. Enclosures were anchored to the substrate with boulders and spaced at 5 m intervals along the shoreline. Renewal of water within the enclosures occurred through ambient flow.

In the food supplementation experiment, supplemental food, in the form of lake zooplankton, was made available to the experimental fish through a centrally located feeding container suspended at mid-depth. The rectangular feeding container was constructed of opaque plastic and was 10 cm^2 and 35 cm in length. Zooplankton were introduced into the feeder through a hinged lid at the top of the feeder. Zooplankton were able to escape through 1 - 4 mm holes (n = 32) in the sides of the containers.

Experimental Fish, Sampling

To reduce the genetic contribution to variation in growth and survival among experimental treatments, I used larvae from a single 'donor' brood in Lake Opeongo. Young from the donor brood had transformed from embryos into larvae two days prior to being collected (see Chapter 2 for description of developmental intervals). Larvae were collected with aquarium dip nets, placed into nine 5 l containers filled with lake water and transported directly to the experimental site to minimize handling mortality. Containers were randomly assigned to the enclosures and larvae were introduced into the enclosures.

Some larvae (n=15) were collected from the donor brood and preserved in 5% buffered formalin to determine initial mean total length (TL) and dry weight (W_d) of larvae. Offspring from each enclosure were sampled midway through the larval period, at the end of the larval period and again at the termination of the experiment for growth determination. I removed a total of 10 and 15% of the initial number of larvae stocked in each enclosure at the two larval period sampling times in the stocking density and supplemental feeding experiments, respectively. At the termination of the experiment all surviving fish were enumerated and placed in a 5% formalin solution. A sub-sample (n = 25) from each enclosure was removed for total length and dry weight determinations. Sampled fish were dried at 60°C for 24 h and weighed individually to the nearest 0.1 mg.

Zooplankton Sampling

Zooplankton densities in the enclosures were quantified prior to the start of the experiments and again immediately following termination of the experiment. On each occasion, zooplankton densities were determined for three randomly chosen enclosures. Triplicate 5-L samples were collected and pooled from each enclosure on each date. Samples were collected using an electric bilge pump (Jabsco, Par Model; capacity 40 l min^{-1}), filtered through a 40 μm screen and preserved in a 5% buffered formalin solution.

Enclosure and littoral-zone zooplankton samples from the lake were processed similarly. In the laboratory, samples were adjusted to a constant volume, randomly sub-sampled, after which 200-300 individuals were identified, counted, and measured using a dissecting microscope connected to a computer-assisted caliper system (Sprules, et al.

1981). Zooplankton densities were converted to biomass by using species-specific length-weight regressions for crustacean zooplankton (Culver, et al. 1985). Total zooplankton biomass included all cladocerans, copepods and copepod nauplii and copepodites.

Analysis

Growth in length (mm d^{-1}) and weight (mg d^{-1}) were estimated by linear regression of length and weight against time (days). As individual enclosures were the experimental units, analyses for stocking density and food level effects were based on average growth within each enclosure. Growth rates were estimated by the slope of the regression of mean fish length versus age. Instantaneous growth rate was calculated as:

$$G = (\ln TL_t - \ln TL_i)/t$$

where G = instantaneous growth rate; TL_i = mean total length of fish for a given enclosure at the start of the growth period, Tl_t = mean total length of fish at time t, and t = duration (days) of the growth period.

Mortality rate was estimated for each enclosure. At the termination of the experiments, enclosures were lifted and surviving juveniles were collected and counted. Instantaneous total mortality (Z) was calculated as Z = S + M, where S is sampling mortality and M represents natural mortality. Sampling mortality was standardized across treatments in the stocking density experiment by removing an equal proportion (10%) of the fish from each enclosure. Thus, a total of 10, 20, and 40 fish were sampled in the low, medium and high density treatments, respectively. In the supplemental feeding study, in which all enclosures were equally stocked (n = 100), 15 (15%) fish were sampled from each enclosure. The following equation was used to determine survival:

$$N_f = N_i\, e^{-(S + M)t}$$

where N_f = number of survivors at the termination of the experiment, N_i refers to the initial number of larvae stocked in the enclosures and t = duration of the experiment in days. Knowing N_f, N_i, S and Z, I estimated natural mortality (M). Finally, I solved for expected survivors (N_{exp}), if no fish had been sampled, using the expression

$$N_{exp} = N_i\, e^{-Mt}.$$

Growth and mortality of fish from the enclosure experiments and field study were analyzed with analysis of variance (ANOVA) to compare differences among treatments. Statistical analysis consisted of separate 1-way ANOVAs for each of the dependent variables and significance was determined at alfa = 0.05 (Zar 1984). Tukeys' multiple comparison test was used to detect differences among experimental treatments.

5.2.1 Stocking Density Experiment

The experiment was conducted over a 25 d period and consisted of a balanced experimental design using three stocking densities (Table 5.1), with three replicates per treatment. Treatments were designed to detect the effects of increasing stocking density on growth and survival of young SMB. Nine enclosures, each randomly assigned to one of the three stocking densities, were placed in the water 2 d before larvae were stocked. YOY densities within the enclosures were comparable with densities observed in natural broods (see Chapter 3).

5.2.2 Food Supplementation Experiment

The experiment was conducted over a 22-d period and consisted of a balanced design using three food levels, control (Control$_{encl}$), low supplement (Food$_{Low}$), high supplement (Food$_{High}$), with three replicates per treatment. Additionally, I measured the growth rate of YOY from the donor brood, which served as a second control (Control$_{lake}$). Treatments were designed to detect the effects of increasing food levels on YOY growth and survival. Nine enclosures, each randomly assigned to one of the three food treatments, were placed in the water 2 d prior to being stocked. Enclosures were stocked with 100 larvae (50 m^{-2}), which approximated the density (45 m^{-2}) of YOY in SMB broods in Lake Opeongo immediately following metamorphosis (Chapter 3). Fish in the control treatments received no additional food.

Supplemental Feeding

Zooplankton for supplemental feeding was collected from the nearshore zone in Lake Opeongo. Fish in low and high food treatment groups received supplemental food on the first day of the experiment, and daily thereafter, until the experiment was terminated. Fish were fed three times daily (1000, 1300 and 1600 h).

Zooplankton samples were collected using Student plankton nets (100 μm mesh) towed from a boat. Nets were attached to each side of the boat using a bridle and set at a depth of 1.0 m. Transect lines for collecting zooplankton were 50 m in length, their locations marked with flagging tape attached to shoreline trees. A speed of 1 - 1.5 ms^{-1} was maintained while sampling. Samples for all six enclosures were collected, washed into 500 ml jars and immediately transferred to feeding containers.

The volume of water filtered in each net along a 50 m transect was:

$$V = pi \times r^2 \times L$$

where V = volume of water sampled, r = radius of the mouth of the plankton net and L = length (m) of the transect. Thus, the combined volume of water sampled by both nets along a 50 m transect was approximately 20 m^{-3}.

At each feeding, low and high food treatment enclosures received zooplankton collected in 20 and 40 m^{-3} of water, respectively. Based on the mean biomass of littoral zone zooplankton in Lake Opeongo in 1993 (67 mg m^{-3}; Chapter 4) and three daily feedings, low and high food treatment enclosures received approximately 4000 and 8000 mg of zooplankton each day, respectively. By comparison, the volume of water occupied by an average-sized brood at metamorphosis (15 m^3) in Lake Opeongo, contained approximately 1000 mg of zooplankton (Chapter 3).

Preliminary trials were conducted to determine the clearance time of zooplankton from the feeding containers. Nine zooplankton samples (20 m^{-3}) were collected, sub-sampled for initial abundance, and transferred to feeding containers suspended in enclosures. Feeding containers (n = 3) were removed from the water 1.0 1.5 and 2.0 h after the trials began. A plastic sleeve was slipped over the feeding containers to minimize loss of zooplankton while sampling. Feeding containers and plastic bags were rinsed with filtered water and poured through a 40 μm filter. Samples were adjusted to a constant volume (500 ml) and sub-sampled to determine abundance.

5.2.3 Field Study

To assess patterns in growth and survival, young-of-year SMB were sampled from natural broods in Jones Bay, Lake Opeongo at regular 4 d intervals throughout the 1992 and 1993 reproductive seasons. Sampled fish were preserved in 5% buffered formalin solution and measured for total length to the nearest 0.1 mm.

Zooplankton was sampled weekly or bi-weekly from fixed stations in the littoral zone. Zooplankton samples (20-L) were collected with a plankton pump operated from the bow of an outboard boat (see Chapter 2). Seven samples were collected at each site on each sampling date. Samples were passed through a 40 μm screen, preserved in 5% buffered formalin solution and returned to the laboratory for enumeration.

5.3 Results

5.3.1 Zooplankton Abundance

Zooplankton biomass varied seasonally in Lake Opeongo with peak values occurring prior to the occurrence of first-feeding SMB larvae in both 1992 and 1993 (Fig. 5.2). Dry weight biomass of littoral-zone zooplankton in Lake Opeongo at the time of the field experiments averaged 44 and 40 mg m^{-3} in 1992 and 1993, respectively. Zooplankton biomass in the enclosures, averaged over the two sampling times, was within 10% of the littoral zone lake values in both years, averaging 40 and 39 mg m^{-3} in 1992 and 1993, respectively. With regard to body size, adult cladocerans represented the largest potential zooplankton prey items available to young-of-year SMB in the littoral zone of Lake Opeongo. Cladocerans also dominated the biomass of littoral-zone zooplankton during the summers, and comprised 73% (1992) and 83% (1993) of the total biomass. In both years, *Polyphemus pediculus* and *Bosmina longirostris* were the most abundant cladocerans. Cladocerans also dominated within the enclosures, comprising, 77 and 71% of the zooplankton biomass in 1992 and 1993, respectively. Thus, the largest zooplankton prey items available to young-of-year SMB were not excluded from the enclosures.

5.3.2 Stocking Density Experiment

YOY Growth

Growth of larvae appeared density dependent, averaging 0.40, 0.36 and 0.24 mm d^{-1} for low, medium and high density treatments, respectively (Table 5.2; Fig. 5.3). Daily instantaneous growth rates of larvae averaged 0.032, 0.029 and 0.021 for low, medium and high density treatments, respectively and differed significantly ($F_{2,6} = 24.25$; $p =<0.001$). Tukeys' test showed that larvae in the high density treatment grew at significantly lower rates than larvae in low and medium treatments. In comparison, brood-specific growth rates of larvae from Lake Opeongo ranged from 0.03 to 0.52 mm d^{-1} in 1992, and averaged 0.37 mm d^{-1}. Thus, the average growth rate of larvae from natural broods in Lake Opeongo most closely approximated the growth rate of larvae in the medium and low density treatments. ANOVA and Tukey's post-hoc test showed that growth rates of larvae in Lake Opeongo were significantly higher than those of larvae in the high-density treatment ($F_{3,77} = 14.44$; $p = 0.011$).

Mean length and weight of fish showed increasing divergence among density treatments following metamorphosis (Table 5.2). Mean length of juveniles at the termination of the experiment ranged from a low of 16.6 mm in the high density treatment to 21.3 mm in the low density treatment. Absolute growth rates during the juvenile period of development averaged 0.56, 0.44 and 0.32 mm d^{-1} for the low, medium and high density treatments, respectively. Daily instantaneous growth rates of juveniles in low, medium and high density treatments averaged 0.030, 0.025 and 0.021; ANOVA followed by Tukeys' post-hoc test showed that instantaneous growth rates differed significantly among all three treatments ($F_{2,6} = 84.57$; $p < 0.0005$). Brood-specific growth rates of juveniles in Lake Opeongo ranged from 0.19 to 1.01 mm d^{-1} and averaged 0.69 mm d^{-1}. ANOVA showed that daily instantaneous growth rates of juveniles in Lake Opeongo differed significantly from enclosure-held juveniles ($F_{3,39} = 31.36$; $p = 0.001$). Tukeys' test showed that the brood-specific growth rate of juveniles in Lake Opeongo was significantly higher than those of juveniles from the medium and high density experimental treatments.

YOY Survival

Expected survival of young-of-year at the termination of the stocking density experiment ranged from 73 to 91% (Table 5.3). Mean percentage survival equalled 85, 81 and 77% for low, medium and high stocking densities, respectively. Mean instantaneous mortality rate averaged 0.007, 0.008 and 0.011 for low, medium and high density treatments, respectively and differed significantly among stocking densities ($F_{2,6} = 1.86$; $p = 0.236$). In contrast to experimental fish, only 29% of first-feeding larvae from the Lake Opeongo population survived to metamorphosis in 1992 (Fig. 5.4). Expressed as daily instantaneous mortality, the larval mortality rate for the 1992 year-class equalled 0.075, an order of magnitude higher than values for enclosure-held fish .

5.3.3 Food Supplementation Experiment

YOY Growth

Mean larval growth rates of Control$_{encl}$, Control$_{lake}$, Food$_{low}$ and Food$_{high}$ treatment groups averaged 0.62, 0.66, 0.76 and 0.83 mm d^{-1}, respectively (Table 5.4; Fig. 5.5). Thus, absolute growth rates of larvae tended to increase with prey abundance. In comparison, larval growth rates for natural broods in Lake Opeongo ranged from 0.24 to 1.00 mm d^{-1} and averaged 0.70 mm d^{-1}. Instantaneous growth rates of Control$_{encl}$, Control$_{lake}$, Food$_{low}$ and Food$_{high}$ treatment groups equalled 0.043, 0.045, 0.051 and 0.054, but did not differ significantly from one another ($F_{3,8} = 3.33$; $p = 0.08$).

Juvenile growth rates for Control$_{encl}$, Control$_{lake}$, Food$_{low}$ and Food$_{high}$ treatment groups averaged 1.23, 1.44, 1.66 and 1.85 mm d^{-1}. By comparison, brood-specific growth rates of juveniles in Lake Opeongo ranged from 0.23 to 1.76 mm d^{-1} and averaged 1.46 mm d^{-1} (Chapter 4). Daily instantaneous growth rates of juveniles in the Control$_{encl}$, Control$_{lake}$, Food$_{low}$ and Food$_{high}$ treatment groups averaged 0.065, 0.059, 0.069 and 0.073, respectively and differed significantly ($F_{3,8} = 35.20$; $p < 0.0005$). Tukeys' test showed that; 1) the growth rate of juveniles in the Control$_{encl}$ treatment was significantly lower than the growth rate of juveniles in other treatments and 2) growth rate of juveniles in the Food$_{high}$ treatment was significantly higher than the growth rate of juveniles in the donor brood.

YOY Survival

Expected survival of fish at the termination of the supplemental feeding experiment averaged 79, 88 and 86% for the Control$_{encl}$, Food$_{low}$ and Food$_{high}$ treatment groups, respectively (Table 5.5). The mean expected daily instantaneous mortality rate for the Control$_{encl}$, Food$_{low}$ and Food$_{high}$ treatment groups at the conclusion of the experiment equalled 0.012, 0.006 and 0.007, respectively, but did not differ significantly ($F_{2,6} = 1.52$; $p = 0.29$). In contrast to the high survival of enclosure-held fish, only 38% of the larvae from the donor brood (Control$_{lake}$) survived to the end of the 3 wk experiment. Survival in the donor brood was relatively high compared with survival in the population as a whole, as only 32% of the larvae in Lake Opeongo survived the 14 d period between first-feeding and metamorphosis in 1993 (Fig. 5.6). The instantaneous mortality rate of Lake Opeongo larvae was 0.071, an order of magnitude higher than values for enclosure-held fish.

5.4 Discussion

5.4.1 Stocking Density Experiment: Growth

Employing in situ enclosures, I demonstrated that density significantly influenced the growth of larval and early juvenile SMB. Larvae reared at high densities were significantly smaller than those reared at low and medium densities, while juveniles differed in size across all three stocking densities. Growth of YOY in the enclosures fell within the range of values previously observed for YOY SMB in both laboratory and field studies (Rowan 1962; Peek 1965; MacLean, et al. 1981) and were also similar to those from natural broods in Lake Opeongo (see Chapter 4). Growth rates of larval capelin *Mallotus villosus*, reared in enclosures in the Gulf of St. Lawrence were similar to those estimated for natural populations (Frank and Leggett 1986). Despite the similarity in growth rates between enclosure and lake YOY, it is possible that the density-dependent pattern of growth observed among experimental treatments may have resulted from experimental artifacts of the enclosure environment. For instance, fine-mesh walls can quickly become blocked by growth of algae or sedentary animals (de Lafontaine and Leggett 1987; Kneib 1993); however, the large size of SMB larvae permitted the use of a relatively large mesh size, allowing zooplankton to move freely through the enclosure walls. In addition, treatment densities remained within the range of values observed in natural broods in Lake Opeongo and as larvae and early juveniles typically remain in family shoals within the littoral zone, it was unlikely that their behaviour was seriously altered by the enclosures.

The effects of stocking density on growth of larval and juvenile SMB have not been investigated; however, Johnson and McCrimmon (1967) demonstrated density-dependent growth in pond-reared juvenile largemouth bass, a closely related centrarchid. Density-dependent growth has also been shown for other species, including larval weakfish *Cynoscion regalis,* raised in large enclosures (Duffy and Epifanio 1994), juvenile walleye *Stizostedion vitreum* (Fox and Flowers 1990) and bluegills *Lepomis macrochirus* (Breck 1993), raised in ponds. Evidence regarding density-dependent first-year growth in natural popultions however, remains contentious. Some studies have confirmed density-dependent growth (Carlander and Payne 1977), others have not (Kramer and Smith 1960; Forney 1974), including SMB in a small Wisconsin lake (Serns 1982). My results showed no consistent pattern between initial larval abundance and mean growth rates among years (see Chapter 4). In contrast, DeAngelis et al. (DeAngelis, et al. 1991) demonstrate a strong negative feedback loop between density of larvae and prey availability, growth and survival, using an individual-based model.

Whether or not density-dependent growth occurs in a population may depend on the details of the community structure within which the species in question lives. Competition in aquatic communities is commonly invoked and may arise from size-structured interactions, where similar-sized individuals of different species compete for a limited resource (Stein, et al. 1988; DeVries and Stein 1992). For instance, Forney (1972) found that growth rates of YOY SMB were negatively related to abundances of young yellow perch, which may compete or food resources with YOY SMB. In Lake Opeongo, the abundance of YOY yellow perch and other potential competitors in the littoral zone was extremely low (pers. obs.), reducing the likelihood of strong interspecific competition for food resources.

The density dependent nature of growth rates among the experimental treatments are particularly interesting when examined with regard to growth rates of YOY from natural broods. Growth rates of larvae from natural broods did not differ from those in the low and medium-density treatments, despite the higher density of larvae in natural broods. This result was intriguing, and suggested that YOY in the lake may not be food-limited during the larval period. In contrast, the extremely low growth rates of larvae in the high-density treatment, relative to larvae in the lake, implied food limitation. The density of larvae in the high-density treatment reflected those observed for natural broods at first-feeding. The increase in dispersion area of larval broods between first-feeding and metamorphosis may, therefore, be critical in allowing larvae to achieve adequate growth rates in natural conditions.

Juvenile growth was strongly density-dependent in this experiment as length and weight showed an increased divergence among treatments following metamorphosis. Importantly, growth rates of juveniles in the lake were higher than those at all stocking treatments. The stocking densities chosen for the experiment were based on density estimates of natural broods at three developmental times: early larval phase, late larval phase and metamorphosis. Due to the low mortality of YOY in the enclosures, densities remained higher than those estimated for natural broods, even though initial stocking densities (low and medium treatments) were low relative to those of first-feeding larvae in the lake. One possible explanation for the high juvenile growth rates in natural broods is that density continued to decrease following metamorphosis, reducing competition for food. A further decline in density could have resulted from increased dispersion of broods, predation, or through their combined effects. Predators may have mitigated the effects of competition within natural broods by maintaining juvenile densities below the carrying capacity of the spawning habitat (Mills, et al. 1987).

A second explanation for the high growth rates of juveniles in natural broods is that they were able to forage in an unrestricted manner. Optimal foraging theory suggests that in order to sustain maximum growth rates, predators should shift to larger prey items as they grow (Wilbur 1988). In Lake Opeongo, YOY larvae fed solely on suspended zooplankton in the littoral zone; however, a gradual shift to foraging on benthic prey began just prior to dispersal (pers. obs.). The shift from planktivory to benthivory by juvenile SMB in Lake Opeongo followed the decline in peak zooplankton biomass values each season (see Chapter 4), suggested that a reduction in zooplankton biomass may cause increased feeding on benthic prey. Similar shifts to benthic prey occur among juvenile yellow perch during periods of zooplankton decline (Mills and Forney 1983; Wu and Culver 1992), but may also result from intense interspecific competition for food resources (Post and McQueen 1994). While diet shifts in other species are often accompanied by switches across littoral-pelagic habitats (Werner and Hall 1988), I had little evidence to suggest that YOY SMB moved into offshore waters at dispersal. Rather, juveniles remained in the littoral zone, but shifedt from a shoaling lifestyle to a solitary one. My enclosure experiment showed that high juvenile growth rates could be achieved over a short time period with only limited access to benthic prey; however, it is not clear whether these rates could be sustained over a longer time period.

The lower mean growth rates in the high-density treatment may have resulted from depression of feeding rates. Fenderson and Carpenter (1971) found social interaction to be the main factor that depresses feeding rates in salmonids. Alternatively, low growth rates in the high-density treatment may have resulted from inadequate prey resources or from increased activity levels due to increased competition for food. Research has shown that the energetic costs of interference competition can be high in stream salmonids defending territories (Fausch and White 1986; Grant and Noakes 1988) and may also explain some of the variation in growth rates among populations (Boisclair and Leggett 1989). Post and McQueen (1994), employing in situ enclosures, found that fish density was the principle factor influencing first-year growth of yellow perch; however, energetic costs of interference explained only 2% of the observed variability in growth. Post and McQueen (1994) attribute the low energetic cost of interference competition to the shoaling nature of yellow perch. I made no systematic effort to measure the costs of interference competition; however, casual observations revealed few instances of agonistic behaviour among experimental fish, consistent with estimates of agonistic behaviour in the field (see Chapter 3) and with observations on closely related centrarchids (Brown 1985). SMB exhibit shoaling behaviour during the parental care period and it is likely that reduced search times, through social facilitation and local enhancement (Pitcher, et al. 1982; Pitcher 1986; Ryer and Olla 1992) may offset potential competitive interactions under natural conditions. Brown (1985) and Brown and Colgan (1985), show that the level of agonistic behaviour during early life history in closely related centrarchids increases dramatically following metamorphosis, and suggest that it may enhance dispersal of juveniles from natal territories The apparent absence of interference competition among experimental fish suggests that much of the variability in growth rates of larval and early juvenile SMB may be attributable to variability in availability of prey.

5.4.2 Supplemental Feeding Experiment: Growth

My enclosure experiment revealed that YOY SMB growth was strongly related to prey abundance, especially during the juvenile period. The effect of prey density on SMB growth has not been previously demonstrated using in situ enclosures, but my results are consistent with research on other species (Hart and Werner 1987; Fox 1989; Welker, et al. 1994; Johnson and Dropkin 1995). As in the stocking density experiment, growth rates of YOY in the experimental treatments were similar to those previously reported in the literature. Survival rates of YOY in the enclosures were again an order of magnitude above field estimates, but survival rates were unrelated to prey abundance.

Larval growth rates did not differ among experimental treatments, including those in the Contol$_{lake}$ treatment, suggesting that larvae were not food limited. This result was consistent with the pattern observed in the stocking density experiment, with the exception of the high-density treatment. Following metamorphosis, juvenile growth rates differed significantly among treatments, showing a strong positive relationship with prey abundance. Juvenile growth rates in the Food$_{high}$ treatment differed significantly from Control$_{encl}$ and Contol$_{lake}$ treatments as well as from YOY in the lake population.

In addition to prey abundance, the high growth rates of YOY in the Food$_{low}$ and Food$_{high}$ treatments may have been partly due to differences in the amount of energy expended in foraging activities. The amount of energy expended for activity, including foraging, has been shown to influence growth in fish (Ware 1975; Kitchell, et al. 1977). Mobility (percent time spent moving) in juvenile salmonids decreases rapidly as current velocity increases and encounter rate with food increases (Grant and Noakes 1988). Activity levels in the Food$_{\text{low}}$ and Food$_{\text{high}}$ treatments were likely low, as the source of supplemental food was predictable, both spatially and temporally. YOY receiving supplemental food were often observed to be stationed near the feeding containers, in contrast to YOY in the Control$_{\text{encl}}$ treatment, that actively searched for prey throughout the enclosure volume. Furthermore, the activity level of YOY foraging in the lake was extremely dynamic, relative to that of enclosure-held fish. This was evident at both the brood (dispersion) and individual (swimming speed) levels (see Chapter 3).

Previous experiments have shown variation in growth to be negatively related to ration size in fishes (Davis and Olla 1987; Letcher and Bengtson 1996). This relationship is not universal however, as variability in growth depends not only on the amount of food, but also on its defensibility and the intensity of interference competition among individuals (Magnuson 1962; Koebele 1985). In laboratory-reared coho salmon *Oncorhynchus kisutch*, variability in growth was greater in groups receiving localized as compared to dispersed food at a low ration level, but no difference was found at the high ration level (Ryer and Olla 1996). The ephemeral nature of both the supplemental food source and of prey patches in the lake provided little opportunity for competition or patch monopolization (Grant and Kramer 1992).

The relationship between prey abundance and variability in length was not investigated in this experiment; however, I suspect that variability in growth would not have been strongly related to prey abundance, as I observed little aggressive behaviour between YOY in the enclosures, consistent with field observations (see Chapter 3). YOY SMB are a shoaling species during the parental care period of development and the prevailing social behaviour I observed in the field and in the enclosures was mutual attraction (pers. obs.). Lack of a relationship between variability in growth and ration level has also been observed in young sockeye salmon *Oncorhynchus nerka*, a schooling fish that showed no aggressive behaviour under limited prey levels (Brett, et al. 1969). More recently, medians for length, weight and growth rate of juvenile chum salmon *Onchorhynchus keta*, did not differ between the highest ration levels, although variability in growth, as measured by the coefficient of variation for these variables, did differ (Davis and Olla 1987). Competition can accentuate individual differences in members of a population and the effects of competition on growth are not necessarily revealed by measures of mean or median population growth, which assume equal competitive abilities of individuals (Rubenstein 1981).

An increase in variability in growth with decreased ration also depends on the quantity of food available and is therefore most likely to occur under limited prey concentrations. In contrast to the studies that have demonstrated variability in growth under limiting ration levels, my experiment was designed to test for differences in growth rates under supplemental feeding conditions. Thus, it is unlikely that the magnitude of variability in growth among the Food_{low} and $\text{Food}_{\text{high}}$ treatments would have been large. However, higher coefficients of variation in length of YOY at the low prey levels

(Control$_{encl}$ and Contol$_{lake}$) are more likely, and would suggest that food resources were unevenly partitioned by YOY. Assuming faster growth and larger size reduce susceptibility to predation (Werner and Gilliam 1984; Bailey and Houde 1989), a growth advantage may translate into a survival advantage for those individuals that consume a greater proportion of the food resources.

The absence of predators in the enclosures may have contributed to the difference in growth rates between enclosure-held fish and those from natural broods. Tradeoffs between foraging and predator avoidance may occur if a group is at risk while foraging and individuals may choose to forage in a less profitable area if the risk of predation is lower (Milinski 1986). Predation risk has repeatedly been shown to affect habitat selection by foraging animals (Caldwell 1986; Ferguson, et al. 1988; Cowlishaw 1997), including fishes (Gilliam and Fraser 1987; Werner and Hall 1988). Predation risk has also been shown to cause a significant reduction in the foraging activity of juvenile bluegill *Lepomis macrochirus*, within and among food patches within a habitat (Gotceitas and Colgan 1990). Gotceitas and Colgan (1990) show that within-patch foraging activity of bluegills is less affected by the presence of a predator than between-patch foraging activity. In contrast to the artificial patches constructed by Gotceitas and Colgan (1990) and for natural situations where vegetation patches themselves provide a varying amount of protection, the ephemeral patches of zooplankton utilized by YOY SMB offer no refuge potential. Therefore, it is less clear that reductions in the foraging activity of YOY SMB and other fishes that feed on ephemeral food patches lacking physical protection, could be so clearly divided into between- and within-patch components as a consequence of predation risk. When exposed to predators, YOY SMB moved to safer areas, decreased or stopped foraging, remained motionless near the substrate or sought refuge in crevices between rocks and boulders (pers. obs.). These antipredator behaviours constrain foraging rates of YOY and further studies are needed to determine the magnitude of the predator-mediated reduction in foraging rate.

5.4.3 YOY Mortality

My results indicated that neither stocking density nor prey abundance had a strong impact on larval and early juvenile mortality rates. These results were not surprising given the significant negative relationship between larval abundance and instantaneous mortality rate for the Lake Opeongo SMB population (see Chapter 4). Density-independent survival has been shown for other freshwater and marine species reared in ponds (Swingle 1950; Rubenstein 1981; Fox 1989; Fox and Flowers 1990) and mesocosms (Duffy and Epifanio 1994). Evidence supporting density-dependent larval mortality in natural populations however, remains equivocal (Ware 1975) largely because its effects are often obscured by stronger density-independent factors (Sissenwine 1984). Several studies of YOY SMB indicate density-dependent survival, including Serns's (1984) empirical study in Nebish Lake, Wisconsin and DeAngelis et al's. (1993) application of an individual-based model, which shows strong density dependence of mortality rate early in the growing season.

Similar to the stocking density experiment, little of the variation in mortality in the supplemental feeding experiment could be accounted for by prey level, although survival tended to increase in the treatments that received supplemental food. My results differed from those of Hart and Werner (1987), who demonstrated a positive relationship between prey density and survival of white sucker *Catostomus commersoni* and pumpkinseed *Lepomis gibbosus* larvae in the laboratory. The discrepancy may be due to differences in initial stocking density; Hart and Werner (1987) used 15 l tanks stocked at four larvae l^{-1} (4000 m^{-3}) compared with 100 m^{-3} in my experiment. In a more recent study , Welker et al. (1994) show survival to be related to prey abundance in larval gizzard shad *Dorosoma cepedianum*, but not in larval bluegill *Lepomis macrochirus*, using 750 l fibreglass tanks. Unlike the constant renewal of prey in my enclosures, Welker et al. (1994) added no additional zooplankton to the fibreglass tanks after the 2 wk experiment was initiated.

Slight size differences can confer considerable advantages in resistance to food limitation and starvation and may also have important consequences to a fish's vulnerability to predators (Mittelbach and Chesson 1987; Miller, et al. 1988). Larval yellow perch, which are slightly smaller than SMB larvae can survive food deprivation for up to 2 wks after hatching (Hokanson and Kleiner 1974). Larval bluegills are less susceptible to mortality by starvation than gizzard shad, and the high variation in year-class strength of gizzard shad, relative to other reservoir species, may stem from its sensitivity to prey availability during the larval period (Welker, et al. 1994). Hart and Werner (1987) suggest that white sucker larvae are better able to survive short term reductions in prey availability than pumpkinseed larvae because of their larger yolk reserves at first-feeding. First-feeding SMB larvae also possess large yolk reserves (Meyer 1970; Wallace 1972) and like white sucker, may be less sensitive to temporary reductions in prey resources than species with smaller larvae. Indeed, prey abundance explained little of the annual or inter-annual variability in larval mortality rates (see Chapter 4).

Daily instantaneous mortality rates of enclosure-held fish in both experiments were an order of magnitude lower than values estimated for SMB from natural broods in Lake Opeongo. Johnston and Mathias (1993) report that mortality rates of walleye larvae in natural lakes are typically an order of magnitude above values reported for larvae raised in culture ponds. The low mortality rates of enclosure-held fish was likely due to the absence of large predators in the enclosures. Low mortality rates in the absence of predators has also been reported for both marine (Oiestad 1985) and freshwater (Karjalainen 1991) fishes raised in mesocosms. Hart and Werner (1987) report mortality rates of white sucker and pumpkinseed in the laboratory to be similar to estimates of natural mortality in other species and suggest that feeding conditions in the laboratory did not deviate from natural conditions. However, their highest prey density (3000 prey l^{-1}) was 50 - 100 times greater than estimates of littoral-zone zooplankton in Lake Opeongo.

My estimates of mortality for enclosure-held fish were based on samples collected at the termination of the experiments. Consequently, I was unable to partition the mortality between the larval and juvenile periods, nor did I attempt to identify sources of mortality. However, my results suggested that food limitation was not a major source of mortality. I did not quantify prey abundance in the enclosures during the course of the experiments; however, I assumed that renewal of zooplankton via shoreline current was similar for all enclosures. Comparison of zooplankton samples taken in the enclosures, prior to and following termination of the experiment, with samples collected in the littoral zone of the lake, confirmed my assumption.

Although larval density and prey abundance both had a significant influence on growth of YOY, mortality remained unrelated to either factor. Thus, reduced growth during early development does not necessarily imply an increase in mortality as suggested by Beyer and Laurence (1981). Survival of YOY was high in the enclosures, even at high stocking densities and ambient prey levels, which indicated that most YOY captured sufficient food to prevent starvation. Summer zooplankton densities in Lake Opeongo ranged between 25 and 81 l^{-1} and averaged 50 l^{-1} over four spawning seasons, similar to those in other temperate lakes of similar latitude (Watson and Carpenter 1974; Patalas 1992; Patalas and Salki 1993). The high growth rates of YOY in Lake Opeongo also suggest that zooplankton densities must be lower than previously thought for starvation to occur.

Unpublished results from my field research suggested that predation may play an important role in mortality of YOY SMB. In 1993, I conducted shoreline transect swims in Jones Bay in conjunction with a field experiment to determine spatial and temporal patterns in relative predation risk. Results showed significant temporal and spatial variation in both predator densities and relative predation risk within the study area. Previous studies have shown that numerous species of fish prey on SMB offspring during the parental care period of development (Scott and Crossman 1973; Lukas and Orth 1995), and that removal of guarding males results in complete loss of broods to predators within 24 h (Neves 1975). During the 1988 and 1991 field seasons, I sampled sub-adult

SMB from the study area for diet analysis. Remains of larval SMB bass were found in 11 and 5 % of the stomachs examined in 1989 and 1991, respectively, and confirmed the existence of heterospecific cannibalism (Dominey and Blumer 1984). The frequency of occurrence of larval remains in sub-adult stomachs was low, but may have constituted a significant fraction of the year-class, given the low density of larval bass in Lake Opeongo. Although I did not witness a single occasion of parental males feeding on their offspring, filial cannibalism is relatively common in fish (Dominey and Blumer 1984), and is best known in species with parental care (Belles-Isles and FitzGerald 1991; FitzGerald 1991). Filial cannibalism could explain the dramatic and nearly 'instantaneous' (overnight) loss of entire SMB broods in Lake Opeongo. The fact that cannibalism has not been reported as an important factor influencing survival and recruitment in SMB bass may stem from the difficulties in detecting and quantifying its occurrence in the field.

Conclusions

The conclusions that can be drawn from the two enclosure experiments, in combination with field results may be summarized as follows: (1) prey densities in temperate lakes such as Lake Opeongo may be sufficient to support adequate growth of YOY SMB; (2) SMB have a very high potential survival rate, despite high stocking densities and marginal prey availability; (3) given the lack of evidence for food limitation and the large discrepancy in mortality rates between enclosure-held YOY and those from natural broods, many healthy YOY may be susceptible to predation in Lake Opeongo.

The relevance of my experimental results to studies of natural populations of SMB is clear. The high growth rates achieved by YOY SMB in natural broods may depend on changes in the ontogeny of foraging behaviour and on social interactions of individuals within a brood. The association of conspecifics within a brood and their interaction with potential predators and zooplankton prey are key components to understanding growth and survival of YOY SMB. These interactions are complex, and future studies are required to verify competition for food resources and to conclusively link reductions in foraging rate to the presence of predators. Exclusion of piscine predators from enclosures has underlined the importance of predation as a major source of mortality in YOY SMB. Further investigations of the role of predation in growth and mortality are required to more fully understand the population dynamics of YOY SMB.

Table 5.1. Description of treatments in the (a) stocking density and (b) supplemental feeding experiment conducted in 1992 and 1993, respectively. Three replicates per treatment were used in each experiment.

(a)

Stocking Density Experiment

Treatment (density)	Number of Fish	Density (m^{-3})
Low	100	67
Medium	200	133
High	400	267

(b)

Supplemental Feeding Experiment

Treatment	Supplement Level (mg dry wt d^{-1})	Number of Fish	Density (m^{-3})
$\text{Control}_{\text{lake}}$	ambient	2300	----
$\text{Control}_{\text{encl}}$	ambient	100	67
Low Supplement	4000	100	67
High Supplement	8000	100	67

Table 5.2. Means (± SD) of total length (TL), dry weight (W_d), growth rate in length (G_l) and growth in weight (G_w) for larval and juvenile smallmouth bass stocked at 3 densities employing in situ replicate (n = 3) enclosures in Lake Opeongo, 1992. Values are also presented for larval (n = 72) and juvenile (n = 34) broods of smallmouth bass in Lake Opeongo. For each of the developmental periods (larval, juvenile), means with a common superscript are not significantly different ($P<0.05$) by Tukey's multiple comparison test.

Density (fish m^{-2})	TL (mm)	W_d (mg)	G_l (mm d^{-1})	G_w (mg d^{-1})
Larval				
50	16.2^a	6.57^a	0.40^a	0.088^a
	(0.46)	(0.50)	(0.031)	(0.005)
100	15.5^a	5.69^a	0.36^a	0.078^a
	(0.40)	(0.40)	(0.031)	(0.005)
200	13.8^b	4.13^b	0.24^b	0.056^b
	(0.40)	(0.30)	(0.025)	(0.005)
Lake	15.7	6.12	0.37	0.081
	(1.07)	(0.66)	(0.122)	(0.007)
Juvenile				
50	21.3^a	14.38^a	0.56^a	0.087^a
	(0.65)	(1.22)	(0.027)	(0.003)
100	19.4^b	10.74^b	0.44^b	0.070^b
	(0.66)	(1.09)	(0.031)	(0.005)
200	16.6^c	6.78^c	0.32^c	0.055^c
	(0.50)	(0.56)	(0.024)	(0.004)
Lake	22.0	15.98	0.69	0.094
	(1.78)	(1.93)	(0.211)	(0.010)

Table 5.3. Survival of YOY smallmouth bass reared in enclosures at three densities (Low = 50 m^{-2}, Medium (Med) = 100 m^{-2} and High = 200 m^{-2} in Lake Opeongo, 1992. Instantaneous mortality rate and expected survival were calculated for the entire duration (25 days) of the experiment. Larvae used in the experiment were 2-day post first-feeding at the start of the experiment.

Treatment	Density (m^{-2})	Number sampled	Number of survivors	Expected number[1] of survivors	Expected instant mortality rate (Z)[2]	Expected survival (%)
Low	50	10	82	91	0.004	91
Low	50	10	78	87	0.006	87
Low	50	10	70	78	0.010	78
Low (mean)			77	85	0.007	85
Med	100	20	147	163	0.008	82
Med	100	20	153	170	0.007	85
Med	100	20	138	153	0.011	77
Med (mean)			146	162	0.008	81
High	200	40	261	290	0.013	73
High	200	40	296	329	0.008	82
High	200	40	271	301	0.011	75
High (mean)			276	307	0.011	77

[1] Expected number of survivors accounts for fish sampled for growth determination.

[2] Expected instant mortality rate is the adjusted instantaneous mortality rate, accounting for fish sampled for growth determination.

Table 5.4. Means (± SD) of total length (TL), dry weight (W_d), growth rate in length (G_l) and growth in dry weight (G_w), for larval and juvenile smallmouth bass for Control$_{lake}$, Control$_{encl}$, Food$_{low}$ and Food$_{high}$ treatments employing in situ replicate enclosures (n = 3) in Lake Opeongo in 1993. See Table 5.1 for details of supplemental feeding levels. The Control$_{lake}$ treatment refers to young sampled from the donor brood. For each of the developmental periods (larval, juvenile), means with a common superscript are not significantly different ($P < 0.05$) by Tukey's multiple comparison test.

Prey Abundance	TL (mm)	W_d (mg)	G_l (mm d^{-1})	G_w (mg d^{-1})
Larval				
Control$_{lake}$	16.3^{a}	6.80^{a}	0.66^{a}	0.14^{a}
	(0.72)	(0.86)	(0.08)	(0.017)
Control$_{encl}$	15.9^{a}	6.26^{a}	0.62^{a}	0.13^{a}
	(0.81)	(0.92)	(0.09)	(0.013)
Food$_{low}$	17.2^{a}	8.06^{a}	0.76^{a}	0.16^{a}
	(0.85)	(1.11)	(0.10)	(0.016)
Food$_{high}$	17.8^{a}	8.87^{a}	0.83^{a}	0.17^{a}
	(0.95)	(1.30)	(0.11)	(0.016)
Juvenile				
Control$_{lake}$	$29.4^{a,b}$	$44.61^{a,b}$	$1.44^{a,b}$	0.21^{a}
	(1.98)	(7.65)	(0.12)	(0.010)
Control$_{encl}$	26.9^{a}	32.99^{a}	1.23^{a}	0.18^{b}
	(1.74)	(8.82)	(0.11)	(0.009)
Food$_{low}$	$32.1^{b,c}$	$60.50^{b,c}$	$1.66^{b,c}$	$0.22^{ab,c}$
	(1.58)	(10.46)	(0.09)	(0.006)
Food$_{high}$	34.4^{c}	76.51^{c}	1.85^{c}	0.24^{c}
	(1.41)	(11.03)	(0.06)	(0.002)

Table 5.5. Survival of young-of-year smallmouth bass during 25 d supplemental feeding experiment employing in situ enclosures in Lake Opeongo, 1993. Treatment levels included; ($Control_{encl}$) = ambient prey levels within enclosures, $Food_{low}$ = low food supplement and $Food_{high}$ = high food supplement. See Table 5.1 for details of food treatment levels.

Treatment	Density (m^{-2})	Number sampled	Number of survivors	Expected number[1] of survivors	Expected instant mortality rate $(Z)^2$	Expected survival (%)
$Control_{encl}$	50	15	68	80	0.006	80
$Control_{encl}$	50	15	75	88	0.011	88
$Control_{encl}$	50	15	60	71	0.017	71
Cont (mean)			68	79	0.012	79
$Food_{low}$	50	15	73	86	0.008	86
$Food_{low}$	50	15	77	91	0.005	91
$Food_{low}$	50	15	75	88	0.006	88
$Food_{low}$ (mean)			75	88	0.006	88
$Food_{high}$	50	15	68	80	0.011	80
$Food_{high}$	50	15	75	88	0.006	88
$Food_{high}$	50	15	77	91	0.005	91
$Food_{high}$ (mean)			73	86	0.007	86

[1] Expected number of survivors accounts for fish sampled for growth determination.

[2] Expected instant mortality rate is the adjusted instantaneous mortality rate, accounting for fish sampled for growth determination.

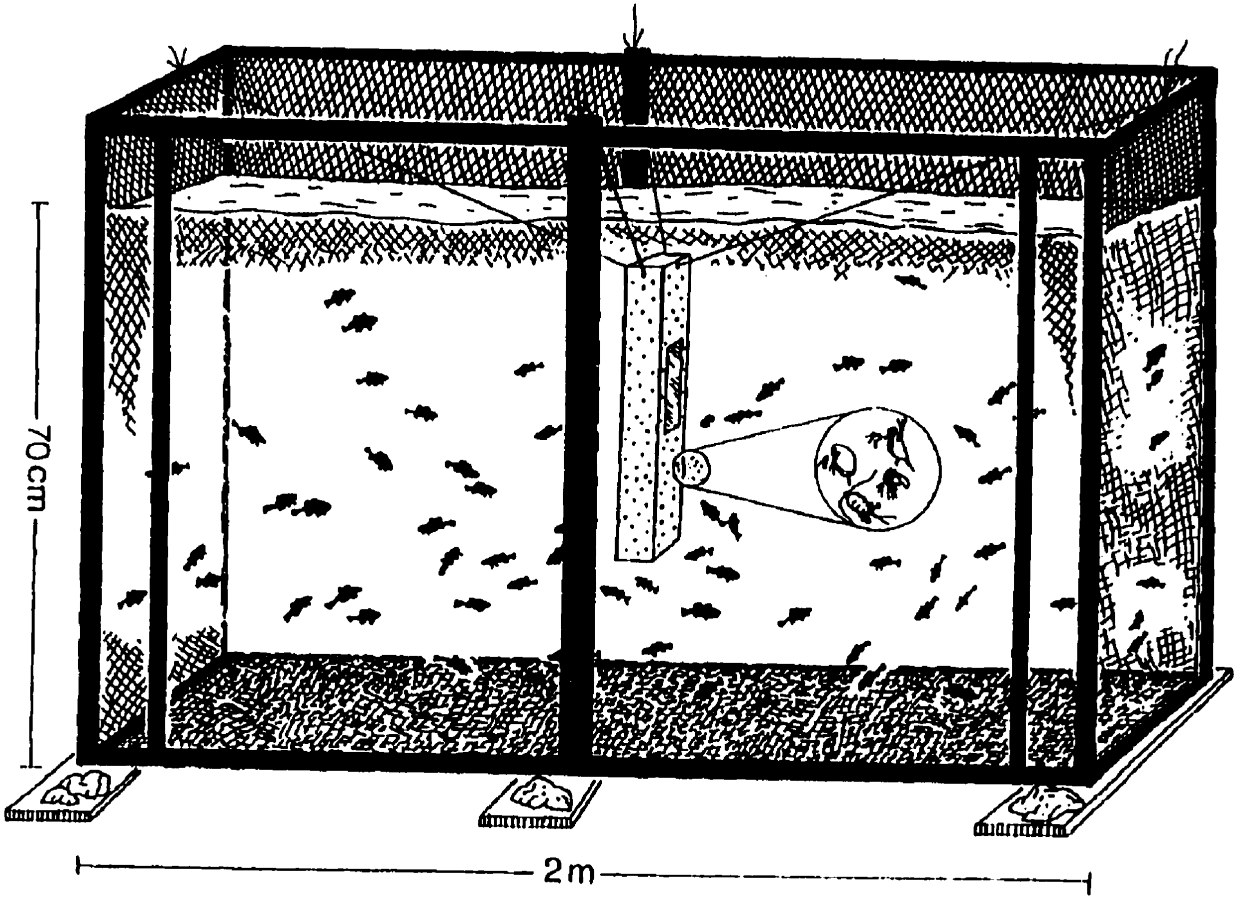

Figure 5.1. Design of in situ enclosures employed in stocking density (1992) and supplemental feeding (1993) experiments in Lake Opeongo.

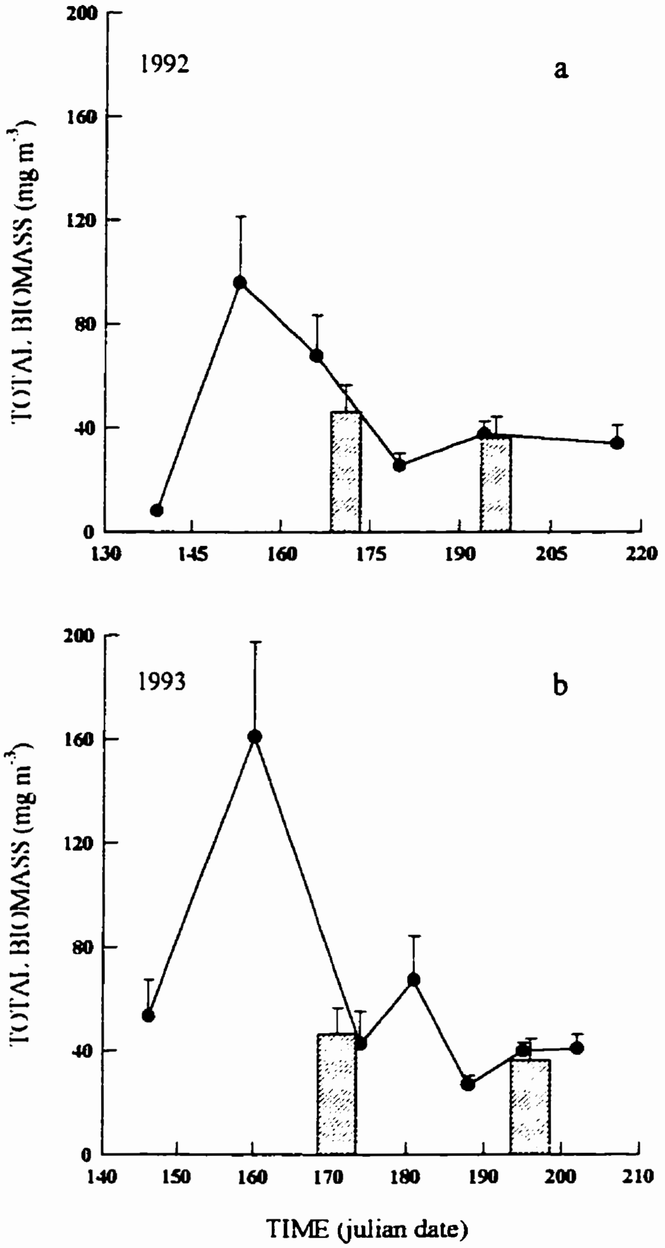

Figure 5.2. Seasonal changes in littoral-zone zooplankton biomass (solid circles) from May - August in (a) 1992 and (b) 1993 in Lake Opeongo. Hatched bars indicate zooplankton biomass within enclosures prior to and immediately following termination of the stocking density (1992) and supplemental feeding experiment. Data for seasonal changes in zooplankton biomass are from Chapter 4. Error bars indicate +1 SE.

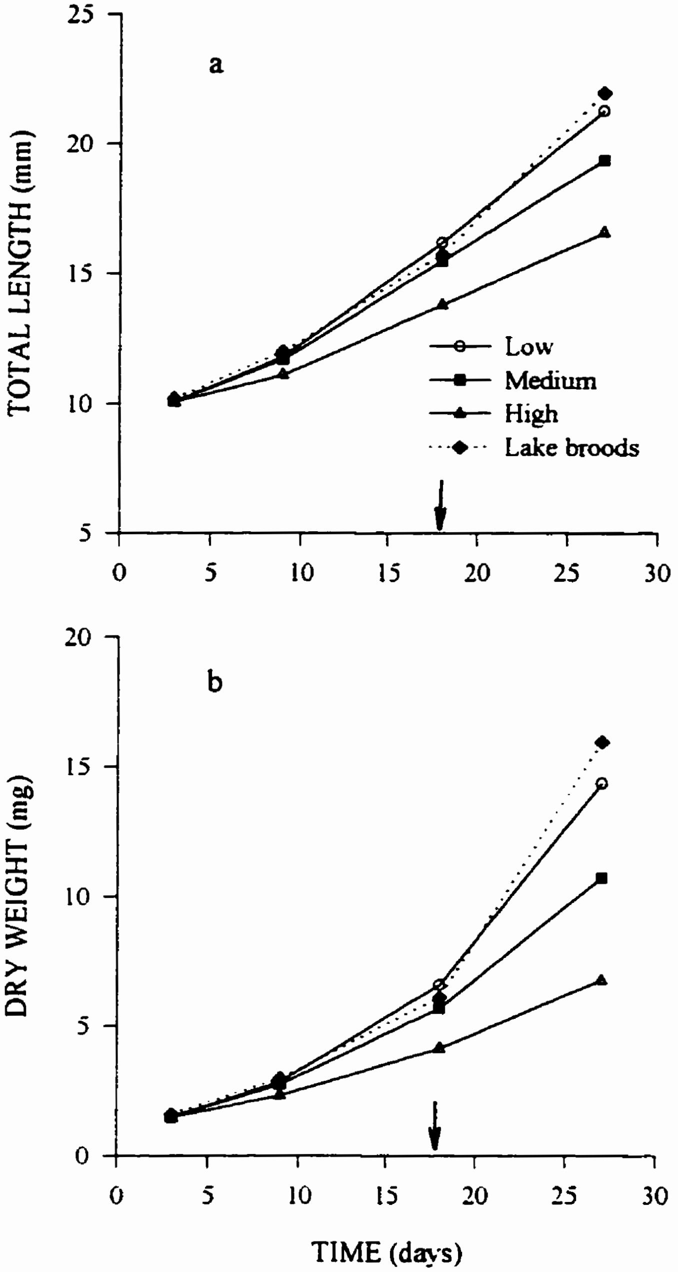

Figure 5.3. Changes in (a) mean total length and (b) mean dry weight of larval and juvenile smallmouth bass in Low (50 m^{-2}), Medium (100 m^{-2}) and High (200 m^{-2}) density treatments in the stocking density experiment. Values are also presented for young-of-year smallmouth bass from the Lake Opeongo population in 1992 (hatched line-closed diamond). Vertical arrow indicates mean time to metamorphosis.

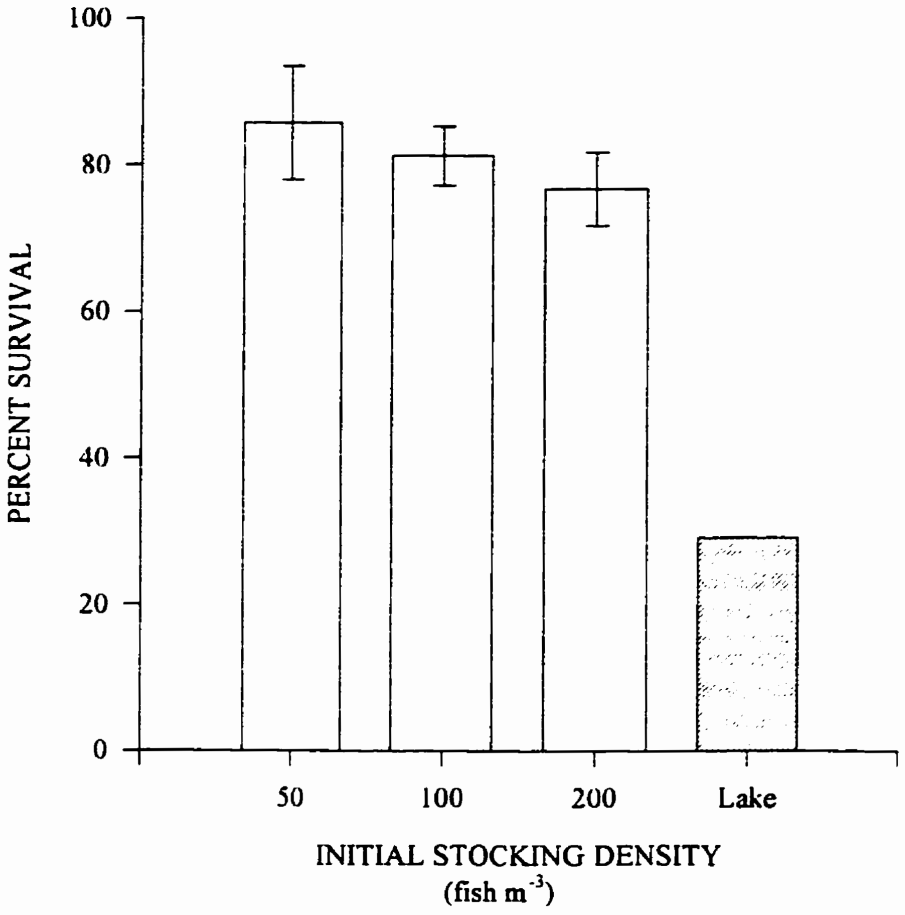

Figure 5.4. Relationship between stocking density and percent survival for Low (50), Medium (100) and High (200 fish m^{-3}) treatments in the stocking density experiment conducted in Lake Opeongo, 1992. For comparison, percentage survival of larvae from the Lake Opeongo population in 1992 is shown (hatched bar). Error bars indicate ±1 SD.

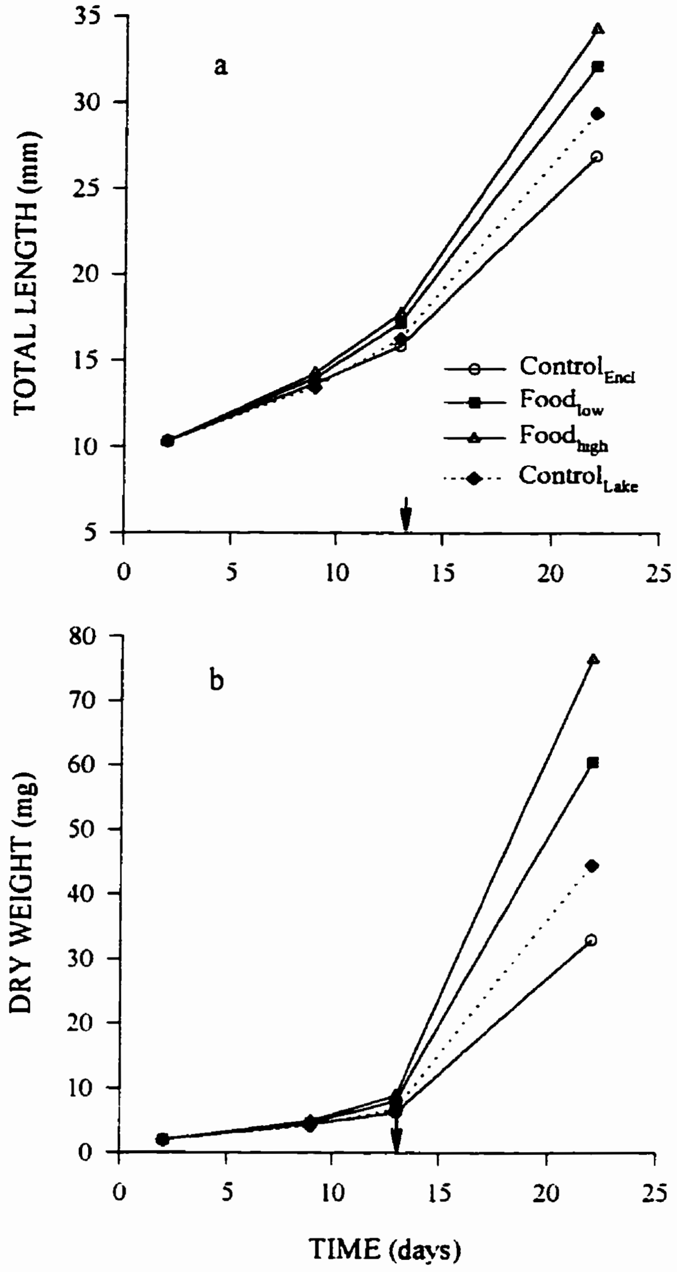

Figure 5.5. Changes in (a) mean total length and (b) mean dry weight of larval and juvenile smallmouth bass for Control$_{encl}$ (pen circle), Control$_{lake}$ (closed diamond-dashed line), Food$_{low}$ (closed square) and Food$_{high}$ (open triangle) treatments in the supplemental feeding experiment. See Table 5.1 for details of food treatment levels. Vertical arrow indicates average time of larval-juvenile transformation (metamorphosis) in 1993.

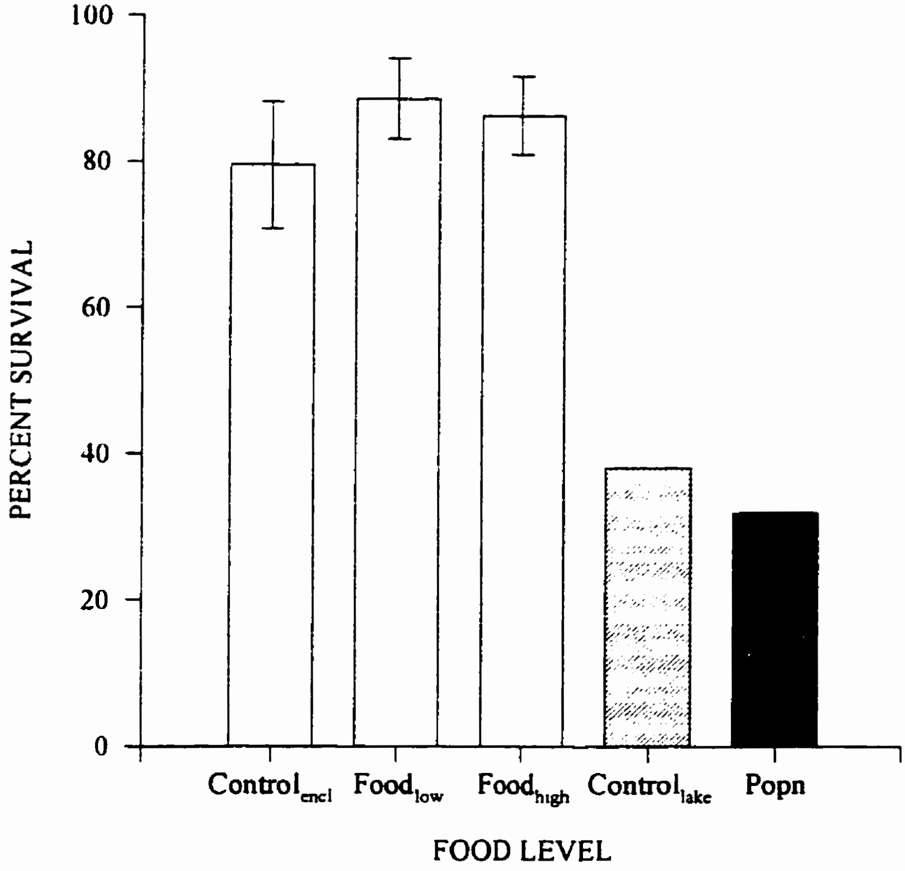

Figure 5.6. Relationship between food abundance and percentage survival for Control$_{encl}$, Control$_{lake}$, Food$_{low}$ and Food$_{high}$ treatments in the supplemental feeding experiment in Lake Opeongo, 1993. See Table 5.1 for details of supplemental feeding levels. For comparative purposes, percentage survival through the 2-week larval period is shown for the Lake Opeongo population (solid bar).

Chapter 6

Summary

This study addressed a variety of issues of specific relevance to YOY SMB growth and survival, as well as of general relevance to the study of fish early life history and its role in the population dynamics of freshwater species. The primary objective of this study was to determine the importance of food limitation in larval fish ecology. Results of this research offered strong support to the idea that food limitation is a relatively minor phenomenon in natural populations of SMB during the larval and early juvenile periods of development and that the most important cause of mortality may be predation.

I base this conclusion on the following evidence. First, swimming speed, foraging rate, agonistic interactions and nearest neighbour distance of individual YOY were unrelated to brood size, suggesting that competition for prey resources did not increase with brood size. Importantly, the dispersion of SMB broods within natal territories may be critical in allowing young bass to find sufficient prey resources and in achieving adequate growth under natural conditions. Second, no evidence was found to indicate that prey resources were being depressed as a consequence of foraging by juvenile SMB. I propose that wind-generated water motion in the littoral zones of freshwater lakes, through its potential to influence predator-prey contact rates (MacKenzie, et al. 1990), may explain the lack of effect of foraging by YOY SMB on prey resources.

Third, my data showed a distinct temporal mismatch between the seasonal abundance of first-feeding larvae and their prey, suggesting that food limitation of early larvae may not be the dominant force constraining the timing of spawning and subsequent growth, mortality and abundance patterns of YOY SMB. To the degree that SMB face energetic constraints on their spawning behaviour (Ridgway 1991), my results suggest that food limitation during the early larval phase, implicit in both the critical period hypothesis and the match-mismatch hypothesis, may not be as important in determining the timing of spawning and the seasonal patterns in growth and mortality of YOY SMB as predation.

A fourth reason I believe food limitation plays a minor role in larval and early juvenile population dynamics, is because of the high levels of supplemental food required to elevate growth rates of enclosure-held YOY above those in natural broods. Further, survival of YOY within the predator-free enclosures was an order of magnitude higher than that of YOY in natural broods, suggesting that predation during the larval and early juvenile periods may be a process of greater importance to survival than prey availability.

In addition to the immediate concerns of this dissertation, the results of this study may allow insights to be gained into how growth, mortality and abundance interact to influence recruitment variability in SMB. To date, initial abundance and growth rates during early life history have not been clearly linked to year-class strength in SMB, but a general lack of correlation between the abundance of larvae and subsequent recruitment has been noted in other species (Sissenwine 1984). It is clear that no one process controls larval and juvenile survival and subsequent recruitment. I suggest that a more complete understanding of recruitment variability in SMB will require research into a wider range of developmental periods, including later juvenile phases of development, and that particular consideration must be given to the role of predation during the first year of life.

Behaviour of YOY

- Swimming speed, foraging rate, agonistic interactions and nearest neighbour distance of individuals were all positively related to YOY body size, but unrelated to brood size.

- At the brood level, dispersion was positively related to body size and brood size. In contrast density within broods was inversely related to body size and did not differ across brood-size category.

- Estimates of zooplankton biomass did not differ 'within' and 'outside' broods, suggesting that YOY SMB were not food-limited.

Development of YOY

- Mean size and age of YOY at metamorphosis were positively correlated among years.

- The duration of both the early and late larval phases were inversely related to temperature. Temperature effects on larval phase duration influenced juvenile production; year classes that grew most rapidly during the larval period had the lowest cumulative mortality.

- The mean duration of the embryonic, larval and juvenile periods differed significantly among years. There was a strong negative relation between water temperature and period duration among years.

Production of YOY

- Annual differences in total production of first-feeding larvae were related to both spawning stock abundance and mean brood size.

- Annual differences in abundance estimates of first-feeding larvae paralleled annual changes in early juvenile abundance estimates, indicating that year-class strength of YOY SMB may be fixed during the larval period.

Growth of YOY

- Mean length of first-feeding larvae differed significantly among years.

- Brood-specific growth rates were highly variable within each spawning season. Growth rates showed a weak to moderate positive relationship with water temperature in 4 of 5 years.

- Inter-annual differences in growth rates were attributed primarily to differences in water temperature as growth rates were close to temperature-predicted values (Peek 1965) and therefore did not appear to be food-limited.

- Brood-specific growth rates of larvae were not significantly related to the match between the timing of production of larvae and their prey, nor did prey biomass account for much of the inter-annual variability in larval growth rates.

- No evidence was found for density-dependence in growth or mortality rates of YOY SMB, as annual differences in growth and mortality rates were not related to initial larval abundance. In fact, growth rates of YOY were highest in 1989, a year in which the number of spawning males in Jones Bay surpassed the previous 50-year high by nearly 30% (Ridgway 1986). It is possible that density-dependent regulation of SMB populations may operate during the early juvenile period when young disperse from the nesting territories, or later in the juvenile period, through changes in the timing of first reproduction.

- Growth rates of enclosure-held YOY were positively related to prey level and negatively related to larval stocking density, particularly following metamorphosis. The absence of density and prey level effects on growth rates of YOY from natural broods contrasted with those of enclosure-held fish and appeared to be related, in part, to changes in the behaviour of YOY. For instance, swimming speed, foraging rate and nearest neighbour distance of individuals increased significantly with body size. At the brood-level, mean area of water occupied by broods increased by an order of magnitude between first-feeding and metamorphosis, while the mean density of YOY within broods decreased significantly.

- Mean annual growth rates below temperature-predicted values in some years and the high brood-specific variability in growth rate within years suggested that factor(s) other than temperature affected YOY growth rates. Sub-maximal growth rates may have been due to variability in zooplankton distributions or predator-prey contact rates that were not evident at the scale of sampling in my study.

Mortality of YOY

- Brood-specific mortality rates were highly variable within each spawning season . Brood-specific mortality distributions were highly skewed to the right in all years, indicating that a small percentage of nests experienced high mortality each season.

- Within-season mortality rates of YOY were not consistently related to prey abundance or temperature, but tended to increase seasonally in all years.

- Within-season brood-specific mortality rates of larvae were negatively related to growth rates.

- The mortality rate of YOY SMB in natural broods was an order of magnitude higher than estimates for enclosure-held fish in Lake Opeongo. As piscivore predators were excluded from the enclosures, these results suggested that predation may be the dominant source of mortality of YOY SMB.

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IMAGE EVALUATION
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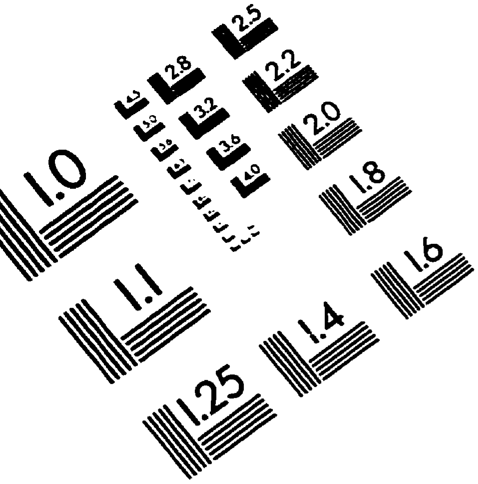

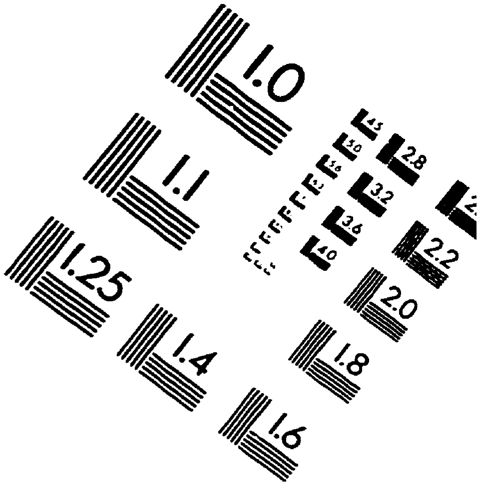

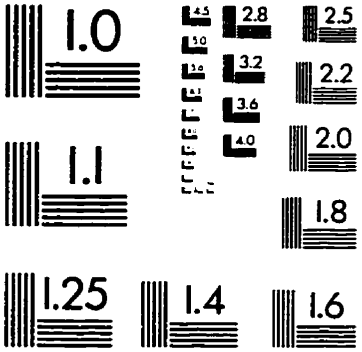

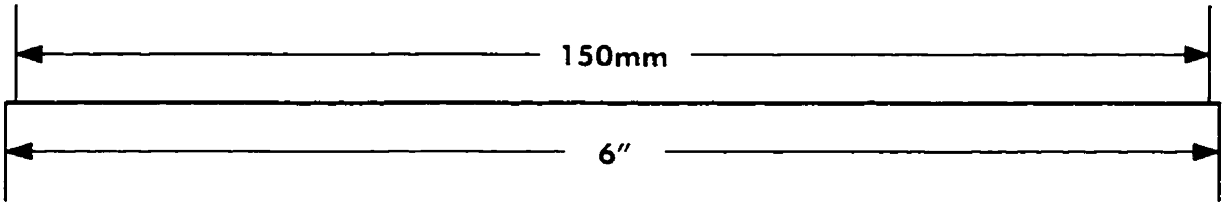

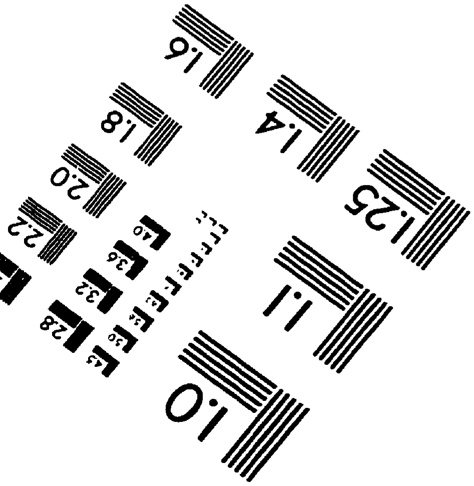

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