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Growth Dynamics of Smallmouth Bass in Lake Billy Chinook, Oregon

Abstract

During May-October, 2001, we analyzed the growth patterns and diet overlap of different ages of smallmouth bass in Lake Billy Chinook, Oregon to identify periods within the growing season when temperature or competition for food might limit growth. Bass of various ages were sampled during three 6-wk periods with a boat-mounted electroshocker from nearshore sites in two separate habitat types. Age 0 bass consumed smaller prey items, while older and larger fish were able to consume an increasingly wider size range of prey, predominantly crayfish. Bass consumed fewer crayfish through the study. Age 1 smallmouth bass consumed only age 0 crayfish, while older bass were not as limited. Diets of age 3 and age 4 smallmouth bass were similar with crayfish constituting at least 70% of the diets by volume, although amphipods and other invertebrates were important prey items to individual fish. During all periods of the study, realized consumption, defined as actual consumption divided by theoretical metabolic maximum consumption and indexed by the *P*-value generated from bioenergetic modeling, was generally higher for smaller fish than for larger bass. Consumption rates for juvenile and adult bass dropped dramatically in the fall demonstrating potential food limitation during this period. Our study suggests that during the fall, high densities of age 0 bass may affect the availability of alternative prey (chironomids and amphipods) and consequently, the growth of older age classes of smallmouth bass.

Introduction

Since their introduction into the upper Willamette River drainage in the early 1900s, the distribution and abundance of smallmouth bass (*Micropterus dolomieu*) in Oregon has increased substantially. Oregon Department of Fish and Wildlife (ODFW) acknowledges that warmwater fish such as smallmouth bass are a resource that supports important recreational fisheries in the face of declining traditional coldwater salmonid fisheries. Effective management of warmwater fisheries to optimize user benefits, while remaining consistent with conservation strategies for naturally produced native fish species, will require a better understanding of the regulatory mechanisms that limit and control warmwater fish populations in Oregon.

Smallmouth bass in Lake Billy Chinook, a large reservoir in central Oregon, exhibit low annual survival and slow growth, which is typical of other Pacific Northwest smallmouth bass stocks (Bennett et al. 1991). The reservoir appears to provide favorable conditions for the development of a high-quality smallmouth bass fishery—fairly stable water levels, large areas of cobble/boulder substrate, and abundant crayfish (*Pacifastacus leniusculus*) for forage (Lewis 1997).

The success of a fishery and or a fish population may be driven by the availability of key or preferred prey, with growth and survival being regulated by availability of certain key or preferred prey (Mills et al. 1989, Post and McQueen 1994). Crayfish are a preferred prey of smallmouth bass. Where they are abundant, crayfish often account for >60% of the diet of adult smallmouth bass (Scott and Crossman 1973, Carlander 1977). Bass consumed almost one-third of total crayfish production and one-half of the total crayfish biomass in an Ozark stream (Rabeni 1992). With an abundance of a preferred prey species (crayfish), growth rates of smallmouth bass in Lake Billy Chinook should be nearly optimal. However, annual ODFW inventories of the Lake Billy Chinook smallmouth bass population show a limited number of fish >250 mm, and previous ODFW studies suggest that annual mortality of adults is ~50%. While the reservoir supports a recreational fishery for smallmouth bass, it is unlikely that angling mortality is the major factor limiting the increase in older, larger bass. Based on ODFW creel data, only an estimated 618 smallmouth bass ≥ 300 mm were harvested annually from the reservoir between 1996-1998. While there is evidence of intraspecific competition limiting smallmouth bass recruitment and survival in other systems

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(Dong and DeAngelis 1998), no data exist, however, to evaluate the relative importance of competition and environmental factors in determining patterns of smallmouth bass growth in Lake Billy Chinook.

Wild fish have endogenous seasonal rhythms in growth (Baker and Wigham 1979) that are largely determined by temperature and food supply (Coble 1977), although other factors such as parasites, disease, and pollution may restrict realization of ultimate growth rates. Smallmouth bass growth rates in Lake Billy Chinook are similar to the slowest growing population investigated by Coble (1977) and Carlander (1977) at Fall Creek, New York where age 2, 3 and 4 bass were 140, 178, and 216 mm. Optimal growth for smallmouth bass occurs at 25°-29°C (Coble 1977, Wren 1980, Edwards et al. 1983, Casselman 2002), and faster growth of smallmouth bass is generally associated with higher summer temperatures for populations in northern latitudes (King et al. 1999). We used bioenergetic modeling to separate temperature limitation on growth of smallmouth bass in Lake Billy Chinook from other possible factors such as limited prey availability.

Bioenergetic models that incorporate estimates of thermal history, diet composition, and prey energy density provide a simple method to evaluate effects of temperature on fish dynamics and to explore seasonal and ontogenetic patterns in predator-prey interactions (Hanson et al. 1997, Whitledge and Hayward 1997). Growth and survival of different age-classes of smallmouth bass can be affected by competition for key prey (Dong and DeAngelis 1998). Bass utilize strategies such as prey switching or niche segregation to lessen competition for limited prey (Collier et al. 1973), but often at an energetic cost (Ihssen et al. 1981, Pothoven et al. 2001). Prey switching could result in the consumption of prey items that return less energy to a predator than energy expended in the pursuit and capture of that prey (Hoyle and Keast 1987). Investigation of possible competitive interaction between different age-classes of smallmouth bass requires identification of significant diet overlap for prey items, which are limited in abundance (Bowen 1983). Diet overlap is easily quantified with various indices (Crowder 1990), but measures of food limitation are more difficult to establish. However, because growth rates of fish are highly sensitive to per capita resource availability (Backel and Le Cren 1978), bioenergetic simulations are an indirect way of measuring resource limitation within the bounds set by the temperature regime. Our objective for this study was to use bioenergetic simulations of the patterns of smallmouth bass growth to identify periods within the growing season indirectly when temperature or competition for food might affect growth of different ages of smallmouth bass.

Study Site

Lake Billy Chinook is a multi-purpose reservoir in Central Oregon created in 1964 by impoundment of the Deschutes River just below its confluence with the Crooked and Metolious Rivers, thus forming three narrow arms (maximum width < 600 m; Figure 1). At full pool, the reservoir has a surface area of 1,585 ha and a volume of 493 x 10^6 m^3 (Johnson et al. 1985). The reservoir generally has steep-sloping, alternately cobble or sand banks resulting in a shoal area of 5% of the total surface area of the reservoir, an average depth of 31.1 m, and a maximum depth of 126.5 m (Johnson et al. 1985).

In addition to smallmouth bass, the fish assemblage in Lake Billy Chinook comprises 17 native and introduced species (Lewis 1999). Principal gamefish species include smallmouth bass, kokanee (*Oncorhynchus nerka*), and bull trout (*Salvelinus confluentus*), as well as smaller numbers of redband trout (*O. mykiss*) and brown trout (*Salmo trutta*). Primary nongame fish species present include large numbers of northern pikeminnow (*Ptychocheilus oregonensis*), and bridgelip and largescale sucker (*Catastomus columbianus* and *C. macrocheilus*).

The limnological character of each arm of the reservoir reflects the land use and physiographic nature of the watershed for that arm. The Metolious watershed is forested and the least disturbed of the three, the Deschutes watershed is most heavily influenced by human development, and the Crooked River, which contributes around 40% of the reservoir inflow, is impacted by extensive agriculture and grazing, (Johnson et al. 1985). Below each river inlet, each arm has a several hundred meter-long transition zone of unstratified water with temperatures similar to the river. Farther down the arm, these cold water masses plunge below the warmer surface water to depths with water of similar temperature and density (Beauchamp and Van Tassel 1999), thus forming

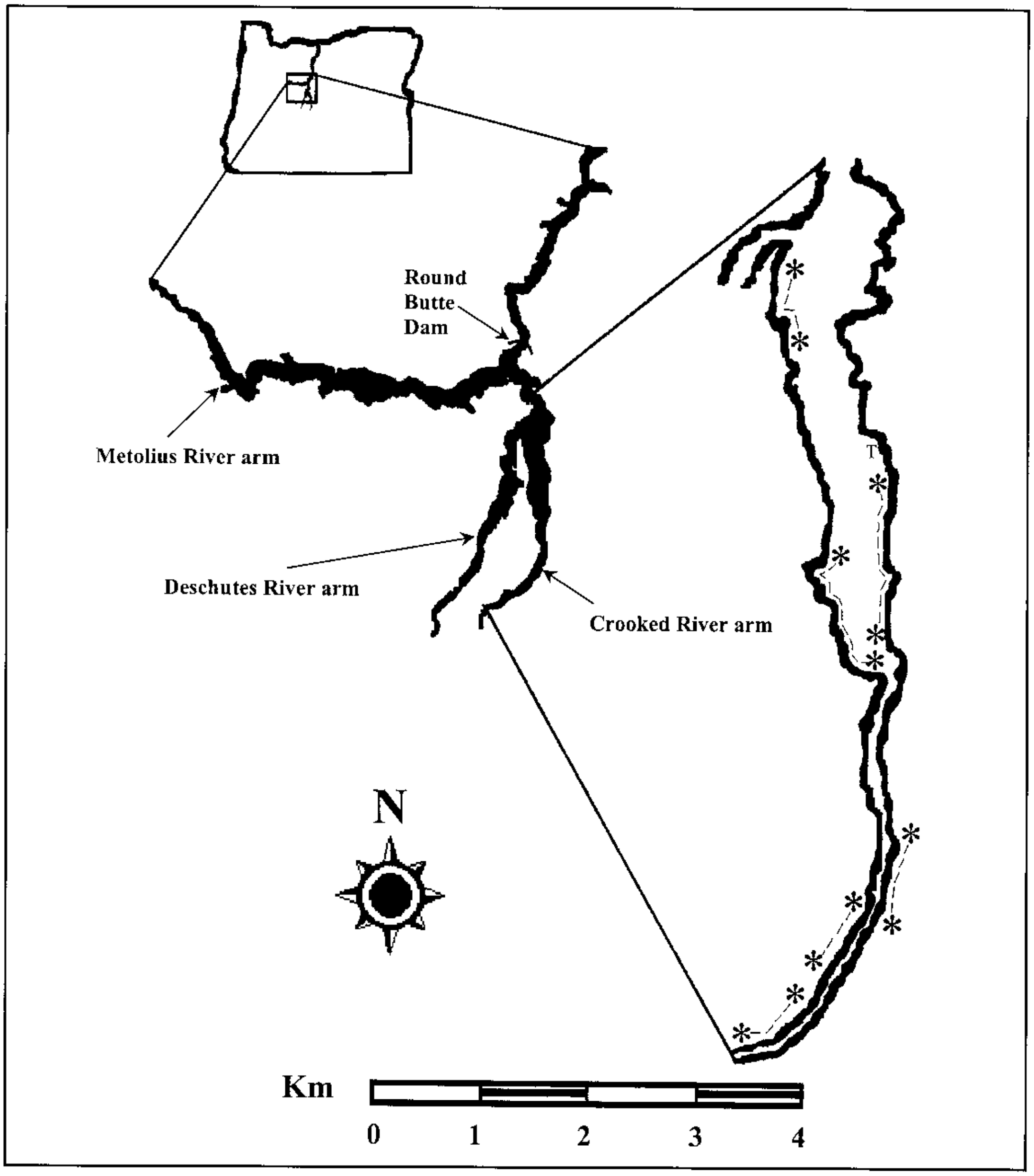

Figure 1. Lake Billy Chinook and the Crooked River arm showing location of the recording thermograph (T) and electrofishing transects (*) during May to October, 2001.

a vertical thermal barrier and effectively segregating the habitat between warmwater and coldwater species (Lewis 1999). Our study focused on the smallmouth bass in the 10 km long Crooked River arm because previous sampling indicated this population represented the smallmouth bass populations in the rest of the lake.

Methods

Fish Collection

We identified six littoral sections of the Crooked River arm as sampling sites (Figure 1). These sites were chosen by general reservoir nature (three open reservoir sites versus three canyon sites), accessibility to shocking boat (shallow areas with scattered, large boulders were too dangerous to sample at night), and probability of encountering bass (deep water associated with cliffs rendered electrofishing gear ineffective). On any given sampling occasion, smallmouth bass were collected by night electrofishing two or four sites (randomly selected and equally divided between open reservoir and canyon sites) with a 5 KW boat electrofisher set for DC operation. Sampling was conducted at night because high water clarity increased fish avoidance of the electrofishing boat during the day and severely reduced daytime capture efficiency. Both open reservoir and canyon sites were sampled to encompass inter-site variation in bass growth or diet to model the Crooked River population as a whole.

Total length (TL; mm) of all bass captured was measured along with weight (g) of a subsample of fish. Prior sampling indicated that smallmouth bass < 150 mm could be accurately aged by modes in the length frequency distribution. Scales were taken from bass with a goal of 10 fish sampled in each 10-mm length interval greater than 150 mm. An age-length key was developed from non-regenerative scales impressed in acetate and aged by two readers using a microfiche viewer.

Diet Composition

Smallmouth bass diet was summarized for each of the four sample dates (May 4, June 21, August 14, and October 2) by 50-mm TL bass intervals (Figure 2). Our target was to collect stomach contents from 10 bass from successive 50-mm TL size groups, although this sample size was not achieved for all size groups on all sample occasions. Stomach contents of smallmouth bass > 200 mm were recovered through gastric lavage followed by a visual inspection of the mouth and esophagus for large items not flushed clear. Contents recovered were rinsed through a sieve (1-mm opening) and preserved in 10% formalin. Bass < 200 mm were killed, their digestive tracts were removed, and were similarly preserved.

Recovered prey items were examined using a variable power binocular dissecting microscope and were identified to the lowest practical taxonomic level (species for fish and crayfish, and order for other invertebrates), and counted. In most cases separate tallies were kept for adult insects and their larval stages; dipterans, other than chironomid larvae, were the primary exception. Fish prey in advanced states of digestion were identified through diagnostic bones such as the cleithrum, dentary, and vertebrae (Hansel et al. 1988, Frost 2000). Age of crayfish consumed was determined to be age 0 or older after consideration of crayfish length and time of year it was consumed (Scott Lewis, Portland General Electric, personal communication).

Bass diets were derived from the volumetric contribution of each prey category to the total volume of food consumed by smallmouth bass in each 50-mm size category on any of the four sample dates. Volume of zooplankton consumed was measured directly, while chela length-volume and chela length-total length regressions for crayfish, and number-volume regressions for small prey items, e.g., chironomids and amphipods, were developed using intact, undigested individuals. Despite limitations, this allowed approximate volume calculations even if only partial remains of a prey item were found in a stomach.

Diet Overlap

Diet overlap was quantified for each sample date using the Schoener index (Wallace 1981), which was calculated as follows:

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} \left| px_i - py_i \right|\right),$$

where

n = number of prey categories,

px_i = proportion, by volume, of prey type i in the diet of smallmouth bass of age class x, and

py_i = proportion, by volume, of prey type i in the diet of smallmouth bass of age class y.

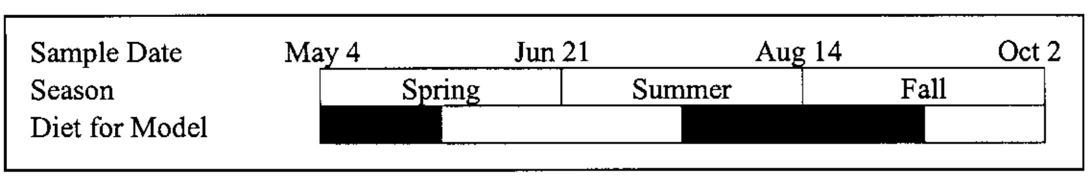

Figure 2. Relationship between sampling dates, designated seasons, and transformed seasonal smallmouth bass diet used in bioenergetic modeling for this study during 2001.

This index ranges from a value of 0.0 (no overlap) to 1.0 (complete overlap) and is considered to indicate significant resource overlap when the index exceeds 0.60 (Zaret and Rand 1971, Mathur 1977).

Bioenergetic Modeling

For the purpose of bioenergetic modeling, the growing season was divided into three 6-wk periods: spring (May 4 to June 20), characterized by increasing water temperatures and productivity; summer (June 21 to August 13), characterized by thermal stratification of the water column and declining phytoplankton production; and fall (August 14 to October 2), characterized by decreasing water temperatures, the breakdown of thermal stratification, and temporary increase in productivity related to greater nutrient availability. Hereafter, these periods will be referred to as spring, summer, and fall (Figure 2).

Although we initially summarized smallmouth diet on each sample occasion by 50-mm predator length increments, for modeling purposes we needed the diet summarized on a seasonal basis to fit the growth increments observed for each smallmouth bass age class. This transformation required several steps. Sampling occurred at the breaks between seasons, so we assumed that the diet observed on each sampling occasion represented the diet for the period halfway between prior and subsequent sampling (Figure 2). For example, diet composition for 150 - 200 mm bass on June 21 (beginning of summer period) was assumed to represent the diet for 150 – 200 mm bass during the latter half of spring and the first half of the summer period (Figure 2). However because the bioenergetic modeling was performed on the basis of growth of age classes during each season, the next step was to determine the average size of each age class of bass at the beginning of each season. Once the average size of each bass age class was calculated, we could determine which 50-mm diet category best represented the diet of each age class during each season. For the purposes of bioenergetic model input, when the average size of a smallmouth bass age-class crossed the boundary of a 50-mm interval during a season, we assumed linear growth and apportioned the time spent consuming each diet accordingly.

The index output by the Wisconsin bioenergetics model (Hanson et al. 1997), a *P*-value, is a proportionate measure of a species' observed consumption to its theoretical consumption (as limited by the ambient thermal regime). If the *P*-value of a species is 1.0, the species is growing at its theoretical metabolic maximum, while if it is below 1.0, in the absence of other physical or biological limiting factors, it is likely that growth is being limited by competition.

Thermal history was estimated by recording water temperature at 1 m depth at 15 min intervals over the period of the study using a HOBOTEMP. Age-specific weight of bass on each sampling occasion was determined either directly from data collected on that occasion or, when sample size of weighed fish was too small, indirectly using a period-specific, length-weight regression equation. Values for predator and prey caloric densities (Richman 1958, Davis and Warren 1971, Hewett and Johnson 1992) were held constant for predator and prey since seasonal energy density data were not available.

Results

Fish Collection

Smallmouth bass in Lake Billy Chinook generally increased in length and weight during each season, except during the fall (Figure 3). Age-0 smallmouth bass did not recruit to the gear until the fall at which point they became extremely abundant. Too few age-5 smallmouth bass were collected during the study to include them in the modeling.

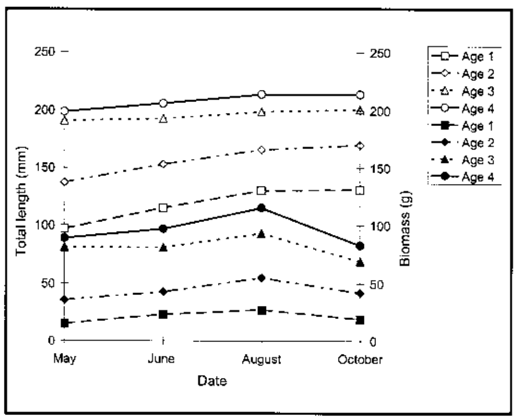

Figure 3. Seasonal growth for smallmouth bass age-classes in Lake Billy Chinook during May-October, 2001 (open symbols = total length, closed symbols = biomass).

Diet Composition

Prey consumed by smallmouth bass varied as a function of predator size and sample date (Figure 4). Age 0 bass consumed smaller prey items such as zooplankton, chironomids, and amphipods, while older and larger fish were able to consume an increasingly wider size range of prey (predominantly crayfish). Size range of crayfish consumed was also restricted by predator size; age 1 smallmouth bass consumed only age 0 crayfish (Scott Lewis, Portland General Electric,

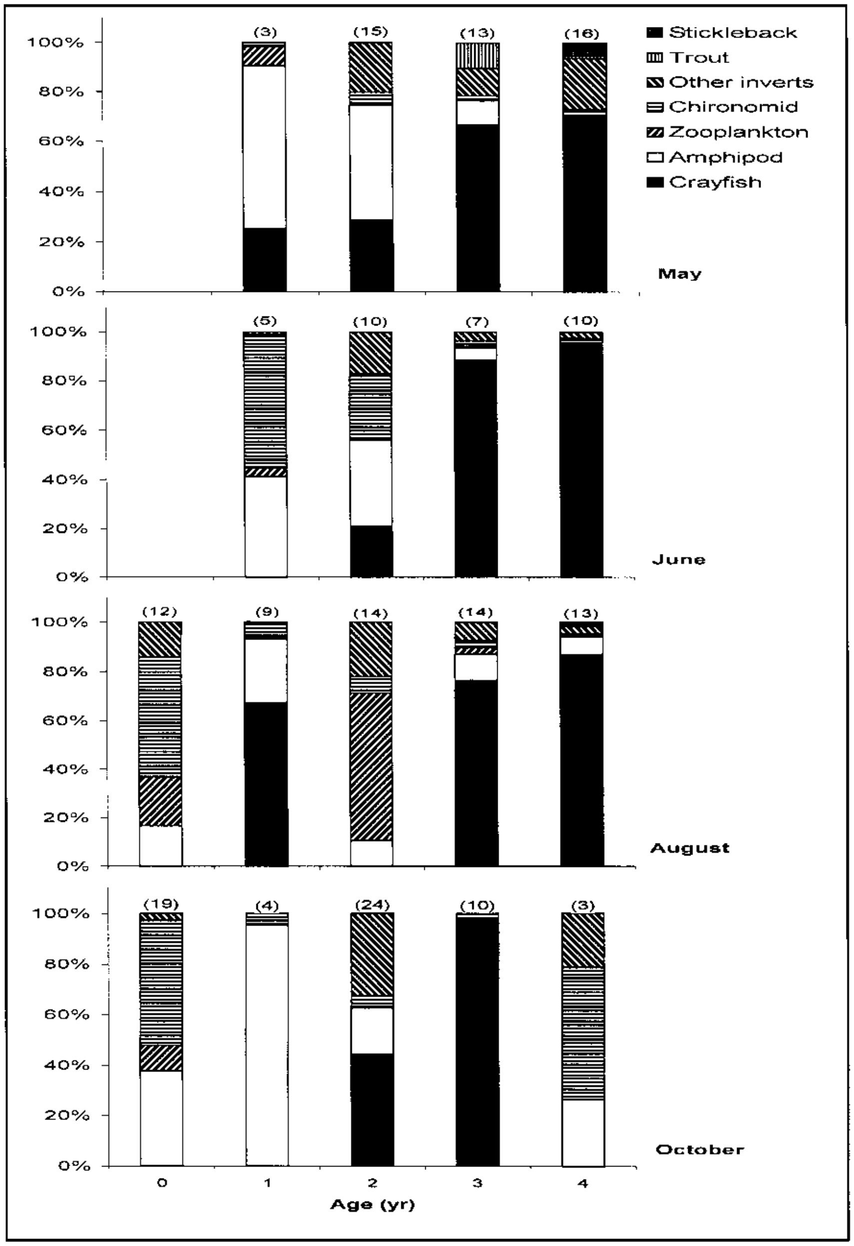

Figure 4. Percent composition (by volume) of diets for age classes of smallmouth bass from Lake Billy Chinook during May, June, August, and October, 2001. Number in parentheses represent number of non-empty stomachs in the sample.

personal communication), while older bass were not as limited (Figure 5).

Consumption of age 0 crayfish by smallmouth bass was heavy early (63% of the crayfish consumed in May were age 0), but generally declined through the year (50% in June and less than 45% in August and October; Figure 4). Except for age 4 fish in October (when sample size was small), crayfish constituted at least 70% of the stomach contents by volume of age 3 and age 4 smallmouth bass, although amphipods and other invertebrates continued to be important prey items to individual fish.

Diet Overlap

Although the degree of diet overlap between age classes of smallmouth bass varied with sampling occasion (Table 1), Schoener's index showed similarity of feeding among different age classes. Generally when Schoener indices exceed 0.6 (except for the age 1 and 2 bass in June when they consumed primarily amphipods and chironomids), amphipods or crayfish were the prevalent prey items in the diets of the two age-classes. Diet

TABLE 1. Schoener diet-overlap indices for various age classes of smallmouth bass in Lake Billy Chinook during May to October, 2001. No age 0 bass were collected in May or June.

	Age class			
Age class	1	2	3	4
		May		
0	—	—	—	—
1		0.73	0.38	0.28
2			0.46	0.39
3				0.80
		June		
0	—	—	—	—
1		0.63	0.08	0.02
2			0.29	0.24
3				0.92
		August		
0	0.23	0.46	0.17	0.09
1		0.17	0.81	0.76
2			0.18	0.09
3				0.88
		October		
0	0.42	0.25	0.02	0.51
1		0.23	0.17	0.30
2			0.46	0.44
3				0.02

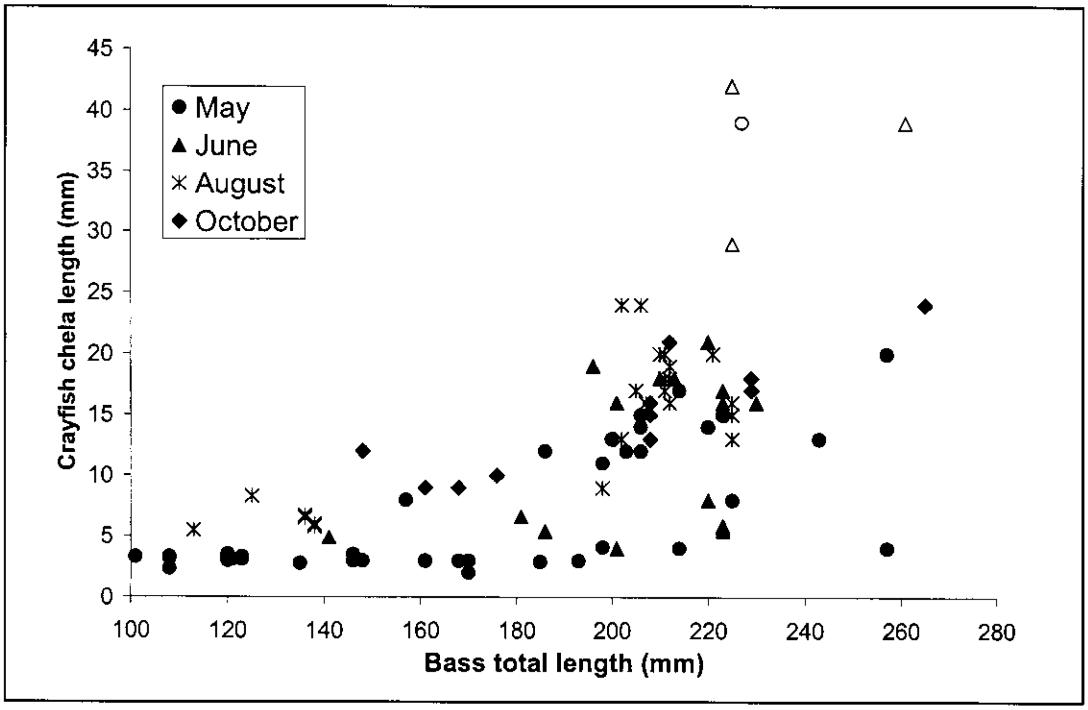

Figure 5. Length of crayfish chela found in smallmouth bass stomachs from Lake Billy Chinook during May to October, 2001. Open symbols denote crayfish that were freshly molted.

overlap between age 3 and 4 bass is high reflecting the degree of similarity in size of these fish, except for October when the small sample size of age 4 fish confounded the analysis. Overlap values between age 1 bass and age 3 and 4 fish for August are misleading because the predominant prey item, crayfish, is partitioned between the juvenile and adult bass by size. Due to a smaller mouth gape, age 1 bass are morphologically limited to consuming smaller crayfish than older fish (Figure 5).

Bioenergetic Model Results

P-values for smallmouth bass varied by age and season, but only in age 1 smallmouth bass during the spring was consumption limited only by temperature (Table 2). During all seasons, realized consumption, defined as actual consumption divided by theoretical metabolic maximum consumption, was generally higher for smaller (younger) fish than for larger bass. Consumption rates for juvenile and adult bass dropped dramatically in the fall demonstrating potential food limitation during this period.

TABLE 2. *P*-values generated from bioenergetic modeling of growth of smallmouth bass in Lake Billy Chinook during spring, summer, and fall, 2001.

Period	Age-0	Age-1	Age-2	Age-3	Age-4
Spring	—	1.01	0.72	0.54	0.57
Summer	—	0.75	0.60	0.53	0.53
Fall	0.64	0.62	0.43	0.34	0.26

Discussion

Thermal regime places limitations on the biological growth potential and, consequently, management options for smallmouth bass in Lake Billy Chinook. With a mean temperature of 17.6°C for the period of July through September, we could expect age 3 to 5 fish in Lake Billy Chinook to grow ~23 mm according to Coble (1967). This slow growth alone effectively eliminates quality or trophy fisheries as viable management options for the fishery. Additionally, in 2001, age 3 and 4 smallmouth bass realized only 45%-65% of their potential growth based on temperature alone, which suggests, given no overt evidence of disease or parasitism, some degree of resource limitation during the growing season.

Crayfish, particularly age 0 individuals, were an important prey item for bass in Lake Billy Chinook. However, certain factors may act to affect the availability of crayfish as forage for bass. Only half of the total annual crayfish production in an Ozark stream was available to smallmouth bass and rock bass (*Ambloplites rupestris*) as a result of size-selective predation and prey behavioral traits (Rabeni 1992). During our study, 61%, 69%, 48%, and 32% of age 3 and 4 smallmouth bass ate crayfish in May, June, August, and October. For age 2 fish, during the same periods, 47%, 20%, 0%, and 17% ate crayfish. This decline in crayfish consumption mirrors the exponential decline in the survivorship curve of age 0 crayfish in Lake Billy Chinook (Lewis 1997) and suggests some level of competition for available crayfish may occur at certain times during the growing season.

In Lake Billy Chinook, as the contribution of crayfish to bass diets decreased, chironomids and amphipods became increasingly important alternative prey. Whereas chironomid larvae have been noted as important food items for smallmouth bass in other waters (Clady 1974, Carlander 1977), reliance of smallmouth bass on amphipods, as demonstrated in this study, is uncommon. For age 1-4 smallmouth bass in Lake Billy Chinook, however, the switch from crayfish may come with an energetic cost. Prey size consumed by smallmouth bass tends to increase as fish grow (Scott and Crossman 1973, Olson and Young 2003), although larger smallmouth bass will still consume small prey items (Long and Fisher 2000). However, while the energy density of amphipods is greater than crayfish (Hanson et al. 1997), pursuit, capture and consumption of small prey (amphipods) undoubtedly requires higher energy expenditure than for a diet of larger prey items (crayfish) (Ibssen et al. 1981, Pothoven et al. 2001, Tyson and Knight 2001). Hoyle and Keast (1987) theorized that largemouth bass (*Micropterus salmoides*) should consume prey items that are ~29% of their body length, to optimize energy gained relative to energy expended. When feeding on amphipods and chironomids, age 1-4 smallmouth bass in Lake Billy Chinook are consuming prey items ~6% of their body length, potentially much smaller than that required for optimum energy gain. Additionally, during the period of prey switching (fall), juvenile and adult smallmouth bass in this study that had consumed only chironomids or amphipods typically were not satiated, consuming an average of only one amphipod and 4-5 chironomids. This is reflected in low fall P-values and decreases in juvenile and adult bass weights during this period suggesting limited prey availability.

Interspecific competition likely was not responsible for the decrease in smallmouth bass condition in the fall as other potential fish competitors were not numerous enough or were segregated from smallmouth bass by habitat or food preferences. Kokanee, although the most numerous species in the lake, primarily consume zooplankton (Theisfeld et al. 1999) and, as a pelagic species, are spatially segregated from smallmouth bass. Although bull trout, brown trout and northern pikeminnow consumed crayfish or amphipods seasonally (Beauchamp and Van Tassell 1999, Lewis 1999), lower thermal preferences for those species minimized spatial overlap with smallmouth bass during summer and fall (Lewis 1999). Redband trout are potential year-around competitors with age 0 bass for *Daphnia* and with all ages of bass in the fall for chironomid larvae (Groves et al. 1999). However, despite thermal tolerances (Raleigh et al. 1984) that would allow for spatial overlap with smallmouth bass, their low numbers in the reservoir and the absence of redband trout observed during sampling suggests minimal potential significance as competitors with bass.

The source of this resource limitation for older smallmouth bass contrasts with findings from Dong and DeAngelis (1998), who demonstrated that high densities of older juveniles could suppress the growth and recruitment of age-0 fish. Our study suggests that during the fall, high densities of age 0 bass may affect the availability of limited alternative prey (chironomids and amphipods) and growth of older age classes of smallmouth bass. During the same time period when juvenile and adult bass consumption was severely limited, fingerling (age 0 and age 1) bass had P-values/consumption rates 50%-130% higher than older bass, thus demonstrating a greater efficiency than older bass at capturing and utilizing these prey items. This integration of amphipods into age 0 bass diets occurred at the same time that amphipods were becoming increasingly important to older age classes of bass due to the disappearance of age 0 crayfish and decreased morphological availability of larger crayfish to older smallmouth bass.

Elucidation of factors limiting growth and potentially survival of smallmouth bass in Lake Billy Chinook allows a more relevant contemplation of potential management direction and actions. Presently managed as a basic yield fishery, Lake Billy Chinook smallmouth bass do not realistically have the biological potential to produce a quality or trophy fishery given their limited growth potential as defined by the temperature regime combined with high mortality rates. Assuming that angler harvest (Theisfeld et al. 1999) is an insignificant portion of total mortality, imposition of common restrictive regulations used to increase the quality of bass fisheries—minimum-length or slot limits—will not address temperature or food limitations identified in this study. As a result, given ODFW's direction to provide a variety of fishing opportunity, Lake Billy Chinook smallmouth bass could be managed as a high-yield fishery, i.e., increasing the bag limit above the five-fish limit currently in effect. This would allow better angler utilization of limited smallmouth bass production in the reservoir. Increased angler harvest could potentially result in better bass growth and over-winter survival through lower bass density and reduced inter-age class competition during the critical fall period. However, given temperature limitations on smallmouth bass growth in Lake Billy Chinook, it is unlikely that the quality of the fishery, i.e., density of fish > 300 mm, would increase substantially.

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