2005

An Empirical Model for Estimating Annual Consumption by Freshwater Fish Populations

Hongsheng Liao
Iowa State University

Clay L. Pierce
United States Geological Survey, cpierce@iastate.edu

Joe G. Larscheid
Iowa Department of Natural Resources

An Empirical Model for Estimating Annual Consumption by Freshwater Fish Populations

Abstract

Population consumption is an important process linking predator populations to their prey resources. Simple tools are needed to enable fisheries managers to estimate population consumption. We assembled 74 individual estimates of annual consumption by freshwater fish populations and their mean annual population size, 41 of which also included estimates of mean annual biomass. The data set included 14 freshwater fish species from 10 different bodies of water. From this data set we developed two simple linear regression models predicting annual population consumption. Log-transformed population size explained 94% of the variation in log-transformed annual population consumption. Log-transformed biomass explained 98% of the variation in log-transformed annual population consumption. We quantified the accuracy of our regressions and three alternative consumption models as the mean percent difference from observed (bioenergetics-derived) estimates in a test data set. Predictions from our population-size regression matched observed consumption estimates poorly (mean percent difference = 222%). Predictions from our biomass regression matched observed consumption reasonably well (mean percent difference = 24%). The biomass regression was superior to an alternative model, similar in complexity, and comparable to two alternative models that were more complex and difficult to apply. Our biomass regression model, $\log_{10}(\text{consumption}) = 0.5442 + 0.9962 \cdot \log_{10}(\text{biomass})$, will be a useful tool for fishery managers, enabling them to make reasonably accurate annual population consumption predictions from mean annual biomass estimates.

Keywords

predator populations, prey resources, population consumption, freshwater fish

Disciplines

Aquaculture and Fisheries | Environmental Indicators and Impact Assessment | Environmental Monitoring | Natural Resources and Conservation | Natural Resources Management and Policy | Population Biology

Comments

This article is from *North American Journal of Fisheries Management* 25 (2005): 525, doi:10.1577/M03-213.1.

North American Journal of Fisheries Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

An Empirical Model for Estimating Annual Consumption by Freshwater Fish Populations

Hongsheng Liao [a], Clay L. Pierce [b] & Joe G. Larscheid [c]

[a] Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa, 50011, USA

[b] U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, 339 Science II, Iowa State University, Ames, Iowa, 50011, USA

[c] Iowa Department of Natural Resources, 611 252nd Avenue, Spirit Lake, Iowa, 51360, USA

Published online: 08 Jan 2011.

To cite this article: Hongsheng Liao, Clay L. Pierce & Joe G. Larscheid (2005) An Empirical Model for Estimating Annual Consumption by Freshwater Fish Populations, North American Journal of Fisheries Management, 25:2, 525-532, DOI: 10.1577/M03-213.1

To link to this article: http://dx.doi.org/10.1577/M03-213.1

North American Journal of Fisheries Management 25:525–532, 2005

DOI: 10.1577/M03-213.1

[Article]

An Empirical Model for Estimating Annual Consumption by Freshwater Fish Populations

HONGSHENG LIAO[1]

Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa 50011, USA

CLAY L. PIERCE*

U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, 339 Science II, Iowa State University, Ames, Iowa 50011, USA

JOE G. LARSCHEID

Iowa Department of Natural Resources, 611 252nd Avenue, Spirit Lake, Iowa, 51360, USA

Abstract.—Population consumption is an important process linking predator populations to their prey resources. Simple tools are needed to enable fisheries managers to estimate population consumption. We assembled 74 individual estimates of annual consumption by freshwater fish populations and their mean annual population size, 41 of which also included estimates of mean annual biomass. The data set included 14 freshwater fish species from 10 different bodies of water. From this data set we developed two simple linear regression models predicting annual population consumption. Log-transformed population size explained 94% of the variation in log-transformed annual population consumption. Log-transformed biomass explained 98% of the variation in log-transformed annual population consumption. We quantified the accuracy of our regressions and three alternative consumption models as the mean percent difference from observed (bioenergetics-derived) estimates in a test data set. Predictions from our population-size regression matched observed consumption estimates poorly (mean percent difference = 222%). Predictions from our biomass regression matched observed consumption reasonably well (mean percent difference = 24%). The biomass regression was superior to an alternative model, similar in complexity, and comparable to two alternative models that were more complex and difficult to apply. Our biomass regression model, $\log_{10}(\text{consumption}) = 0.5442 + 0.9962 \cdot \log_{10}(\text{biomass})$, will be a useful tool for fishery managers, enabling them to make reasonably accurate annual population consumption predictions from mean annual biomass estimates.

Effective management of freshwater fisheries requires knowledge of the fish populations to be managed and an understanding of the processes that define their relationships with the environment and control their dynamics. Fisheries managers routinely survey population characteristics, such as abundance, size, and other factors, in search of this information (Kohler and Hubert 1999). For a variety of reasons, however, analyses focusing on the important processes and relationships are attempted far less frequently in routine management. A major reason is the lack of accessible and versatile tools.

* Corresponding author: cpierce@iastate.edu

[1] Present address: Center for Quantitative Fisheries Ecology, 800 West 46th Street, Old Dominion University, Norfolk, Virginia 23508, USA.

Received November 5, 2003; accepted September 30, 2004
Published online May 3, 2005

Population consumption is an important process linking consumer populations to their prey populations (Gerking 1994). Population consumption is a measure of the impact a population has on its trophic base and is necessary to evaluate the food requirements of consumer populations in relation to the carrying capacity of the system. Unfortunately, population-level consumption information is difficult to obtain (Ney 1990). Direct consumption estimation via diet data and evacuation models is far too costly and time-consuming for management use, and even bioenergetics modeling is beyond reach of most routine management applications. Simple tools are needed to enable managers to incorporate this important aspect of fisheries dynamics into their routine decision-making (Ney 1990).

Our primary purpose was to develop simple regression models for estimating annual consumption in freshwater fish populations. Because bioenergetics modeling has become commonplace in research applications and results are now prominent in the literature, we sought to develop simple regression models that would approximate consumption estimates obtained from bioenergetics modeling. Our objectives were to (1) obtain data from the literature on population size, biomass, and annual population consumption estimated with bioenergetics models, (2) develop regressions predicting annual population consumption from either population size or biomass, and (3) compare predictions from our regression models with predicted consumption from other relatively simple models.

Methods

Literature search.—We searched the fisheries literature for reports of annual food consumption estimated by bioenergetics modeling, along with estimates of population size and biomass for entire populations of freshwater fishes. In some cases we calculated biomass from reported population size and mean fish weight, and population size was sometimes calculated from reported density and area in some cases.

Spirit Lake data collection.—Liao et al. (2004) recently assessed population size, biomass, diet, energy density, and water temperatures for black crappies *Pomoxis nigromaculatus*, largemouth bass *Micropterus salmoides*, northern pike *Esox lucius*, smallmouth bass *M. dolomieu*, walleyes *Sander vitreus*, and yellow perch *Perca flavescens* for 3 years in Spirit Lake, Iowa, and used the Fish Bioenergetics model 3 software package (FBM3; Hanson et al. 1997) to estimate population consumption for each species in each year. This yielded 18 estimates for development of our regression models and 18 populations with cohort data, which allowed us to generate consumption estimates from models requiring cohort data.

Regression models.—We developed simple linear regressions of annual population consumption versus population size and biomass. Predicted annual consumption estimates from the regression models were calculated for the Spirit Lake data set and compared with observed (FBM3-derived) consumption and estimates from other models (see below). Variables were $\log_{10}(X)$ transformed for analysis. Regression analyses were performed using the REG procedure (SAS Institute 1996).

Model comparisons.—We found three alternative models in the literature to compare with our regression models. Ney (1990, 1993) suggested that an estimate of annual cohort consumption could be obtained as

$$C = 5 \cdot B, \tag{1}$$

where C is annual cohort consumption and B is average cohort biomass. As a refinement to equation (1), Ney (1990, 1993) proposed that annual cohort consumption could also be estimated as

$$C = 2 \cdot P + 3 \cdot B, \tag{2}$$

where P is annual cohort production. Here, P is calculated as

$$P = g \cdot B, \tag{3}$$

where g is cohort specific growth rate. Here, g is calculated as

$$g = \log_e(W_2/W_1), \tag{4}$$

where W_2 is mean fish weight at the end of the year and W_1 is mean fish weight at the beginning of the year. Carline (1987) developed regression models estimating individual annual consumption of largemouth bass and northern pike as functions of initial mean weight and mean weight gain over the year. These models are solved for each cohort and expanded by cohort size to give cohort consumption. The form of these models is

$$C = a + b_1 \cdot W_1 + b_2 \cdot \Delta W, \tag{5}$$

where W_1 is as above and ΔW is the mean weight change during the year. Parameters for largemouth bass are as follows: $a = -176$, $b_1 = 0.95$ and $b_2 = 4.18$. Parameters for northern pike are $a = 211$, $b_1 = 2.45$, and $b_2 = 3.63$. Equation (1) is subsequently referred to as ''Ney model 1,'' equation (2) as ''Ney model 2,'' and equation (5) as the ''Carline model.'' All three of these models require cohort-level data and provide annual cohort consumption estimates. Population-level estimates are obtained by summing over cohorts.

Using data from the six species studied in Spirit Lake (Liao et al. 2004), we calculated predicted annual consumption by each population in each of the three study years using Ney model 1 and Ney model 2. For largemouth bass and northern pike, we also calculated predicted annual population consumption using the Carline model. These predictions, along with corresponding predicted consumption from the population size and biomass regressions were compared graphically with observed consumption (FBM3-derived) in each combination of species and year. Percent differences (D) between predicted (C_p) and observed (C_o) consumption were quantified as

$$\%D = [(C_o - C_p)/C_o] \cdot 100. \quad (6)$$

For an overall comparison of percent differences among prediction methods, we calculated means of the absolute values of percent differences. Absolute values were used to express the average percent difference, avoiding cancellation of positive and negative differences.

Results

Data Sets

Our literature search yielded 74 annual population-consumption estimates with corresponding estimates of population size (Table 1). Biomass estimates were available for 41 of these annual consumption estimates. Our data set included 14 different species, ranging from large-bodied (e.g., striped bass *Morone saxatilis* and lake trout *Salvelinus namaycush*) to small-bodied (e.g., black crappie and yellow perch). The estimates come from 10 different bodies of water, ranging from Lake Superior, the world's largest body of freshwater, to 88-ha Sparkling Lake, Wisconsin. The bodies of water include natural lakes and reservoirs, and range from coldwater to warmwater systems. Annual population-consumption estimates ranged from 97 kg/year to 94×10^6 kg/year (Table 1).

The study by Liao et al. (2004) in Spirit Lake yielded 18 annual population-consumption estimates with corresponding estimates of population size and biomass (Table 1). These estimates represented six different species, ranging from relatively large-bodied species (e.g., northern pike) to relatively small-bodied species (e.g., black crappie and yellow perch). Annual population-consumption estimates in Spirit Lake ranged from 2,500 to 595,000 kg/year.

Regressions

The regression of log-transformed annual consumption versus log-transformed mean annual population size was statistically significant ($P < 0.0001$) and explained 94% of the variation in log-transformed consumption. The regression equation for annual population consumption (C_p) was

$$\log_{10}(C_p) = -0.3018 + 1.0932 \cdot \log_{10}(S), \quad (7)$$

where S is annual average population size. This regression was based on 74 observations.

The regression of log-transformed annual consumption versus log-transformed mean annual biomass was also statistically significant ($P < 0.0001$) and explained 98% of the variation in log-transformed consumption (Figure 1). Here, the regression equation for C_p was

$$\log_{10}(C_p) = 0.5442 + 0.9962 \cdot \log_{10}(B), \quad (8)$$

where B is annual average biomass. This regression was based on 41 observations. Fit of the literature data and Spirit Lake data to the regression relationship calculated from all the observations was similar (Figure 1).

Model Comparisons

When applied to the Spirit Lake data set, annual population consumption predicted by the population-size regression varied from observed (FBM3-derived) consumption estimates by an average percent difference of 222%. Fifteen of the 18 consumption predictions were higher than observed consumption (Figure 2). In contrast, annual population consumption predicted by the biomass regression varied from observed consumption estimates by an average percent difference of only 24%. Individual percent differences ranged from 7% to 59%. In addition, the signs of differences were more balanced than for the population-size-based predictions; 10 of the 18 consumption predictions were higher than observed consumption (Figure 2).

Annual population consumption predicted by Ney model 1 varied from observed consumption estimates by an average percent difference of 58% and a range of 14–107%. Fourteen of the 18 consumption predictions from Ney model 1 were higher than observed consumption (Figure 2). Annual population consumption predicted by Ney model 2 varied from observed consumption estimates by an average percent difference of 24%, and a range of less than 1% to 67%. Six of the 18 consumption predictions from Ney model 2 were higher than observed consumption (Figure 2). Annual population consumption predicted by the Carline model, possible only for largemouth bass and northern pike, varied from observed consumption estimates by an average percent difference of 18%, and a range of 4–40%. Four of the six consumption predictions from the Carline model were higher than observed consumption (Figure 2).

Discussion

We assembled a data set consisting of 74 individual estimates of annual population consumption and mean annual population size, 41 of which also included estimates of mean annual biomass. The data set included 14 freshwater fish species from

TABLE 1.—Data used for developing regression models predicting annual fish population consumption. Data were obtained from the literature and from a recent study in Spirit Lake, Iowa.

Species	Population Year	Population Size	Population Biomass (kg)	Annual consumption (kg)
Stonewall Jackson Lake, West Virginia (Perry et al. 1995)				
Largemouth bass	1989	16,750	6,501	19,000
Sparkling Lake, Wisconsin (Lyons and Magnuson 1987)				
Walleye	1982	823	38	97
	1983	492	25	334
Lake Mendota, Wisconsin (Johnson et al. 1992)				
Walleye	1987	13,449	5,323	12,110
	1989	25,097	9,393	26,520
Northern pike	1987	1,314	1,778	4,500
	1989	13,065	9,193	42,800
Largemouth bass	1987	2,112	1,594	5,030
	1989	2,112	1,594	4,300
Norris Reservoir, Tennessee (Raborn et al. 2002)				
Striped bass *Morone saxatilis*	1996	96,901	192,418	719,836
Western Lake Erie, Ohio (Hartman and Margraf 1992)				
Walleye	1986	478,300,000	29,044,870	94,300,000
	1987	142,200,000	18,982,645	83,700,000
	1988	89,800,000	19,943,975	86,000,000
Bear Lake, Idaho and Utah (Ruzycki et al. 2001)				
Cutthroat trout *Oncorhynchus clarki*	1993	30,845	16,322	47,265
Lake trout *Salvelinus namaycush*	1993	15,738	36,596	46,420
Lake Superior, Minnesota (Negus 1995)				
Atlantic salmon *Salmo salar*	1989	159,255	38,262	114,080
Chinook salmon *O. tshawytscha*	1989	598,777	230,992	752,100
Coho salmon *O. kisutch*	1989	187,500	86,750	376,300
Kamloops trout (subspecies of rainbow trout)	1989	176,709	116,675	512,000
Steelhead (anadromus rainbow trout)	1989	32,412	18,834	101,810
Lake trout	1989	2,731,766	982,284	2,838,900
Flaming Gorge Reservoir, Utah and Wyoming (Yule and Luecke 1993)				
Lake trout	1990	120,600	258,935	331,000
Spirit Lake, Iowa (Liao et al. 2004)				
Black crappie	1995	7,735	1,077	4,040
	1996	14,841	2,159	6,887
	1997	5,889	681	2,500
Largemouth bass	1995	2,797	1,043	2,696
	1996	4,489	1,561	4,227
	1997	13,012	3,250	10,095
Northern pike	1995	1,748	1,098	4,255
	1996	3,072	1,943	7,305
	1997	2,280	1,846	7,462
Smallmouth bass	1995	6,056	871	2,518
	1996	6,711	1,119	2,868
	1997	8,137	1,329	3,590
Walleye	1995	106,873	16,620	105,802
	1996	561,757	57,227	464,815
	1997	774,766	101,360	594,567
Yellow perch	1995	206,009	13,256	35,603
	1996	720,653	50,519	152,229
	1997	298,991	18,237	45,249
Lake Michigan, Michigan (Rudstam et al. 1995)				
Burbot *Lota lota*	1988	3,155,000	1,056,000	3,476,000

TABLE 1.—Continued.

Species	Population			Annual consumption (kg)
	Year	Size	Biomass (kg)	
Lake Michigan, Michigan (Stewart and Ibarra 1991)				
Chinook salmon	1978	7,670,000		37,000,000
	1979	8,444,000		39,000,000
	1980	9,817,000		45,000,000
	1981	9,111,000		43,500,000
	1982	9,911,000		53,500,000
	1983	10,450,000		55,000,000
	1984	11,673,000		43,500,000
	1985	11,044,000		49,000,000
	1986	10,326,000		45,000,000
	1987	9,856,000		55,000,000
	1988	9,900,000		44,000,000
Coho salmon	1978	3,591,000		18,000,000
	1979	4,837,000		20,000,000
	1980	4,142,000		20,000,000
	1981	3,366,000		16,500,000
	1982	2,961,000		15,500,000
	1983	3,055,000		15,700,000
	1984	3,497,000		14,000,000
	1985	3,534,000		17,000,000
	1986	3,024,000		13,500,000
	1987	2,985,000		15,500,000
	1988	3,302,000		14,000,000
Lake trout	1978	5,193,000		7,400,000
	1979	5,210,000		7,400,000
	1980	5,234,000		7,400,000
	1981	4,817,000		7,400,000
	1982	4,859,000		7,350,000
	1983	4,531,000		7,000,000
	1984	3,291,000		6,000,000
	1985	3,702,000		6,000,000
	1986	4,292,000		5,500,000
	1987	3,875,000		5,400,000
	1988	3,422,000		6,000,000

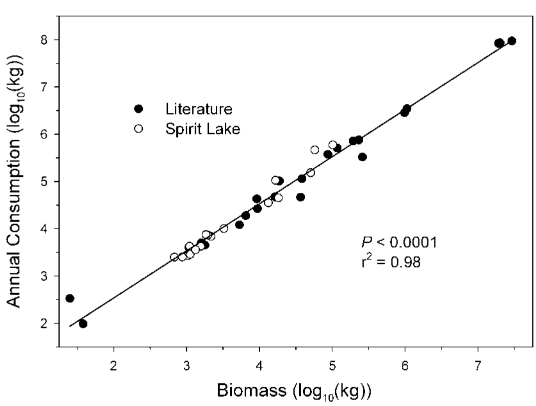

FIGURE 1.—Relationship of annual fish population consumption and mean annual biomass (data are from Table 1). Although literature and Spirit Lake, Iowa, observations are distinguished for visual comparison, the regression line was calculated from all observations.

10 different bodies of water. Broad ranges of consumption, population size, biomass, and body size were represented in our data set from systems ranging from small lakes to the Great Lakes, natural lakes to reservoirs, and warmwater to coldwater systems. The extent and breadth of our data set provided a strong basis for developing empirical models applicable to a wide variety of lake and reservoir fish populations, including many species of management concern.

We believe our biomass regression model (equation 8) will be a useful tool for fishery managers, enabling them to make reasonably accurate annual population-consumption predictions from mean annual biomass estimates. Compared with the complexity and considerable input data requirements of bioenergetics models such as FBM3, our biomass regression model is simple; requires only two input values; and can be applied to a variety of species, body sizes, and systems.

Other models have been proposed as simplified

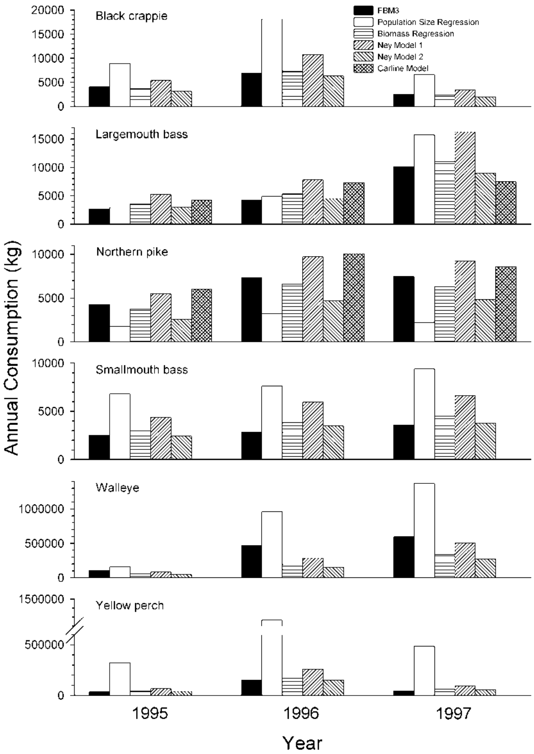

FIGURE 2.—Predictions of annual population consumption for Spirit Lake, Iowa, from five simple models versus the Fish Bioenergetics model 3 (FBM3; obtained from Liao et al. 2004). The population-size and biomass regressions were developed in our study.

alternatives to bioenergetics modeling, such as the models of Ney (1990, 1993) and Carline (1987). Comparisons of our regression models with the models of Ney and Carline reveal a tradeoff of complexity versus accuracy with respect to how closely they match FBM3-derived estimates. Our population-size regression requires only population size and, thus, would be the simplest model to apply, requiring the least amount of input information. Of the five models compared, it had by far the largest average percent difference from FBM3 estimates. Although the population-size regression explained a large percentage of the variance in log-transformed consumption, the poor match of predicted values with FBM3 estimates in our Spirit Lake data set suggests it is probably too crude to be useful. The two biomass-based models, our biomass regression and Ney model 1, are of intermediate complexity. In addition to population size, they also require mean fish weight to calculate biomass. Predictions of both models matched FBM3 estimates much more closely than the population-size regression, but the mean percent difference for the biomass regression model was less than half that of Ney model 1. The remaining two models, Ney model 2 and the Carline model, are the most complex, requiring information on population size, mean fish weight and growth. The mean percent difference for Ney model 2 was identical to that of our biomass regression model. The Carline model had a slightly lower mean percent difference than the biomass regression model and Ney model 2. Inclusion of additional information about the population does appear to result in increased accuracy of the predictions. However, this increase in accuracy comes at a price. Whereas our regression models are applied to whole-population data directly, Ney's models and the Carline model are applied to cohort data, which requires partitioning the population by age-class. Consumption is estimated for each cohort separately and then summed to give population consumption. This involves more effort than is required by our regression models. Our biomass regression model was superior to Ney model 1, equal to the more complex Ney model 2, and nearly as accurate as the more complex and species-specific Carline model; however, because our model is applied directly to whole-population data, it would be far easier to use than any of the other models.

A key assumption of our study is that bioenergetics-derived estimates of consumption are an appropriate standard for comparing estimates from simpler and presumably less accurate methods. Although we believe this assumption was reasonable for our purposes, we acknowledge the shortcomings of bioenergetics-based consumption estimates. Ney (1993) and Hansen et al. (1993) outlined numerous problems with the bioenergetics approach, ranging from error accumulation (due to the large number of input parameters) to potentially variable, but largely unknown, activity costs. A major determinant of the accuracy of population-consumption estimates is the accuracy of population abundance estimates, regardless of what approach is used (Hansen et al. 1993). Unfortunately, achieving accurate and precise estimates of population abundance remains one of the greatest challenges in many fisheries. Although we considered bioenergetics-derived consumption estimates as reasonably good standards, it is perhaps worth paraphrasing Ney's (1993) warning against thinking of them as a gold standard.

The three consumption models we compared with our regressions are not the only alternatives to bioenergetics modeling for estimation of consumption. Using a data set of 108 marine and freshwater fish populations, Palomares and Pauly (1998) developed a regression model predicting relative food consumption (consumption per unit biomass) as a function of growth, habitat temperature, caudal fin aspect ratio, and food type. Unfortunately, the habitat temperature and food type requirements of their model make it much more difficult to use than our biomass regression model. These additional requirements make the Palomares and Pauly model comparable with bioenergetics models in complexity.

Our biomass regression model of annual population consumption (equation 8) provides freshwater fishery managers with a simple, useful tool for routine applications. Similar empirical models have been developed for a variety of phenomena in ecology and fisheries (e.g., Hanson and Leggett 1982; Peters 1983; Carline 1987; Pauly 1989; Peters 1991; Downing and Plante 1993; He and Wurtsbaugh 1993; Randall et al. 1995; Palomares and Pauly 1998). In contrast to the exhaustive diet, growth, mortality, age structure, and thermal data required for bioenergetics modeling, population size and mean fish weight are routinely assessed by management agencies. Using our model, these data can be easily converted to annual population-consumption estimates, allowing analysis of trophic relationships and, ultimately, to more insightful management decision-making. In a review of trophic supply and demand issues in fisheries, Ney (1990) suggested that for routine management applications, methods simpler than bioenergetics modeling are needed for routine management assessments of population consumption. We believe our biomass regression model fulfills this need.

Acknowledgments

We thank Don Bonneau, Jim Christianson, and Tom Gengerke for agency support and encouragement; Phillip Dixon and Paul Hinz for statistical advice; and Phillip Dixon, John Downing, Bill Clark, Carolyn Griswold, Michael Hansen, Barry Johnson, Joe Morris, John Ney, Mark Pelham and several anonymous reviewers for ideas and comments on earlier drafts of this manuscript. Financial support was provided by the Iowa Department of Natural Resources and Iowa State University.

References

Carline, R. F. 1987. Simplified method based on bioenergetics modeling to estimate food consumption by largemouth bass and northern pike. Transactions of the American Fisheries Society 116:224–231.

Downing, J. A., and C. Plante. 1993. Production of fish populations in lakes. Canadian Journal of Fisheries and Aquatic Sciences 50:110–120.

Gerking, S. D. 1994. Feeding ecology of fish. Academic Press, San Diego, California.

Hansen, M. J., D. Boisclair, S. B. Brandt, S. W. Hewett, J. F. Kitchell, M. C. Lucas, and J. J. Ney. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here? Transactions of the American Fisheries Society 122: 1019–1030.

Hanson, J. M., and W. C. Leggett. 1982. Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences 39:257–263.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish Bioenergetics Model 3. University of Wisconsin Sea Grant Institute, Technical Report WISCU-T-97-001, Madison.

Hartman, K. J., and F. J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie. Transactions of the American Fisheries Society 121:245–260.

He, E., and W. A. Wurtsbaugh. 1993. An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. Transactions of the American Fisheries Society 122:717–730.

Johnson, B. M., S. J. Gilbert, R. S. Stewart, L. G. Rudstam, Y. Allen, D. M. Fago, and D. Dreikosen. 1992. Piscivores and their prey. Pages 319–351 *in* J. F. Kitchell, editor. Food web management: a case study of Lake Mendota. Springer-Verlag, New York.

Kohler, C. C., and W. A. Hubert, editors. 1999. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Liao, H., C. L. Pierce, and J. G. Larscheid. 2004. Consumption dynamics of the adult piscivorous fish community in Spirit Lake, Iowa. North American Journal of Fisheries Management 24:890–902.

Lyons, J., and J. J. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. Transactions of the American Fisheries Society 116: 29–39.

Negus, M. T. 1995. Bioenergetics modeling as a salmonine management tool applied to Minnesota waters of Lake Superior. North American Journal of Fisheries Management 15:60–78.

Ney, J. J. 1990. Trophic economics in fisheries: Assessment of demand-supply relationships between predators and prey. Reviews in Aquatic Sciences 2: 55–81.

Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Transactions of the American Fisheries Society 122:736–748.

Palomares, M. L., and D. Pauly. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Marine and Freshwater Research 49: 447–453.

Pauly, D. 1989. Food consumption by tropical and temperate fish populations: some generalizations. Journal of Fish Biology 35(Supplement A):11–20.

Perry, W. B., W. A. Janowsky, and F. J. Margraf. 1995. A bioenergetics simulation of the potential effects of angler harvest on growth of largemouth bass in a catch-and-release fishery. North American Journal of Fisheries Management 15:705–712.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK.

Peters, R. H. 1991. A critique for ecology. Cambridge University Press, Cambridge, UK.

Raborn, S. W., L. E. Miranda, and M. T. Driscoll. 2002. Effects of simulated removal of striped bass from a southeastern reservoir. North American Journal of Fisheries Management 22:406–417.

Randall, R. G., J. R. M. Kelso, and C. K. Minns. 1995. Fish production in freshwaters: are rivers more productive than lakes? Canadian Journal of Fisheries and Aquatic Sciences 52:631–643.

Rudstam, L. G., P. E. Peppard, T. W. Fratt, R. E. Bruesewitz, D. W. Coble, F. D. Copes, and J. F. Kitchell. 1995. Prey consumption by the burbot (*Lota lota*) population in Green Bay, Lake Michigan, based on a bioenergetics model. Canadian Journal of Fisheries and Aquatic Sciences 52:1074–1082.

Ruzycki, J. R., W. A. Wurtsbaugh, and C. Luecke. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah−Idaho. Transactions of the American Fisheries Society 130: 1175–1189.

SAS Institute. 1996. SAS user's guide: version 6.03. SAS Institute, Cary, North Carolina.

Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. Canadian Journal of Fisheries and Aquatic Sciences 48:909–922.

Yule, D. L., and C. Luecke. 1993. Lake trout consumption and recent changes in the fish assemblage of Flaming Gorge Reservoir. Transactions of the American Fisheries Society 122:1058–1069.