Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats

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Abstract: Species-specific production rate per unit biomass (P/B, per year) ratios were calculated for 79 freshwater fish species of eastern Canada. P/B (per year) ratios were calculated using two methods, which were based on allometry with fish weight-at-maturity and life expectancy, respectively. P/B (per year) values obtained by the two methods were significantly correlated, as expected from life history theory, since the two predictors (longevity, size-at-maturity) were themselves correlated. Species-specific P/B (per year) ratios were also significantly correlated with field observations of P/B from published sources. The estimation of P/B based on allometry with fish size is recommended because of its utility; the predictive equation is P/B (per year) $= 2.64 W_{\mathrm{mat}}^{-0.35}$, where W_{mat} is weight-at-maturity. Both the coefficient 2.64 and the exponent –0.35 of this equation are provisional and require further validation from field studies of fish production. More accurate estimates of P/B are possible if population-specific information on size-at-maturity or mean size is known. The product of average fish biomass and estimated P/B coefficients (habitat productivity index (HPI) $= B \times P/B$) is a proposed measure of habitat productive capacity.

Résumé : Nous avons calculé les rapports spécifiques à l'espèce P/B (an^{-1}) (taux de production par unité de biomasse) pour 79 espèces de poissons dulcicoles de l'est du Canada. Les rapports P/B (an^{-1}) ont été calculés par deux méthodes, fondées sur l'allométrie avec respectivement le poids à la maturité du poisson et l'espérance de vie. Les valeurs de P/B (an^{-1}) obtenues par les deux méthodes étaient significativement corrélées, comme on pouvait le prévoir théoriquement, car deux prédicteurs (longévité, taille à la maturité) étaient eux-mêmes corrélés. Les rapports spécifiques P/B (an^{-1}) étaient aussi significativement corrélés aux observations de terrain fournies par diverses sources publiées. Nous recommandons l'estimation de P/B basée sur l'allométrie avec la taille des poissons, du fait de son utilité; l'équation prédictive est : P/B (an^{-1}) $= 2{,}64 W_{\mathrm{mat}}^{-0.35}$, W_{mat} correspondant au poids à la maturité. Le coefficient 2,64 et l'exposant –0,35 sont provisoires et doivent être validés par des travaux de terrain sur la production des poissons. Il est possible d'obtenir des estimations plus précises de P/B si on dispose d'information spécifique à la population sur la taille à la maturité ou sur la taille moyenne. Nous proposons, pour mesurer la capacité productive d'un habitat, de faire le produit de la biomasse moyenne de poisson et des coefficients estimés de P/B (indice de productivité de l'habitat $= B \times P/B$).

[Traduit par la Rédaction]

Introduction

Fish production is the best indicator of the quantitative performance of a fish population in any type of habitat, and it is a measure of productive capacity (Jones et al. 1996; Minns et al. 1996). However, estimation of production in the field is time consuming and costly, and often, surrogates of production are used to evaluate habitat suitability or capacity. For any defined time period, fish production is the product of average biomass and specific growth rate, and therefore, fish biomass and fish production are correlated (Downing et al. 1990; Downing and Plante 1993; Randall et al. 1995). Animal biomass is sometimes used as a surrogate of production (Banse and Mosher 1980). For freshwater fish, the slope of the regression of production versus biomass is not significantly different from unity, indicating that specific production does not vary systematically with biomass, and therefore, fish production can be approximated by using an average production to biomass ratio (Downing and Plante 1993). Specific or population production (i.e., production per unit biomass, P/B) varies with fish size, however, and a more accurate estimate of production is possible if both biomass and fish size are used as predictors (Boudreau and Dickie 1989; Downing and Plante 1993; Randall et al. 1995). Fish growth and mortality are related to fish size (Peters 1983), and consideration of fish size accounts for some of the variability in specific production.

Specific production (P/B) considered in this paper is based on a 1-year time frame (annual production divided by mean annual biomass), and it applies to populations in steady state (not increasing or decreasing in abundance with time). The P/B (per year) ratio indicates how quickly biomass is potentially changing. For fish populations in lakes, most P/B ratios varied between 0.2 and 5.0, and were inversely related to maximum size of the fish in the populations and positively related to lake productivity (Downing et al. 1990; Downing and Plante 1993). Most P/B ratios were within this range for fishes inhabiting rivers as well (Mann and Penczak 1986). In a population dynamic context, maxi-

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Table 1. Life history characteristics of 79 species of fish that inhabit the freshwaters of eastern Canada.

Species	Code	L_{mat} (SL, mm)	L_{max} (SL, mm)	T_{mat} (years)	T_{max} (years)	W_{mat} (g)	W_{max} (g)	Method	P/B_Z	P/B_W	P/B
Longnose gar	F0041	500	1830	6	32	1945.3	78 548.0	LMAT	0.14	0.09	0.19
Bowfin	F0051	610	870	4	25	3055.4	8 977.4	LW	0.18	0.08	0.16
Alewife	F0061	138	205	3	6	36.6	108.8	LW	0.73	0.37	0.75
Gizzard shad	F0063	279	521	2	6	472.5	3 100.4	LW	0.73	0.15	0.31
Pink salmon	F0071	411	508	2	2	1105.3	2 057.38	LMAT	2.14	0.11	0.23
Coho salmon	F0073	635	900	3	3	3875.7	10 452.2	LMAT	1.43	0.07	0.15
Chinook salmon	F0075	750	968	3	9	5463.0	11 550.8	LW	0.49	0.06	0.13
Rainbow trout	F0076	349	915	4	8	681.5	12 331.6	LW	0.55	0.13	0.27
Atlantic salmon	F0077	800	1550	3	5	7545.0	48 997.3	LMAT	0.87	0.06	0.12
Brown trout	F0078	258	874	3	18	361.6	11 505.4	LW	0.25	0.17	0.34
Brook trout	F0080	156	350	3	9	52.9	627.1	LWL	0.49	0.33	0.66
Lake trout	F0081	510	1310	5	20	2059.6	30 376.3	LMAT	0.22	0.09	0.18
Lake whitefish	F0091	236	526	4	17	229.2	2 771.4	LWL	0.26	0.20	0.39
Lake herring	F0093	246	395	3	13	251.5	1 006.4	LMAT	0.34	0.19	0.38
Round whitefish	F0102	183	468	3	14	107.2	1 629.6	LMAT	0.32	0.26	0.51
Rainbow smelt	F0121	125	297	3	6	15.7	192.9	LW	0.73	0.50	1.01
Northern pike	F0131	534	1000	3	12	1349.8	8 889.8	LW	0.37	0.11	0.21
Muskellunge	F0132	650	1426	4	22	4145.6	38 659.6	LMAT	0.20	0.07	0.14
Grass pickerel	F0133					9.7	75.3	WMAX		0.60	1.19
Central mudminnow	F0141	110	132	1	4	24.7	44.7	LMAT	1.08	0.43	0.86
Quillback	F0161	472	660	6	12	2501.8	7 615.4	LW	0.37	0.09	0.17
Longnose sucker	F0162	240	583	6	24	234.3	3 042.8	LMAT	0.19	0.20	0.39
White sucker	F0163	253	487	4	15	280.3	1 983.4	LW	0.30	0.18	0.37
Chubsucker	F0164					15.9	128.3	WMAX		0.50	1.00
Silver redhorse	F0168	391	635	5	14	957.2	3 879.1	LMAT	0.32	0.12	0.24
Shorthead redhorse	F0171	195	620	3	14	138.7	4 818.8	LW	0.32	0.23	0.47
River redhorse	F0173					147.0	1 400.5	WMAX		0.23	0.46
Goldfish	F0181	175	457	4	30	274.4	2 384.7	LW	0.15	0.18	0.37
Redbelly dace	F0182	46	61	1	8	2.0	5.0	LMAT	0.55	1.03	2.07
Finescale dace	F0183	59	80	2	8	4.1	10.8	LMAT	0.55	0.80	1.61
Lake chub	F0185	108	189	3	5	23.4	123.9	LMAT	0.87	0.44	0.88
Carp	F0186	353	800	4	20	1199.7	13 424.8	LW	0.22	0.11	0.22
Brassy minnow	F0189	57	158	1	4	3.7	74.4	LMAT	1.08	0.83	1.67
Hornyhead chub	F0192	93	188	3	4	15.2	122.0	LMAT	1.08	0.51	1.02
Golden shiner	F0194	64	211	2	7	4.2	164.6	LW	0.62	0.80	1.59
Emerald shiner	F0196	42	124	1	4	0.9	21.3	LW	1.08	1.38	2.76
Common shiner	F0198	74	169	1	5	7.9	90.1	LMAT	0.87	0.64	1.28
Blackchin shiner	F0199	37	71	1	4	0.9	4.6	LW	1.08	1.37	2.73
Blacknose shiner	F0200	24	81	1	3	0.3	11.2	LMAT	1.43	2.00	4.00
Spottail shiner	F0201	55	137	1	4	2.6	38.8	LW	1.08	0.94	1.89
Mimic shiner	F0206	35	63	1	2	0.9	5.5	LMAT	2.14	1.36	2.73
Bluntnose minnow	F0208	50	78	1	3	1.7	7.3	LW	1.43	1.10	2.21
Fathead minnow	F0209	54	73	1	4	4.9	9.7	LWL	1.08	0.76	1.51
Blacknose dace	F0210	49	58	2	3	2.4	4.3	LMAT	1.43	0.97	1.94
Longnose dace	F0211	74	118	2	5	7.9	32.5	LMAT	0.87	0.64	1.28
Creek chub	F0212	87	240	2	5	13.6	185.0	LWL	0.87	0.53	1.06
Fallfish	F0213		420			140.5	1 198.2	LMAX		0.23	0.47
Pearl dace	F0214	94	132	2	4	15.9	37.6	LWL	1.08	0.50	1.00
Brown bullhead	F0233	161	297	3	8	79.5	488.9	LW	0.55	0.29	0.57
Channel catfish	F0234	337	1004	7	24	623.5	14 261.9	LMAT	0.19	0.14	0.28
Tadpole madtom	F0236	62	110	1	3	4.7	26.6	LMAT	1.43	0.77	1.53
American eel	F0251	457	1520	9	27	462.3	4 390.5	LW	0.17	0.15	0.31
Banded killifish	F0261	53	102	2	3	3.0	21.5	LMAT	1.43	0.95	1.80
Burbot	F0271	370	775	3	13	816.3	6 833.5	LMAT	0.34	0.13	0.25
Brook stickleback	F0281	50	87	1	3	2.5	13.7	LMAT	1.43	0.95	1.90
Threespine stickleback	F0282					0.5	2.9	WMAX		1.72	3.45
Ninespine stickleback	F0283	35	68	2	3	0.9	6.8	LMAT	1.43	1.36	2.73

Table 1 (*concluded*).

Species	Code	L_{mat} (SL, mm)	L_{max} (SL, mm)	T_{mat} (years)	T_{max} (years)	W_{mat} (g)	W_{max} (g)	Method	P/B_Z	P/B_W	P/B
Fourspine stickleback	F0284	41	52	2	2	1.4	3.2	LMAT	2.14	1.16	2.33
Trout-perch	F0291	78	123	2	4	6.5	51.7	LW	1.08	0.69	1.37
White perch	F0301	254	482	2	12	412.1	3 067.7	LW	0.37	0.16	0.32
White bass	F0302	115	322	3	8	47.0	684.6	LW	0.55	0.34	0.69
Rock bass	F0311	54	222	2	10	4.9	338.7	LW	0.44	0.75	1.51
Green sunfish	F0312	76	169	2	9	8.5	90.1	LMAT	0.49	0.62	1.25
Pumpkinseed	F0313	59	219	2	9	6.5	391.2	LW	0.49	0.68	1.37
Bluegill	F0314	93	250	3	9	25.3	502.2	LW	0.49	0.43	0.85
Smallmouth bass	F0316	264	423	4	12	380.8	1 509.0	LW	0.37	0.16	0.33
Largemouth bass	F0317	272	453	3	15	429.0	2 014.6	LW	0.30	0.16	0.32
Black crappie	F0319	192	300	3	9	150.5	563.7	LW	0.49	0.23	0.46
Yellow perch	F0331	175	334	4	10	96.1	650.0	LW	0.44	0.27	0.53
Sauger	F0332	283	593	4	13	376.8	3 193.5	LMAT	0.34	0.17	0.33
Walleye	F0334	328	641	4	20	527.7	3 998.7	LW	0.22	0.15	0.29
Iowa darter	F0338	43	58	1	3	1.6	4.3	LMAT	1.43	1.11	2.22
Johnny darter	F0341	37	60	1	4	1.1	4.8	LMAT	1.08	1.29	2.58
Logperch	F0342	106	150	2	3	14.9	39.6	LW	1.43	0.51	1.03
Tessellated darter	F0346	43	77	1	4	1.6	9.7	LMAT	1.08	1.11	2.22
Brook silverside	F0361	74	81	1	2	7.9	11.2	LMAT	2.83	0.64	1.28
Freshwater drum	F0371	292	940	5	17	393.6	19 172.6	LW	0.26	0.16	0.33
Mottled sculpin	F0381	60	82	2	4	4.3	11.5	LMAT	1.08	0.79	1.58
Slimy sculpin	F0382	63	120	3	7	5.0	34.1	LMAT	0.62	0.75	1.51

Note: Code, unique identification for each species; Method, method for estimating W_{mat} and W_{max} (LW, weight estimated using length–weight coefficients from the productive capacity database (Appendix 1); LWL, length–weight coefficients from Appendix 2; LMAT, weight estimated from eq. 3 or 4 (Table 2); WMAX, W_{mat} estimated from eq. 2; LMAX, weight estimated from eqs. 1, 3, and 4); P/B_Z and P/B_W, ratio of production to biomass as estimated from longevity and weight-at-maturity, respectively; P/B, production to biomass ratio based on weight-at-maturity, with an adjusted coefficient (see text).

mum P/B is equal to the maximum rate of population increase (R, i.e., $P/B_{max} = R_{max}$ (Peters 1983)). Rate of population growth (and P/B) can be used to estimate the amount of time required for a population to establish itself after a catastrophic decline, to colonize a new habitat, or to withstand exploitation (Peters 1983; Charnov 1993). Both P/B and R_{max} are expressions of growth potential (biomass and numbers) and are linked to the productive capacity of the habitat.

As will be seen, the P/B ratio varies inversely with fish size-at-maturity and longevity and is therefore specific for species and populations. P/B has been calculated for species based on their life span (Waters 1977), body size (Dickie 1972; Banse and Mosher 1980), and life history growth and mortality patterns (Allen 1971; Waters 1977; van Straalen 1985). The objective of this study was to calculate species-specific P/B (per year) ratios for several species of fishes ($n = 79$) that inhabit the freshwaters of eastern Canada. P/B (per year) ratios are calculated and compared using two methods that are based on allometry with fish size and longevity. The generalized species-specific P/B (per year) ratios are compared with actual field estimates (literature) for a subset of the species. Finally, a potential application for the use of species-specific P/B ratios to evaluate habitat suitability and capacity is proposed and examined.

Methods

Fish database sources

Three databases were used to obtain species-specific informa-

tion on life history traits. Fish lengths were given as standard length (SL), fork length (FL), or total length (TL) in millimetres, depending on the database (see below). Where necessary, TL and FL were converted to SL by dividing by 1.2 and 1.1, respectively (Portt et al. 1991). Weights are in grams.

Portt et al. (1991) and Minns et al. (1993) summarized the life history characteristics of 75 species of freshwater fishes that inhabit inland lakes in Ontario. Hereafter, the Portt et al. (1991) and Minns et al. (1993) database is referred to as the LakeDB. Species-specific length-at-maturity (L_{mat}) (SL, millimetres), maximum length (L_{max}) (SL, millimetres), age-at-maturity (T_{mat}, years), and maximum age (T_{max}, years) from the LakeDB were used for this study. Recognizing that these traits are population dependent, the authors used medial values for each species when possible (for further details, see Minns et al. 1993).

Parameters a and b for the length–weight regression $W = aL^b$ for a subset of the species were derived from a productive capacity fish database, which was based on electrofishing samples from the lower Great Lakes (Moore et al. 1998) (hereafter referred to as the CapacityDB). Species for which at least 10 individuals were measured for length (usually FL; Valere 1996) and for which the coefficient of determination was >0.50 were used (Appendix 1). The total number of species meeting these criteria was 36, of which four were found in the CapacityDB but not in the LakeDB. The total number of freshwater species considered in this study was therefore 79. Length–weight data for an additional five species (used for validation, see below) were obtained from the literature (Appendix 2). The length–weight parameters were used to convert the LakeDB length data (maturity and maximum) to weights. For the remaining species for which the length–weight coefficients were not known ($n = 38$), weight-at-maturity (W_{mat}) or maximum weights (W_{max}) were estimated by regression (Table 1). The CapacityDB was also used to estimate the L_{max} of fish for each

taxon, based on the arithmetic average of the 10 largest individuals in the sample (Pauly 1984). Maximum fish lengths from CapacityDB were compared with the maximum sizes reported by Portt et al. (1991) and Minns et al. (1993) to test for consistency in the species size data between data sets.

For a subset of species, asymptotic lengths (L_{inf}) and asymptotic weights (W_{inf}) were obtained from a published database (FishBase 98; Froese and Pauly 1998). These parameters were available for 142 populations of 28 species (Froese and Pauly 1998). Maximum size of fish species in the LakeDB was compared with these asymptotic sizes.

Estimation of *P/B* ratios

Data from the three databases were used to estimate species-specific *P/B* ratios using the life history information on fish W_{mat} (grams) and longevity (years).

Allometric theory based on animal energetics predicts that *P/B* declines with weight as $W^{-0.25}$ (Lavigne 1982). However, Banse and Mosher (1980) showed that the weight exponent was significantly different from –0.25 within taxonomic groups with similar production efficiencies; they found an exponent of –0.37. Other researchers have also found coefficients that were different than expected from allometric theory (Dickie et al. 1987; Boudreau and Dickie 1989; Randall et al. 1995). Dickie et al. (1987), Boudreau and Dickie (1989), and Boudreau et al. (1991) showed that the different slopes were related to the influence of both primary (physiological) and secondary (ecological) scaling factors. A regression (log *P/B* versus log *W*) across taxonomic groups (e.g., invertebrates and fish) gave a lower slope (about –0.2) than a regression within a taxonomic group (e.g., fish with a slope of about –0.3) (see fig. 1*a* and table 1 in Boudreau and Dickie 1989). The secondary scaling factor was related to predator–prey interactions and energy transfer between trophic positions (Thiebaux and Dickie 1992, 1993). For this paper, *P/B* was estimated using an allometric equation developed by Randall et al. (1995) for fish inhabiting lakes and rivers: $\log P/B = 0.12 - 0.35 \log W_{mat} + 0.18H$, where W_{mat} is the weight-at-maturity (grams) and *H* is a habitat indicator variable (0 for lakes, 1 for rivers). (Note that in the original paper, Randall et al. (1995) used average fish weight of fish in the community rather than W_{mat}.) The partial slope of –0.35 with W_{mat} in this regression is consistent with the exponent of the within-fish subgroup discussed above. Retransformed assuming a lake habitat gives the allometric formula $P/B_W = 1.32 W_{mat}^{-0.35}$. The estimate of P/B_W was applied to all 79 species of fishes.

Hoenig (1983) demonstrated that plots of total mortality versus T_{max} were negatively correlated for three taxonomic groups, mollusks, fishes, and cetaceans, and could be described by the predictive equation $\ln Z = 1.44 - 0.982 \ln T_{max}$, where *Z* is the instantaneous mortality rate (annual) and T_{max} is the maximum age in the population. Mortality rate is inversely related to longevity. Parameters for the regression were similar for all three groups of animals, and Hoenig recommended that the combined data set be used for prediction. For balanced populations, annual *P/B* is approximately equal to instantaneous mortality, if mortality is constant with age (Dickie 1972; van Straalen 1985; Mertz and Myers 1998), i.e., *P/B* = *Z*, and therefore, the Hoenig equation can also be used as a first-order estimate of population production (reexpressed in a nonlog form: $P/B_Z = 4.22 T_{mat}^{-0.982}$). The estimate of P/B_Z was applied to 75 of 79 species for which T_{max} was known. The two estimates of *P/B* (per year) were compared by correlation analysis (Pearson product-moment) and were validated by interspecies correlation with field estimates of *P/B* from Downing and Plante (1993).

Results

Life history characteristics

The L_{max} varied among species from 52 to 1830 mm (Ta-

ble 1). Many of the species were small and short-lived; about 70% of the 79 species matured at age 3 or less.

The L_{mat} was related to L_{max} as described by the equation $\log L_{mat} = -0.005 + 0.880 \log L_{max}$ ($n = 74$, $F = 642.2$, $R^2 = 0.90$, $P < 0.001$) (Fig. 1; Table 2). The L_{max} and L_{inf} predicted from the von Bertalanffy growth equation should be reasonably close (say ±30%; Froese and Pauly 1998). In conformity with this, L_{max} (LakeDB) and L_{inf} (FishBase98) were significantly correlated (Fig. 2), confirming that L_{max} provided an approximation of L_{inf} and that the sizes in the LakeDB were approximately medial values for each species (Minns et al. 1993). The corresponding equation for the relationship between W_{mat} and W_{max} for the subset of species was $\log W_{mat} = -0.762 + 0.931 \log W_{max}$ ($n = 38$, $F = 191.6$, $R^2 = 0.84$, $P < 0.0001$) (Table 2).

Species-specific L_{max} values from the LakeDB were also significantly correlated with maxima for 35 species calculated from field data collected from the Great Lakes in the CapacityDB (Fig. 3). This result was consistent with the hypothesis that maximum size can be estimated from field samples by using the 10 largest individuals in large samples (Pauly 1984). Together, Figs. 2 and 3 confirmed that all three databases were consistent and provided roughly similar trends in maximum size.

P/B ratios

For the 79 species of fishes, *P/B* (per year) ratios as calculated by the two methods were significantly correlated (Fig. 4). The average *P/B* values were least for P/B_W and highest for P/B_Z (Table 3). Most of the values for P/B_Z were within the bounds of 0.2 and 5, consistent with field observations of fish biomass and production in lakes around the world (Downing and Plante 1993). However, this was not the case for the P/B_W estimates, which were lower (37% were less than 0.2). The slope of $\log P/B$ on $\log W_{mat}$ was –0.19 for P/B_Z, which was different from the slope of –0.35 used for P/B_W (Table 3).

P/B ratios estimated by the two methods were correlated with published information on *P/B* ratios for fish species in lakes (Downing and Plante 1993). A subset of data from Downing and Plante (1993), which included nine species that were also found in our database, were used for this comparison. The subset included 24 populations from nine lakes in Canada; average biomass (kilograms per hectare), annual production (kilograms per hectare per year), and *P/B* (per year) ratios were given for each population. Both the P/B_Z and P/B_W estimates were correlated with the observed ratios in the published field studies (Table 4; where more than one estimate of *P/B* was available for three of the nine species, an average was used). Although the sample size was small ($n = 9$ species), these results suggested that the species-specific estimators of P/B_Z and P/B_W were useful predictors of actual *P/B* ratios. Both methods, however, underestimated on average the actual specific production coefficients as measured in the field.

Theoretically, *P/B* estimates based on population size-at-maturity data would be more accurate than the above estimates that are based on species "average" size-at-maturity data. For the published data on fish production in lakes, Downing and Plante (1993) also reported the maximum individual size of fish in the populations. Population size-at-

Fig. 1. Scatterplot matrices of life history traits of the species of fishes listed in Table 1. Each point represents one of 79 species. The traits are L_{mat} (SL), L_{max} (SL), T_{mat}, T_{max}, and Z. Species length and age data were from Portt et al. (1991) and Minns et al. (1993). Mortality was estimated from T_{max} (see text). Data are plotted on a $\log_{10}$ scale.
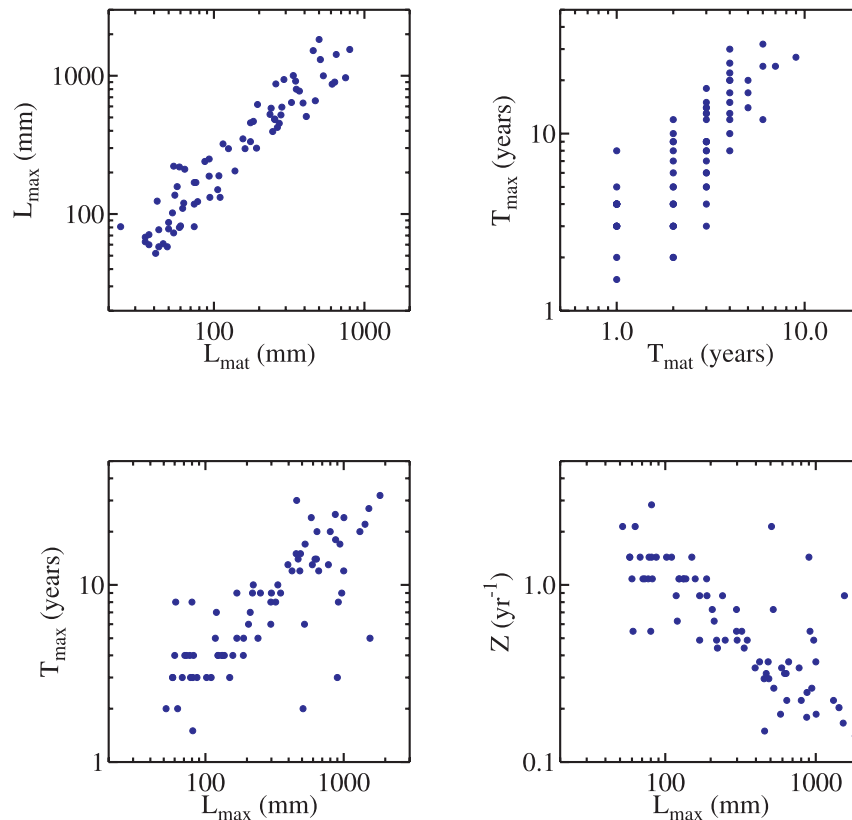
Table 2. Regressions used to estimate W_{mat} and W_{max} in Table 1.

Equation	Dependent	Independent	n	F statistic	Intercept	Slope	R^2
1	$\log L_{mat}$	$\log L_{max}$	74	642.2	–0.005	0.880	0.90
2	$\log W_{mat}$	$\log W_{max}$	38	191.6	–0.762	0.931	0.84
3	$\log W_{mat}$	$\log L_{mat}$	38	1098.1	–4.491	2.884	0.97
4	$\log W_{max}$	$\log L_{max}$	38	625.6	–4.372	2.842	0.94

maturity for 16 of the 24 populations (maximum size was constant in eight populations) was estimated using the regression of W_{mat} on W_{max} (Table 2, eq. 2). Coefficients of determination for the regression of P/B on species and population W_{mat} for the 16 populations were $R^2 = 0.65$ and $R^2 = 0.62$, respectively, and thus, there was little difference in the predictors in this case. This was likely due to the significant correlation between the species average and the population-specific maturity weights for the species in this data set ($n = 16$, $F = 27.7$, $R^2 = 0.67$, $P < 0.0001$).

For the 24 populations, production rate was estimated as the product of the reported biomass (kilograms per hectare from Downing and Plante 1993) and the species-specific P/B_W ratios that were determined in this study. The correlation between the expected and observed production rates was highly significant ($n = 24$, $F = 61.8$, $R^2 = 0.74$, $P < 0.0001$) (Fig. 5). One species (*Perca flavescens*) was a significant outlier (studentized residual = 4.26) in this regression. The coefficient of determination for the regression of biomass alone on production for the 24 populations was 0.65, and therefore, the precision of the prediction increased

by 9% (from 0.65 to 0.74, $n = 24$) if a species-specific rather than an average P/B ratio was used. First-order approximations of production of a variety of fish species can be estimated from information on field biomass and species P/B ratios.

Discussion

Species-specific P/B (per year) ratios are potentially useful to fisheries biologists for determining first-order estimates of production from field biomass data. The following topics that relate to the application and limitations of the P/B coefficients developed in this study are discussed below: characteristics of the species database, validation of the species-specific P/B ratios, and finally the potential use of P/B coefficients for determining habitat suitability and productive capacity from field estimates of fish biomass.

Database characteristics and limitations

The P/B (per year) ratios that have been generated are applicable to freshwater fish populations inhabiting the differ-

Fig. 2. Correlation between L_{max} (SL) as reported in the LakeDB (Portt et al. 1991; Minns et al. 1993) and L_{inf} (SL) as reported for a number of species and populations in FishBase 98 (Froese and Pauly 1998). The vertical row of circles for some of the species values of L_{max} shows the range of L_{inf} values reported for individual populations (Froese and Pauly 1998). The broken line is the least-squares regression and the solid line shows the 1:1 relationship.
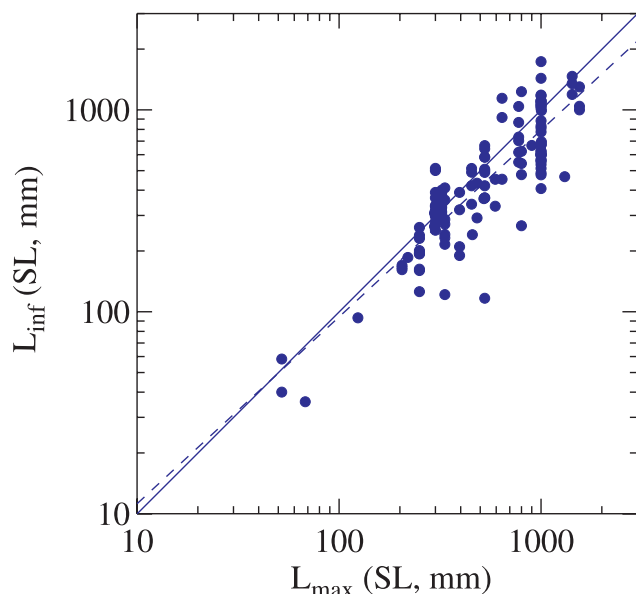

Fig. 3. Comparison of L_{max} (SL) as estimated as the average of the 10 largest individuals in the CapacityDB and as reported for 35 species in the LakeDB. The broken line is the least-squares regression and the solid line shows the 1:1 relationship.
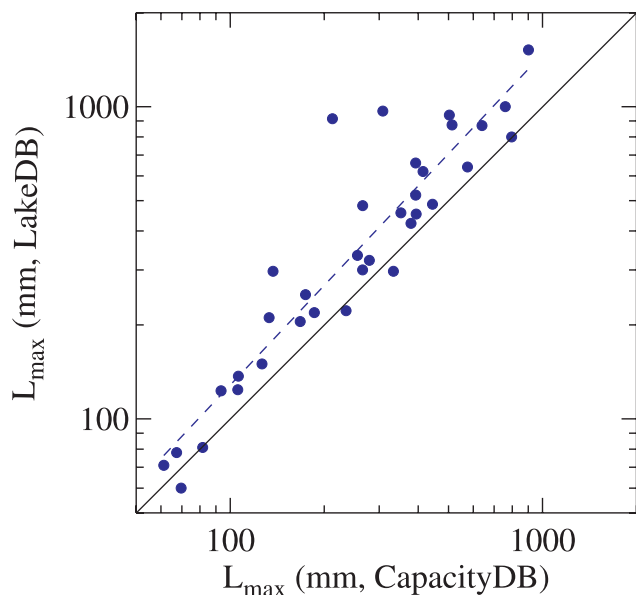
ent areas of eastern Canada. Data on life history parameters summarized by Portt et al. (1991) and Minns et al. (1993) were originally collated because of an interest in the taxocene assemblage structure of the fish species commonly found in inland lakes in Ontario. Additional growth data (length–weight) were available for several of the same spe-

Fig. 4. Comparison of P/B ratios for 79 species of fish as estimated from mortality (P/B_Z) and allometry with weight-at-maturity (P/B_W, using the adjusted coefficient of 2.64; see text). Axes are on a $\log_{10}$ scale.
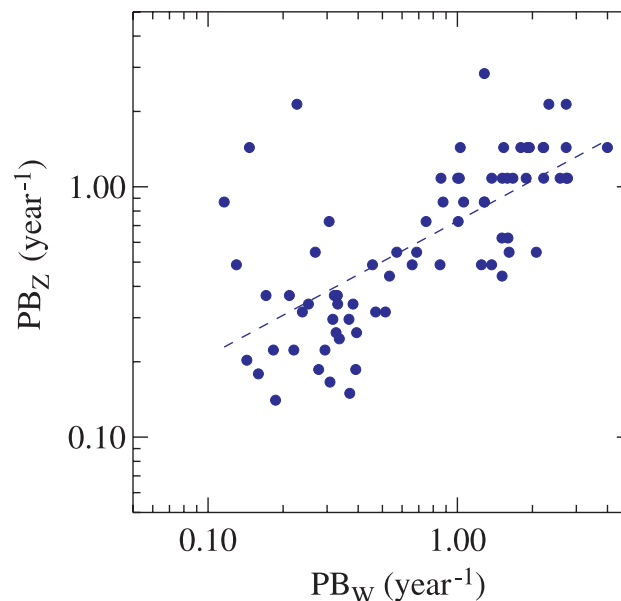
Table 3. Comparison of P/B ratios calculated from information on longevity (P/B_Z) and fish weight-at-maturity (P/B_W).

Method	Average	Range	Percent	Slope (95% CL)
P/B_Z	0.8	0.1–2.8	92	−0.19 (−0.14, −0.24)
$P/B_W{}^a$	0.5	0.1–2.0	63	−0.35 (−0.23, −0.47)
$P/B_W{}^b$	1.1	0.1–4.0	90	

Note: Percent is the percentage of values between 0.2 and 5.0 (see text). The slope of the regression of log P/B on log weight-at-maturity is indicated.
[a] Slope and 95% CL from Randall et al. (1995).
[b] P/B calculated using the adjusted proportionality coefficient (see text). The slope remains as −0.35.

cies from samples collected from the lower Great Lakes. Many of the 79 species also occur elsewhere in eastern Canada, and some occur in both lake and river habitats. Zoogeographically, all of these species are listed as part of the Atlantic drainage basin in eastern Canada (Scott and Crossman 1973), and they include many of the common species that inhabit this Atlantic region. The 79 species comprised 48% of the 165 species reported for Ontario (Mandrak and Crossman 1992) and a large proportion of the freshwater species found in Quebec, Newfoundland, and the Maritime Provinces. The species life history traits in Table 1 are not unique to Ontario populations.

Several of the life history traits covaried among species, as expected from life history theory. Comparison of the correlations among traits from this study with the literature-based expectations is informative. The ratio L_{mat}/L_{inf} is considered to be one of three life history invariants (Charnov 1993). The ratio of L_{mat}/L_{max} ($\cong L_{mat}/L_{inf}$) of 0.53 (95% confidence limits (CL) = 0.5–0.6), determined by the arithmetic average using the data in Table 1, was within the range of

Table 4. Comparison of P/B of nine species of fishes as estimated from allometry with weight-at-maturity (P/B_W) and longevity (P/B_Z) and as observed in field populations (from Downing and Plante 1993).

Species	T_{mat}	T_{max}	P/B_W	P/B_Z	P/B_{field}
Lake whitefish	4	17	0.39	0.26	0.21 (0.11–0.31, 8)
Brook trout	3	9	0.66	0.49	0.82 (0.55–2.00, 7)
White sucker	4	15	0.37	0.30	0.23 (0.17–0.31, 3)
Creek chub	2	5	1.06	0.87	2.50
Fathead minnow	1	4	1.51	1.08	2.87
Golden shiner	2	7	1.59	0.62	2.00
Yellow perch	4	10	0.53	0.44	2.52
Pearl dace	2	4	1.00	1.08	2.08
Walleye	4	20	0.29	0.22	0.36

Note: Values of P/B_{field} for the first three species are averages with ranges and the number of populations, respectively, in parentheses. For the remaining species, only one population was studied.

0.4–0.8 for L_{mat}/L_{inf} observed for fishes in general (Beverton and Holt 1959; Charnov 1993), although the overall ratio was lower than that predicted by ecological theory (L_{mat}/L_{inf} constant of 0.66; Jensen 1996). The average value of $Z \times T_{mat}$ indicated a product of 1.6 (95% CL = 1.4–1.8), which was similar to the theoretical value of 1.65 (Jensen 1996) but was less than the range of 1.75–2.2 reported for "typical fish" by Charnov (1993). Generally, the life history traits were correlated as expected from life history theory. The reason for the lower values of L_{mat}/L_{max} and $Z \times T_{mat}$ in our data set compared with some reported values is unknown, although it may be related to the taxonomic diversity of our species database, as noted below.

The above comparison of life history traits among species has limitations. Normally, the life history traits are considered to be constants within taxonomic groups (Charnov 1993). Some of the variability between L_{mat} and L_{max}, for example, was probably attributable to the diversity of taxonomic groups and species that were considered in Table 1. The relationship may be less variable if the same taxonomic group was considered (e.g., salmonids or cyprinids). Despite these limitations, the covariance among life history traits was useful for determining W_{mat} and first-order P/B coefficients for the diverse group of species considered in this study.

Estimates of species-specific P/B ratios can be applied to population biomass, but they will be approximations of specific production. Life history traits vary among populations of the same species. Variability in L_{inf} among populations in different habitats, for example, is clearly illustrated in Fig. 2. Variability in traits among populations is particularly evident for long-lived species of fishes. Shuter et al. (1998) found a twofold variation in L_{inf} and a fourfold variation in Z for lake trout (*Salvelinus namaycush*) populations in Ontario, and they cited similar variation in size and mortality traits for walleye (*Stizostedion vitreum*) populations. Applying a species constant P/B to specific populations is therefore an approximation. The potential error will be highest for long-lived species and least for short-lived species.

Nevertheless, we advocate the use of generic species P/B coefficients, in the absence of population-specific information on life history traits. If population-specific traits (such

Fig. 5. Comparison of predicted versus observed production for 24 populations of freshwater fishes. Predicted production was estimated as the product of population biomass (from Downing and Plante 1993) and species-specific P/B_W (where $P/B_W = 2.64W^{-0.35}$; see text). The broken line is the regression line and the solid shows the 1:1 relationship. The highest observed production value was an outlier (see text).
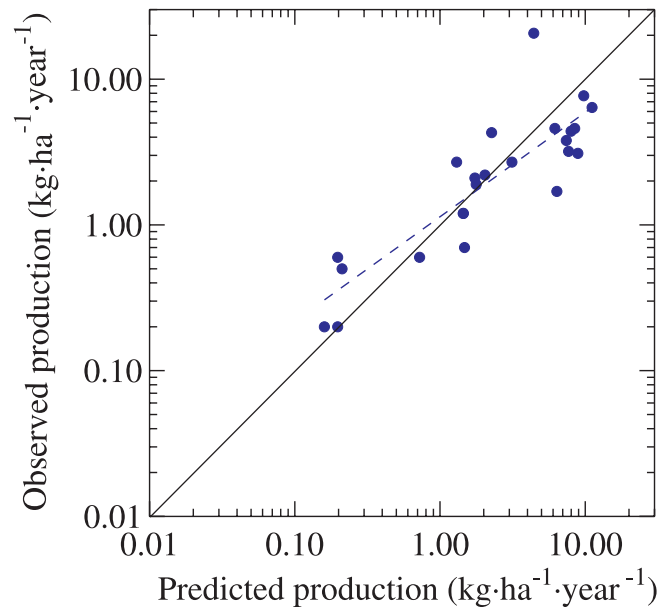
as W_{mat}) are known for a particular population and area, they should be used to estimate P/B (using the allometric equation) rather than the generic species P/B coefficients.

Validation and calibration

P/B ratios can be validated by intercorrelation of the two methods and by comparison with published empirical data. The significant correlation between the two estimates of P/B was expected, as the two predictors (longevity and size-at-maturity) were themselves correlated, as discussed above. Both methods use different predictors to estimate the same parameter. The second method (P/B_W) is favoured because the predictor population trait (size-at-maturity or maximum size) is often available from population studies of age and growth and because the empirical relationship between animal size and P/B is well founded in the literature (Banse and Mosher 1980; Peters 1983).

Assuming that fish weight is potentially the most useful predictor of P/B, the allometric coefficient that relates P/B to size is important. The $\log P/B_Z$ scaled with log fish weight with a slope of –0.19, which was similar to the physiological scaling (–0.25) discussed earlier. For their whole data set, Downing and Plante (1993) found that P/B and weight were related with an exponent of –0.22 ($n = 100$ populations, major axis regression). However, for the subset of data that were used for validation in this study, P/B scaled with fish size as $W^{-0.35}$, after adjustment for biomass ($n = 24$ populations). This greater coefficient is consistent with the allometric coefficient used to calculate P/B_W in this study. The wide confidence interval in the regressions of P/B on weight is a reminder that body size is an inexact predictor of P/B (Banse and Mosher 1980; Randall et al. 1995), and predic-

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tions of specific production from body mass are approxima-
tions. The latter slope of –0.35 is similar to the within fish
group (population production) coefficients discussed by
Dickie et al. (1987) and Boudreau and Dickie (1989). Until
further validation with field data is possible, the coefficient
of –0.35 will be used to estimate P/B_W (= $aW^{-0.35}$).

The P/B_W consistently underestimated the observed field
P/B ratios. This suggests that the proportionality coefficient
(a) of the allometric equation could be adjusted upwards.
There are two reasons why this may be the case. First,
Randall et al. (1995) used average fish weight rather than
W_{mat}. Average fish weight in populations of actively growing
fish would be less than maturity weight, and average P/B
based on maturity weight would be underestimated accord-
ingly. Second, Randall et al.'s (1995) equation relating fish
weight to P/B was based on community measures of fish
production. Downing and Plante (1993) showed that com-
munity production, adjusted for fish biomass, was margin-
ally lower than population production. Again, this would
lead to an underestimate of P/B. The average ratio of ob-
served to predicted production, using the unadjusted propor-
tionality coefficient, was 2.04 (excluding yellow perch); P/B
ratios adjusted by a factor of 2 (coefficient of 2.64 rather
than 1.32) produced a reasonably good fit with the P/B ratios
observed from the field studies. Use of the published data
for calibration would suggest that P/B from species W_{mat}
data can be estimated as $2.64W^{-0.35}$. Given the above uncer-
tainties, both the proportionality coefficient and exponent of
this equation may be modified in future.

P/B values estimated for all 79 species of fish using this
equation are reported in Table 1. Further validation of these
ratios is needed, particularly for species that mature at a
large size and live for many years, since our data set was
based primarily on short-lived species. P/B coefficients in
Table 1 are provisional. Fishes inhabiting rivers would have
higher P/B ratios for any given biomass; P/B coefficients
may have to be adjusted upwards by 1.5 for river habitats
(Randall et al. 1995). Populations of young fish (e.g., juve-
nile anadromous salmonids) would have higher P/B ratios
than indicated in Table 1. Additional adjustments to the P/B
ratios could be made to account for differences in water nu-
trient levels (total phosphorus concentrations) or water tem-
perature (Downing and Plante 1993). Although P/B
coefficients for freshwater species of fishes are considered in
this study, the same principle and methodology for estimat-
ing P/B would apply to marine fishes, but the coefficients
would have to be validated by comparison with estimates of
fish production in marine habitats.

Application

A first-order habitat productivity index (HPI), a proposed
measure of habitat suitability and productive capacity, can be
calculated as the product of average fish biomass and the
species P/B coefficient (HPI = $B \times P/B$). This fish produc-
tion index assumes that fish production is correlated with av-
erage fish biomass and that biomass is linked to habitat
productivity, and the P/B coefficient is a further refinement
to adjust for the effects of fish size on population production.

As an example, HPI values were calculated for a number
of samples from boat electrofishing transects in nearshore
areas of Lake Erie (n = 30) and Lake Ontario (n = 33). The

Fig. 6. Top panel: correlation between average fish biomass from
electrofishing samples and the HPI. Fish catches were from sam-
ples collected by boat electrofishing at 100-m line transects in
nearshore habitats of Lakes Erie and Ontario (R.G. Randall, per-
sonal observation). HPI was the product of average biomass and
species P/B (per year) ratios, summed for all species captured at
the transect. Axes are on a $\log_{10}$ scale. Bottom panel: relation-
ship between the calculated HPI and macrophyte density (% bot-
tom cover, arcsine square root transformed) at the transects. Only
transects where macrophytes were present were included (n = 43).
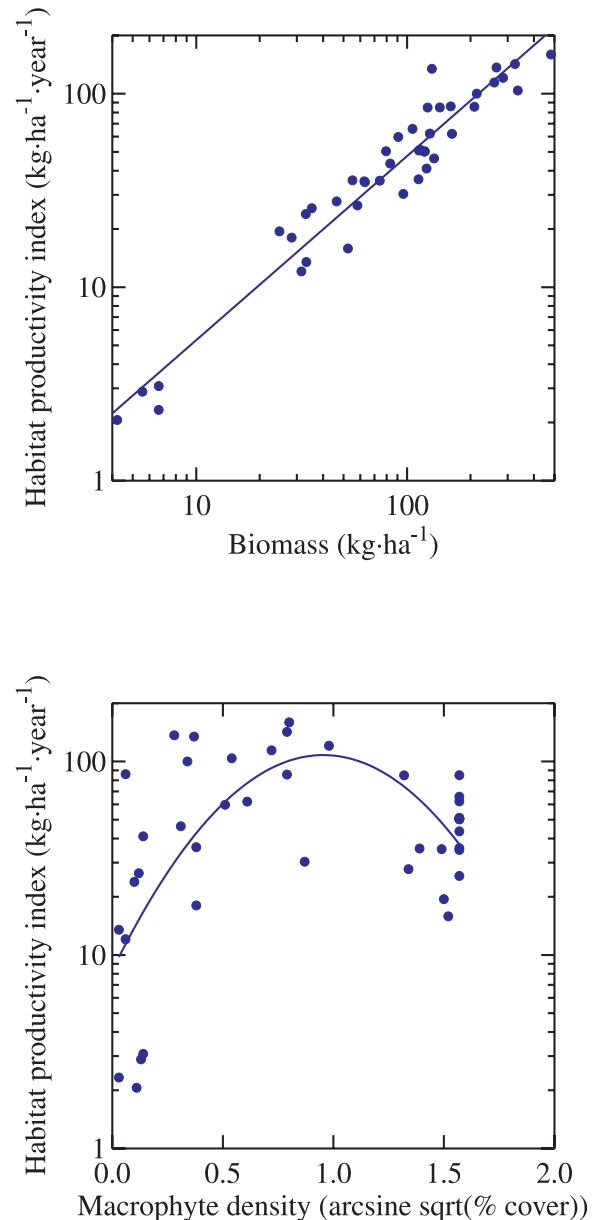
fish samples were collected by boat electrofishing at 100-m
line transects in shallow waters (1.5 m depth). The habitats
surveyed included coastal wetlands (with submerged macro-
phytes), harbour breakwalls, and exposed shorelines adja-
cent to the harbours (R.G. Randall, personal observation).
Sixty-three transects were surveyed on three occasions at
monthly intervals during the summer of 1994. For calcula-
tion of biomass density, we assumed that the effective width

of each transect was 10 m, and the average catch efficiency was 0.3 (Randall et al. 1993). Average biomass (kilograms per hectare) for the three visits was calculated for each transect, by species. HPI was calculated as the product of the average biomass and the species P/B ratios, summed for all species captured at each transect. Transects that included an average of at least five fish were included in the analysis ($n = 54$).

HPI was highly correlated ($R^2 = 0.93$) with biomass, as expected by calculation, but it varied for any specific level of biomass because of differences in fish size (Fig. 6). For a transect where the total catch in biomass was 30 kg·ha^{-1}, for example, the 95% confidence interval for HPI ranged between 10.7 and 29.5 kg·ha^{-1}·year^{-1}, a factor of about 3. Both biomass and fish size were significant predictors of HPI ($P < 0.05$), confirming that HPI was related to fish size in the field catch data. Preliminary investigation showed that the residuals from the regression of HPI versus biomass were weakly correlated with macrophyte abundance ($r = 0.27$, $P = 0.05$), indicating that HPI was related to habitat cover after adjustment for biomass. Macrophyte abundance affects fish assemblage structure and possibly habitat productivity (Randall et al. 1996) (Fig. 6, bottom panel). These observations suggest that although HPI provided a similar measure of habitat capacity as biomass, it also accounted for fish size structure. Areas with similar biomass but with smaller fish size had a higher HPI than areas with larger fish. HPI is a more direct fish assemblage measure of habitat productive capacity than biomass alone, although this hypothesis has yet to be tested in an area where fish production has been estimated in the littoral zone of a lake. These preliminary results suggest that further investigation and testing of the HPI could be worthwhile.

A more sensitive fish metric of production would be to adjust P/B for the size of the fish in the catches rather than using a constant P/B coefficient for each species. This refinement will require investigation of the relationship between fish size and P/B within and among cohorts of different populations and species, as has been initiated by Boudreau and Dickie (1989). HPI as an index of habitat productive capacity requires further validation by comparison with biomass spectra (Boudreau and Dickie 1992) and field estimates of population and community production.

Acknowledgements

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Appendix 1. Length–weight regression coefficients for fish species collected as part of the Productive Capacity fish database. Species codes are defined in Table 1.

Species code	n	L_{min}	L_{max}	W_{min}	W_{max}	b	SE_b	a	SE_a	R^2	$SE_{estimate}$
F0051	75	267	762	175	6 000	3.04	0.08	−5.10	0.21	0.95	0.07
F0061	9873	15	192	1	71	2.75	0.01	−4.44	0.02	0.93	0.08
F0063	679	31	455	1	1 700	3.01	0.01	−4.82	0.03	0.99	0.10
F0075	101	73	850	3	8 100	2.93	0.11	−4.82	0.21	0.89	0.12
F0076	32	65	565	3	2 440	3.00	0.04	−4.93	0.08	0.99	0.05
F0078	38	73	617	11	3 180	2.84	0.12	−4.40	0.31	0.94	0.19
F0121	75	47	185	1	29	2.90	0.16	−5.00	0.32	0.82	0.20
F0131	269	44	955	1	5 540	3.00	0.02	−5.19	0.06	0.99	0.07
F0133	47	99	277	6	144	3.08	0.08	−5.37	0.17	0.97	0.06
F0161	25	243	533	220	2 400	3.32	0.13	−5.62	0.33	0.97	0.05
F0163	1036	65	513	3	1 594	2.99	0.01	−4.86	0.02	0.99	0.05
F0164	15	66	237	2	231	3.27	0.17	−5.37	0.36	0.97	0.13
F0171	59	163	541	56	2 800	3.07	0.08	−5.01	0.20	0.96	0.05
F0173	26	308	620	408	3 610	3.06	0.11	−5.00	0.30	0.97	0.03
F0181	76	121	563	46	3 000	2.25	0.20	−2.71	0.49	0.64	0.15
F0186	1807	115	910	32	15 360	2.95	0.02	−4.56	0.06	0.91	0.08
F0194	394	36	164	1	62	3.07	0.05	−5.05	0.09	0.91	0.14
F0196	2506	35	154	1	29	2.95	0.03	−4.96	0.06	0.79	0.13
F0199	214	33	84	1	6	2.49	0.16	−4.05	0.27	0.53	0.13
F0201	1054	32	120	1	24	2.96	0.04	−4.85	0.08	0.82	0.16
F0208	88	43	83	1	10	3.32	0.22	−5.55	0.39	0.72	0.13
F0233	3928	70	430	5	1 066	2.97	0.01	−4.77	0.03	0.92	0.07
F0251	143	53	1030	90	3 260	1.87	0.13	−2.39	0.37	0.59	0.22
F0291	16	67	125	2	28	4.56	0.36	−8.01	0.71	0.92	0.09
F0301	2730	38	330	1	680	3.13	0.01	−5.05	0.02	0.97	0.07
F0302	71	80	335	8	710	2.60	0.13	−3.80	0.31	0.85	0.12
F0311	931	42	268	1	450	2.99	0.02	−4.62	0.03	0.98	0.07
F0313	5154	22	256	1	225	3.12	0.01	−4.85	0.01	0.98	0.08
F0314	529	8	196	1	222	3.02	0.03	−4.67	0.06	0.95	0.16
F0316	527	28	432	1	1 346	2.92	0.02	−4.61	0.04	0.98	0.09
F0317	1859	30	457	1	1 830	3.03	0.01	−4.87	0.02	0.99	0.09
F0319	362	29	318	1	585	2.96	0.02	−4.70	0.04	0.98	0.11
F0331	4797	37	350	1	560	2.96	0.01	−4.77	0.02	0.95	0.09
F0334	290	70	682	4	5 300	3.02	0.03	−5.01	0.06	0.98	0.13
F0342	1479	52	142	1	33	2.82	0.03	−4.66	0.07	0.82	0.13
F0371	181	138	570	25	3 980	3.32	0.06	−5.74	0.15	0.95	0.07

Note: Coefficients are for the regression log weight = log a + b(log length), where length is FL (mm) and weight is wet weight (g).

Appendix 2. Length–weight coefficients for five species of fish, as obtained from the literature.

Species	Code	n	a	b	Units	Reference
Fathead minnow	F0209	387	−3.26	2.28	log weight (g); log SL (mm)	Chadwick 1976*
Pearl dace	F0214	405	−3.79	2.53	log weight (g); log SL (mm)	Chadwick 1976
Creek chub	F0212	235	−3.85	2.57	log weight (g); log SL (mm)	Chadwick 1976
Brook trout	F0080		−5.1142	3.06	log weight (g); log FL (mm)	Carlander 1969[†] (mean of 6 populations)
Lake whitefish	F0091		−5.1483	3.11	log weight (g); log FL (mm)	Carlander 1969 (mean of 8 populations)

*Carlander, K.D. 1969. Handbook of freshwater fishery biology. Vol. 1. Iowa State University Press, Ames, Iowa.
[†]Chadwick, E.M.P. 1976. Ecological fish production in a small Precambrian shield lake. Environ. Biol. Fishes, 1: 13–60.