PERSPECTIVES

A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario[1]

B.J. Shuter, M.L. Jones, R.M. Korver, and N.P. Lester

Abstract: Life history characteristics of 54 Ontario lake trout (*Salvelinus namaycush*) populations vary with differences in lake area (range 25–450 000 ha) and total dissolved solids (TDS) (range 15–180 mg·L^{-1}). Populations from large lakes exhibit greater maximum sizes, greater ages and sizes at first maturity, lower natural mortality rates, and lower sustainable yields. Populations from high-TDS lakes exhibit higher growth rates in early life, lower ages at first maturity, larger sizes at first maturity, and higher natural mortality rates. Angler catchability increases significantly at low population densities. With these relationships included in an age-structured population model, we found that the fishing mortality rate at maximum equilibrium yield ranges from 0.12·year^{-1} for a 100-ha, low-TDS lake to 0.37·year^{-1} for a 10 000-ha, high-TDS lake; the fishing effort level at maximum equilibrium yield ranges from 6.6 angler-h·ha^{-1}·year^{-1} for a 100-ha, low-TDS lake to 4.0 angler-h·ha^{-1}·year^{-1} for a 10 000-ha, high-TDS lake. Populations from small, low-TDS lakes are more sensitive to overexploitation than populations from large, high-TDS lakes. Easily measured, environmental correlates of life history characters may be common among fish species and are useful in developing exploitation guidelines for populations that are not well studied.

Résumé : Certaines caractéristiques du cycle vital de 54 populations de touladi (*Salvelinus namaycush*) de l'Ontario varient en fonction de la superficie des lacs (fourchette de 25 à 450 000 ha) et des solides dissous totaux (SDT) (fourchette de 15 à 180 mg·L^{-1}). Les poissons des populations des grands lacs ont des tailles maximales plus élevées, sont plus âgés et plus gros à la première maturité, ont des taux de mortalité naturelle moins élevés et donnent des rendements équilibrés inférieurs. Les poissons des populations des lacs à forte teneur en SDT ont dans leurs premiers stades des taux de croissance plus élevés, sont plus jeunes et plus gros à la première maturité et ont des taux de mortalité naturelle plus élevés. Le potentiel de capture par les pêcheurs sportifs s'accroît de façon significative quand les densités des populations sont faibles. En incluant ces relations dans un modèle de population structuré selon l'âge, nous avons établi que le taux de mortalité par pêche au rendement maximal équilibré varie de 0,12·an^{-1} pour un lac de 100 ha à faible teneur en SDT à 0,37·an^{-1} pour un lac de 10 000 ha à forte teneur en SDT; l'effort de pêche au rendement maximal équilibré varie de 6,6 h-pêcheurs·ha^{-1}·an^{-1} pour un lac de 100 ha à faible teneur en SDT à 4,0 h-pêcheurs·ha^{-1}·an^{-1} pour un lac de 10 000 ha à forte teneur en SDT. Les populations des petits lacs à faible teneur en SDT sont plus sensibles à la surexploitation que les populations des grands lacs à forte teneur en SDT. Des corrélats environnementaux facilement mesurables de paramètres du cycle vital peuvent être communs à des espèces de poisson et sont utiles pour l'élaboration de lignes directrices en matière d'exploitation des populations qui ne sont pas bien étudiées.

[Traduit par la Rédaction]

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Fig. 1. Locations of about 2200 lake trout lakes in Ontario; the 54 lakes sampled for this studied are circled.
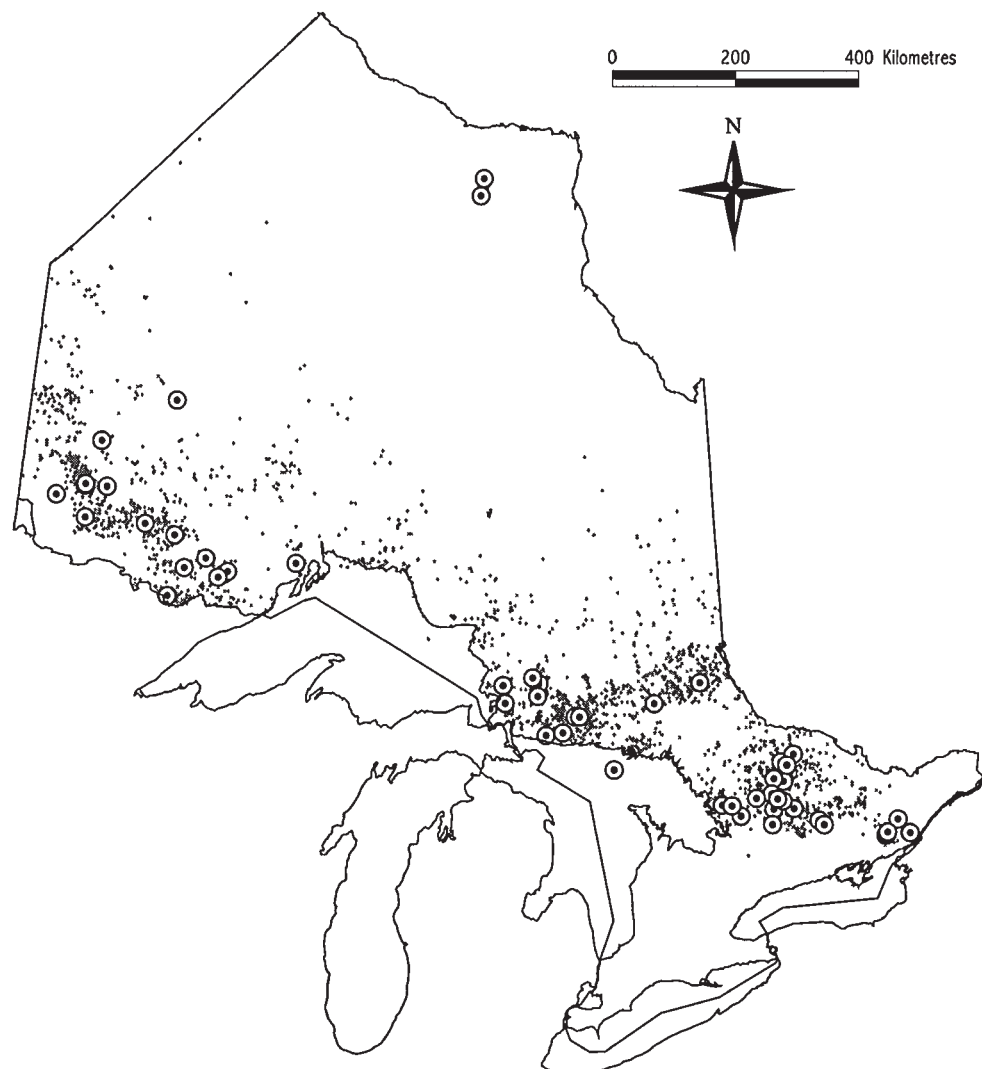
Introduction

The principal challenge of managing exploitation of fish in the numerous inland lakes of eastern North America lies in the problem of generalization. Overall, the size and economic importance of the resource is large, but it is divided into so many small, isolated populations (Fig. 1) that it is impractical to carry out detailed stock assessments on each of them, and this, in turn, makes it impossible to manage these populations on a lake by lake basis. As a result, we are faced with the necessity of generalizing about sustainable levels of exploitation for all populations on the basis of knowledge from a very limited sample of populations. In this paper, we develop a general approach to this problem by examining the degree of demographic variation in a relatively large and representative sample of Ontario lake trout (*Salvelinus namaycush*) populations and exploring the implications of this variation for developing effective strategies for regional management of exploitation.

Recognition of the challenge of generalization is not new. Development of empirical models to predict potential fish yield from individual lakes began in the 1940s (reviewed by Leach et al. 1987). The most well-known and widely uti-

lized model of this type is the morphoedaphic index (MEI: Ryder et al. 1974). The success of such models hinges on the fact that measures of nutrient availability, or trophic state, are repeatedly correlated with indices of lake-wide fish production (at least to within an order of magnitude). More recent investigations have shown that species-specific yields can be predicted from climate variables (Schlesinger and Regier 1983) and from measures of the amount of thermally suitable habitat (Christie and Regier 1988). These relationships can be used to predict the yield potential of a lake from a relatively easily measured set of lake characteristics. However, they do not allow prediction of sustainable levels of fishing mortality or effort. This requires a model based on explicit descriptions of both the demographics of the exploited populations and the relationship between fishing mortality and fishing effort. Our objective is to develop such a model for managing angling exploitation of lake trout on the inland lakes of Ontario.

The lake trout is the only major indigenous sport species adapted to the deep, cold waters of oligotrophic lakes. It exists in about 2200 inland Ontario lakes (Fig. 1) and is fished during winter, spring, and summer seasons. Lake trout are characterized by slow growth, late maturity, low repro-

ductive potential, and a slow replacement rate. These attributes make the species especially vulnerable to overexploitation. For lake trout populations in the southern part of the province, levels of fishing effort are often high, harvests often exceed annual production, and the quality of many fisheries is in decline (Evans et al. 1991). Populations in northern Ontario are in better condition, but similar trends are expected in the future if angling effort (E, angler-hours per hectare) and fishing mortality rate (F, per year) are not held within appropriate bounds.

Recent work on both freshwater (brook trout *Salvelinus fontinalis*: Hutchings 1993, 1996) and marine fish species (Atlantic cod *Gadus morhus*: Myers et al. 1997) has demonstrated that interpopulation variation in demographic parameters can be large enough to affect intrinsic rates of population growth and hence influence the sensitivity of individual populations to exploitation. In several studies, significant portions of this variation were associated with simple habitat characteristics (e.g., water temperature: Myers et al. 1997; conductivity/fish community: Trippel and Beamish 1989, 1993). We begin our study by demonstrating that the life history parameters for a lake trout population can be predicted from simple environmental characteristics of the lake that it lives in. We use these relationships to construct a population model that can be calibrated to individual lakes with minimal lake-specific information. We go on to define empirically the relationship between fishing mortality and angling effort for Ontario lake trout angling fisheries and embed that relationship in our model, thus creating a structure that explicitly acknowledges the respective roles that life history, habitat, and the fishery play in determining abundance, harvest, and sustainable levels of exploitation. We use this model to predict sustainable levels of fishing mortality and fishing effort for typical Ontario lake trout lakes. Finally, we identify and discuss those aspects of our approach that may be applicable to other species in different geographic regions.

Methods

Population yield model

To identify the parameters needed to predict yield as a function of fishing mortality, we developed an age-structured equilibrium yield model. It was derived by combining a generalized stock–recruitment relationship (Shepherd 1982) with conventional yield-per-recruit and biomass-per-recruit functions (Appendix 1). The result is a yield equation of the following form:

$$Y = f(W_\infty, \omega, t_m, f_{max}, \alpha_{max}, M; \beta, B_0; t_c, F)$$

where the parameters can be grouped as follows.

(*i*) Life history parameters, defining rates of growth, mortality, and reproduction, characteristic of specific habitats in the absence of intraspecific competition: W_∞, asymptotic mass of an adult fish (kilograms); ω, rate of length growth (centimetres per year) in early life (Gallucci and Quinn 1979), the product of the von Bertalanffy growth parameters K (per year) and L_∞ (centimetres); t_m, age of maturation, knife-edge transition to maturity assumed; f_{max} fecundity, number of eggs per kilogram for a mature female at low population density; α_{max}, survival from egg to age 1 at low population density; M, instantaneous natural mortality rate (per year) for fish aged 1 year and over.

(*ii*) Habitat quantity parameters, defining the rates at which early survival and (or) fecundity are reduced from their maximal

values as the population fills available habitat and approaches its carrying capacity: β, a parameter that sets the rate at which early survival and (or) fecundity declines as the population approaches its carrying capacity (i.e., a higher β value produces a more rapid decline); B_0, a scaling parameter (kilograms per hectare) that reflects the amount of habitat available to the population, and hence is directly related to both the carrying capacity of the population and its maximum sustainable harvest.

(*iii*) Fishery parameters, defining the part of the population that is exploited and the intensity of exploitation: t_c, age of first capture by the fishery, knife-edge transition to full vulnerability assumed; F, instantaneous fishing mortality (per year) applied to all fish aged $\geq t_c$.

Each of these parameters must be estimated to characterize the model for a specific lake. Our objective is to find a basis for estimating their values for lakes lacking extensive stock assessment information. To address this objective, we examined existing data on Ontario lake trout populations with two questions in mind. (1) Are there empirical relationships that link any of the yield model parameters to some readily measured lake attribute such that those parameters could be predicted from that attribute and would not have to be measured directly? (2) Do the life history parameters covary in a consistent fashion among lake trout populations such that an estimate of the value for at least one parameter could be used to predict the values of others?

Our data come from a set of 54 lakes (Table 1) widely distributed throughout Ontario (Fig. 1) and include estimates of growth rates, mortality rates, maturation schedules, and fecundity. Much of this information was assembled as part of a concerted effort by the Ontario Ministry of Natural Resources to summarize existing knowledge pertinent to the management of Ontario's inland lake trout populations (Payne et al. 1990).

Describing lifetime growth pattern

We chose to describe the lifetime growth pattern of lake trout in terms of the von Bertalanffy equation, parameterized according to the scheme first suggested by Gallucci and Quinn (1979):

$$L_t = L_\infty \cdot (1 - e^{-(\omega/L_\infty) \cdot t})$$

We chose the von Bertalanffy equation because it is simple, it typically provides superior fits to fish growth data (Chen et al. 1992), and it has a form that is very similar to the form predicted by detailed growth models that explicitly describe the accumulation of energy and its optimal allocation to activity, somatic growth, and reproductive products (Roff 1983; Kozlowski 1996). We chose the Gallucci–Quinn parameterization because the two parameters (ω, L_∞) have tangible units (e.g., centimetres per year, centimetres) and are easily interpretable, statistical estimates for both parameters are not intrinsically intercorrelated, as are the traditional von Bertalanffy parameters K and L_∞ (Chen et al. 1992), and the parameters cleanly separate lifetime growth data into the growth rate prior to sexual maturity (ω) and an index of the amount of growth that occurs after maturity (L_∞); this separation satisfies the objections raised by authors who have criticized use of the von Bertalanffy equation in life history studies (Roff 1984; Day and Taylor 1997).

Results

Parameter estimates for Ontario lake trout populations

Growth (ω, W_∞)

Payne et al. (1990) observed that the lifetime growth patterns of lake trout populations are correlated with lake area. To further explore this relationship, we summarized each of the growth patterns in our 54 lakes with two parameter esti-

Table 1. Summary of the lakes used to explore relationships among lake trout demographic and fishery parameters.

Lake	Surface area (ha)	TDS (mg·L^{-1})	Aging method	No. of fish aged	L_∞ (cm)	ω (cm·year^{-1})	Z (year^{-1})	Maturity	Vulnerability	Catchability
Adelaide	137	28	S	299	43.8	12.75	—	—	—	—
Basswood (Wakwekobi)	2 709	—	S	278	74.8	13.02	1.57	—	×	×
Big Clear	187	50	S	264	47.9	11.54	0.52	×	×	×
Big Rideau	5 761	138	S	270	62.1	14.47	0.49	×	×	×
Big Salmon	148	58	S	225	59.4	9.80	0.39	—	×	×
Bone	121	30	S	708	43.0	10.75	1.08	×	×	×
Boshkung	716	35	S	132	63.2	7.84	—	—	—	—
Buddell	194	28	O	64	62.2	6.53	0.12	—	—	—
Burnt Island	110	25	O	87	61.0	7.93	—	—	×	—
Charleston	2 517	137	S	285	64.9	11.75	0.64	×	×	×
Chiblow/ Denmans	2 725	31	S	1255	70.6	11.79	1.11	×	×	×
Christman (Jim Christ)	59	46	S	204	50.9	15.42	1.03	×	×	×
Devil	1 062	109	S	272	58.8	11.64	0.44	—	×	×
Dickey	214	90	S	240	40.4	14.34	0.93	×	×	×
Eagle	27 691	39	S	35	78.4	9.02	—	—	—	—
Flack	951	22	S	2142	64.0	10.62	1.06	×	×	×
Gong	385	24	S	79	81.2	10.31	—	—	—	—
Goulais	240	31	S	111	54.0	9.83	—	—	—	—
Greenwater	3 060	44	O	189	74.0	8.07	—	—	—	—
Greenwich	484	20	O	283	50.8	7.16	—	—	—	—
Gull	995	30	S	447	54.5	8.94	—	—	—	—
Happy Isle	536	23	S	2993	58.2	9.14	—	—	—	—
Hawley	1 235	134	O, F	451	63.1	8.77	0.18	—	×	—
Islets	189	16	O	100	57.8	9.08	—	×	—	—
Kawagama	2 819	22	S	155	48.8	12.01	—	—	—	—
Kennisis	1 417	23	S	312	56.2	9.16	—	—	—	—
Lake 223	30	—	F	799	46.0	16.10	0.38	—	—	—
Lake 224	25	—	F	522	41.0	12.30	0.36	—	—	—
Lake Joseph	5 156	45	S	602	72.0	8.06	—	—	—	—
Lake Lavieille	2 402	32	S	569	79.2	9.19	—	×	×	×
Lake Louisa	490	23	S	571	49.5	11.73	0.90	×	×	×
Lake Manitou	10 461	180	K	—	73.0	20.44	0.22	×	—	—
Lake Muskoka	12 215	61	S	133	66.0	12.41	—	—	—	—
Lake Nipigon	448 060	102	O	364	90.3	16.53	—	×	×	—
Lake Opeongo	5 860	29	S	6015	87.2	8.02	0.43	×	×	×
Lake Rosseau	6 374	33	S	111	64.9	12.98	—	—	—	—
Lake Temagami	20 972	49	S	344	79.3	10.86	0.67	—	×	×
Lake of Bays	6 904	23	S	51	68.8	8.46	—	—	—	—
Lake of the Woods (shoal)	25 856	138	O	199	81.5	11.17	—	—	×	—
Little Gull	325	16	O	67	52.5	10.82	—	—	—	—
Little Joe	221	52	O	97	61.9	12.69	—	—	×	—
Loch Erne	165	67	O	118	68.4	10.60	—	—	×	—
Miskwabi	264	62	S	94	55.8	10.77	—	—	—	—
Nelson	316	32	S	410	61.9	9.35	—	—	—	—
Pickerel	6 059	20	O	174	59.6	8.52	—	—	—	—
Ranger	2 254	25	S	251	55.5	13.04	0.69	—	×	×
Redstone	1 130	64	S	80	48.8	9.91	—	—	—	—
Robinson	421	15	O	48	59.8	7.65	—	—	×	—
Semiwhite	304	28	S	605	61.1	10.26	1.07	—	×	×

Table 1 (*concluded*).

Lake	Surface area (ha)	TDS (mg·L^{-1})	Aging method	No. of fish aged	L_∞ (cm)	ω (cm·year^{-1})	Z (year^{-1})	Maturity	Vulnerability	Catchability
Smoke	607	25	S	282	76.3	8.39	—	×	—	—
South Otterskin	214	115	O	91	63.9	14.63	—	×	—	—
Squeers	384	28	O	1009	55.0	7.54	0.39	×	—	×
Sutton	3 764	154	O, F	188	63.7	9.24	0.15	—	×	—
Wollaston	363	162	S	153	40.2	10.37	—	—	×	—

Note: The ×'s in the last three columns indicate which lakes were used to examine a particular parameter. All 54 lakes were used in the lake size and growth analyses. Aging methods: S, scale; O, otolith; F, fin ray; K, known (clips). Estimates of total instantaneous mortality rate (Z) were obtained from catch at age data (Chapman and Robson 1960; Robson and Chapman 1961).

mates, ω and L_∞, with ω estimated as the product of the standard von Bertalanffy growth parameters K and L_∞ (Galucci and Quinn 1979). Estimates for 10 of these lakes were taken from Trippel and Beamish (1989). Estimates for the remaining 44 lakes were derived using the methods outlined below.

For most populations, age determination was done using scales, otoliths, or fin rays. For populations with scale ages only, mean size at age 8 and older was probably biased high (Casselman 1983). This bias would lead to a strong positive bias in L_∞ estimates derived from methods that involve extrapolating size at age curves to infinite age (e.g., direct nonlinear fit of the von Bertalanffy equation) or extrapolating annual size increments to the point where they vanish (e.g., Walford linear regression). To avoid these biases, we followed Pauly's (1984) approach and estimated L_∞ as the mean length of the 10 largest fish sampled from the lake. For 13 of our 54 lakes, we had accurate size at age data from otoliths over a range of ages large enough to permit us to estimate L_∞ by a nonlinear fit of the von Bertalanffy equation to the data. Estimates of L_∞ derived using this method were highly correlated ($r^2 = 0.81$, $p \le 0.0001$) and similar to estimates derived using the Pauly approach. We also checked for negative bias in the Pauly estimates of L_∞ for populations with high total mortality (Z) rates, where larger older fish might be rare. For the 23 populations with both L_∞ and Z estimates (range of Z estimates 0.15–1.6; see Table 1), there was no significant correlation ($r^2 < 0.001$, $p > 0.90$) between the two variables and thus no indication of bias.

All size at age data were derived from harvest samples. To avoid potential biases inherent in such samples, K was estimated using size at age data for ages that were old enough to be well represented in the fishery, but young enough to be reliably aged. This was done by fitting the following equation to observed, lake-specific data on length at age (L_i) using simple linear regression:

$$-\ln\left(1 - \frac{L_i}{L_\infty}\right) = K \cdot i$$

derived by rearranging the conventional von Bertalanffy equation and setting $t_0 = 0$. If ages were obtained from scales, we based our K estimate on size at age for ages 4–7. If ages were obtained from otoliths or fin rays, we used size at age data for all ages > 4 because lake trout otolith and fin ray ages are reliable over a very broad age range, while scale ages are reliable to age 8 (Casselman 1983).

With lifetime growth pattern summarized in terms of ultimate size (L_∞) and early growth rate ($\omega = K \cdot L_\infty$), we found that a pair of empirical relationships could be used to predict these parameters from two simple lake characteristics.

(*i*) A log–log regression analysis ($r^2 = 0.459$, $p < 0.001$, $n = 54$) of the association between L_∞ and lake area (median = 661 ha, range 25.4 – 44 810 ha) generated the following equation for predicting L_∞:

(1) $L_\infty = 37.15 \cdot \text{area}^{0.071}$

(*ii*) A log–log regression analysis ($r^2 = 0.227$, $p < 0.001$, $n = 51$) of the association between ω and total dissolved solids (TDS) (median = 34.3 mg·L^{-1}, range 15–180 mg·L^{-1}) generated the following equation for predicting ω:

(2) $\omega = 5.60 \cdot \text{TDS}^{0.162}$.

Parameter L_∞ was essentially independent of TDS and ω was essentially independent of lake size. Therefore, with TDS constant, asymptotic length will increase with lake size, early growth rate will remain constant, and growth differences among lakes will emerge only as fish reach older ages. In contrast, with lake size constant, early growth rate will vary with TDS, asymptotic length will remain constant, and growth differences among lakes will disappear as fish reach older ages.

Length–mass regression parameter estimates were available for 23 Ontario lake trout populations (Payne et al. 1990). Among-lake variation in these parameter estimates was not correlated with variation in other lake trout biological parameters, with lake area, or with TDS. Therefore, we used the provincial average length–mass relationship (Payne et al. 1990) to estimate W_∞ (kilograms) from L_∞ (centimetres):

(3) $W_\infty = 5.87 \times 10^{-6} \cdot L_\infty^{3.18}$.

Thus, the first two life history parameters of our model, W_∞ and ω, can be predicted from lake area and TDS.

Maturation (t_m)

Life history theory predicts that age and size at maturity should vary with lifetime growth pattern. We looked for such relationships in our data set using female length at maturity data from 22 lakes (Payne et al. 1990; Trippel 1993): 13 estimates of length (or age) at which 5% of females are mature, 12 estimates of length (or age) at which 50% of females are mature, and 11 estimates of length (or age) at which 95% of females are mature. If only age at maturity

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data were available for a population, we used its von Bertalanffy growth equation to convert ages to lengths. We used analysis of covariance on these estimates of length at 5, 50, and 95% maturity (L_{m5}, L_{m50}, L_{m95}) to assess the relationship between size at maturity and lifetime growth pattern. With $\log(L_i, i = m5, m50, m95)$ as dependent variable, $\log(L_\infty)$ and $\log(\omega)$ as covariates, and 5% maturity, 50% maturity, and 95% maturity as treatments, we found that $\log(L_\infty)$, $\log(\omega)$, and the treatment variables each explained significant portions (overall multiple $R^2 = 0.725$, $p < 0.0001$, $n = 36$) of the observed variation in $\log(L_i)$. This analysis produced the following equation for predicting L_{m50}:

$$(4) \qquad L_{m50} = 1.56 \cdot \omega^{0.257} \cdot L_\infty^{0.665}.$$

Given L_{m50} for a particular lake, age at 50% maturity (t_m) can be estimated using the von Bertalanffy growth equation for the lake. Thus, we can estimate our third life history parameter, t_m, from lake area and TDS using the relationships that link these characters to L_∞, ω, and L_{m50}.

Early survival and fecundity (α_{max}, f_{max})

Few estimates are available for age 0 survival (α_{max}) of lake trout, but the few that exist are surprisingly consistent. In Lake Opeongo, Matuszek et al. (1990) found that age 0 survival at low population densities fell in the range from 0.0035 to 0.0055. M. Fruetel (Ontario Ministry of Natural Resources, Thunder Bay, Ont., personal communication) found a value of 0.00425 for Squeers Lake, a 400-ha lake in northwestern Ontario. For the period of lowest lake trout abundance in Lake Superior (prelamprey control), Ferreri et al. (1995) found a value of 0.00416, a value similar to that (0.004) by Walters et al. (1980) in an earlier assessment of Lake Superior lake trout. The mean of these four separate estimates is 0.0043.

Fecundity data were available for 13 lakes (Payne et al. 1990; Trippel 1993; E.A. Trippel, DFO Biological Station, personal communication). Although the range of values in this data set is quite wide (883–2226 eggs·kg body mass^{-1}), most estimates cluster around the mean value of 1506 eggs·kg body mass^{-1}.

In the results presented below, we have assumed fixed values of 0.0043 and 1506 for α_{max} and f_{max}, respectively. Given the sources of these values, we judge them to be representative of habitats where water quality parameters lie well within lake trout tolerance zones.

Natural mortality (M)

In his synthesis of demographic statistics from populations of 84 exploited fish species, Pauly (1980) found that M suffered by a population could be estimated from its von Bertalanffy growth parameters K and L_∞ plus an estimate of the annual average water temperature experienced by its members. We reanalysed his data set, generating a log–log regression equation that could use estimates for ω, L_∞, and water temperature to predict values for M ($R^2 = 0.718$, $n = 175$). Given an annual average water temperature of 6°C for lake trout (Shuter et al. 1987), we arrived at the following equation for predicting M:

$$(5) \qquad M = 2.064 \cdot \omega^{0.655} \cdot L_\infty^{-0.933}.$$

The water temperature estimate of 6°C was derived as follows: (*i*) in Lake Opeongo, the ice-free period is about 7 months long; for much of this time, the lake is stratified with an average hypolimnetic temperature of about 8°C; if we assume that lake trout occupy the hypolimnion during stratification (Martin and Olver 1980) and that water temperatures during ice cover are of the order of 3°C, then the annual average temperature that lake trout experience is about 6°C (Shuter et al. 1987) and (*ii*) values close to 6°C were calculated for our other lake trout lakes, using ice-free times and surface water warming rates estimated from the equations in Shuter et al. (1983).

Estimates of M, derived from eq. 5, were similar to independent, direct estimates of M (Table 2) obtained for eight Ontario lake trout populations as follows: (*i*) in six lakes, exploitation rates were effectively zero, and hence, we could assume that total mortality and natural mortality were equivalent; we estimated (Chapman and Robson 1960; Robson and Chapman 1961) total mortality from the average catch curve obtained from at least 3 years of catch at age data; data sets containing only 1 or 2 years of data were rejected because the presence of a single strong or week year-class in such a data record can produce severely biased mortality estimates (Ricker 1975) and (*ii*) for the more heavily exploited populations in Squeers and Opeongo, M estimates were obtained by subtracting estimates of fishing mortality from estimates of total mortality (Squeers: Ball 1988) or by estimating total mortality rates in years of very low fishing effort (Opeongo: Shuter et al. 1987).

Given this validation of M estimates based on eq. 5, we conclude that our sixth life history parameter (M) can be estimated from lake area and TDS using the relationships that link these characters to L_∞, ω, and M.

Habitat quantity (β and B_0)

A common assumption in both the fisheries literature (Ricker 1954; Cushing 1988) and the life history literature (Roff 1992; Charnov 1993) is that density-dependent effects on population growth rate act on the reproductive rate directly, either by increasing juvenile mortality or by reducing adult fecundity. This assumption is embodied in our population model through a stock–recruitment relationship that does not distinguish between effects on early mortality and fecundity. It simply assumes a negative effect of adult population density (B, kilograms of mature female biomass in the population per hectare) on the efficiency (maximum = $\alpha_{max} \cdot f_{max}$) with which mature female biomass produces 1-year-old fish:

$$N_1 = \frac{\alpha_{max} \cdot f_{max} \cdot B}{1 + \left(\dfrac{B}{B_0}\right)^\beta}.$$

Parameter B_0 establishes the range of population densities where significant declines in efficiency begin to be felt, and β defines the rate of decline as density increases through, and beyond, this range. We adopted the β value (2.0) used by Matuszek et al. (1990) in their long-term study of the Lake Opeongo lake trout population.

Parameter B_0 establishes the carrying capacity for a population and its value reflects the amount of limiting habitat

Table 2. Estimates of lake trout natural mortality rates for eight Ontario lakes.

Lake	L_∞ (cm)	ω (cm·year^{-1})	Pauly M (year^{-1})	Observed M (year^{-1})	Data source	Comments
Opeongo	87.2	8.0	0.13	0.12	M from Shuter et al. 1987	M for 1964–1983 estimated by regression of Z on effort
Squeers	55.0	7.5	0.18	0.24	M from Ball 1988	M is average for 1982–1986 mark–recapture estimates
Hawley	63.1	8.8	0.18	0.18	K. Armstrong, Ontario Ministry of Natural Resources, Cochrane, Ont., unpublished data	M from catch curve for 1989–1991 data; exploitation light and assumed negligible
Sutton	63.7	9.2	0.18	0.15	K. Armstrong, Ontario Ministry of Natural Resources, Cochrane, Ont., unpublished data	M from catch curve for 1989–1991 data; exploitation light and assumed negligible
Manitou	73.0	20.2	0.27	0.22	Budd et al. 1968	M from 1959–1962 mark–recapture data; growth parameters fitted visually to line on graph in paper
Lake 223	46.0	16.1	0.36	0.40	K. Mills, Department of Fisheries and Oceans, Winnipeg, Man., unpublished data	M from catch curve for 1975–1978 data; unexploited lake
Lake 224	41.0	12.3	0.33	0.25	K. Mills, Department of Fisheries and Oceans, Winnipeg, Man., unpublished data	M from catch curve for 1976–1980 data; unexploited lake
Buddell	62.2	6.5	0.15	0.12	J. Casselman, Ontario Ministry of Natural Resources, Picton, Ont., unpublished data	M from catch curve; unexploited lake

Note: The Pauly M estimates were derived from $\log_e(M) = -0.0238 - 0.9326 \log_e(1.094\, L_\infty) + 0.6551 \log_e(\omega) + 0.4646 \log_e(T)$, where T is mean annual water temperature and L_∞ is measured as total length. This equation was derived by reanalysing the variation in M, in Pauly's (1980) collection of M, K, L_∞, and T values, in terms of ω, L_∞, and T. In deriving our Pauly M estimates for lake trout, T was fixed at 6°C and L_∞ values were multiplied by 1.094 to convert from fork length to total length. Sources for observed M estimates are described in the table. The estimate for Lake 223 was based on data collected in the time period before the population was impacted by experimental acidification.

available (Shuter 1990; Minns et al. 1996) for use by that population. The value of B_0 sets the absolute yields associated with specific fishing mortality rates (Appendix 1) such that the maximum equilibrium yield (MEY) varies directly with the value of B_0. Conversely, given the MEY value for a population (plus estimates for W_∞, ω, t_m, f_{max}, α_{max} M, β, t_c), its B_0 value can be derived. This useful property provides a simple means of formally incorporating empirical relationships between population yield and limiting habitat into our population model. It permits such a relationship to be translated into a formula that predicts the value of B_0 appropriate to a particular amount of limiting habitat (Appendix 1).

Payne et al. (1990) (cf. Marshall 1996) extended Christie and Regier's (1988) lake yield (kilograms per hectare) data for lake trout by including long-term, sustained lake yield values from five smaller Ontario lakes. They found that annual lake yield could be accurately predicted from lake area ($r^2 = 0.923$, $p < 0.001$, $n = 20$):

(6) $\log_{10}(\text{yield}) = 0.50 + 0.83 \cdot \log_{10}(\text{area})$

and we incorporated this relationship into our model by translating it (Appendix 1) into a relationship that predicts B_0 from lake area:

(7) $B_0 = 84.33 \cdot \text{area}^{-0.76 + 0.038 \cdot \log_{10}(\text{area})}$.

This was done using all the relationships developed so far plus the relationship between ω, L_∞, and t_c described below.
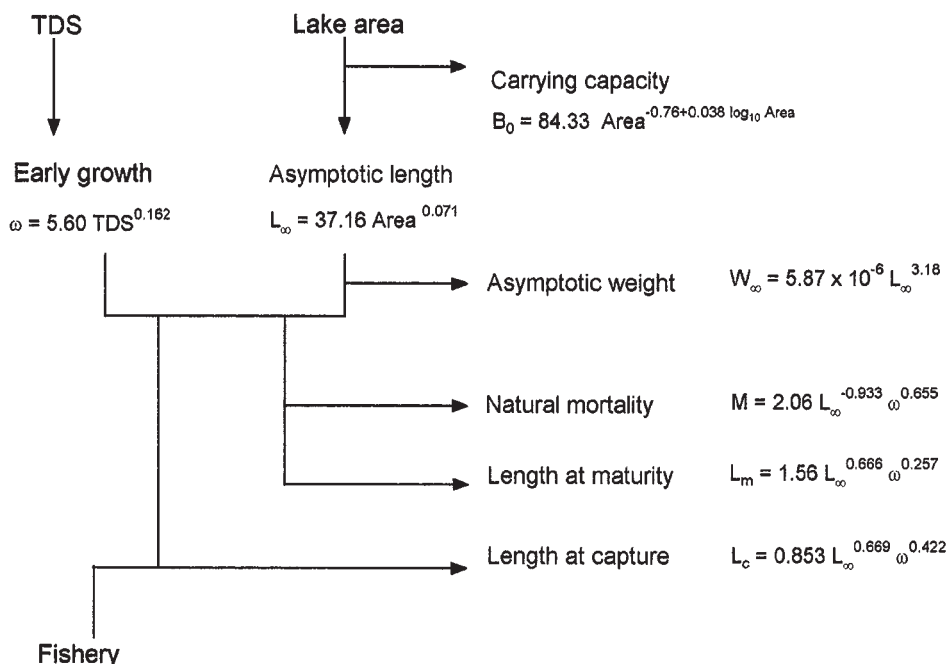
Vulnerability (t_c)

We used total angling mortality estimates and catch at age data to determine age-specific vulnerability for the lake trout in 21 lakes. Beginning with the modal age in the catch at age data (assumed to be the age of full vulnerability: $v_i = 1$), we back-calculated the expected catch in the preceding age-class from

$$C_i \approx \frac{v_i}{v_{i+1}} \cdot C_{i+1} \cdot e^{v_i \cdot F + M}.$$

We estimated the values of v_i for each age prior to the modal age by trial and error such that the computed C_i from the above equation most closely corresponded to the observed catch at age. We then used these age-specific vulnerabilities to estimate length at 5, 50, and 95% vulnerability (L_{c5}, L_{c50}, L_{c95}) for each of the 21 populations. We used analysis of covariance on these data, with $\log(L_i, i = c5, c50, c95)$ as dependent variable, $\log(L_\infty)$ and $\log(\omega)$ as covariates, and 5, 50, and 95% vulnerability levels as treatments. All independent variables were statistically significant ($p < 0.01$), with the full covariance model explaining 64% ($p < 0.0001$, $n = 63$) of the variation in observed sizes at the three levels of vul-

Fig. 2. Schematic diagram showing how eqs. 1–8 can be used to translate information on the area and TDS of a lake into a fully parameterized population model for the lake trout living in that lake.

nerability estimated. This analysis leads to the following equation for predicting size at 50% vulnerability (L_c):

$$(8) \qquad L_c = 0.853 \cdot \omega^{0.421} \cdot L_\infty^{0.669}.$$

Thus, for any lake, L_c can be estimated from ω and L_∞ using eq. 8 and t_c can then be estimated from L_c using the von Bertalanffy growth equation for the lake. The data used in this analysis come from fisheries that were free of regulations on the size of individual fish harvested. Hence, eq. 8 captures the "natural" size preference of fishers for their prey and suggests that this preference varies from population to population depending on the size range of fish available. Using eq. 8, we can estimate t_c from lake size and TDS using the relationships that link these characters to ω and L_∞.

Yield as a function of fishing mortality

We observed that L_∞ varies with lake size, that ω varies with TDS, and that other life history parameters vary in a consistent fashion with these variations in growth. Given this variation, the sensitivity of lake trout populations to exploitation may also vary with lake size and lake fertility. We explored this possibility using a population yield model based on eqs. 1–8 (Fig. 2). Model output showed that lake size has a substantial influence on the level of fishing mortality associated with MEY (F_{MEY}) and on the level of fishing mortality associated with stock extinction (F_{ext}). Yield curves for three lake sizes at a median level of TDS (32 mg·L^{-1}) demonstrate this (Fig. 3a; Table 3). For small lakes (100 ha), $F_{MEY} = 0.13$ and $F_{ext} = 0.20$, while for large lakes (10 000 ha), $F_{MEY} = 0.30$ and $F_{ext} = 0.43$. Lake trout populations in large lakes can apparently sustain approximately three times the fishing mortality that populations in small lakes can sustain. The effect of an increase in TDS on

sustainable F values is similar to that of an increase in lake size (Fig. 3b; Table 3).

The influence of lake size on the yield–F relationship stems from two separate effects. First, asymptotic mass (W_∞) is greater in large lakes (Table 3), and therefore, the egg production of a typical adult is greater. Other factors being equal, this ensures that the typical adult is more efficient at producing offspring and hence that the population can sustain higher total mortality rates. Second, natural mortality rates are lower in large lakes due to the positive association between lake size and adult fish size and the inverse relationship between adult size and natural mortality (eq. 5). Other factors being equal, lower natural mortality ensures lower prereproductive mortality, a longer reproductive lifetime, and thus, higher sustainable fishing mortality rates. Sensitivity analyses have shown that it is the differences in individual growth that contribute most to the differences in sustainable exploitation rates. To summarize, in large lakes, higher total mortality rates are sustainable because egg production per adult is greater, and a larger proportion of this mortality can be allocated to fishing because natural mortality is lower.

The influence of TDS on the yield–F relationship stems from three similar effects. First, mass at first maturity (W_m) is greater and age at first maturity is lower in high-TDS lakes. Hence, adult egg production is greater and exposure to prereproductive mortality is reduced. In addition, the difference between age at first capture and age at first maturity is smaller in high-TDS lakes (Table 3), and this leads to a decrease in prereproductive fishing mortality. All these changes lead to an increase in the range of sustainable total mortality rates and consequently an increase in the range of sustainable fishing mortality rates. The latter increase is diminished but not eliminated by the higher natural mortality

Fig. 3. Predicted relationships between equilibrium yield and fishing mortality for (*a*) lakes with a TDS value of 32 mg·L^{-1} and surfaces areas of 100 ha (solid line), 1000 ha (dashed line), and 10 000 ha (dotted line) and (*b*) lakes with a surface area of 1000 ha and TDS values of 15 mg·L^{-1} (solid line), 32 mg·L^{-1} (dashed line), and 180 mg·L^{-1} (dotted line). Predictions were derived using the lake trout population model, parameterized according to the scheme outlined in Fig. 2.
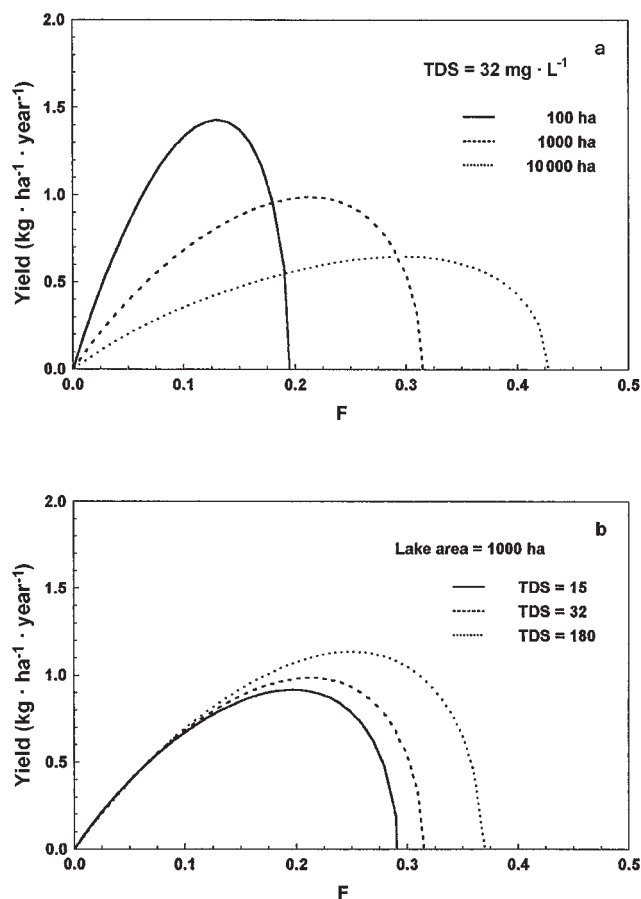
Fishing mortality as a function of fishing effort and stock abundance

Effort levels on a lake are often used as indicators of exploitation intensity. To consider the effort implications of this model, the relationship between fishing mortality rate (*F*) and angling effort (*E*) must be described. Classical fisheries theory (Beverton and Holt 1957; Ricker 1975) assumes that these variables are directly related, $F = qE$, where the catchability coefficient (*q*) is a constant. Many theoretical (e.g., Paloheimo and Dickie 1964; Condrey 1984) and empirical (e.g., Peterman and Steer 1981; Beaumont et al. 1991) studies have shown that, under a wide variety of circumstances, it is more reasonable to expect that *q* will vary inversely with the abundance of the exploited population. We constructed three independent tests of the hypothesis that

angling *q* is negatively related to lake trout population abundance (number per hectare).

We examined variation in catchability for two lakes where annual, independent estimates of both catchability and population abundance could be obtained (Fig. 4*a*). Time series data from the lake trout populations in Lake Opeongo and Squeers Lake included annual estimates of effort, yield, population abundance (*N*, number per hectare), and fishing mortality. For the Opeongo population, *F* and *N* estimates were based on catch at age analysis, supplemented with a series of mark–recapture experiments (Shuter et al. 1987) (Appendix 2). For the Squeers population, annual *F* and *N* estimates were based on annual mark–recapture experiments (Appendix 2). For each lake, we found a negative correlation between *q* and *N* ($p < 0.001$).

We examined variation in catchability among 17 lakes where estimates of average values for both catchability and population abundance (*N*, number per hectare) could be obtained (Fig. 4*b*). For lakes other than Opeongo and Squeers, we obtained annual estimates of effort intensity by multiplying nominal effort per hectare by the proportion of the catch that was kept. We averaged annual effort and yield values across years to get mean values for annual effort intensity and annual harvest (*H*, number kept per hectare) for each lake. We used pooled catch at age data to estimate total mortality (*Z*) (Chapman and Robson 1960; Robson and Chapman 1961) and eq. 5 to estimate natural mortality (*M*). From these mortality components, we generated lake-specific estimates of *F*, *q*, and *N*:

$$F = Z - M$$

$$q = \frac{F}{E}$$

$$N = \frac{H}{F}.$$

These *q* and *N* estimates were also negatively correlated ($p < 0.001$).

All three analyses demonstrate a strong, negative relationship between catchability and population abundance. This finding suggests that density-dependent angler catchability is a common feature of lake trout populations in Ontario.

Yield as a function of fishing effort: influence of density-dependent catchability

Paloheimo and Dickie (1964) were the first to consider the consequences for catchability of a more realistic picture of predation by fishers. Given that fish are distributed in patches (i.e., schools, aggregations) and that fishing involves the search for patches and the capture of fish within patches, they showed that catchability should be modelled by an equation of the form
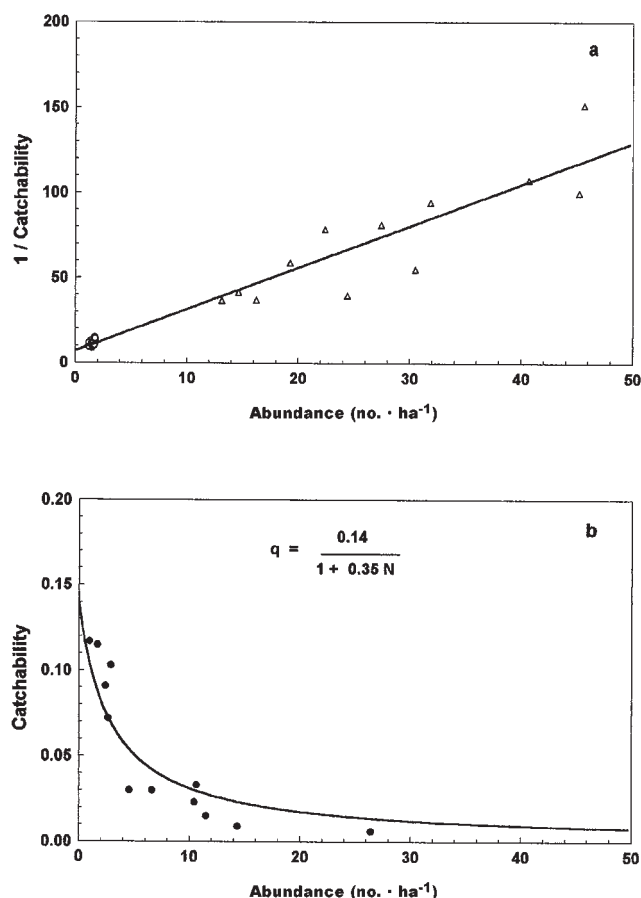
$$q = \frac{a}{1 + bN}.$$

Linearizing this equation by plotting q^{-1} against *N*, we see that the relationship defined by pooling the Squeers and Opeongo data sets roughly matches not only the within-lake variation in *q* observed in the two lakes (Fig. 4*a*), but also

rates that also accompany the shift in growth pattern characteristic of higher TDS values. The net result of all these changes is higher F_{MEY} and F_{ext} values among populations with higher TDS values.

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Table 3. Predicted parameter values (W_∞, M, t_m, t_c) and model results (F_{MEY}, F_{ext}, E_{MEY}, E_{safe}) for various lake sizes (100, 1000, 10 000 ha) and levels of TDS (15, 32, 180 mg·L^{-1}).

Lake size (ha)	W_∞ (kg)	TDS (mg·L^{-1})	M (year^{-1})	t_m (years)	t_c (years)	$t_m - t_c$ (years)	F_{MEY} (year^{-1})	F_{ext} (year^{-1})	E_{MEY} (angler-h·ha^{-1})	E_{safe} (angler-h·ha^{-1})
100	1.63	15	0.22	7.8	5.1	2.7	0.12	0.19	6.6	1.3
		32	0.23	7.3	4.9	2.4	0.13	0.20	6.3	1.4
		180	0.28	6.6	4.5	2.1	0.14	0.21	5.4	1.5
1 000	2.74	15	0.18	8.2	5.5	2.7	0.20	0.29	4.2	2.1
		32	0.20	7.7	5.3	2.4	0.21	0.32	4.2	2.3
		180	0.24	6.8	4.8	2.0	0.25	0.37	4.2	2.6
10 000	4.61	15	0.16	8.7	6.0	2.7	0.27	0.39	3.3	2.8
		32	0.17	8.2	5.7	2.5	0.30	0.43	3.4	3.1
		180	0.21	7.1	5.2	1.9	0.37	0.53	3.9	3.8

Note: W_∞ is shown only once for each lake size because it is not affected by TDS.

Fig. 4. (*a*) Observed relationship between the inverse of catchability and population abundance for the lake trout populations of Lake Opeongo (circles) and Squeers Lake (triangles). The line is the regression line derived from all the data points. Note that the fitted line closely matches the trend evident in the Squeers Lake data alone while also passing through the centres of the two clusters of data. (*b*) Fitted relationship (from Fig. 4*a*) between catchability (*q*) and abundance (*N*) compared with observed values for average catchability and abundance for 12 Ontario lake trout lakes.

Fig. 5. Predicted relationships between equilibrium yield and fishing effort for lakes with a TDS value of 32 mg·L^{-1} and surface areas of 100 ha (solid line), 1000 ha (dashed line), and 10 000 ha (dotted line). Predictions were derived using the lake trout population model, parameterized according to Fig. 2, plus the relationship between catchability and population abundance given in Fig. 4.
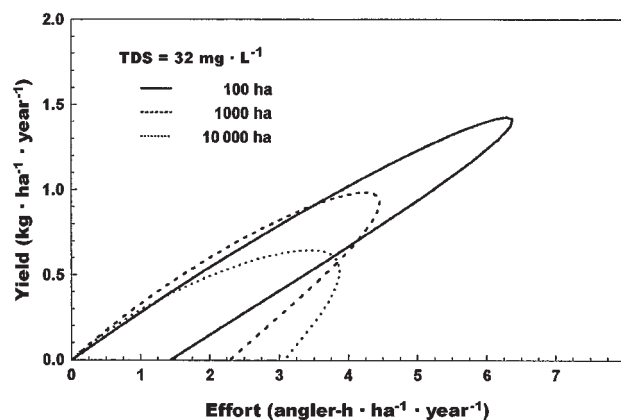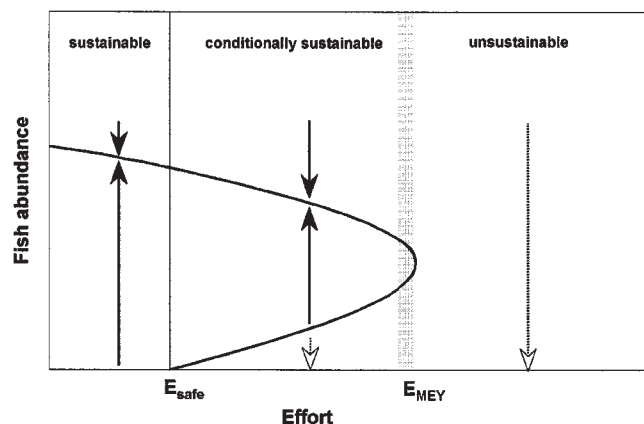

density (<0.5 individual·ha^{-1}) lakes in our data set (predicted $q = 0.15$, mean observed $q = 0.31$). Given the many factors that can influence catchability, it is perhaps surprising that a single relationship is capable of describing so much of the joint variation observed among *q* and *N* values.

We used this relationship to reexpress the yield–*F* curves in Fig. 3 in terms of yield–*E* curves: we substituted the equilibrium population abundance at each *F* value (Appendix 1) into the following equation to calculate the appropriate equilibrium effort value:

$$E = \frac{F}{\dfrac{0.14}{1 + 0.35N}}.$$

This leads to a set of unusual yield–*E* curves (Fig. 5). As effort increases toward E_{MEY}, equilibrium yield rises almost linearly to a maximum (MEY). Small increases in effort beyond E_{MEY} are unstable and lead to stock collapse if maintained. These curves are the product of the strong interaction between population abundance and sustainable effort levels explained below (Fig. 6).

the among-lake variation in *q* observed for the 12 lakes with mean densities >1 individual·ha^{-1} (Fig. 4*b*). The relationship does, however, underestimate *q* values for the three low-

Fig. 6. Schematic diagram illustrating changes in equilibrium population abundance (N) with changes in fishing effort (E). If $E < E_{safe}$, there is a single equilibrium value for N and that equilibrium value is stable. If N lies between E_{safe} and the maximum equilibrium value for E, there are two equilibrium values for N, a higher one that is stable and a lower one that is unstable. If N is greater than the maximum equilibrium E, there are no equilibrium values for N. The open and solid arrows show how N will change if it does not lie on one of the equilibrium curves.

Fig. 7. (*a*) Changes in predicted benchmark mortality values (F_{MEY}, F_{ext}) with changes in lake size and TDS. The elevated pair of dashed lines represents F_{ext} (top line) and F_{MEY} (bottom line) values for lakes with a TDS of 180 mg·L^{-1}. The pair of solid lines represents F_{ext} (top line) and F_{MEY} (bottom line) values for lakes with a TDS of 15 mg·L^{-1}. (*b*) Changes in predicted benchmark fishing effort (E_{safe}, E_{MEY}) levels with changes in lake size and TDS. The pair of dashed lines represents E_{MEY} (top line) and E_{safe} (bottom line) values for lakes with a TDS of 180 mg·L^{-1}. The pair of solid lines represents E_{MEY} (top line) and E_{safe} (bottom line) values for lakes with a TDS of 15 mg·L^{-1}.

(*i*) There is a critical effort level, E_{safe}, below which all effort values are unconditionally sustainable; for each effort level in this interval, population abundance will move toward a stable, equilibrium value that is well above zero.

(*ii*) Values of E in the interval (E_{safe}, E_{MEY}) are conditionally sustainable; for each effort level in this interval, there is a critical value for population abundance, N^*, such that (*a*) if $N > N^*$ and the effort level is maintained, the population will move toward a stable equilibrium value that is well above zero and (*b*) if $N < N^*$ and the effort level is maintained, the population will collapse.

(*iii*) Values of $E > E_{MEY}$ are unsustainable; if such effort levels are maintained, the population will collapse.
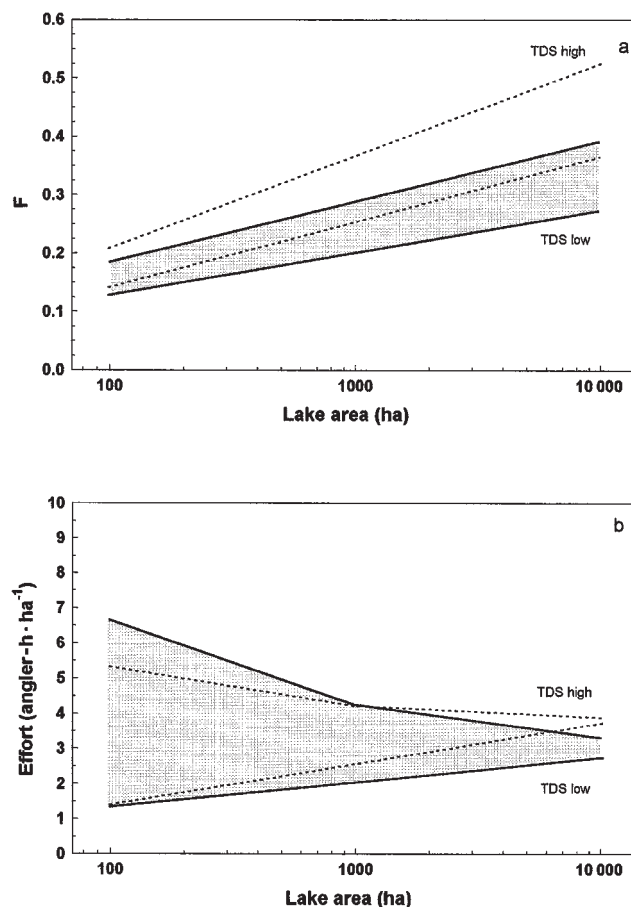
This pattern of behaviour has the important consequence that, when effort is at unsustainable levels ($N < N^*$, given E), hesitation in implementing effort reductions will ensure that larger reductions are necessary to permit stock recovery. This occurs because when $N < N^*$, N will decline and as N declines, the effort level that it can sustain also declines. The longer this decline is allowed to continue, the greater the effort reduction required to stabilize N and permit it to increase. In the absence of information on stock abundance, E must be reduced below E_{safe} to ensure stock recovery. The highly stochastic nature of many real systems greatly augments the danger of inadvertently entering a region of unsustainable effort levels. Once this happens, the dynamics outlined above will take over, leading to the all too familiar situation of a collapsed population and a closed fishery.

Discussion

Managing Ontario lake trout populations: strategic considerations

We had two primary objectives in this study. First, we identified predictable differences in the biology of Ontario lake trout populations and in the character of Ontario lake trout angling fisheries. Second, we demonstrated the effects of such differences on the sensitivity of individual populations to overexploitation. Some of our findings have significant implications, at the strategic level, for exploitation management in the province.

Our analysis shows that small lakes with low TDS values are quite sensitive to overexploitation and hence require more stringent exploitation controls than large lakes with high TDS values. Both sustainable fishing mortality levels and sustainable effort levels vary significantly with lake area and with TDS (Table 3; Fig. 7). As lake size decreases or as TDS decreases, values for F_{MEY} and F_{ext} decline and converge, while values for E_{MEY} and E_{safe} diverge. These shifts indicate that large, high-TDS lakes are least sensitive to exploitation, while small, low-TDS lakes are most sensitive: as

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F_{ext} approaches F_{MEY}, small variations in F around F_{MEY} are more likely to exceed F_{ext} and hence lead to stock collapse; similarly, as E_{safe} diverges further from E_{MEY}, larger reductions in fishing effort will be required to ensure stock recovery, once collapse has begun.

Values for E_{safe} and E_{MEY} vary in a complex fashion with both lake area and TDS. For any TDS value, E_{MEY} decreases with lake area, while E_{safe} increases (Fig. 7b). For small lakes, E_{MEY} decreases with TDS, while E_{safe} remains essentially unchanged. For large lakes, E_{safe} and E_{MEY} increase and converge with TDS. This interactive effect arises because both growth rate and size at maturity increase with TDS and these changes permit numerical density at MEY to decline. For small lakes, numerical density is high to begin with and, therefore, catchability is particularly sensitive to density differences. For such lakes, the lower numerical densities associated with higher TDS values lead to increases in catchability that are large enoough to produce lower E_{MEY} values. In large lakes, density is low to begin with and, therefore, catchability is relatively insensitive to density differences. In such lakes, higher TDS values are accompanied by increases in benchmark effort levels that roughly parallel increases in benchmark fishing mortality rates.

Our analysis shows that the catchability coefficient associated with angling effort is strongly dependent on lake trout abundance, and therefore, catch per unit effort (CUE) figures are not proportional to fish abundance. Preliminary work with a dynamic version of our model shows that the density dependence of catchability is strong enough to permit maintenance of unsustainable effort levels for extended periods before a detectable decline in CUE occurs. These results demonstrate that angler CUE cannot be used to accurately assess the status of lake trout populations subjected to angling fisheries.

Another important aspect of the interaction between angling catchability and population abundance is the fact that sustainable effort levels decrease with lake size, while sustainable fishing mortality levels increase (Fig. 7). Observed effort levels for Ontario lake trout lakes tend to follow this trend; however, they are often greater than predicted E_{MEY} values: predicted E_{MEY} values lie in the range from 3 to 7 angler-h·ha^{-1}·year^{-1}. In the Goddard et al. (1987) study of 80 Ontario lake trout angling fisheries, about half the recorded effort values (median effort = 7.7 angler-h·ha^{-1}) exceeded this range. Thus, existing angling effort levels appear to be well in excess of sustainable limits on many of Ontario's lake trout lakes. The effects of overexploitation are obvious in the southern part of the province, where high effort levels have existed for many years, severe reductions in angling CUE values have occurred, and these reductions have led to both new regulations and an increased demand for stocking. Effects are less obvious in the north, where lakes have a shorter history of exploitation.

Critical elements in regional management models for fish populations

Density-dependent catchability and effort management

Classical fisheries theory (Beverton and Holt 1957; Ricker 1975) and common management practice begin with the assumption of a constant catchability coefficient. Strictly

speaking, this assumption is only valid if the movements of either predator (the fisher) or prey (the fish) are purely random. While some fisheries may approximate this ideal condition, many do not. The behavioural repertoire of many fish species is as complex as that of any of the vertebrates, with habitat preference, habitat defense, and schooling commonly exhibited. These very nonrandom movement habits of the prey are complemented by the ability of typical fishers to find and efficiently exploit concentrations of fish.

Early theoretical work by Paloheimo and Dickie (1964) showed that more realistic pictures of the predation process in fisheries require that catchability be represented as a negative function of fish population density. This early result has been reinforced by a long list of additional theoretical work, plus many empirical studies (e.g., MacCall 1976; Hutchings and Myers 1994). The theoretical studies suggest that, given the character of real fisheries, density-dependent catchability should often be expected. The empirical studies show that, when looked for, such an effect is more often present than absent (Lester and Shuter 1993).

The weight of this evidence suggests that the appropriate null hypothesis for most situations is that catchability is density dependent. This conclusion is reinforced by the precautionary principle that effort management strategies predicated on a false assumption of constant catchability can lead directly to stock collapse (e.g., Fig. 6).
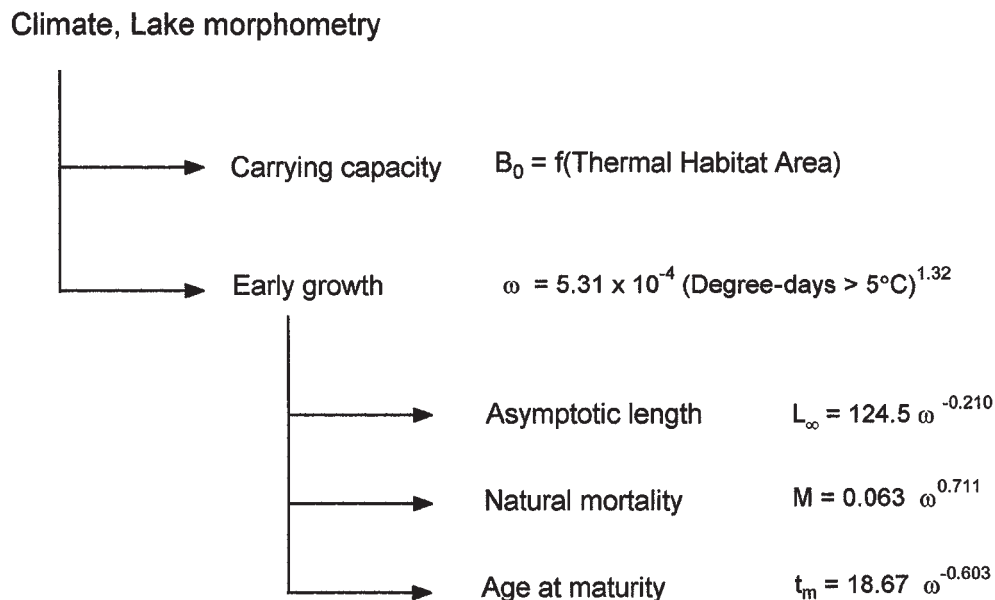
Yield, carrying capacity, and habitat quantity

Our yield model explicitly identifies the linkages between the amount of habitat available to a population and the sustainable yields that the population can generate. We do this using a very simple version of the approach to habitat modelling discussed by Shuter (1990) and Minns et al. (1996). This approach permits easy scaling of model output to match empirical relationships that predict sustainable yields from indices of available habitat. In our lake trout analysis, this was done by making B_0 a function of lake area so that model-generated MEY values would match values predicted from an empirical relationship linking long-term sustained yield to lake area. Such empirical relationships have been demonstrated for other species. Christie and Regier (1988) found strong links between sustainable yield and amount of thermally suitable habitat for walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*), and lake whitefish (*Coregonus clupeaformis*). Thus, it seems likely that habitat-based predictors for MEY can be developed for other species. Incorporating such relationships into yield models greatly extends model usefulness by allowing explicit consideration of the effects of habitat loss on sustainable yield.

Predictability of interpopulation differences in life history characters

Our work on lake trout has shown that interpopulation differences among life history characters can be large enough to significantly affect sustainable exploitation rates. Within the relatively narrow geographic confines of Ontario, lake trout populations exhibit a twofold variation in both ω and L_∞ and a fourfold variation in M (Tables 1 and 2). Given this degree of variation in life history parameters, we can infer up to a fourfold variation in benchmark (F_{MEY}, F_{ext}) exploitation rates. This degree of variation is not unique to lake

Fig. 8. Empirical relationships linking environmental variables to carrying capacity and life history parameters for walleye populations. The carrying capacity relationship refers to the finding of Christie and Regier (1988) that sustainable yields from walleye populations were tightly correlated with a measure of the annual average amount of habitat thermally suitable for walleye (i.e., their "thermal habitat area"). The life history relationships were derived from regression analysis of walleye life history data reported in Beverton (1987). Natural mortality rates were estimated from longevity values using a relationship between mortality and longevity reported by Hoenig et al. (1987).

Climate, Lake morphometry

Carrying capacity $\quad B_0 = f(\text{Thermal Habitat Area})$

Early growth $\quad\quad \omega = 5.31 \times 10^{-4} (\text{Degree-days} > 5^\circ\text{C})^{1.32}$

Asymptotic length $\quad L_\infty = 124.5\, \omega^{-0.210}$

Natural mortality $\quad M = 0.063\, \omega^{0.711}$

Age at maturity $\quad t_m = 18.67\, \omega^{-0.603}$

trout. Life history data from walleye populations in 13 lakes spanning the much wider geographical range from Ontario to Texas (Beverton 1987, based on data from Colby et al. 1979 and Colby and Nepszy 1981) exhibit a twofold range in L_∞, a 10-fold range in ω, and a fourfold range in M. Given the potential effects of such variation on sustainable exploitation rates, it is obvious that exploitation could be more effectively managed if this variation could be predicted and used to identify geographical regions and (or) categories of water bodies that require different regulations.

In general, interpopulation variation in demographic parameters can arise from two sources: variation in the abiotic characteristics of the habitats occupied by the populations or variation in the biota that share those habitats. The walleye data mentioned above suggest an abiotic linkage: life history parameters are strongly correlated with an index of environmental temperature, and with each other (Fig. 8). This set of demographic–environmental linkages is quite similar to the set that characterizes Ontario lake trout populations (Fig. 2): growth (ω) is predictable from environmental conditions, and maturity and mortality are predictable from growth.

For lake trout, the effects of TDS and lake area on growth probably reflect differences in associated biota rather than differences in abiotic conditions. Lake trout are strongly stenothermal and tend only to be found in lakes (and habitats within lakes) that provide abiotic conditions that are well suited to their requirements (e.g., low temperatures, high dissolved oxygen levels). Higher TDS levels are associated with higher zooplankton productivity, and zooplankton are the primary food for lake trout during their first few years of life. Hence, the TDS effect on ω may reflect a relatively simple link between food availability and growth. The lake area effect on L_∞ is a bit more difficult to interpret.

However, there is considerable evidence that lake trout lakes with greater community complexity (most notably the presence of a broad size range of abundant prey) tend to produce populations with larger asymptotic sizes (Martin 1966; Matuszek et al. 1990). Our data are consistent with this trend. For the 54 populations that we examined, the log–log correlation between L_∞ and lake area is matched by similar log–log correlations between L_∞ and species richness ($r^2 = 0.39$, $p < 0.001$) and between species richness and lake area ($r^2 = 0.53$, $p < 0.001$). Also, the fact that the growth differences among populations become more apparent as fish reach older ages is consistent with the expectation that in larger lakes, greater fish species richness will provide a wide prey size range and hence promote increased growth among larger, piscivorous lake trout (Kerr and Martin 1970; Kerr 1971; Roff 1986).

Both of our examples exhibit strong intercorrelations among life history parameters. This is consistent with many empirical and theoretical studies that support the existence of significant covariation among the primary life history parameters of fish, most notably those that describe growth (ω, L_∞), sexual maturity (L_m, t_m) (Roff 1992, Charnov 1993), and natural mortality (e.g., Beverton 1987; Charnov and Berrigan 1991; Roff 1991). Qualitatively similar relationships seem to describe both inter- and intra-specific variation in these characters (e.g., Pauly 1980; Roff 1992; Charnov 1993).

Life history theory (Roff 1992; Charnov 1993) seeks to explain such intercorrelations by suggesting that optimization of lifetime reproductive output requires that variation in growth rate produce changes in size at first maturity and that these changes will, in turn, affect postreproductive mortality. Similarly, variation in mortality rate should produce changes

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Fig. 9. Observed and predicted values for size at maturity. Observed values represent the lengths at which 50% (solid circles) and 95% (open circles) of females are mature; predicted values were derived from von Bertalanffy growth parameters using an equation (eq. 9) developed by Roff (1986).
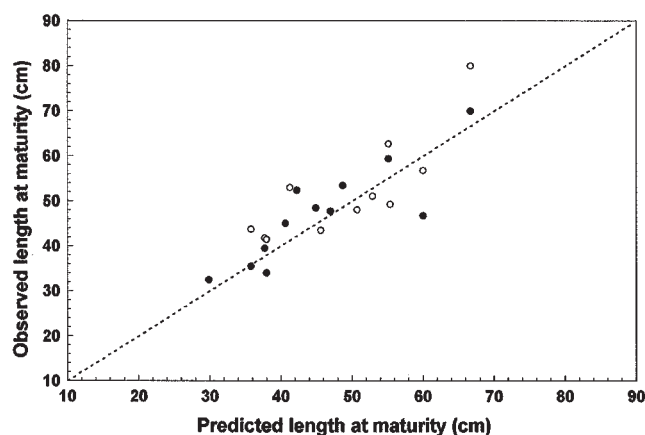
in age and size of maturity and these changes should, in turn, affect the overall growth pattern of the animal. Much of the covariation among life history characters observed in our examples is consistent with Roff's (1984, 1986) model for predicting optimal size at first reproduction. Roff found that, for a wide range of circumstances, the size at first reproduction that maximizes lifetime reproductive output is

$$(9) \qquad L_m = L_\infty \cdot \left(\frac{3 \cdot \omega}{3 \cdot \omega + M \cdot L_\infty} \right)$$

and the corresponding age at first reproduction is

$$(10) \qquad t_m = \frac{L_\infty}{\omega} \cdot \log_e \left(\frac{3 \cdot \omega}{L_\infty \cdot M} + 1 \right)$$

We used these equations to predict L_m and t_m values from our estimates for L_∞, ω, and M. We found good correspondence (Fig. 9) between predicted L_m values and our observed values for L_{m50} and L_{m95} and reasonable correspondence between estimated and predicted t_m values ($R^2 = 0.334$, $p < 0.003$, $n = 23$, relationship between estimated and predicted values not significantly different from the 1:1 line).

Equations 9 and 10 predict that growth rate changes at different points in the life cycle can have different effects on life history parameters: an increase in L_∞ will cause both L_m and t_m to increase, while an increase in ω will cause L_m to increase and t_m to decrease. These predictions are confirmed by our lake trout data. Increases in lake size are accompanied by parallel increases in both L_m and t_m; increases in TDS are accompanied by increases in L_m and decreases in t_m. These effects have been observed in earlier studies. Matuszek et al. (1990) observed an increase in both size and age at maturity in the Lake Opeongo lake trout population after the introduction of cisco (*Coregonus artedi*) produced increased growth among lake trout > 35 cm in length. Trippel (1993) and Trippel and Beamish (1993), in a comparative study of three low-TDS and three high-TDS lakes,

found higher early growth rates, higher sizes at maturity, and lower ages at maturity in the three high-TDS lakes.

Thus, fish species that typically undergo ontogenetic shifts in diet (e.g., lake trout, walleye) may respond to a growth rate increase with either an increase or a decrease in age at maturity, depending on where in the life cycle the growth rate change occurs (Hutchings 1993). Fish that do not exhibit ontogenetic diet shifts are more likely to exhibit growth rate changes throughout the life cycle and hence are more likely to decrease age of maturity in response to an increase in growth. These conclusions are a simple consequence of the basic trade-off that underlies optimization for age of maturity in fish: the benefits gained by delaying maturity to a later age (and hence, growing to a larger size) are increased fecundity and decreased cost of reproduction, while the cost incurred is a decrease in the overall probability of surviving to that later age. An increase in potential growth for age groups near the current age of maturity would increase the benefit of growing older without affecting the cost, and hence would move both the optimum age and size of maturity upward. An increase in growth rate early in life would decrease the benefit in growing older without decreasing the cost, and hence would move the optimum age of maturity downward and size at maturity upward, as the increase in growth compensates for the decrease in age.

Our results suggest that the search for useful environmental correlates of life history characters should focus on those factors most likely to influence the lifetime growth pattern of the species being studied. Our results support the prediction of life history theory that a common consequence of natural selection for reproductive efficiency is a high degree of intercorrelation among life history parameters. Thus, once such a correlation pattern has been identified in a representative sample of populations from a region, that pattern can be used with some confidence to forecast behaviour of other populations in that region.

Acknowledgments

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Appendix 1. Derivation of equilibrium yield equation

Our model combines yield per recruit and stock–recruitment functions to construct yield curves relating equilibrium yield to fishing mortality, following methods described by Shepherd (1982). We will focus on the situation where the age of first capture by the fishery (t_c) is less than or equal to the age of maturity (t_m).

First, we note that yield (Y) equals yield per recruit (YPR) times number of recruits (R):

(A1) $\quad Y = \text{YPR} \cdot R$

and that the number of recruits equals female spawner biomass (S) divided by female spawner biomass per recruit (SPR):

(A2) $\quad R = \dfrac{S}{\text{SPR}}.$

Therefore, yield can be expressed as

(A3) $\quad Y = \text{YPR} \cdot \dfrac{S}{\text{SPR}}.$

Given any stock–recruitment relationship, spawner biomass can be expressed as a function of SPR. This is illustrated using Shepherd's generic model which accommodates various functional forms proposed by Ricker (1954, 1975) and Beverton and Holt (1957):

(A4) $\quad R = \dfrac{\alpha_{max} \cdot f_{max} \cdot S}{1 + \left(\dfrac{S}{B_0}\right)^{\beta}}$

where α_{max} is survival from conception to recruitment, f_{max} is fecundity, and B_0 and β together control the rate at which the number of recruits per unit spawner biomass declines with increases in spawner biomass. Because SPR is defined as S/R, eq. A4 can also be expressed in the form

(A5) $\quad S = B_0 \cdot \left(\alpha_{max} \cdot f_{max} \cdot \text{SPR} - 1\right)^{\frac{1}{\beta}}.$

Substituting for S in eq. A3 gives

(A6) $\quad Y = \dfrac{\text{YPR}}{\text{SPR}} \cdot B_0 \cdot \left(\alpha_{max} \cdot f_{max} \cdot \text{SPR} - 1\right)^{\frac{1}{\beta}}.$

The variables in this equation, YPR and SPR, are in fact functions that depend on life history parameters (i.e., growth, age at maturity, and natural mortality) and fishery parameters (i.e., initial age of capture and fishing mortality). A function for YPR is available from Beverton and Holt (1957):

(A7) $\quad \text{YPR} = F \cdot e^{-M \cdot (t_c - t_r)} \cdot W_\infty$

$$\times \left(\frac{1}{Z} - \frac{3 \cdot e^{-K \cdot t_c}}{Z + K} + \frac{3 \cdot e^{-2 \cdot K \cdot t_c}}{Z + 2 \cdot K} - \frac{e^{-3 \cdot K \cdot t_c}}{Z + 3 \cdot K} \right)$$

where F is fishing mortality, M is natural mortality, t_c is initial age of capture, t_r is the age of a recruit (whose abundance is indicated by R in previous equations), W_∞ is asymptotic mass, K is the von Bertalanffy growth rate parameter, and Z is total mortality ($= M + F$). To simplify the notation, the bracketed expression in eq. A7 will be referred to as function $g(t)$ where

(A8) $\quad g(t) = \left(\frac{1}{Z} - \frac{3 \cdot e^{-K \cdot t}}{Z + K} + \frac{3 \cdot e^{-2 \cdot K \cdot t}}{Z + 2 \cdot K} - \frac{e^{-3 \cdot K \cdot t}}{Z + 3 \cdot K} \right)$

An equation for SPR can be derived from the YPR function given that (*i*) catchable biomass (*B*) equals yield divided by fishing mortality:

$$(A9) \quad B = \frac{Y}{F}$$

and (*ii*) spawner biomass equals catchable biomass times the proportion (by mass) of mature fish in the catchable segment of the population (p_m) times the proportion (by mass) of females (i.e., 0.5):

$$(A10) \quad S = 0.5 \cdot B \cdot p_m.$$

Substitute eq. A9 into eq. A10 and divide both sides by *R* to obtain

$$(A11) \quad SPR = \frac{YPR \cdot p_m}{2 \cdot F}.$$

To obtain an equation for p_m, we note that the proportion of mature fish in the catchable segment equals the proportion of mature fish in the catch. An expression for the latter is available by an extension of eq. A7 which gives the yield provided by fish that are aged *t* or older ($t > t_c$) as a function of the number of fish that survive to age *t* (N_t):

$$(A12) \quad Y_t = F \cdot N_t \cdot W_\infty \cdot g(t).$$

Since

$$(A13) \quad p_m = \frac{Y_{t_m}}{Y_{t_c}}$$

it follows that, when $t_c \leq t_m$:

$$(A14) \quad p_m = \frac{N_{t_m} \cdot g(t_m)}{N_{t_c} \cdot g(t_c)}$$

Given that the number of fish surviving to maturity is less than or equal to the number at initial age of capture:

$$(A15) \quad N_{t_m} = N_{t_c} \cdot e^{-Z \cdot (t_m - t_c)}$$

and therefore:

$$(A16) \quad p_m = e^{-Z \cdot (t_m - t_c)} \cdot \frac{g(t_m)}{g(t_c)}$$

and

$$(A17) \quad SPR = \frac{YPR}{2 \cdot F} \cdot e^{-Z \cdot (t_m - t_c)} \cdot \frac{g(t_m)}{g(t_c)}$$

Substitute the expression in eq. A7 for YPR to get

$$(A18) \quad SPR = 0.5 \cdot W_\infty \cdot e^{-M \cdot (t_c - t_r)} \cdot e^{-Z \cdot (t_m - t_c)} \cdot g(t_m)$$

An explicit formulation for yield is then obtained by substituting for YPR and SPR in eq. A6:

$$(A19) \quad Y = \frac{2 \cdot B_0 \cdot F \cdot g(t_c)}{e^{-Z \cdot (t_m - t_c)} \cdot g(t_m)}$$

$$\times (0.5 \cdot \alpha_{max} \cdot f_{max} \cdot W_\infty \cdot e^{-M \cdot (t_c - t_r)} \cdot e^{-Z \cdot (t_m - t_c)} \cdot g(t_m) - 1)^{\frac{1}{\beta}}$$

Thus:

$$(A20) \quad Y = B_0 \cdot f(M, K, W_\infty, t_m, \alpha_{max}, f_{max}, \beta, t_c, F)$$

$$(A21) \quad = B_0 \cdot f°(F)$$

given all other parameters held constant.

Now, given biologically reasonable values for (M, K, W_∞, t_m, α, f, β, t_c), $f°(F)$ has a single maximum at F_{MEY} and this equals the maximum equilibrium yield (MEY). Therefore:

$$(A22) \quad Y_{MEY} = B_0 \cdot f°(F_{MEY})$$

and

$$(A23) \quad B_0 = \frac{Y_{MEY}}{f°(F_{MEY})}$$

Therefore, if Y_{MEY} is an empirical function (*g*) of the amount of limiting habitat (hab) and if $f°(F_{MEY})$ is known for each value of hab, then

$$(A24) \quad B_0 = \frac{g(hab)}{f°(F_{MEY})} = g°(hab)$$

Appendix 2. Estimating lake trout density on Squeers Lake and Lake Opeongo

Mark–recapture studies have been conducted since 1985 on Squeers Lake. We used the Peterson–Chapman method to estimate initial abundance (*N*) of the exploitable stock in each year. Since the fishery is restricted to a 10-day period in March each year, we assumed negligible natural mortality during this period and calculated fishing mortality rate (*F*) as

$$F = -\log_e \left(1 - \frac{H}{N} \right)$$

and average abundance ($\overline{N}$) as

$$\overline{N} = \frac{H}{F}$$

where *H* is the annual harvest.

The Lake Opeongo fishery has been monitored since 1937, and estimates of population size and fishing mortality were calculated as described in Shuter et al. (1987) using catch at age analysis and periodic independent assessments with mark–recapture studies. We used only the more recent years (post-1967) in our analysis because the character of the fishery has been relatively stable since then. The fishery operates over a 4-month period (May–August), so we assumed that natural mortality during the fishing period was one third of the annual estimate ($M = 0.11$) and $\overline{N}$ calculated as

$$\overline{N} = N \cdot \frac{(1 - \exp(-F + 0.33 \cdot M))}{(F + 0.33 \cdot M)}.$$