



Baseline demographics of a non-native lake trout population and inferences for suppression from sensitivity-elasticity analyses

B. S. COX

Montana Cooperative Fishery Research Unit, Department of Ecology, Fish and Wildlife Management Program, Bozeman, MT, USA

C. S. GUY

Montana Cooperative Fishery Research Unit, Department of Ecology, Fish and Wildlife Management Program, US Geological Survey, Bozeman, MT, USA

W. A. FREDENBERG

U.S. Fish and Wildlife Service, Creston, MT, USA

L. R. ROSENTHAL

Montana Fish, Wildlife, and Parks, Kalispell, MT, USA

Abstract Management agencies in several western states of the United States are implementing suppression programmes to control non-native lake trout, *Salvelinus namaycush* (Walbaum), for the conservation of native species. This study was implemented to ascertain the population demographics of an expanding lake trout population and use those data to construct an age-structured model to inform suppression efforts. Population projection matrices were used to model population growth and identify age or stage classes with the greatest influence on population growth. The size and age structure of lake trout sampled was skewed towards juveniles, indicating strong recruitment and a growing population. Matrix-model simulations corroborated the observed size and age structure, as the lake trout population was predicted to grow exponentially ($\lambda = 1.35$, 95% CL: 1.25–1.43) with no suppression efforts. Elasticity analysis of matrix models indicated the relative contribution of survival rates to population growth among immature age classes was equal from age 0 to age at first maturity, but immature survival rates contributed more than adult survival and fertility rates. These results emphasise the importance of targeting juvenile lake trout for suppression efforts during exponential growth in recently established populations.

KEY WORDS: demographics, elasticity, matrix model, *Salvelinus namaycush*, sensitivity, suppression.

Introduction

The lake trout *Salvelinus namaycush* (Walbaum) was widely distributed outside its native range in the late 19th Century because it was a desirable sport fish (Crossman 1995). However, this top-level predator has

had detrimental effects on native ecosystems in the western USA (Crossman 1995; Martinez *et al.* 2009). The bull trout *Salvelinus confluentus* (Suckley), a native predator, has consistently been displaced by non-native lake trout in lakes of the upper Columbia River Basin (Donald & Alger 1993; U.S. Fish & Wildlife Service

Correspondence: Benjamin S. Cox, Department of Ecology, Fish and Wildlife Ecology and Management Program, 301 Lewis Hall, Bozeman, MT 59717, USA (e-mail: benjamin.s.cox@state.or.us)

¹Current address: Oregon Department of Fish and Wildlife, Clackamas, OR, USA

(USFWS) 1998; Fredenberg 2002). Predation by non-native lake trout on Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* (Jordan & Gilbert), and kokanee *Oncorhynchus nerka* (Walbaum), has altered linkages between terrestrial and aquatic food webs by reducing spawning runs of lacustrine-adfluvial species predated by birds and mammals (Spencer *et al.* 1991; Koel *et al.* 2005). Introduced lake trout has also had cascading ecosystem effects, altering communities of aquatic invertebrates (Ellis *et al.* 2011).

Although much historical work on lake trout population dynamics has focused on conservation of native populations, management agencies in the western USA seek to develop an understanding of lake trout population dynamics in relation to suppression efforts. Lake trout exhibit a relatively long-lived, late-maturing, life-history strategy (Healey 1978; Martin & Olver 1980) that makes populations vulnerable to overharvest (Musick 1999). In Lake Superior, lake trout populations were in decline from overexploitation prior to the introduction of sea lamprey *Petromyzon marinus* (L.) (Hansen 1999; Wilberg 2004). The collapse of the lake trout population in Lake Erie was related exclusively to exploitation because sea lamprey never became abundant (Hartman 1972). Thus, intentionally collapsing lake trout populations in lakes of the western USA should be feasible with enough effort. Collecting baseline data on multiple aspects of lake trout population demographics is necessary for managers to evaluate the efficacy of suppression programmes and may provide further insight into the responses of exploited lake trout populations.

The objectives of this study were to describe baseline biological characteristics of a non-native lake trout population in Swan Lake, Montana, at the onset of an experimental suppression programme, and construct age-structured matrix models. These models allowed estimates of the population growth rate (λ) and conduct sensitivity-elasticity analyses to help identify age or stage classes on which to focus suppression efforts (Benton & Grant 1999; Caswell 2001). Population characteristics including size and age structure, growth, condition, maturity schedules and fecundity were quantified to describe the population and construct matrix models.

Methods

Study area

Swan Lake (47.9628° N, 113.9033° W) is a natural, glacially formed lake in the Flathead drainage in northwest Montana (Fig. 1). The Swan River is the primary tributary and outlet of Swan Lake (1335 ha), flowing for 22 km and discharging into Flathead Lake. In 1902, Big

Fork Dam was constructed on the Swan River ≈ 1.6 km upstream of the confluence with Flathead Lake (Baxter *et al.* 1999). In the 1950s, a fish ladder was constructed around Bigfork Dam. Lake trout would have had access to Swan Lake by migrating upstream from Flathead Lake until the fish ladder was removed in 1992. It is uncertain whether lake trout populated Swan Lake by illegal introduction(s) or by natural colonisation. Two lakes in the upper Swan River drainage approximately 50 km upstream from Swan Lake, Holland Lake and Lindbergh Lake, also contain bull trout populations. Lake trout were discovered in Lindbergh Lake in 2009 and in Holland Lake in 2012 by Montana Fish, Wildlife and Parks (MFWP).

The morphometry of Swan Lake is characterised by two relatively deep basins (>30 m) at the north and south ends and a shallower mid-lake section. Mean depth is 16 m and maximum depth is 43 m. Bottom substrates are dominated by fine sand and silt in depositional zones, with several reefs consisting of larger substrates scattered throughout the lake, particularly in the mid-lake region. Shoreline substrates are dominated by glacial till, with a section of large angular cobble and boulders along Montana Highway 83 on the southeast edge of the lake.

Dissolved nutrient levels (TDS = 112 mg L⁻¹) in Swan Lake are relatively high compared with lakes containing lake trout populations (Shuter *et al.* 1998; McDermid *et al.* 2010). Swan Lake is dimictic and stratifies during summer months, with a thermocline at ≈ 18 m in late summer. Hypolimnetic oxygen deficiencies have been recorded in the deep basins with the highest deficits (e.g. <0.1% O₂ saturation) in the south basin (Butler *et al.* 1995). Oxygen deficiencies in the hypolimnion are attributed to nutrient inputs from the Swan River from historical logging and road construction within the drainage (Butler *et al.* 1995).

Swan Lake contains a diverse fish assemblage with several native and non-native species. Native fish species include bull trout, westslope cutthroat trout *Oncorhynchus clarkii lewisi* (Pratt & Graham), mountain whitefish *Prosopium williamsoni* (Girard), pygmy whitefish *Prosopium coulterii* (Eigenmann & Eigenmann), northern pikeminnow *Ptychocheilus oregonensis* (Richardson), peamouth *Mylocheilus caurinus* (Richardson), redbelt shiner *Richardsonius balteatus* (Richardson), longnose sucker *Catostomus catostomus* (Forster), largescale sucker *Catostomus macrocheilus* (Girard) and slimy sculpin *Cottus cognatus* (Richardson). Introduced species include lake trout, kokanee, rainbow trout *Oncorhynchus mykiss* (Walbaum), brook trout *Salvelinus fontinalis* (Mitchill), northern pike *Esox lucius* (L.), brook stickleback *Culaea inconstans* (Kirtland) and central mudminnow *Umbra limi* (Kirtland). Introduced opossum shrimp

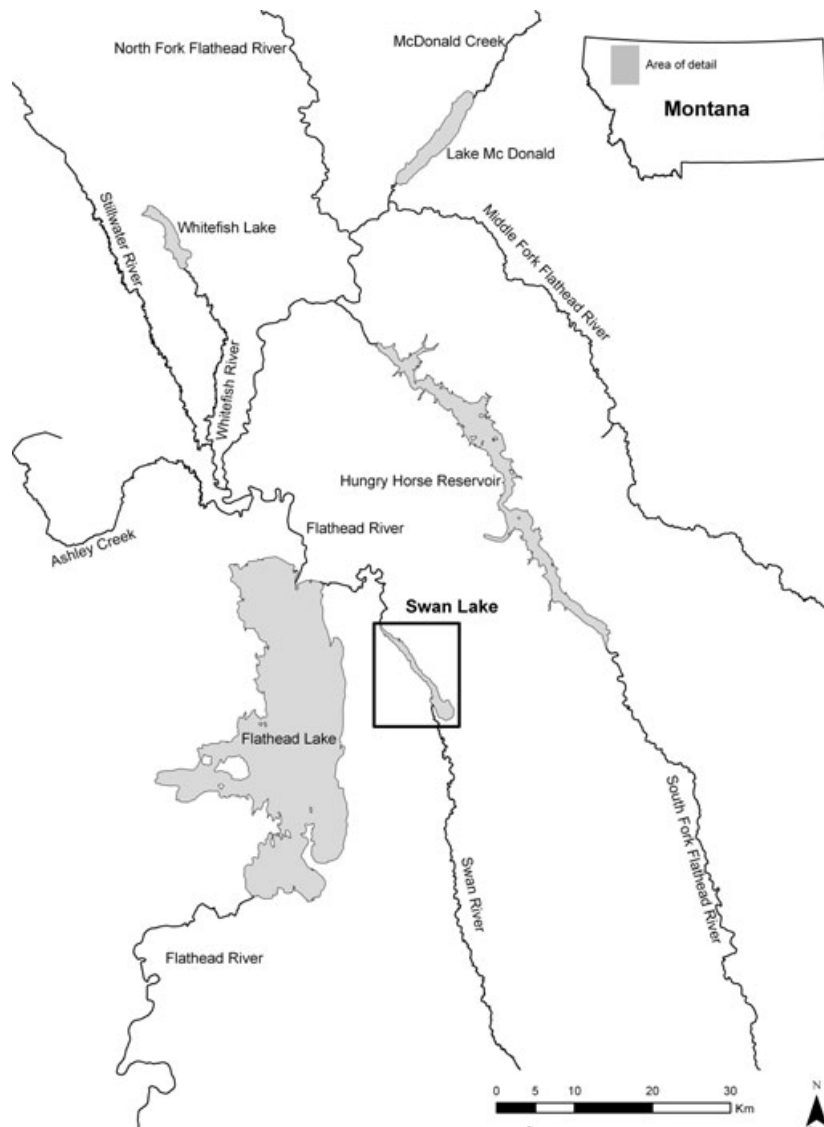


Figure 1. Geographical location of Swan Lake in the Flathead River drainage, northwest Montana.

Mysis diluviana (Audzijonyte & Vainola) are also part of the food web in Swan Lake.

Population demographics

A stratified random sampling design was developed to sample lake trout in 2007 and 2008. The sampling stratum was designated as all of the lake at or below thermocline depth (≈ 18 m), where lake trout were expected to occur during lake stratification (Martin & Olver 1980). Sampling occurred from 19 September to 4 October in 2007 and from 9 September to 25 September in 2008. Three, 91.4-m panels of each 2.5, 3.2, 3.8, 4.5 and 5.1 cm (bar measure) mesh sinking monofilament gill net were combined to form a 1371 m long gang in 2007. In 2008, the

length of the gang was doubled, and an additional six, 91.4-m panels of 1.9-cm bar mesh were added, forming a gang 3290 m long. The gang fished for an average of 2.4 h per set in 2007 and 3.5 h per set in 2008. Short sets were conducted to minimise bycatch mortality of bull trout. The gang was set from a random starting location within the sampling stratum during morning and evening crepuscular hours in 2007 and 2008.

All lake trout captured were measured for total length (TL, nearest mm). Ten lake trout per centimetre length group were weighed (nearest 1.0 g) each year ($n = 580$) to quantify body condition using relative weight as an index (Piccolo *et al.* 1993; Anderson & Neumann 1996). Age information was used to describe the age structure of the population as well as somatic growth. Ten sagittal

otoliths per centimetre TL group ($n = 611$) were aged to construct an age-length key and calculate an age-frequency distribution (DeVries & Frie 1996). TL-at-age data were used to model growth with a von Bertalanffy growth model (VBM) for both sexes:

$$TL = L_{\infty} \cdot (1 - e^{-K \cdot (\text{Age} - t_0)}).$$

Sexual maturity was visually assessed after dissection on all fish used for age analyses. Length and age at 50% and 90% maturity were estimated with logistic regression to describe the maturity schedule of lake trout in Swan Lake. Models were developed by sex because male lake trout generally mature at younger ages than females (Martin & Olver 1980). Confidence limits for length and age at 50 and 90% maturity were calculated using a bootstrap procedure (Wang *et al.* 2008). The probability of maturity at age (pm_t) predicted from the logistic regression for females was used to model fertility in matrix population models.

Fecundity was estimated gravimetrically for all gravid female lake trout ($n = 26$) captured in 2008 (Murua *et al.* 2003). Age was determined for all female lake trout with corresponding ovary samples. Mean fecundity at age (f_t) was calculated from fecundity-at-age data for age classes with more than one observation. Mean fecundity at age (f_t) was used as a vital rate in fertility elements in matrix models.

Population modelling

Matrix population models were female based and structured after a post-breeding census to consider age-0 survival explicitly in sensitivity-elasticity analyses. Data were available for lake trout up to age 16 in Swan Lake; however, it is not uncommon for lake trout to live longer than 20 years (Martin & Olver 1980). An age 16+ stage was included so that the life span of lake trout in the model was not limited to 16 years. Projection matrices were of the form:

$$\mathbf{A} = \begin{bmatrix} F_0 & \dots & \dots & F_{16+} \\ S_0 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \ddots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & S_{15} & S_{16+} \end{bmatrix},$$

where F_0 – F_{16+} are fertility rates for lake trout age 0–16+, S_0 – S_{15} are annual survival rates for lake trout ages 0–15 and S_{16+} is annual survival in the 16+ stage. Fertility elements (F_1 – F_{16+}) for each age t were modelled as:

$$F_t = f_t \cdot pm_t \cdot p_f,$$

where f_t is mean fecundity at age t , pm_t is the probability of maturity for females age t , and p_f is the proportion of

offspring that are female (assumed to be 0.5). Reproductive female lake trout in each age class were assumed to spawn every year in simulations.

A simulation approach was used to account for uncertainty in fertility and survival rates used to parameterise matrices. Fertility elements were calculated from randomly generated fertility vital rates in each simulation. Probabilities of maturity at each age (pm_t) were constrained between 0 and 1 by generating values from a beta distribution with mean and SD equal to the predicted pm_t and SE from the logistic regression of maturity at age (Morris & Doak 2002). Fecundity at age (f_t) was generated in each simulation from a stretched beta distribution with mean and SD calculated from fecundity-at-age data (Morris & Doak 2002).

Information on natural mortality was needed for population models, but no direct estimates of age-specific natural mortality were possible with sample data. The lake trout population was assumed to follow a type-III survivorship curve, reaching an asymptotic survival rate at age 3 (Sitar *et al.* 1999). Age-specific survival rates for lake trout ages 0–3 were obtained from the literature. Survival from age 0 to age 1 (S_0) was the mean of five separate studies reported in Shuter *et al.* (1998). Survival rates for lake trout ages 1–2 were obtained from Sitar *et al.* (1999). Instantaneous natural mortality (M) was predicted using VBM growth parameters L_{∞} and K in a model to predict M for lake trout populations in Ontario lakes (equation 5 in Shuter *et al.* 1998):

$$M = 2.064 \cdot \omega^{0.655} \cdot L_{\infty}^{-0.933},$$

where ω is the product of von Bertalanffy parameters L_{∞} and K (Galucci & Quinn 1979; Shuter *et al.* 1998). To obtain estimates of uncertainty in M , the von Bertalanffy growth parameters ω and L_{∞} were generated 5000 times from normal distributions with mean and SD equal to the parameter estimates ($L_{\infty} = 1112$, $K = 0.1496$) and predicted SEs (SE $L_{\infty} = 32.44$, SE $K = 0.0087$) of the VBM. Instantaneous natural mortality (M) was then calculated for the 5000 simulations of ω and L_{∞} in equation (1) and converted to conditional annual natural survival (S) as $S = e^{-M}$ (Miranda & Bettoli 2007).

Uncertainty in survival rates was incorporated in population matrices by generating random age-specific survival rates in each simulation. Age-0 survival (S_0) was generated with the mean and standard deviation calculated from data in Shuter *et al.* (1998) using a beta distribution. No measure of variation in survival rates for ages 1 and 2 was available for Lake Huron data (Sitar *et al.* 1999), so annual survival rates for ages 1 and 2 (S_1 , S_2) were generated from a beta distribution with

mean equal to the rates in Sitar *et al.* (1999) and SD equal to 20% of the estimates. Natural survival rates for lake trout age 3 and greater were generated using mean and SD of the simulated conditional annual S rates.

To model population growth, 5000 projection matrices were generated given the uncertainty in vital rates. The per capita population growth rate (λ) was calculated as the dominant eigenvalue of each matrix (Caswell 2001). Approximate 95% confidence limits of the mean population growth rate were calculated as the 2.5 and 97.5 percentiles of the 5000 simulations. Population growth rates and sensitivity-elasticity matrices were calculated using the `eigen.analysis` function in the `popbio` package (Stubben & Milligan 2007). Sensitivity represents the effect of an absolute change in matrix element a_{ij} on λ , relative to equal absolute changes in other elements (de Kroon *et al.* 1986):

$$S_{ij} = \partial\lambda/\partial a_{ij},$$

Sensitivity was calculated using the analytical solution of Caswell (1978) as follows:

$$S_i = v_i \cdot w_j / \langle \mathbf{w}, \mathbf{v} \rangle .$$

where v_i is the i th element of the left eigenvector of matrix \mathbf{A} , w_j is the j th element of the right eigen vector of matrix \mathbf{A} , and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of the left and right eigen vectors of matrix \mathbf{A} respectively. Elasticity (e_{ij}) is the proportional change in λ resulting from a proportional change in a matrix element a_{ij} (Caswell *et al.* 1984; de Kroon *et al.* 1986):

$$\begin{aligned} e_{ij} &= \partial \log \lambda / \partial \log a_{ij} \\ &= (a_{ij} / \lambda) \cdot (\partial \lambda / \partial a_{ij}) \end{aligned}$$

Elasticity represents the proportional contribution of matrix elements to the population growth rate λ (de Kroon *et al.* 1986). Confidence limits (95%) on sensitivity and elasticity values were calculated as the 2.5th and 97.5th percentiles of the sensitivity and elasticity of each element for the 5000 simulations. Matrix simulations were programmed in R using functions from the 'popbio' package (Stubben & Milligan 2007; R Core Development Team 2009).

Results

In 2007, 2156 lake trout were captured and 3785 were captured in 2008. Samples were comprised mostly of immature-planktivorous fish in both years. Lake trout varied in length from 166 (age 2) to 945 mm TL (age 16), but fish 220 to 400 mm (ages 3, 4 and 5) contrib-

uted 94% of the sample. Less than 5% of the lake trout captured in 2007 and 2008 were greater than 500 mm (age 6) and less than 1% were greater than 700 mm (age 8). Relative weights (W_r) for lake trout 280–699 mm were between the 50th and 60th percentiles among lake trout populations (Hubert *et al.* 1994). Mean W_r for adult lake trout larger than 700 mm in Swan Lake exceeded 110, which corresponded to the 92nd percentile among lake trout populations (Hubert *et al.* 1994). The estimated VBM was as follows:

$$TL = 1112(1 - e^{-0.1496 \cdot (Age - 1.387)}).$$

Male lake trout matured at smaller sizes and younger ages than female lake trout. Mature males varied from 385 to 945 mm and mature females varied from 665 to 899 mm. Fifty per cent of males were mature at 590 mm (547–604, 95% CL) and 90% were sexually mature at 712 mm (670–727, 95% CL), whereas 50% of females were mature at 708 mm (697–727, 95% CL) and 90% were mature at 753 mm (731–780, 95% CL). The maturity schedule of male lake trout was described by the logistic regression:

$$pm_t = e^{1.53 \cdot Age - 9.22} / (1 + e^{1.53 \cdot Age - 9.22}).$$

Age at 50 and 90% maturity for males was predicted to be 6.1 (5.7–6.3, 95% CL) and 7.6 (7.0–8.0, 95% CL) respectively. Age at 50 and 90% maturity for females was predicted to be 7.4 (7.0–7.8, 95% CL) and 8.1 (7.1–8.6, 95% CL), respectively, with the logistic regression:

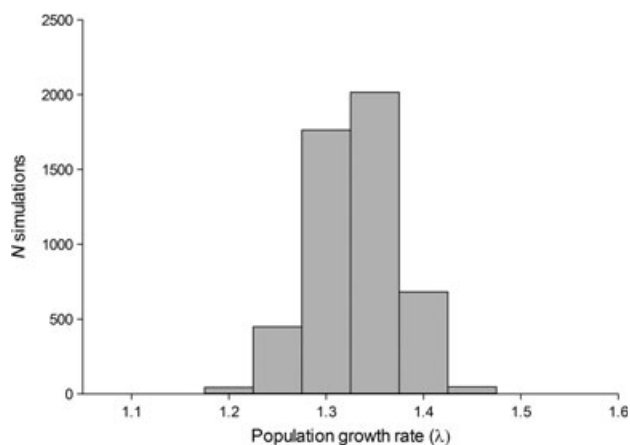
$$pm_t = e^{3.15 \cdot Age - 23.48} / (1 + e^{3.15 \cdot Age - 23.48}).$$

Fecundity varied from 1390 to 14 717 eggs for female lake trout sampled from 680 to 900 mm (ages 7–15). Mean fecundity was 8464 (7124–9804, 95% CL) eggs per fish. In general, fecundity increased with age for the age classes sampled (Table 1). Mean relative fecundity was 1396 (1241–1551, 95% CL) eggs \cdot kg⁻¹ body mass.

The per capita annual population growth rate (λ) of the lake trout population in Swan Lake was estimated at 1.35 (1.25–1.43, 95% CL) based on matrix-model simulations (Fig. 2). At this rate, lake trout abundance in Swan Lake would double every 2.3 years (1.9–2.9, 95% CL). Conditional natural annual mortality for age classes 3 and greater was estimated at 8.1% (7.5–8.7; 95% CL) using the estimated VBM parameters. Sensitivity analysis indicated that population growth was more sensitive to changes in survival rates than to changes in fertility rate (Table 2). The population growth rate was most sensitive to changes in the survival of age-0 lake trout (Table 2). Population growth was less sensitive to changes in survival rates with increasing age. The relative contribution

Table 1. Vital rates used to construct population matrices for the lake trout population in Swan Lake, Montana. Errors for vital rates are SD for sample data and SE for model predictions

Symbol	Definition	Age(<i>t</i>)	Value	Error	Source
Fertility elements					
f_t	Fecundity at age <i>t</i>	7	5571	2371	This study ovary sample data
		8	6182	3388	
		9	10 367	2703	
		10	9789	665	
pm_t	Probability of maturity at age <i>t</i>	11+	12 793	951	This study, logistic regression of maturity at age for females.
		1–6	0	N/A	
		7	0.19	0.073	
		8	0.84	0.099	
p_f	Proportion of offspring that are female	8–16+	0.5	N/A	Martin & Olver (1980)
		9–16+	1	N/A	
Transition elements					
S_0	Egg to age 1 survival	0	0.0043	0.00084	Shuter <i>et al.</i> (1998)
S_1	Age 1 survival	1	0.45	0.09	Sitar <i>et al.</i> (1999)
S_2	Age 2 survival	2	0.78	0.16	
S_{3-16+}	Asymptotic survival	3–16+	0.92	0.0035	Model from Shuter <i>et al.</i> (1998) using von Bertalanffy growth parameters from this study

**Figure 2.** Distribution of population growth rates from 5000 simulations of projection matrices for lake trout in Swan Lake, Montana. Survival rates for ages 0–3 were from the literature, survival rates for ages 3+ were estimated from von Bertalanffy growth parameters estimated for this population. Fecundity data and maturity schedules from this study were used to model fertility rates**Table 2.** Sensitivity of population growth to matrix elements from 5,000 simulated projection matrices for lake trout in Swan Lake, Montana. Matrix elements are survival (S_t) and fertility rates (F_t) at age *t*

Matrix element	Mean sensitivity	95% CL	
		Lower	Upper
S_0	27.799	19.804	38.753
S_1	0.267	0.189	0.396
S_2	0.156	0.115	0.262
S_3	0.126	0.109	0.143
S_4	0.126	0.109	0.143
S_5	0.126	0.109	0.143
S_6	0.126	0.109	0.143
S_7	0.120	0.103	0.135
S_8	0.099	0.084	0.114
S_9	0.071	0.058	0.084
S_{10}	0.052	0.041	0.063
S_{11}	0.036	0.027	0.044
S_{12}	0.024	0.017	0.032
S_{13}	0.017	0.011	0.023
S_{14}	0.014	0.007	0.017
S_{15}	0.008	0.005	0.012
S_{16+}	0.018	0.009	0.033
F_7	1.11×10^{-5}	7.30×10^{-6}	1.49×10^{-5}
F_8	7.52×10^{-6}	5.33×10^{-6}	9.75×10^{-6}
F_9	5.10×10^{-6}	3.86×10^{-6}	6.42×10^{-6}
F_{10}	3.47×10^{-6}	2.78×10^{-6}	4.27×10^{-6}
F_{11}	2.36×10^{-6}	1.95×10^{-6}	2.87×10^{-6}
F_{12}	1.61×10^{-6}	1.32×10^{-6}	1.96×10^{-6}
F_{13}	1.10×10^{-6}	8.74×10^{-7}	1.36×10^{-6}
F_{14}	7.53×10^{-7}	5.71×10^{-7}	9.56×10^{-7}
F_{15}	5.15×10^{-7}	3.70×10^{-7}	6.78×10^{-7}
F_{16+}	1.13×10^{-6}	6.73×10^{-7}	1.78×10^{-6}

of survival rates to λ (i.e. elasticity) was constant for juvenile fish age 0 to age 6, but decreased with age for reproductive age classes age 7 and older (Table 3). Confidence intervals among sensitivity and elasticity values did not overlap, indicating the pattern observed in the sensitivity-elasticity analysis would not change at the level of uncertainty incorporated into simulations. Summed elasticities were greatest for juvenile survival rates (0.602), followed by survival rates of reproductive age classes (0.311). Thus, in the model, survival rates from birth to sexual maturity made the largest relative contribution to λ , followed by survival of reproductive age classes. Fertility rates had the lowest summed elasticity (0.087) and made the smallest relative contribution to λ .

Discussion

At the onset of this experimental suppression programme, the lake trout population in Swan Lake appeared to be growing rapidly. When non-native species

Table 3. Elasticity of population growth to matrix elements from 5000 simulated projection matrices for lake trout in Swan Lake, Montana. Matrix elements are survival (S_t) and fertility rates (F_t) at age t

Matrix element	Mean elasticity	95% CL	
		Lower	Upper
S_0	0.086	0.080	0.092
S_1	0.086	0.080	0.092
S_2	0.086	0.080	0.092
S_3	0.086	0.080	0.092
S_4	0.086	0.080	0.092
S_5	0.086	0.080	0.092
S_6	0.086	0.080	0.092
S_7	0.082	0.075	0.088
S_8	0.068	0.056	0.076
S_9	0.048	0.038	0.058
S_{10}	0.036	0.027	0.044
S_{11}	0.024	0.017	0.032
S_{12}	0.017	0.011	0.023
S_{13}	0.011	0.007	0.017
S_{14}	0.008	0.005	0.012
S_{15}	0.005	0.003	0.009
S_{16+}	0.012	0.006	0.024
F_7	0.004	0.0009	0.011
F_8	0.014	0.003	0.030
F_9	0.020	0.009	0.027
F_{10}	0.013	0.010	0.016
F_{11}	0.011	0.009	0.013
F_{12}	0.008	0.006	0.009
F_{13}	0.005	0.004	0.006
F_{14}	0.004	0.003	0.005
F_{15}	0.003	0.002	0.003
F_{16+}	0.005	0.003	0.009

colonise novel systems, there is an inherent time lag between the initial establishment of the population and onset of exponential growth (Crooks & Soulé 1999; Sakai *et al.* 2001). Lake trout were first documented in the Swan River system in 1998, but juvenile lake trout did not appear in MFWP annual gillnet surveys until 2003. The size and age structure of the population demonstrated that lake trout had been reproducing in Swan Lake since 1992, but juvenile recruitment had increased in recent years. The sinking gillnets used in this study may have contributed to the skewed size and age structure observed through selectivity of the mesh sizes or due to the behaviour of piscivorous lake trout pursuing pelagic prey (e.g. kokanee) suspended in the water column (Dunlop *et al.* 2010; Dux *et al.* 2011). However, the size and age structure dominated by juveniles was consistent with invasive species in a favourable environment (Deering & Vankat 1999; Caswell 1984; Charlesworth 1994).

Growth and condition within lake trout populations are dependent on food availability, which can be limited

at high densities (Matuszek *et al.* 1990; Johnson & Martinez 2000). The size at age of juvenile lake trout in Swan Lake was similar to populations throughout North America (Martin & Olver 1980). The moderate size at age and condition of juvenile lake trout in Swan Lake may reflect increased intraspecific competition among the large cohorts produced in recent years. Adult lake trout attained large maximum sizes and were in exceptional condition in Swan Lake (Shuter *et al.* 1998; McDermid *et al.* 2010). The large size at age and high condition of adult lake trout likely reflected abundant food resources and a relatively low density in Swan Lake (Matuszek *et al.* 1990; Johnson & Martinez 2000).

Somatic growth rates also influence the maturity schedule of lake trout populations (Matuszek *et al.* 1990; Ferreri & Taylor 1996). Fast-growing, piscivorous lake trout populations mature at younger ages and larger sizes than slow-growing planktivorous populations (Martin & Olver 1980). Age at maturity in Swan Lake was comparable with most lake trout populations across North America (Healey 1978; Martin & Olver 1980; McDermid *et al.* 2010), but the size at which female lake trout reached maturity was among the largest reported in the literature. Length at 50% maturity was greater than populations in the Great Lakes (Madenjian *et al.* 1998), inland lakes in Ontario (Trippel 1993), and inland lakes in Alaska (Burr 1991). By contrast, female lake trout in Lake McDonald, Glacier National Park (a relatively unproductive lake with a long-established lake trout population) did not reach sexual maturity until age 15, and individuals in this population were generally in poor condition (Dux *et al.* 2011). The size at maturity in Swan Lake was similar to the size at maturity of lake trout in Yellowstone Lake, Yellowstone National Park at the onset of the suppression programme there (Syslo *et al.* 2011). The maturity schedule observed in Swan Lake indicated favourable somatic growth conditions for adult lake trout during this study. The maturity schedule in Swan Lake is likely to shift towards younger, smaller individuals as a compensatory response to suppression efforts (Trippel 1995; Syslo *et al.* 2011).

Lake trout in Swan Lake had relatively high length and age-specific fecundity compared with other lake trout populations. A 790-mm lake trout in Swan Lake was as fecund as an 830–900-mm lake trout in Lake Superior (Ferreri & Taylor 1996). Relative fecundity in Swan Lake was similar to the average relative fecundity reported for lake trout populations in the Great Lakes (Martin & Olver 1980), inland lakes in Ontario (Shuter *et al.* 1998) and other populations throughout North America (Martin & Olver 1980). The consistency in relative fecundity (eggs kg^{-1} body weight) among lake trout populations indicate fecundity may be relatively

fixed for lake trout of a given weight (Ferreri & Taylor 1996; Shuter *et al.* 1998). Fecundity at length may be more variable for lake trout due to differences in condition among populations (i.e. weight varies among populations for fish of a given length). Population density has been shown to affect age-specific fecundity through changes in growth (Ferreri & Taylor 1996). It was surmised that the relatively high length and age-specific fecundity in Swan Lake further indicated that resources were not limiting adult lake trout.

Somatic growth varies widely among lake trout populations throughout their geographical range in relation to lake productivity and food web structure (Trippel 1993; Shuter *et al.* 1998; Johnson & Martinez 2000; Lienesch *et al.* 2005; McDermid *et al.* 2010). Lake trout generally grow faster and attain larger sizes in lakes with high productivity and pelagic forage species (Martin & Olver 1980; Shuter *et al.* 1998; McDermid *et al.* 2010). Swan Lake is relatively productive among lakes supporting lake trout populations (Shuter *et al.* 1998; McDermid *et al.* 2010). The food web contains introduced opossum shrimp and several forage fish, including kokanee and pygmy whitefish, which are important diet items to juvenile and adult lake trout in Swan Lake (Guy *et al.* 2011). Given the productivity and food web structure of Swan Lake, lake trout should be expected to have relatively high growth rates. In comparison with other lake trout populations, somatic growth rates, condition and size at maturity of lake trout in Swan Lake were near the upper limit for the species.

Analysis of matrix population models indicated that the lake trout population in Swan Lake is likely growing at an exponential rate, despite the uncertainty in the vital rates used to parameterise the models. The mean per capita population growth rate and doubling time was similar to the growth rate estimated for lake trout in Lake Pend Oreille, Idaho prior to implementing a suppression programme (Hansen *et al.* 2008). The skewed size and age structure of lake trout captured corroborated the relatively high growth rate of the population model (Caswell *et al.* 1984; Charlesworth 1994). However, the mean population growth rate determined with matrix models represents a snap shot of the population at the current estimated survival and fertility rates. Density dependence will ultimately affect the vital rates as the population approaches carrying capacity. If survival rates vary from year to year, the true population growth rate would be less than that estimated with deterministic matrices (Case 2000). Assuming annual spawning would also cause an overestimate of the population growth rate. If the population grows until food resources become limited, then it is plausible that female lake trout would only be capable of intermittent spawning. At the time of

this study, the relatively high somatic growth, condition and size at maturity of lake trout in Swan Lake suggested that density dependence had minimal effect on the population; however, the population growth rate estimated in this study should not be assumed constant.

The population growth rate estimated with these matrix models is likely an underestimate of the true growth rate. Juvenile survival rates in Swan Lake are likely higher than the rates borrowed from Lake Superior. Lake trout populations in Lake Superior are closer to equilibrium densities than the population in Swan Lake, thus density dependence may affect juvenile survival (Corradin *et al.* 2008). Juvenile lake trout in Lake Superior may also be affected by early mortality syndrome (Honeyfield *et al.* 2005) and introduced egg predators (Chotkowski & Marsden 1999). Furthermore, the abundance of introduced opossum shrimp likely provides conditions for high juvenile survival in Swan Lake (Bowles *et al.* 1991; Stafford *et al.* 2002).

Based on sensitivity-elasticity analyses, survival rates from birth to sexual maturity contributed most to population growth followed by survival rates of reproductive adults. Population growth was highly sensitive to changes in the survival of age-0 lake trout, but equal among all survival rates for immature age classes. Uncertainty in juvenile survival rates did not appear to alter the conclusions of sensitivity-elasticity analyses for the level of uncertainty simulated. Although the decreasing trend observed in sensitivity and elasticity with age is a mathematical constraint of the model structure; it is believed that inferences from these analyses are valid because the model is a reasonable representation of lake trout life history under favourable conditions (Carslake *et al.* 2009). These deterministic models indicate targeting juvenile age classes is important for suppression efforts during exponential population growth. Currently, suppression programmes rely on mechanical removal techniques including large-scale gill net programmes and angler incentive programmes to target juvenile and adult lake trout (Martinez *et al.* 2009). Although elasticity matrices showed the relative contribution of age-0 survival rates are equal among immature age classes, targeting age-0 lake trout (i.e. incubating embryos) may be an effective complement to current techniques given that embryos are sensitive to trauma at certain developmental stages and non-motile (Piper *et al.* 1982).

Understanding lake trout population dynamics has been necessary for the management and conservation of native lake trout populations throughout North America (Healey 1978; Shuter *et al.* 1998). The importance of juvenile survival is recognised where conservation or restoration of lake trout populations is the goal (e.g. Ellrott and Marsden 2004). Long-lived, late-maturing species such as lake

trout may be particularly susceptible to overexploitation because individuals are vulnerable to harvest before reaching sexual maturity (Trippel 1995). Knowledge of lake trout life history and management is now being re-examined in the context of controlling lake trout as a non-native species. Baseline data on multiple aspects of population dynamics are necessary to evaluate the efficacy of lake trout suppression programmes in an adaptive management framework. Tracking these metrics through time will provide further insight into compensatory responses of lake trout populations to suppression efforts. Using these baseline data, managers will be able to model various suppression scenarios and determine benchmarks for success in an adaptive management framework.

Acknowledgments

Thanks to R. Lindahl, N. Peterson, M. Gjukis, S. Hawxhurst, D. Daniels, R. Hunt and S. Glutting for their field assistance and to B. Gresswell and J. Rotella for their constructive review of earlier drafts of the manuscript. Reference to trade names does not constitute endorsement by the US Government. This study was performed under the auspices of Montana State University protocol number 28-06. The Montana Cooperative Fishery Research Unit is jointly sponsored by Montana State University, Montana Fish, Wildlife and Parks, and the US Geological Survey.

References

- Anderson R.O. & Neumann R.M. (1996) Length, weight and associated structural indices. In: B.R. Murphy & D.W. Willis (eds) *Fisheries Techniques*, 2nd edn. Bethesda, MD: American Fisheries Society, pp. 447–482.
- Baxter C.V., Frissel C.A. & Hauer F.R. (1999) Geomorphology, logging roads and the distribution of bull trout spawning in a forested river basin: implications for management and conservation. *Transactions of the American Fisheries Society* **128**, 854–867.
- Benton T.G. & Grant A. (1999) Elasticity as an important tool in evolutionary and population ecology. *Trends in Ecology and Evolution* **14**, 467–471.
- Bowles E.C., Rieman B.E., Mauser G.R. & Bennett D.H. (1991) Effects of introductions of *Mysis relicta* on fisheries in northern Idaho. In: T.P. Nesler & E.P. Bergersen (eds) *Mysids in Fisheries: Hard Lessons from Headlong Introductions*. American Fisheries Society Symposium **9**, 65–74.
- Burr J.M. (1991) *Lake trout population studies in interior Alaska, 1990, including abundance estimates of lake trout in Glacier, Sevenmile, and Paxson Lakes during 1989*. Fishery Data Series No. 91–7. Anchorage, AK: Alaska Dept. of Fish and Game, 50 pp.
- Butler N.M., Craft J.A. & Stanford J.A. (1995) *A diagnostic study of the nutrient loading at Swan Lake, Montana*. Flathead Lake Biological Station open file report No. 138-95. Missoula, MT: University of Montana, 76 pp.
- Carlslake D., Townley S. & Hodgson D.J. (2009) Patterns and rules for sensitivity and elasticity in population projection matrices. *Ecology* **90**, 3258–3267.
- Case T.J. (2000) *An Illustrated Guide to Theoretical Ecology*. New York: Oxford University Press Inc., 464 pp.
- Caswell H. (1978) A general formula for the sensitivity of population growth rate to changes in the life history parameters. *Theoretical Population Biology* **17**, 71–79.
- Caswell H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd edn. Sunderland, MA: Sinauer Associates, 722 pp.
- Caswell H.R., Naiman R. & Morin R. (1984) Evaluating the consequences of reproduction in complex salmonid life cycles. *Aquaculture* **43**, 123–143.
- Charlesworth B. (1994) *Evolution in Age-Structured Populations*. 2nd edn. Cambridge: Cambridge University Press, 324 pp.
- Chotkowski M.A. & Marsden J.E. (1999) Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. *Journal of Great Lakes Research* **25**, 26–35.
- Corradin L.M., Hansen M.J., Schreiner D.R. & Seider M.J. (2008) Recruitment dynamics of lake trout in western Lake Superior during 1988–1995. *North American Journal of Fisheries Management* **28**, 663–677.
- Crooks J.A. & Soulé M.E. (1999) Lag times in population explosions of invasive species: causes and implications. In O. T. Sandlund, P.J. Schei & A. Viken (eds) *Invasive Species and Biodiversity Management*. Dordrecht, NL: Kluwer Academic Publishers, pp. 103–125.
- Crossman E.J. (1995) Introduction of the lake trout (*Salvelinus namaycush*) in areas outside its native distribution: a review. *Journal of Great Lakes Research* **21**(Suppl. 1), 17–29.
- Deering R.H. & Vankat J.L. (1999) Forest colonization and developmental growth of the invasive shrub *Lonicera maackii*. *American Midland Naturalist* **141**, 43–50.
- Donald D.B. & Alger D.J. (1993) Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. *Canadian Journal of Zoology* **71**, 238–247.
- Dunlop E.S., Milne S.W., Ridgway M.S., Condiotty J. & Higginbottom I. (2010) In situ swimming behaviour of lake trout observed using integrated multibeam acoustics and biotelemetry. *Transactions of the American Fisheries Society* **139**, 420–432.
- Dux A.M., Guy C.S. & Fredenberg W.A. (2011) Spatiotemporal distribution and population characteristics of a non-native lake trout population, with implications for suppression. *North American Journal of Fisheries Management* **31**, 187–196.
- Ellis B.K., Stanford J.A., Goodman D., Stafford C.P., Gustafson D.L., Beauchamp D.A. *et al.* (2011) Long-term effects of a

- trophic cascade in a large lake ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 1070–1075.
- Ellrott B.J. & Marsden M.J. (2004) Lake trout reproduction in Lake Champlain. *Transactions of the American Fisheries Society* **133**, 252–264.
- Ferreri C.P. & Taylor W.W. (1996) Compensation in individual growth rates and its influence on lake trout population dynamics in the Michigan waters of Lake Superior. *Journal of Fish Biology* **49**, 763–777.
- Fredenberg W.A. (2002) Further evidence that lake trout displace bull trout in mountain lakes. *Intermountain Journal of Sciences* **8**, 143–151.
- Galucci V.F. & Quinn T.J. (1979) Reparameterizing, fitting and testing a simple growth model. *Transactions of the American Fisheries Society* **108**, 14–25.
- Guy C.S., McMahon T.E., Fredenberg W.A., Smith C.J., Garfield D.W. & Cox B.S. (2011) Diet overlap of top-level predators in recent sympatry: Bull trout and non-native lake trout. *Journal of Fish and Wildlife Management* **2**, 183–189.
- Hansen M.J. (1999) Lake trout in the Great Lakes: basin-wide stock collapse and binational restoration. In: W.W. Taylor & C.P. Ferreri (eds) *Great Lakes Fishery Policy and Management: A Binational Perspective*. East Lansing, MI: Michigan State University Press, pp. 417–453.
- Hansen M.J., Horner N.J., Liter M., Peterson M.P. & Maiolie M. (2008) Dynamics of an increasing lake trout population in Lake Pend Oreille, Idaho. *North American Journal of Fisheries Management* **28**, 1160–1171.
- Hartman W.L. (1972) Lake Erie: effects of exploitation, environmental changes, and new species on the fishery resources. *Journal of the Fisheries Research Board of Canada* **29**, 899–912.
- Healey M.C. (1978) The dynamics of exploited lake trout populations and implications for management. *Journal of Wildlife Management* **42**, 307–328.
- Honeyfield D.C., Hinterkopf J.P., Fitzsimmons, J.D., Tillitt D. E., Zajicek J.L. *et al.* (2005) Development of thiamine deficiencies and early mortality syndrome in lake trout by feeding experimental and feral diets containing thiaminase. *Journal of Aquatic Animal Health* **17**, 4–12.
- Hubert W.A., Gipson R.D. & Whaley R.A. (1994) Interpreting relative weights of lake trout stocks. *North American Journal of Fisheries Management* **14**, 212–215.
- Johnson B.M. & Martinez P.J. (2000) Trophic economics of lake trout management in reservoirs of differing productivity. *North American Journal of Fisheries Management* **20**, 127–143.
- Koel T.M., Bigelow P.E., Doepke P.D., Ertel B.D. & Mahony D. L. (2005) Non-native lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. *Fisheries* **30**, 10–19.
- de Kroon H., Plaisier A., van Groenendael J. & Caswell H. (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**, 1427–1431.
- Lienesch P.W., McDonald M.E., Hershey A.E., O'Brien J.W. & Bettes N.D. (2005) Effects of a whole-lake, experimental fertilization on lake trout in a small oligotrophic arctic lake. *Hydrobiologia* **548**, 51–66.
- Madenjian C.P., DeSorcie T.J. & Stedman R.M. (1998) Maturity schedules of lake trout in Lake Michigan. *Journal of Great Lakes Research* **24**, 404–410.
- Martin N.V. & Olver C.H. (1980) The lake charr, *Salvelinus namaycush*. In E.K. Balon (ed) *Charrs: Salmonid Fishes of the Genus Salvelinus*. The Hague, NL: W. Junk, pp. 205–277.
- Martinez P.J., Bigelow P.E., Deleray M.A., Fredenberg W.A., Hansen B.S., Horner N.J. *et al.* (2009) Western lake trout woes. *Fisheries* **34**, 424–442.
- Matuszek J.E., Shuter B.J. & Casselman J.M. (1990) Changes in lake trout growth and abundance after introduction of cisco into Lake Opeongo, Ontario. *Transactions of the American Fisheries Society* **119**, 718–729.
- McDermid J.L., Shuter B.J. & Lester N.P. (2010) Life history differences parallel environmental differences among North American lake trout (*Salvelinus namaycush*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 314–325.
- Miranda L.E. & Bettoli P.W. (2007) Mortality. In C.S. Guy & M.L. Brown (eds) *Analysis and Interpretation of Freshwater Fisheries Data*. Bethesda, MD: American Fisheries Society, pp. 229–271.
- Morris W.F. & Doak D.F. (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sunderland, MA: Sinauer Associates, 480 pp.
- Murua H., Kraus G., Saborido-Rey F., Witthames P. R., Thorsen A. & Junquera S. (2003) Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *Journal of Northwest Atlantic Fisheries Science* **33**, 33–54.
- Musick J.A. (1999) Ecology and conservation of long-lived marine animals. In: J.A. Musick (ed.) *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals, Symposium 23*. Bethesda, MD: American Fisheries Society, pp. 1–10.
- Piccolo J.J., Hubert W.A. & Whaley R.A. (1993) Standard weight equation for lake trout. *North American Journal of Fisheries Management* **13**, 401–404.
- Piper R.G., McElwain I.B., Orme L.E., McCraren J.P., Fowler L. G. & Leonard J.R. (1982) *Fish Hatchery Management*. Washington, DC: U.S. Fish and Wildlife Service, 548 pp.
- R Core Development Team (2009) *R: a language and environment for statistical computing*. Vienna, AU: R Foundation for Statistical Computing, Available at <http://www.R-project.org> (accessed 6 November 2012).
- Sakai A.K., Allendorf F.W., Holt J.S., Lodge D.M., Molofsky J., With K.A. *et al.* (2001) The population biology of invasive species. *Annual Reviews of Ecology and Systematics* **32**, 305–332.
- Shuter B.J., Jones M.L., Korver R.M. & Lester N.P. (1998) A general, life history based model for regional management of fish stocks: the inland lake trout *Salvelinus namaycush*

- fisheries of Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2161–2177.
- Sitar S.P., Bence J.R., Johnson J.E., Ebener M.P. & Taylor W.W. (1999) Lake trout mortality and abundance in southern Lake Huron. *North American Journal of Fisheries Management* **19**, 881–900.
- Spencer C.N., McClelland B.R. & Stanford J.A. (1991) Shrimp stocking, salmon collapse and eagle displacement: Cascading interactions in the food web of a large aquatic ecosystem. *BioScience* **41**, 14–21.
- Stafford C.P., Stanford J.A., Hauer F.R. & Brothers E.B. (2002) Changes in lake trout growth associated with *Mysis relicta* establishment: a retrospective analysis using otoliths. *Transactions of the American Fisheries Society* **131**, 994–1003.
- Stubben C. & Milligan B. (2007) Estimating and analysing demographic models using the *popbio* package in R. *Journal of Statistical Software* **22**, 1–23.
- Syslo J.M., Guy C.S., Bigelow P.E., Doepke P.D., Ertel B.D. & Koel T.M. (2011) Response of non-native lake trout (*Salvelinus namaycush*) to 15 years of harvest in Yellowstone Lake, Yellowstone National Park. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 2132–2145.
- Trippel E.A. (1993) Relations of fecundity, maturation, and body size of lake trout and implications for management in northwestern Ontario lakes. *North American Journal of Fisheries Management* **13**, 64–72.
- Trippel E.A. (1995) Age at maturity as a stress indicator in fisheries: biological processes related to reproduction in northwest Atlantic groundfish populations that have undergone declines. *BioScience* **45**, 759–771.
- U.S. Fish and Wildlife Service (USFWS) (1998) Endangered and threatened wildlife and plants; Determination of threatened status for the Klamath River and Columbia River distinct population segments of bull trout, final rule. *United States Federal Register* **63**, 31647–31674.
- deVries D.R. & Frie R.V. (1996) Determination of age and growth. In B.R. Murphy & D.W. Willis (eds) *Fisheries Techniques*, 2nd edn. Bethesda, MD: American Fisheries Society, pp. 483–512.
- Wang H.Y., Höök T.O., Ebener M.P., Mohr L.C. & Schneeberger P.J. (2008) Spatial and temporal variation in maturation schedules of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 2157–2169.
- Wilberg M.J. (2004) Fleet dynamics of the commercial lake trout fishery in Michigan waters of Lake Superior during 1929–1961. *Journal of Great Lakes Research* **30**, 252–266.