Life History, Maternal Quality and the Dynamics of Harvested Fish Stocks

by

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Abstract

Knowledge of offspring production (recruitment) is fundamental to understanding and forecasting the dynamics of a population. In this thesis, I focus on two demographic characteristics of fish stocks that are important to recruitment: population density and age structure. First, populations produce more recruits at low density, but quantifying this response has proven difficult. Using data from hundreds of populations of walleye (*Sander vitreus*), an economically important freshwater fish, I demonstrate that the growing-degree-day metric (a temperature index) is better than age at explaining variation in density-dependent growth and maturity both within and among populations. I then incorporate multi-lake measures of density-dependent life history change into a temperature-based biphasic model of growth and reproduction to predict sustainable rates of mortality for walleye throughout most of their range. Second, the age (or size) structure of a population may also affect recruitment because of positive effects of maternal age on offspring production and survival; however, evidence for these 'maternal influences' on recruitment is limited. Using both an analytical model and a meta-analysis of stock-recruitment data from 25 species of exploited marine fish, I show that (i) maximum reproductive rate increased with the mean age of adults in a population, and (ii) the importance of age structure increased with a species' longevity. I then demonstrate a similar effect of maternal influences on reproductive rate in a detailed study of Lake Erie walleye. By highlighting the importance of fisheries-induced demographic change to recruitment, this thesis provides insight into past and present failures. However, it also demonstrates clearly the benefits of proactive management strategies that (i) identify and respect the limits of exploitation, (ii) protect from exploitation reproductively valuable individuals—principles that apply generally to any freshwater, marine, or terrestrial species that is of recreational, commercial, or conservation value.

Acknowledgments

As an avid reader of thesis acknowledgements, I have noticed that they almost invariably end with a heart-felt ‘thank you’ to loved one(s), be they animal, vegetable, or mineral. I am breaking from this tradition by making a heart-felt ‘thank you’ to *my* loved one, Jess “Jessga” Ward (who is of the animal variety). Thank you for being my muse, my sounding board, my editor, and my friend. Thank you for leading by example, for making me laugh, and for your support through more rejection letters and letters of ‘reject and resubmit’ than I care to count (10). Thank your for being so understanding, and for giving so much when you had your own thesis to write and life to live; I don’t know how you do it. Thank you for everything.

With the exception of the general introduction (Chapter 1) and the general conclusion (Chapter 6), this thesis is in first person plural instead of first person singular. This is deliberate, not only because changing ‘we’s to ‘I’s and ‘our’s to ‘my’s is a pain, but because so much of this work was collaborative. Beginning with the members of my committee, all of whom were tremendously supportive and gave their precious time to me, especially in the final stages: I thank Peter Abrams for teaching me the basics early on, and for somehow finding a way to fundamentally change every one of the chapters herein (for the better, of course); I thank Helen Rodd for holding me to a higher standard of writing (the antithesis of ‘garbage’), and for encouraging me to look beyond the immediate literature. Your efforts, even after the examining committee was decided, are greatly appreciated; I thank Nigel Lester for being a goal model—for showing by example how to strike a balance between job and family. Thank you for laying the foundations for this work, for taking me under your wing, for introducing me to agency biologists in two provinces, and for encouraging me to collaborate. I hope that there are more road trips; I am equally indebted to Brian Shuter for his foundations, his wing, his introductions, and his encouragement. Thank you for your support and enthusiasm, for treating me like a colleague first and a student second…and for making it so hard to articulate how much your tutelage has meant to me. If I develop into half the researcher that you are, I will consider myself a success.

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Table of Contents

List of Tables

List of Figures

Figure 2.5. Linear ANCOVA models of log-transformed mean total length (log L) of immature walleye (sexes combined) versus log- transformed cumulative annual growing degree-days (GDD_c) for 8 collapsed stocks a) with data divided into periods of high ('+' symbols, solid line) and low (open circles, dashed line) density (Figure 2.1e; showing mean relations within a density period) and b) pooled over the entire time series (Figure 2.1c). Numeric symbols in panel b identify estimated calendar ages in years. Points above the 6 000 GDD_c threshold were excluded from analysis because of the potentially confounding effects of maturity.

Figure 2.6. Linear regression of a) log total length- (L_{50}) and b) log age-at-50%-maturity (t_{50}) on mean annual growing degree days ($\overline{GDD}_a$) for males ('x' symbols, dashed lines) and females (open squares, solid lines). Maturity data are from Figure 2.3. Regression equations and evidence ratios ($E_{i,j}$) are as follows: log male $L_{50} = -0.20 \cdot \log \overline{GDD}_a + 3.18$, $r^2 = 0.07$, $n = 81$, $E_{i,j} = 1.31$; log female $L_{50} = 0.03 \cdot \log \overline{GDD}_a + 2.54$, $r^2 < 0.01$, $n = 78$, $E_{i,j} = 0.35$; log male $t_{50} = -1.30 \cdot \log \overline{GDD}_a + 4.78$, $r^2 = 0.32$, $n = 78$, $E_{i,j} = 290.18$; log female $t_{50} = -0.99 \cdot \log \overline{GDD}_a + 3.97$, $r^2 = 0.40$, $n = 72$, $E_{i,j} = 891.74$. Evidence ratios measure how much more likely one model is relative to another (Burnham and Anderson 2002, Anderson 2008). In this case, we compared each regression model to a horizontal line that intersected the y-axis at the mean value of log L_{50} or log t_{50} (i.e., a model that assumed no relation with $\overline{GDD}_a$).

Figure 3.1. Hypothetical relations between body length and time showing growth trajectories (arrows) and points of maturity (circles) during period 1 (solid arrows, filled circles) and period 2 (dashed arrows, closed circle. According to calendar time (a) growth trajectories and points of maturity are different, regardless of whether periods differ in temperature, per capita food availability, or both. Using thermal time (b), growth and maturity fall along the same trajectory if periods differ only in temperature. If periods differ in both temperature and per capita food availability, then growth and maturity follow different trajectories that describe changes in either (c) length-at-maturity (if thermal time-at-maturity is fixed) or (d) thermal time-at-maturity (if length-at-maturity is fixed).

Figure 3.2. The mean total length (L_{50}) and cumulative annual growing degree days (GDD_{50}) at 50% maturity for male (squares, $n = 4$) and female (triangles, $n = 6$) walleye at high (closed symbols) and low (open symbols) population densities. Error bars are 95 %CI. Solid and dashed

lines show the growth trajectories of immature females at high and low population densities, respectively, as implied by L_{50} and GDD_{50}.

Figure 3.3. Flow diagram for converting GDD_a, GDD_{50}, and L_{50} into an estimate F_{ext} (the F at which $R_o = 1$). Using GDD_{50} and L_{50} at high population density and a given value of GDD_a, we first adjusted M_o until $R_o = 1$ at $F = 0$. We then held M_o constant and re-estimated R_o based on GDD_{50} and L_{50} at low population density. If $R_o \neq 1$ as a result of this change, we adjusted F until $R_o = 1$. We considered two response scenarios for L_{50} and GDD_{50} (mean and maximum) and two strategies of reproductive investment ($g[M_{1+}]$ and $g[Z]$). See text for details. Numbers in parenthesis refer to equations. Symbols are defined in Table 3.3.

Figure 3.4. Predicted relations between female t_{50} and GDD_a when F was absent (thin, solid lines) or present (thin, dashed lines). Shaded areas within a pair of lines define the range of t_{50} values that are predicted by the mean and maximum response scenarios; these lines converge when both response scenarios predict the same t_{50}. Predicted relations can be approximated by the following curves: F absent: $t_{50} = 4672.3 \cdot GDD_a^{-0.886}$, F present: $t_{50} = 3867.6 \cdot GDD_a^{-0.903}$. Thick lines are empirical relations based on data from 11 (Colby et al. 1994; solid line) and 23 (Baccante and Colby 1996; dashed line) populations. See Gangl and Pereira (2003) and Sullivan (2003) for additional data.

Figure 3.5. Predicted relations between g and GDD_a with g optimized to M_{1+} (thin, solid lines) or Z (thin, dashed lines). Shaded areas within a pair of lines define the range of g values that are predicted by the mean and maximum response scenarios; these lines converge as an artifact of rounding such t_{50} in the absence of F (i.e., M_{1+}; see equation 3.2) is the same for both response scenarios. Predicted relations can be approximated by the following curves: $g[M_{1+}]$: $g = 1.01 \cdot 10^{-3} \cdot GDD_a^{0.769}$, $g[Z]$: $g = 4.15 \cdot 10^{-3} \cdot GDD_a^{0.645}$. Open and closed circles are mean observed gonadosomatic index values from heavily and lightly exploited populations, respectively (Colby et al. 1979, Henderson et al. 1996, Moles et al. 2008), after dividing by 0.71 to correct for the higher energy density of gonads relative to soma. Accounting further for additional behavioral and metabolic costs associated with reproduction would shift these points upwards.

Figure 3.6. Predicted relations between L and GDD_c with F absent (solid line), F present and g optimized to M_{1+} (dashed line), and F present and g optimized to Z (dotted line). Dots are empirical data for female walleye from 342 populations in Ontario and Quebec (Chapter 2).

Figure 3.7. Predicted relations between relative fecundity and $\mathrm{GDD_a}$ with g optimized to M_{1+} (thin, solid lines) or Z (thin, dashed lines). Shaded areas within a pair of lines define the range of relative fecundity values that are predicted by the mean and maximum response scenarios; these lines converge as an artifact of rounding such t_{50} in the absence of F (i.e., M_{1+}; see equation 3.2) is the same for both response scenarios. Predicted relations can be approximated by the following curves: $g[M_{1+}]$: relative fecundity = $0.042 \cdot \mathrm{GDD_a} + 14.383$, $g[Z]$: relative fecundity = $0.066 \cdot \mathrm{GDD_a} + 41.069$. Because our model predicted the production of female eggs (equation 3.10), the values presented here were multiplied by 2 assuming a 1:1 sex ratio. The thick line is an empirical relation based on data from 43 populations (Baccante and Colby 1996).

Figure 3.8. Predicted relations between (a) Z_{ext} and (b) F_{ext} and $\mathrm{GDD_a}$. Numbers and numbered lines correspond to model results both in the absence of F ($0 = M_{1+}$; panel a only), and for different combinations of life history change and strategies of reproductive investment when F was present: 1 = mean change and $g[M_{1+}]$, 2 = mean change and $g[Z]$, 3 = maximum change and $g[M_{1+}]$, and 4 = maximum change and $g[Z]$. The thick line in panel b is the F_{ext}-$\mathrm{GDD_a}$ relation proposed by Baccante and Colby (1996). The upper and lower bounds of Z_{ext} and F_{ext} are given by Z_{ext} upper = $1.87 \cdot 10^{-3} \cdot \mathrm{GDD_a}^{0.783}$, Z_{ext} lower = $3.40 \cdot 10^{-4} \cdot \mathrm{GDD_a}^{0.974}$, and F_{ext} upper = $2.24 \cdot 10^{-3} \cdot \mathrm{GDD_a}^{0.672}$, F_{ext} lower = $6.76 \cdot 10^{-5} \cdot \mathrm{GDD_a}^{1.037}$.

Figure 4.1. Hypothetical stock-recruitment relations showing how MI on survival can affect the slope at the origin (α_o), and how this affect increases with reproductive life span (RLS). When MI are absent, α_o is independent of the mean age of spawners ($\bar{A}$) and describes a single (solid) line. When MI are present, α_o decreases with a decrease in $\bar{A}$. Because the decrease in $\bar{A}$ for a fixed reduction in adult survival rate depends directly on RLS (Figure C.1), the decrease in α_o for a species that has a short RLS will be small (i; dashed line) relative to the decrease in α_o for a species that has a long RLS (ii; dotted line). See text and Appendix C for details.

Figure 4.2. Results of a meta-analysis showing the ratio of α_o during growth to α_o during decline (α_o^g / α_o^d) versus reproductive life span (RLS) for (*a*) species ($\alpha_o^g / \alpha_o^d = 0.950 \cdot \mathrm{RLS}^{0.209}$, $r^2 = 0.38$, $n = 25$, $P = 0.001$), and (*b*) families ($\alpha_o^g / \alpha_o^d = 0.878 \cdot \mathrm{RLS}^{0.232}$, $r^2 = 0.61$, $n = 9$, $P = 0.006$). Solid lines were fit by regression analysis. Dashed lines indicate no difference between α_o's (i.e., $\alpha_o^g / \alpha_o^d = 1$). Horizontal error bars are 95 %CI; vertical error bars were not calculated

because of the statistical properties of ratios (Atchley et al. 1976). Note that both axes are logarithmic. Letters and numbers refer to species and families, respectively: A = *Clupea harengus* (Atlantic herring), B = *Engraulis encrasicolus* (European anchovy), C = *Gadus macrocephalus* (Pacific cod), D = *Gadus morhua* (Atlantic cod), E = *Hippoglossus stenolepis* (Pacific halibut), F = *Limanda aspera* (yellowfin sole), G = *Merlangius merlangus* (whiting), H = *Melanogrammus aeglefinus* (haddock), I = *Merluccius productus* (North Pacific hake), J = *Micromesistius poutassou* (blue whiting), K = *Oncorhynchus gorbuscha* (pink salmon), L = *O. keta* (chum salmon), M = *O. kisutch* (coho salmon), N = *O. nerka* (sockeye salmon), O = *O. tshawytscha* (chinook salmon), P = *Ophiodon elongates* (lingcod), Q = *Parophrys vetulus* (English sole), R = *Pleuronectes platessa* (European plaice), S = *P. quadrituberculatus* (Alaska plaice), T = *Pollachius virens* (saithe), U = *Sardinops sagax* (South American pilchard), V = *Scomber japonicus* (chub mackerel), W = *Sebastes alutus* (Pacific Ocean perch), X = *Sprattus sprattus* (European sprat), Y = *Theragra chalcogramma* (Alaska Pollock); 1 = Clupeidae (herring-like fishes), 2 = Engraulidae (anchovies), 3 = Gadidae (cods and haddocks), 4 = Hexagrammidae (greenlings), 5 = Merlucciidae (merluccid hakes), 6 = Pleuronectidae (righteye flounders), 7 = Salmonidae (salmonids), 8 = Scombridae (mackerels), 9 = Scorpaenidae (rockfishes).

Figure 5.1. Independent (closed bars) and joint (open bars) contributions to the variation in relative offspring survival rate that was explained by each female trait, as determined by hierarchical partitioning. Independent and joint contributions refer to effects that were specific to that trait, and effects that were shared with other traits, respectively. The total (independent + joint) variation explained by each trait is given in parenthesis. ES = egg size (mg dry mass), K = condition ($g \cdot mm^{-3} \cdot 10^5$), EL = egg lipid (proportion of dry mass), RG = residual growth (%), LL = arcsine square root liver lipid (proportion of dry mass), SL = arcsine square root somatic lipid (proportion of dry mass), A = age (years), FL = fork length (mm), ED = arcsine square root egg docosahexaenoic acid (proportion of EL), EE = egg residual eicosapentaenoic:arachidonic acid ratio. See text for details.

Figure 5.2. Simulated stock-recruitment relations showing MI on recruitment. Egg production and resulting abundance of age-1 recruits (both expressed as a percentage of unexploited levels) are at two scales: (A) over the full range of values, and (B) near the origin (where egg production was low because of high harvest mortality). Each line is from one of three harvest strategies:

harvest-young (solid line; ages 2, 3, and 4 harvested), harvest-all (long dashes; all age harvested), and harvest-old (short dashes; age classes eliminated in sequence from oldest to youngest). Any point along a line represents the egg production and corresponding recruitment at equilibrium for a given harvest mortality.

Figure 5.3. The stock-recruitment relation of walleye in Lake Erie from 1947-1976 showing MI on recruitment. Each data point is an estimate of total annual egg production and corresponding age-3 abundance when the mean age of adult females was either above (closed circles) or below (open circles) the median value of 3.66 years. Egg production estimates incorporated density-dependent life history changes, and recruitment estimates are presented here with the effects of spring warming rate (ΔT) and water level (W) removed. Curves were predicted using the multiple linear regression model log recruitment = 0.50 · log egg production + 0.31 · mean age + 6.28 · ΔT + 0.65 · W – 121.36, with ΔT and W fixed at mean observed values of $0.21^{o}C\cdot g^{-1}$ and 174.21 m, respectively, and mean age equal to either: minimum observed (3.03 years; thin, dashed line), maximum observed (4.44 years, thin, solid line), mean of values below the median (3.29 years ±0.11; thick, dashed line), and mean of values above the median (4.01 years ±0.14; thick, solid line). The slope at the origin (α_o) of the stock-recruitment relation (10^{-5} age-3 recruits·egg^{-1}) associated with each of these four mean ages was 0.55, 1.52, 0.66, and 1.12, respectively.

List of Appendices

Chapter 1

General introduction: Fisheries-induced demographic change and the dynamics of recruitment

1.1 Background

Fisheries scientists and managers are charged with the difficult task of setting harvest limits that maximize long-term socio-economic gains without compromising the long-term viability of a stock (Hilborn and Walters 1992). From a biological perspective, the success of a management strategy depends on the ability of fisheries scientists to accurately characterize and forecast rates of population growth (i.e., sustainable fishing mortality and the potential yield to the fishery). Because the growth rate of a population is determined, in part, by the ability of that population to produce new recruits (e.g., Ricker 1954, Beverton and Holt 1957), fisheries science has relied heavily on measures of this ‘reproductive potential’ to guide key policy and management decisions (Hilborn and Walters 1992). Paradoxically, complicated ecological interactions, effects of harvesting, and errors in measurement and statistics (Christensen and Goodyear 1988, Hilborn and Walters 1992) are such that both reproductive potential and recruitment are difficult to estimate, and ultimately result in management advice that is ambiguous and unreliable (Needle 2001, Hutchings and Reynolds 2004).

Research to improve our understanding of the dynamics and management of exploited fish stocks has generally focused on (i) identifying mechanisms important to survival early in life (e.g., during the egg, larva, and juvenile stages), (ii) determining the characteristics of an adult stock that most accurately explain and forecast patterns of recruitment, and (iii) quantifying density-dependence in life history and its effects on reproductive potential. In this chapter, I briefly review how research in these three subject areas has contributed to our understanding of stock dynamics, identify some of the existing gaps in our knowledge, and then describe how my doctoral research will address these gaps through a combination of theory, modeling, and empirical data.

Although fisheries science has always been interested in explaining variation in offspring survival and recruitment (Holden and Raitt 1974), recruitment research did not begin in earnest until a committee of the International Council on the Exploration of the Sea proposed that recruitment dynamics depended on where offspring drifted, and whether or not they could find food (Hjort 1914). These hypotheses inspired a great deal of research into the extrinsic causes of recruitment variation that is still ongoing (Houde 2008). In the 1950's, interest in recruitment was again stimulated by the introduction of relations between recruitment and the reproductive potential of a stock (Ricker 1954, Beverton and Holt 1957). These 'stock-recruitment relations' have appeal, first because they relate recruitment to intrinsic factors such as the size of the adult stock, and second because they generate important reference points based on data from an already well-studied segment of the population (Hilborn and Walters 1992). However, because these relationships are notoriously weak (Needle 2001), their use in fisheries science and management has generated a keen interest in explaining residual variation in recruitment.

After almost a century of research on recruitment, we can draw two general conclusions about variation in offspring survival and recruitment. First, this variation is the result of numerous abiotic and biotic mechanisms that are both intrinsic and extrinsic to a stock (Anderson 1988, Houde 2008). Broadly categorized, these mechanisms include (i) adult abundance, which affects the number of offspring that are produced (Ricker 1954, Beverton and Holt 1957); (ii) hydrodynamics, which affect when and where adults spawn, as well as the extent to which their offspring experience conditions that are favourable for survival (e.g., Cushing 1975); (iii) temperature, which affects offspring metabolism, developmental rate, behaviour, and survival (reviewed by Blaxter 1992); (iv) predators and prey, both of which affect rates of offspring growth and survival (Paloheimo and Dickie 1966, Lima 1998); and (v) the size and growth rate of offspring themselves, which affects their ability to both locate and compete for resources, as well as avoid predators (Miller et al. 1988, Sogard 1997, Cowan et al. 2000, Rose et al. 2001). Second, recruitment variation is rarely the result of any one process; rather, it results from numerous mechanisms and their interactions, each of which can affect a different early life stage, or operate at a different spatial or temporal scale (Houde 2008). For example, the 1970's collapse of Peruvian anchoveta (*Engraulis ringens*) is now believed to be the result of a long-term shift in the temperature regime that drastically reduced spawning habitat while simultaneously increasing offspring mortality through starvation, cannibalism, and predation (Alheit and Niquen 2004).

Unfortunately, identifying the general set of factors affecting recruitment does not imply an ability to make accurate forecasts of recruitment. While there is no denying that adults are necessary for recruitment, the strength of this relation varies with the density of a population relative to the carrying capacity of its environment. When exploitation reduces population density relative to carrying capacity, the resultant increase in per capita food availability tends to promote reproduction and recruitment through increased immature growth and survival, reduced predation risk, reduced age-at-maturity, and increased fecundity or egg size. These density-dependent, compensatory life history responses have been observed in gadids (Trippel 1995), salmonids (Ricker 1981, Post et al. 1999), tunas (Polacheck et al. 2004), percids (Muth and Wolfert 1986, Baccante and Reid 1988), and other species (Trippel 1995, Lorenzen and Enberg 2001). However, actually quantifying compensation relative to the milieu of other relevant abiotic and biotic factors such as temperature remains a significant challenge (Rose et al. 2001) and a serious impediment to our ability to accurately explain and forecast the dynamics of exploited populations. Measuring compensation and its effect on population resilience is the focus of Chapters 2 and 3 (see below).

The importance of characterizing the net effect of population density on recruitment is what stimulates much of the interest in stock-recruitment relations (Hilborn and Walters 1992). When first proposed, these relations assumed that egg production was proportional to spawning stock biomass (Ricker 1954, Beverton and Holt 1957). However, this proportionality assumption is being challenged in light of recent evidence from Atlantic cod (*Gadus morhua*; Marshall et al. 1998, Kraus et al. 2000) and other exploited marine fishes (Bobko and Berkeley 2004) that relative fecundity (egg number per gram of female body mass) can increase with female age or length. As population time series lengthen and our ability to analyze them improves, evidence is also accumulating to suggest that recruitment depends on the age structure of spawning adults (Marteinsdottir and Thorarinsson 1998, Marshall and Frank 1999, Marshall et al. 1999). For example, repeat spawning protects individuals (and therefore populations) against recruitment failure in environments in which reproductive success in any given year is unlikely (Stearns 1976, Secor 2000, 2007, Longhurst 2002). Furthermore, recent analyses of a 50 year time-series of 29 stocks of off the California coast (Hsieh et al. 2006, Anderson et al. 2008) also demonstrate how age truncation can destabilize population dynamics.

Age structure might also be important to recruitment because of maternal influences (MI) on egg production and offspring survival. With respect to MI on egg production, I have already mentioned that relative fecundity can increase with maternal age or length (Marshall et al. 1998, Kraus et al. 2000, Bobko and Berkeley 2004). Numerous experiments with fish also suggest that MI on offspring *survival* result from the positive effects of maternal age and length on egg quality (e.g., size and lipid content), the timing and location of egg deposition, and egg fertilization rates (Heath and Blouw 1998, Trippel 1998, Berkeley et al. 2004, Kamler 2005, Scott et al. 2006 and others). If both offspring production and survival increase with the age (or size) of an individual female, then it follows that total recruitment should depend on the age (or size) structure of a spawning population. Although this hypothesis is generally supported by population models that show that MI are important for the dynamics of recruitment, particularly as a result of fisheries-induced demographic change (e.g., Forbes and Peterman 1994, Marteinsdottir and Thorarinsson 1998, Murawski et al. 2001, O'Farrell and Botsford 2006, Lucero 2008), empirical evidence for this phenomenon in any animal is very limited. For example, MI on the population dynamics of fishes has only been demonstrated in Baltic cod (Cardinale and Arrhenius 2000, Vallin and Nissling 2000). In Chapters 5 and 6, I evaluate the importance of age structure in general and MI in particular on the recruitment dynamics of both marine and freshwater fish.

1.2 Outline

This thesis begins with a study that measured density-dependent, compensatory life history responses in numerous populations of walleye (Percidae: *Sander vitreus*), and then used this information to develop a generalized model of maximum sustainable mortality for walleye throughout much of their range (Chapters 2 and 3). The walleye is a slow-growing and long-lived iteroparous teleost whose native North American range approximates a triangle joining the Mackenzie, St. Lawrence, and Mobile rivers (Scott and Crossman 1973). Walleye experience considerable harvesting pressure, especially in Canada, where both commercial and recreational landings rank first in value and second in mass among freshwater species (DFO 2005). This pressure has contributed significantly to the collapse of many populations (e.g., Colby and Nepszy 1981, Baccante and Colby 1996, Sullivan 2003), with concomitant changes in individual growth, maturity, and egg production (e.g., Anthony and Jorgensen 1977, Chevalier 1977, Colby and Nepszy 1981, Reid and Momot 1985, Muth and Wolfert 1986, Colby et al. 1994, Gangl and Pereira 2003, Schueller et al. 2005).

The documented collapse of numerous populations of walleye provides a unique opportunity to develop generalized, life-history based models of sustainable exploitation. Such a generalized approach is necessary in regions such as Ontario, which is home to at least 4898 populations of walleye (MacLeod and Wiltshire 2004); this is far too many to manage individually. However, attributing variation in life history to variation in density, either within or among populations, remains a significant challenge (Rose et al. 2001). In Chapter 2, I argue that progress in this area is hindered by a tendency to focus on time (e.g., age) instead of temperature. Neuheimer and Taggart (2007) recently showed that growing degree-days (GDD; an index of cumulative thermal energy) is superior to cumulative time at explaining variation in fish growth and development because it more accurately accounts for cumulative metabolic rate. By scaling growth and development to temperature, the GDD metric may facilitate the comparison or synthesis of data both within and among populations and, in doing so, simplify the job of estimating the extent to which walleye compensate for fishing mortality. To this end, I evaluate the explanatory power of the GDD metric with respect to variation in walleye growth and development (i) across 417 walleye populations in Ontario and Quebec, and (ii) both within and among 8 populations in which walleye densities have changed dramatically over time. Specifically, I am interested in (i) the GDD (and length) at which walleye tend to mature; (ii) the extent to which GDD is superior to age at explaining variation in immature length; and (iii) whether the GDD approach can elucidate density-dependent changes in immature growth across multiple populations.

In Chapter 3, I proceed to develop a general model of growth and reproduction that combines temperature data with density-dependent life history variation to predict sustainable rates of mortality for walleye throughout most of their range. I begin by using the approach outlined in Chapter 2 to quantify density-dependent changes in age- and size-at-maturity across 6 populations of walleye. I then incorporate this information into a biphasic model of growth and reproduction (Lester et al. 2004) that predicts maximum sustainable mortality in a given thermal environment. By focusing on within-population changes in life history while simultaneously accounting for temperature, this approach is an improvement over other regional analyses that are confounded by among-lake differences (e.g., Sass et al. 2004, Sass and Kitchell 2005).

Chapter 4 marks a change in focus from one kind of fisheries-induced demographic change (density) to another (age structure). Specifically, I test the hypothesis that MI can affect the reproductive capacity of exploited fish stocks through changes in the mean age of spawners. I begin by developing an analytical model to establish under what circumstances and for which life histories we might expect to see MI on population dynamics. Following Myers et al. (1999), I focus on a population’s maximum reproductive rate, which is estimable as the slope at the origin of the stock-recruitment relation. I then conduct a meta-analysis of available stock-recruitment data to determine whether maximum reproductive rate varies (i) between periods of population growth and decline (i.e., when the mean age of spawners is different), and (ii) with the reproductive life span of the species in question. This work is important because it contributes to our understanding of the role that age- and size-selective fisheries can play in shaping recruitment dynamics.

Finally, I return to walleye in Chapter 5 to conduct the kind of thorough, population-specific analysis of MI that was beyond the scope of Chapter 4. This chapter combines a 2-month pond experiment that quantifies MI on the survival of free-swimming larvae and juvenile walleye with an age-structured population model that determines whether MI of this magnitude can influence a population's maximum reproductive rate. After accounting for environmental effects and density-dependent life history changes, I then examine the long-term dynamics of a heavily exploited population of Lake Erie walleye for evidence of MI.

As a whole, my thesis follows closely the hierarchical approach advocated by Rose et al. (2001) in that it explores some of the underlying mechanisms of population dynamics through a combination of theory, modeling, and empirical data. Through the synthesis of walleye population data and temperature data from a variety of sources (e.g., government agencies, the literature), and by analyzing these data both within and among populations, this study provides an improved framework to guide the management of one of North America's most important fisheries. Furthermore, because this research is grounded in life history theory and population biology, the approach and results that are presented herein contribute to a more general understanding of the dynamics of populations, be they marine, freshwater, or terrestrial.

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Chapter 2

Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): Application of the growing-degree-day metric

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2.1 Abstract

Neuheimer and Taggart (2007. Can. J. Fish. Aquat. Sci. 64: 375–385) recently showed that the growing degree-day (GDD; a measure of thermal history) is superior to calendar time at describing growth and development in fishes, but is generally overlooked. In response to their challenge to "…test the GDD metric in all aspects of fish and aquatic invertebrate physiology, growth, and development" (p. 384), we applied the GDD metric to data from 421 populations of walleye (*Sander vitreus*) to reveal (i) 2-fold variation in immature growth rates across 144 populations, (ii) a 20% increase in immature growth rate associated with density declines within 8 populations, (iii) and relatively constant maturity thresholds of 6 300 GDD (~340 mm total length) for males and 6 900 GDD (~470 mm total length) for females in 92 populations. Our results inform the development of generalized management strategies for walleye from south of the Great Lakes to the Arctic coast (~1000 and 2200 GDD per year), and further demonstrate the explanatory and predictive power of the GDD metric with respect to fish growth and maturity.

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[4] The co-authors grant permission to include this chapter and its appendix in the thesis, and authorize the use of the thesis by the National Library.

2.2 Introduction

Fish growth and development is primarily a function of food availability and temperature (Paloheimo and Dickie 1966, Fry 1971, Kitchell et al. 1977). Recently, Neuheimer and Taggart (2007) showed that the growing degree-day (GDD, ^{o}C/day) metric—an index of ambient thermal energy that relates directly to an ectotherm's cumulative metabolic rate but is rarely used in fish science—can account for much of the variation in growth ($r^2 \geq 0.92$) among species and populations of fish.

A corollary of the GDD approach is that unexplained variation is attributable to error and factors other than temperature (e.g., food availability; Neuheimer and Taggart 2007). For decades, fisheries scientists at the Ontario Ministry of Natural Resources (OMNR), Canada, have used the GDD metric to describe fish growth and development (e.g., Colby and Nepszy 1981). Unlike Neuheimer and Taggart (2007), who found that a single GDD function was sufficient to explain 93% of the variation in immature length among 17 stocks of Atlantic cod (*Gadus morhua*), our experience with many long-lived, slow-growing freshwater fishes is that GDD predicts a range of immature lengths that is consistent with spatial or temporal variation in per capita food availability. Given that immature growth rate and length are important determinants of early survival (see reviews by Miller et al. 1988, Sogard 1997, Cowan et al. 2000) and life history parameters such as age-at-maturity, size-at-age, adult size, and longevity (Beverton and Holt 1959), quantifying temperature-independent effect of food on the growth and development of fish from numerous populations is important to understanding the reproductive biology and population dynamics of harvestable species that are distributed over large spatial scales.

In this study, we respond to Neuheimer and Taggart's (2007) challenge to "test the GDD metric in all aspects of fish and aquatic invertebrate physiology, growth, and development" (p. 384) by first showing that GDD is a strong predictor of both the maturity and immature length of walleye (*Sander vitreus*)—an economically important freshwater species that is a research and management priority throughout much of its North American range. Using data from 8 populations in which walleye abundances have changed dramatically over time, we then use the GDD approach in a combined within- and among-population analysis to quantify a general effect of per capita food availability on immature growth rate.

2.3 Methods

2.3.1 Survey data

Walleye data were obtained from 417 waterbodies in Ontario and Quebec (44 to 53^o latitude). These waterbodies were surveyed at least once in fall (surface water 10 to 15^{o}C; Morgan 2002) between 1988 and 2002 by either the OMNR or the Ministere des Ressources Naturelles et de la Faune du Quebec (MRNF). Typically, each survey represented 8 or more depth-stratified, random, overnight sets of multi-mesh gill nets (see Morgan 2002 for details). Walleye total length (L), maturity, and sex were determined in the field, and age at capture was assigned in the lab using otoliths.

For each walleye population in Ontario, we generated a unique time series of the annual growing degree-day (GDD_a) above an air temperature threshold of 5 ^{o}C. We based GDD_a on air temperature because walleye prefer to be above the thermocline (20 to 25 ^{o}C; Colby et al. 1979), where air and water temperatures are strongly correlated over a broad range of lake morphologies (Shuter et al. 1983, Livingston and Lotter 1998, Livingston and Padisak 2007). We used 5 ^{o}C as a base temperature for growth because (i) it defines the walleye growing season in terms of both ice cover (Shuter et al. 1983) and bioenergetics (Kitchell et al. 1977), and (ii) an exploratory analysis following Neuheimer and Taggart (2007; Supplementary Information) showed that the coefficient of determination of the relation between walleye length and GDD was maximized between 0 and 10 ^{o}C (P.A. Venturelli, unpublished results).

To calculate GDD_a for a given population and year of interest, we (i) obtained daily air temperature data from all available Ontario weather stations, (ii) calculated a GDD_a for each station (i.e., the difference between the average daily air temperature and 5 ^{o}C, summed across all days for which the average daily air temperature was $\geq$ 5 ^{o}C), (iii) GIS-interpolated these data to a produce province-wide 1 km^2 GDD_a grid map, and then (iv) assigned a unique GDD_a value according to the population's geographic coordinates. Because grid maps of GDD_a were unavailable for Quebec, we estimated the GDD_a for a given population and year directly from nearby temperature stations (i.e., using steps i and ii above; mean station distance 43 km, range 2 to 173 km).

To calculate the cumulative annual growing degree-day (GDD_c) that each walleye experienced prior to capture, we summed population-specific values of GDD_a across all years in which that walleye was alive. Thus, a 2 year-old walleye from Jessica Lake in fall 2001 experienced three growing seasons (1999, 2000, 2001) prior to capture, each with a specific GDD_a value (1691, 1646 and 1817, respectively) that summed to a GDD_c of 5154. Because each GDD_a value in a time series was unique, a 2 year-old walleye from the same population but a different year would have experienced a different GDD_c.

A summary of waterbody (location, surface area, and mean depth), temperature (GDD_a and GDD_c), and walleye data (sex, age, L, and maturity) is available from the author.

2.3.2 GDD_c and maturity

Because the allocation of surplus energy towards reproduction (Day and Taylor 1997, Lester et al. 2004) is likely to produce adult-specific relations between L and GDD_c, and because the maturity of walleye in some populations and years was unknown, the first step in our analysis of survey data was to define a threshold value of GDD_c below which both males and females were likely to be immature. We began by calculating the mean L of both males and females in each population, year, and age ($n \geq 5$ individuals per mean); associated GDD_c values were calculated accordingly. For both sexes separately, we then fit a locally weighted regression (LOESS; Cleveland and Devlin 1988) curve to the relation between mean L and GDD_c. Curves were fit using a smoothing parameter of 0.6 and an Epanechnikov kernel density estimator (SPSS 2007). Finally, we approximated GDD_c and L values at maturity by determining, via visual inspection, the point at which the LOESS curve for either sex diverged from the linear growth trajectory that was established early in life.

To check that this approach produced reasonably accurate estimates of male and female L-at-maturity, we compared our results to sex-specific distributions of L-at-50%-maturity (L_{50}) that were generated using available survey data. Each estimate of L_{50} in a distribution was derived by probit analysis (Finney 1971, Trippel and Harvey 1991) of the frequency distribution (20 mm length bins) of mature and immature walleye. Because our minimum sample size was 100 males or females pooled across all sample years within a population, some populations were excluded from this analysis.

2.3.3 Immature length and GDD_c

Once we had defined a threshold value of GDD_c below which individual walleye were likely to be immature, we set out to determine how best to describe immature length. Specifically, we were interested in whether GDD_c explained more variation in immature length than age, and whether simple models were better than complex ones. Although Neuheimer and Taggart (2007) found that a single GDD_c function explained 93% of the variation in immature length among 17 stocks of Atlantic cod (*Gadus morhua*), residual variation in relations between immature length and GDD_c among surveyed walleye populations suggests that a more complex model is appropriate. Therefore, we modelled length as

$$L = a \cdot GDD_c^{\,b} \tag{1}$$

or

$$\log_{10} L = \log_{10} a + b \cdot \log_{10} GDD_c \tag{2}$$

where a is a parameter ≥ 0 that depends on food availability. Equation 2 is ideally suited to comparative analyses of growth data because it (i) assumes that L = 0 when time = 0, (ii) allows for both linear and nonlinear growth trajectories (Lester et al. 2004, Quince et al. 2008), (iii) implies a common temperature effect when slopes are consistent, and (iv) implies an effect of food availability when intercepts vary.

Our analysis proceeded as follows. First, we used the threshold value of GDD_c to extract from the survey data all individual walleye that were likely to be immature. We then calculated the mean L of immature walleye in each population, year, and age ($n \geq 5$ individuals, sexes combined); associated values of GDD_c were calculated accordingly. If a population was sampled more than once between 1988 and 2002 (31 of 144 populations in this analysis), mean values were calculated separately for each sampling year and then pooled. We then used linear analysis of covariance (ANCOVA) of log-transformed data to develop 3 models of L for both predictor variables (GDD_c and age): (i) a complex model in which a unique intercept and slope was estimated for each population (Figure 2.1a), (ii) a model of intermediate complexity in which a unique intercept but a common slope was estimated for each population (Figure 2.1b), and (iii) a simple model in which a common intercept and slope was estimated for all populations (Figure 2.1c). To compare the strength of evidence for each of these 6 models, we then used a small-sample, bias-corrected form of Akaike's Information Criterion (AICc) to calculate model probabilities (w_i) (Burnham and Anderson 2002, Anderson 2008).

2.3.4 Immature length, GDD_c, and food availability

The purpose of our final analysis was to determine the efficacy of the GDD metric for quantifying an effect of per capita food availability on immature growth rate among numerous populations of walleye. For this analysis, we focused on 8, well-studied populations in which walleye abundances changed at least 4-fold as a result of overexploitation, experimental overexploitation, invasive species, and (or) recruitment failure stemming from introduced species, pollution, or the degradation of spawning habitat (Table 2.1, Table A.1). Because data were unavailable to quantify food availability directly in these lakes, we used estimates or indices of walleye abundance, together with published accounts of abundances change, to identify periods of time when food availability was likely to be either relatively high or relatively low. As described below, we then used ANCOVA to compare rates of immature growth both between periods and among populations. This approach assumed that, within a population, changes in abundance equated to changes in density and, ultimately, food availability. We based the first assumption on the fact that lake size was effectively constant between periods of abundance in a given population; the second assumption was based on the absence of compelling evidence that, when walleye abundance was low, food availability also increased because of increased lake productivity (Supplemental Table S2). Thus, our analysis controlled for temperature to compare rates of immature walleye growth between periods of high and low food availability in several populations in which confounding effects of lake productivity were probably minor.

We estimated the L-at-age of individual walleye in each population and year primarily from the back-calculation of scales (Tables A.1 and A.2). We used back-calculation because gear size selectivity among young age groups can bias direct measurements of L towards fast-growing individuals. Back-calculations followed the Monastyrsky non-linear method (see Francis 1990). We derived the requisite slope of the relation between body length and scale size via a year-specific log-log regression of L on anterior scale radius. If data from more than one year were available to estimate this slope, we used ANCOVA to calculate a common slope. Because confidence in scale ages tends to be low for older fish, we only back-calculated L-at-age using scales from 4, 5, and 6 yr-old walleye (sexes combined). For each age and year of growth, our minimum sample size was 5 fish per age class (e.g., L-at-age-1 was derived from $n \geq 5$ age-4 walleye from 1977). When more than one age class contributed to back-calculated L in a year (e.g., both 4 and 5 year olds were available to back-calculate L-at-age-1 in 1979), we used a Monte Carlo randomization procedure (up to 10 000 combinations) to test the null hypothesis of no difference between mean L-at-age. If this null hypothesis was rejected, we based L-at-age on the youngest age class; otherwise, data were pooled. Finally, we averaged across individual walleye within each year to produce annual estimates of L-at-age.

Some estimates of L-at-age were obtained from the literature as either back-calculations or direct measures (Table A.1). Estimates were only included if $n \geq 5$ scales (or walleye) per population and year (sexes combined); however, data were not always available to limit back-calculations to scales from 4, 5, and 6 year-olds. When necessary, we developed population-specific regression equations to convert fork length to L.

We obtained GDD_a and GDD_c values for populations in Ontario as described in the section “*Survey data*”. Missing GDD_a values in a time-series were either estimated by linear regression of GIS-interpolated data onto data from the nearest weather station, or obtained from the literature. For Saginaw Bay, Lake Huron, we estimated GDD_a and GDD_c directly from the nearest weather station (Table A.1).

To test for an effect of food availability on growth across all populations, we first used indices of abundances to divide each time series into periods of relatively high and low food availability. Analysis of L data then followed the combined ANCOVA-AICc approach that is described in the previous section—with two important changes. First, we excluded all age-based models by assuming *a priori* that GDD_c was better than age at explaining variation in immature L. This change reduced to three our list of linear ANCOVA models: one complex (Figure 2.1a), one intermediate (Figure 2.1b) and one simple (Figure 2.1c) L-GDD_c relation, each with population as a categorical variable. Second, with the addition of abundance (high or low) as a categorical variable, we were able to evaluate three additional linear ANCOVA models: (i) a complex model in which a unique intercept and a unique slope was estimated for each population in both periods of abundance (Figure 2.1d), (ii) a model of intermediate complexity in which a unique intercept but a common slope was estimated for each population in both periods of abundance (Figure 2.1e), and (iii) a simple model in which a common intercept and a common slope was estimated for all populations in both periods of abundance (Figure 2.1f).

2.4 Results

2.4.1 GDD_c and maturity

Locally weighted regression analysis of 26 481 males from 1 633 age classes across 370 populations in Ontario and Quebec indicated an abrupt decline in growth rate at ~6 300 GDD_c and ~340 mm L (Figure 2.2a). The decline in the growth rate of females was less abrupt (22 256 individuals from 1 388 age classes across 342 populations), but was first noticeable at ~360 L and 6 900 GDD_c (Figure 2.2b). These results were consistent over a broad range of smoothing parameters (0.3 to 0.9, where 1.0 is equivalent to a polynomial fit to all data; P.A. Venturelli, N.P. Lester, T.R. Marshall, and B.J. Shuter, unpublished results). Because 340 mm corresponded to the modal value of L_{50} for males, and was considerably less than the modal values of L_{50} for females (~470 mm; Figure 2.3), we were confident that growth of walleye up to 6 000 GDD_c was not confounded by the allocation of energy towards reproduction. Note that a L_{50} of 470 mm for females (Figure 2.3) corresponds to a GDD_c of ~9400 (Figure 2.2b).

2.4.2 Immature length and GDD_c

Across 144 populations and 9^o of latitude (~1000 to 2200 GDD_a), variation in the log L of walleye that had experienced <6 000 GDD_c was best explained by the intermediately complex linear ANCOVA model based on log GDD_c (Table 2.2, Figure 2.4). However, even when temperature was taken into account, the growth rate of immature walleye from different populations ranged between a low of $\log_{10} L = 0.66 \cdot \log_{10} GDD_c – 0.09$, and a high of $\log_{10} L = 0.66 \cdot \log_{10} GDD_c + 0.22$); a more than 2-fold difference (Figure 2.4). Empirical support for the remaining 5 models was negligible; however, the intermediately complex models always outperformed the simple models, which themselves outperformed the complex models (Table 2.2). Within this hierarchy, log GDD_c was consistently better than log age at explaining variation in immature L. The simple log GDD_c model (which was similar to the simple, un-transformed GDD_c models presented in Neuheimer and Taggart 2007) was ranked third (Table 2.2) and took the form $\log_{10} L = 0.63 \cdot \log_{10} GDD_c + 0.15$.

2.4.3 Immature length, GDD_c, and food availability

For the 8 populations in which walleye abundances changed dramatically over time, empirical support was strongest for the intermediately complex linear ANCOVA model, with a common slope for log GDD_c, but intercept values that were dependent on abundance (Table 3, Fig. 1e). In other words, although growth rates of immature walleye varied among populations, they responded similarly to changes in abundance. On average, the growth rate of immature walleye was described as $\log_{10} L = 0.78 \cdot \log_{10} GDD_c - 0.44$ mm when abundances were high, and then increased to $\log_{10} L = 0.78 \cdot \log_{10} GDD_c - 0.35$ mm when abundances were low (a 1.2-fold increase). Empirical support for the remaining 5 models was negligible, although models that included the categorical variable ‘abundance’ always outperformed the models that ignored it.

Within this abundance-based dichotomy, models ranked intermediate > complex > simple. The simple GDD_c model was again ranked third (Table 3), and took the form $\log_{10} L = 0.79 \cdot \log_{10} GDD_c - 0.42$ (Figure 2.5b).

2.5 Discussion

Our results demonstrate the efficacy of the GDD as a metric for explaining growth in fishes (see also Neuheimer and Taggart 2007). We attribute the consistency with which GDD models outperform age-based equivalents (Table 2.2) to two factors. First, because age data are discrete (age-1, -2, -3, etc.), age-based models severely limit the distribution of L data along the x-axis. For example, if log age was used in place of log GDD_c in Figure 2.4, lenth data would have been restricted to 7 columns; one for each observed age. This change to the structure of the independent variable represents a considerable loss of information with which to explain variation in the dependent variable (Cottingham et al. 2005). Second, L-age relations ignore the fact that aging and growing are distinct processes insofar as a fish that survives over some time interval will age, but the extent to which it increases in L depends, not only on time, but on other factors such as temperature. Put another way, unless the thermal energy (e.g., GDD) that fish are experiencing is known, using age to predict when a fish will reach a certain L is as effective as using a stopwatch alone to predict when a pot of water will boil.

While the GDD metric is clearly superior to age for describing immature growth, our results also demonstrate that a single L-GDD_c relation is not always sufficient. For example, our analysis of survey data from 144 populations of walleye suggests strongly that intercepts were population-specific (Table 2.2) and that predicted growth rates varied two-fold among populations (Figure 2.4). Our analysis of immature L data from 8 populations also shows that log L- log GDD_c relations also differed between periods of high and low abundance within a population (Table 2.3, Figure 2.5a); however, the magnitude of this difference was relatively consistent across populations in that immature walleye tended to grow 1.2 times faster when population densities were low than when population densities were high. Neuheimer et al. (2008) also showed, in a single population of haddock (*Melanogrammus aeglefinus*), that L-GDD_c relations predicted increasingly slower rates of adult growth with increasing population density, but interpreted this change in growth as evidence that size-selective fishing mortality had gradually removed all fast-growing and late-maturing individuals from the population. However, given that fishing mortality in our 8 study lakes was (i) either relatively low or completely absent when densities were low, (ii) relatively high when densities were low, and (iii) altogether negligible in shaping density patterns in some populations (Table 2.1), the observed increase in L at low densities is entirely consistent with a density-dependent increase in the per capita availability of food.

Although density-dependent changes in length-at-age have been observed in many individual populations of walleye (e.g., Anthony and Jorgensen 1977, Colby and Nepszy 1981, Reid and Momot 1985), direct comparisons involving two or more populations are comparatively rare (a trend that is by no means restricted to walleye). To a large extent, individual case studies are common because of a need for detailed information on individual populations in which growth is often the result of numerous factors and their interactions. But it is also a symptom of the age-based approach to growth, which limits the efficacy or even feasibility of among-population analyses by emphasizing, rather than accounting for, differences among populations. Growth models based on GDD, on the other hand, explicitly account for temperature (arguably one of the most important determinants of growth; Paloheimo and Dickie 1966, Fry 1971, Kitchell et al. 1977) and, in doing so, simplify considerably the job of determining how immature growth rates respond to changes in food availability. Furthermore, by relating growth to a common currency (thermal age), the GDD metric facilitates the comparison or even aggregation of data across populations. For example, we observed a consistent, 1.2-fold increase in immature growth rate with large reductions in density; information that is useful for developing management strategies that can be generalized to multiple populations and (or) disturbance scenarios. Curiously, Sass and Kitchell (2005) found that GDD_a contributed negligibly (partial $R^2 = 0.001$ for males and 0.02 for females) to a multiple regression model ($R^2 = 0.34$ for both sexes) that used 7 predictor variables (including walleye density) to explain variation in walleye length across 859 lakes in Wisconsin. Given that this model included no other temperature variables, we suspect that GDD_a performed poorly because it was estimated for a single location, but then applied to an area that spanned $7.5 \cdot 10^4$ km^2 and 3^o of latitude; ideally, a unique GDD_a time series should be developed for each lake. Our results suggest that, when thermal history is accurately accounted for, growth can be used as a surrogate method for monitoring large changes in abundance.

The density-dependent growth response observed in this study is not trivial. Because growth rate and size are critical to the early survival of fish (see reviews by Miller et al. 1988, Sogard 1997, Cowan et al. 2000), even small changes in growth can substantially affect both the timing and number of individuals that recruit into a fishery. For example, the GDD_a in Oneida Lake, New York, is 2 180 (Goddard Institute for Space Studies 2008; our calculation). If we assume that density-dependent growth responses follow Figure 2.5a, then a GDD_a of 2 180 predicts that 1 and 3 year-old walleye will grow to 146 mm and 344 mm L, respectively, when density is high, and 179 and 423 mm L, respectfully, when density is low. Given that walleye in Oneida Lake (i) can experience ~1.5 times more overwinter mortality at 146 mm L than at 179 mm (Rose et al. 1999; our calculation), (ii) become vulnerable to the sport fishery at 381 mm (15 in) L, and (iii) produce ~15 billion $eggs \cdot y^{-1}$ (Forney 1976)—and also assuming that instantaneous rates of natural mortality follow Chapter 5—these relatively small differences in predicted L-at-age translate into dramatic differences in the predicted magnitude and timing of recruitment into the fishery: 3.2 age-3 walleye when food abundance is high for every 1 age-4 walleye when food abundance is low. Conversely, recruitment can be over- or underestimated by this amount if information on density-dependent immature growth is unavailable or ignored.

In addition to immature growth, our results are telling with respect to GDD and other aspects of walleye life history. Relations between L and GDD_c (Figure 2.2) show clearly that the growth of adults is sexually dimorphic over broad temporal and spatial scales (Henderson et al. 2003, Sass and Kitchell 2005, Rennie et al. 2008), and that females tended to mature at a larger size than males (Figure 2.3). These differences are consistent with life history theory (Roff 1992, Charnov 1993), which predicts that the minimum size threshold that an individual must reach before the benefits of maturity outweigh the costs is lower in male fish than it is in female fish. However, GDD_c underestimated the size at which females matured (Figure 2.2b), probably because the tendency for females to mature over a broader range of sizes than males (Figure 2.3) resulted in a relatively smooth female L-GDD_c relation (Figure 2.2b). Although population-specific analyses would be less prone to error, our application of the GDD metric to data from 417 populations between ~1000 and 2200 GDD_a shows clearly that most walleye delay maturation until they reach ~340 mm L (Figure 2.2a, b, Figure 2.3). Thus, ~6 300 GDD_c represents a thermal constant: the thermal energy that walleye must experience in order to reach a maturation size threshold of ~340 mm L.

Furthermore, if the size-at-maturity of walleye and other long-lived species is relatively constant (Rochet 1998, Beverton 2002, this study), then GDD_a (i.e., the rate at which an individual can grow each year) should be a stronger predictor of age-at-50% maturity (t_{50}) than L_{50} because growth rate determines the time that it takes to reach a size threshold, but not that size threshold itself (Roff 1991). Accordingly, we evaluated this *post hoc* hypothesis and found very little support for a relation between L_{50} and GDD_a (the mean GDD_a that an individual experienced prior to maturity; Figure 2.6a), but relatively strong support for a relation between t_{50} (estimated as per L_{50}; see above) and GDD_a (Figure 2.6b; see also Baccante and Colby 1996). Thus, male and female walleye in our study matured at ~340 and ~470 mm L, respectively (Figure 2.3), but, depending on GDD_a, took 2 to 14 years to do so (Figure 2.6a). The extent to which L_{50}, t_{50}, and their relations to GDD vary with walleye density, and how this variation can shape reproductive rates, are addressed in Chapter 3.

2.6 Conclusion

We echo the call by Neuheimer and Taggart (2007) for further research into the GDD metric, the limited use of which in fish science is out of proportion with its demonstrated utility (e.g., Colby and Nepszy 1981, Ridgway et al. 1991, Neuheimer and Taggart 2007, this study). Although the present study shows that the GDD metric can be used to account for variation in temperature when explaining variation in growth and development, it also raises several questions: (i) Are L-GDD relations consistent throughout a species' tolerance limits or geographical range? Recent evidence from walleye suggests that the effects of temperature on growth vary among phylogeographic lineages (Zhao et al. 2008, see also Conover et al. 2006). (ii) Does GDD predict other aspects of life history? If maturity depends on cumulative temperature, then perhaps GDD_c-at-maturity is more informative than age-at-maturity. (iii) How does GDD influence predictions of growth and development under future climate scenarios or in other species? For example, the GDD metric might perform poorly for lake trout (*Salvelinus namaycush*), which seek out thermal refugia (Snucins and Gunn 1995).

We support the results of Neuheimer and Taggart (2007) by demonstrating the explanatory power of the GDD metric with respect to variation in maturity and density-dependent growth across hundreds of populations and a large spatial area. We also expand upon this work be emphasizing the importance of identifying factors that affect growth, to what extent, and under what circumstances. While the GDD metric is by no means a panacea, this statistically powerful, 'common currency' approach has major advantages over relations between growth and calendar time, which must be developed separately for each temperature scenario (e.g., population, treatment, period of time), and generally complicate the synthesis of data from unrelated studies (e.g., through meta-analyses). Given these advantages, and the relative ease with which GDD data can be obtained, we strongly encourage the widespread use of the GDD metric in place of age when studying growth and development in fish.

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Table 2.1. Populations used to relate the immature growth of walleye to GDD$_c$ at high and low abundance.

Population	ID	Location (lat, long)	Area (ha)	Mean depth (m)	Principal cause(s) of change in abundance
Crooked Pine L.	1	48°47'N, 91°05'W	1 604	6.1	Recruitment failure
L. Erie (W and W-central basins)	2	41°49'N, 82°38'W	1.95×10^6	16.6	Overexploitation; recruitment failure
Henderson L.	3	48°49'N, 90°18'W	151	2.5	Experimental overexploitation
L. Huron (Saginaw Bay)	4	43°59'N, 83°29'W	2.96×10^5	10.1	Recruitment failure
Lower Marmion L.	5	48°53'N, 91°31'W	3 982	6.8	Recruitment failure
L. Ontario (Bay of Quinte)	6	44°05'N, 77°05'W	25 740	10.0	Overexploitation; recruitment failure
Savanne L.	7	48°50'N, 90°06'W	364	2.6	Experimental overexploitation
Shoal L.	8	49°33'N, 95°01'W	25 856	9.1	Overexploitation

Note: see Table A.1 for source information.

Table 2.2. The strength of evidence for 6 linear ANCOVA models of immature walleye total length according to survey data from 144 populations in Ontario and Quebec.

Model	Predictor variable	Intercept	Slope	n	K	$\log(\hat{\sigma}^2)$	AICc	AICc rank	Δ_i	w_i	adj. r^2
b	GDD_c	unique	common	642	145	3.201	-1679.916	1	0.000	1.000	0.95
b	age	unique	common	642	145	3.126	-1631.660	2	48.256	<0.000	0.94
c	GDD_c	common	common	642	3	2.480	-1586.235	3	93.680	<0.000	0.81
c	age	common	common	642	3	2.285	-1461.074	4	218.841	<0.000	0.70
a	GDD_c	unique	unique	642	289	3.460	-1167.008	5	512.908	<0.000	0.96
a	age	unique	unique	642	289	3.355	-1099.902	6	580.014	<0.000	0.95

Note: Models correspond to panels in Figure 2.1. Models were ranked according to strength of evidence as determined by a small-sample, bias-corrected form of Akaike's Information Criterion (AICc). Data were log-transformed prior to analysis. n = sample size (number of data points across all populations), K = number of parameters [n + intercept(s) + slope(s) + error estimate], $\hat{\sigma}^2$ = residual variance, Δ_i = AICc differences, w_i = Akaike weight, adj. r^2 = adjusted coefficient of determination, GDD_c = cumulative annual growing degree-day.

Table 2.3. The strength of evidence for 6 linear ANCOVA models of immature walleye total length based on data from 8 populations in which densities have changed dramatically over time.

Model	Density	Intercept	Slope	n	K	$\log(\hat{\sigma}^2)$	AICc	AICc rank	Δ_i	w_i	adj. r^2
e	included	unique	common	339	11	-2.481	-818.377	1	0.000	0.839	0.88
d	included	unique	unique	339	33	-2.621	-815.077	2	3.300	0.161	0.91
f	included	unique	common	339	4	-2.272	-762.167	3	56.210	<0.000	0.82
b	ignored	unique	common	339	10	-2.290	-755.546	4	62.831	<0.000	0.82
a	ignored	unique	unique	339	17	-2.331	-754.300	5	64.077	<0.000	0.83
c	ignored	common	common	339	3	-2.147	-721.729	6	96.648	<0.000	0.76

Note: Models correspond to panels in Figure 2.1. The terms ‘common’ and ‘unique’ apply within a density category for models d and e, but between density categories for model f. Models were ranked according to strength of evidence as determined by a small-sample, bias-corrected form of Akaike’s Information Criterion (AICc). Data were log-transformed prior to analysis. See Table 2.2 for definitions of symbols and abbreviations.

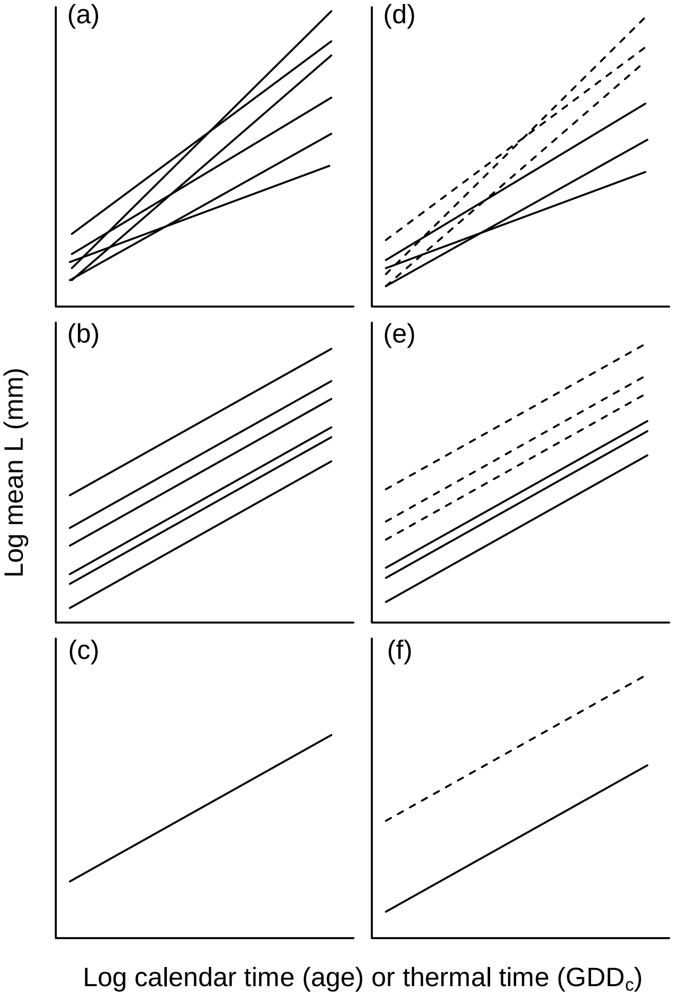

Figure 2.1. Hypothetical examples of the linear ANCOVA models that were evaluated in this study. In our analysis of survey data, we compared among the following 6 models: a) log L vs. log calendar time (age), and log L vs. log thermal time (GDD$_c$), both with the categorical variable ‘population’; b) log L vs. log age, and log L vs. log GDD$_c$, both with no ‘population x time’ interaction term; and c) log L vs. log age, and log L vs. log GDD$_c$, both with no categorical variable. In our analysis of 8 collapsed populations, we compared among the following 6 models: a), b), and c) with only log GDD$_c$ as a covariate; d) log L vs. log GDD$_c$ with the categorical variables ‘population’ and ‘density’; e) log L vs. log GDD$_c$ with the categorical variables ‘population’ and ‘density’ but no interaction terms; and f) log L vs. log GDD$_c$ with ‘density’ as a categorical variable but no interaction terms.

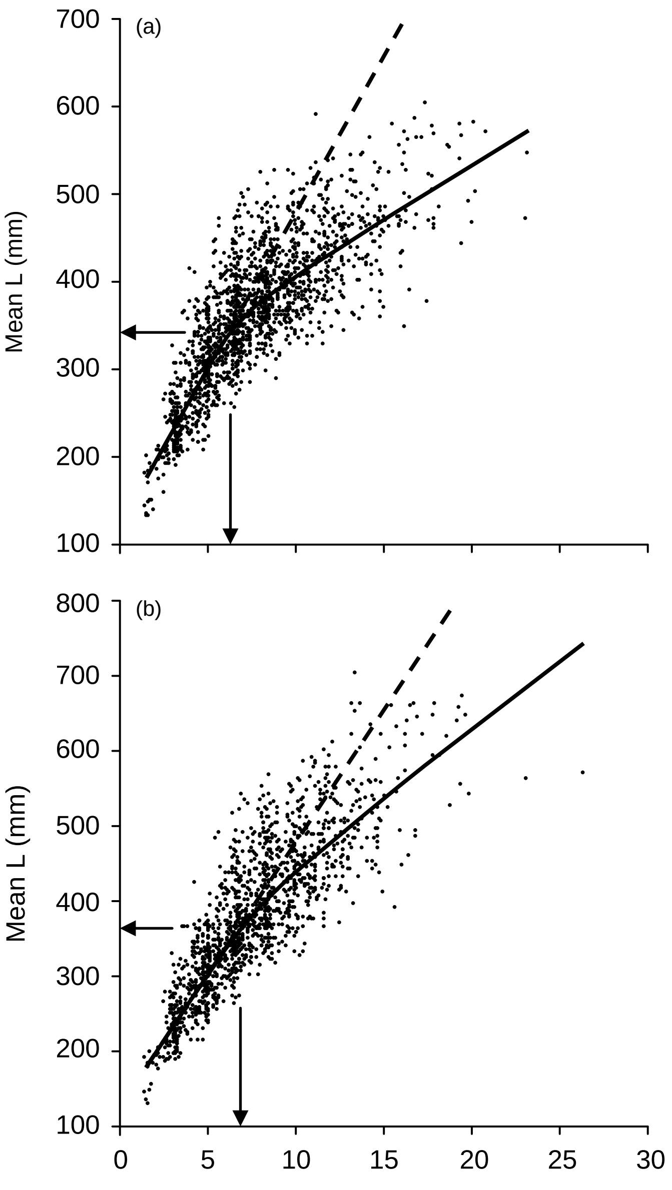

Figure 2.2. Mean total length (L) versus the cumulative annual growing degree-day (GDD$_c$) for a) male (*n* = 1 633 age classes from 370 populations) and b) female walleye (*n* = 1 388 age classes from 342 populations) in Ontario and Quebec. Solid lines were fit by LOESS and dashed lines represent the linear growth trajectory early in life. Arrows indicate the GDD$_c$ and L at which these two lines began to diverge, as determined by visual inspection. These data are available from the author.

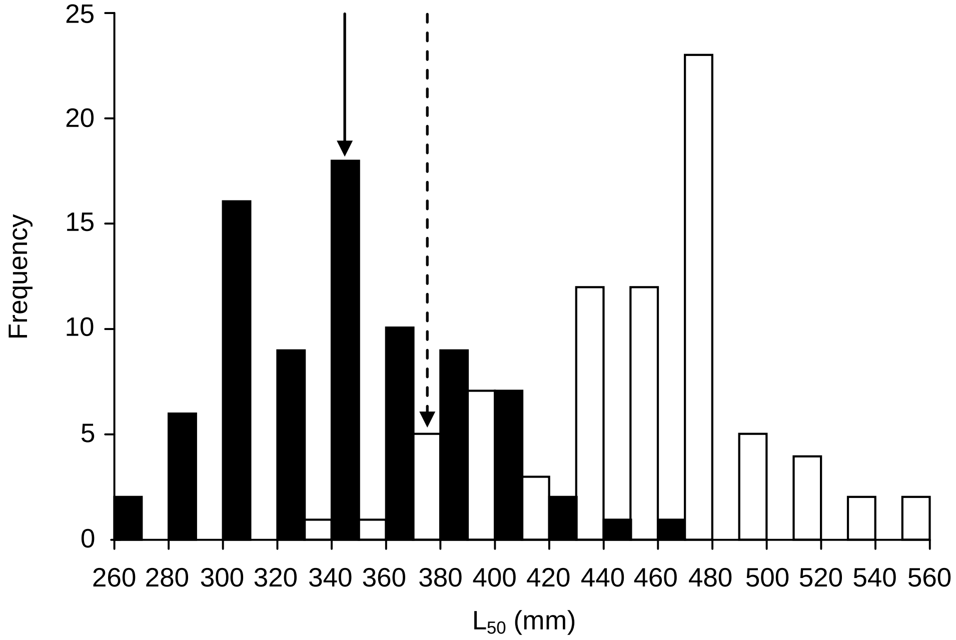

Figure 2.3. The distribution of total length-at-50%-maturity (L_{50}) of male (closed bars, *n* = 81 populations) and female (open bars, *n* = 78 populations) walleye in Ontario and Quebec. Estimates of L_{50} were based on probit analysis with 20 mm L bins and $n \geq 100$. The solid and dashed horizontal arrows indicate, respectively, the L at which the growth trajectories of males and females slowed according to Figure 2.2. These data are available from the author.

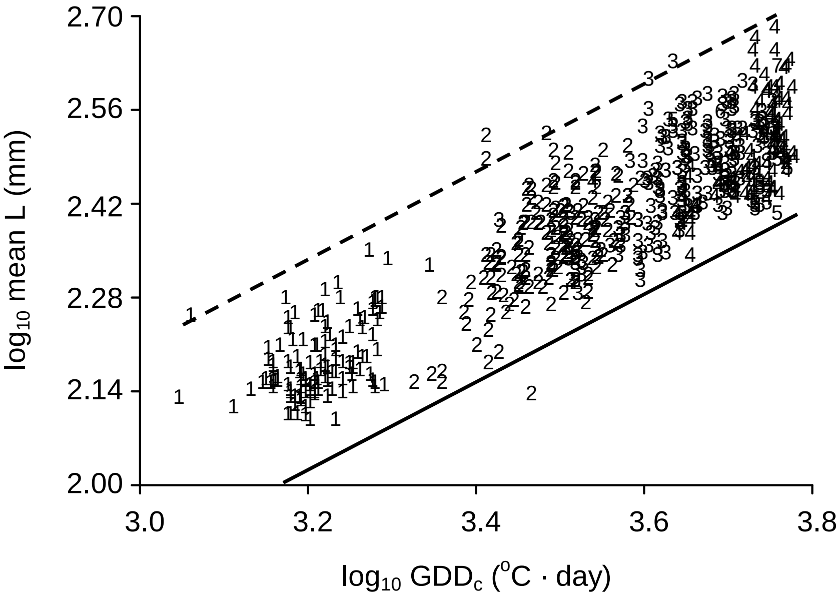

Figure 2.4. Linear ANCOVA model of log-transformed mean total length (L) of immature walleye (GDD$_c$ <6 000, sexes combined) versus log-transformed cumulative annual growing degree-days (GDD$_c$) in 144 surveyed populations. Dashed and solid lines represent the fastest and slowest predicted growth trajectories, respectively, according to model b (Figure 2.1b). Numeric symbols denote age at time of sampling in a population and year. Un-transformed data are available from the author.

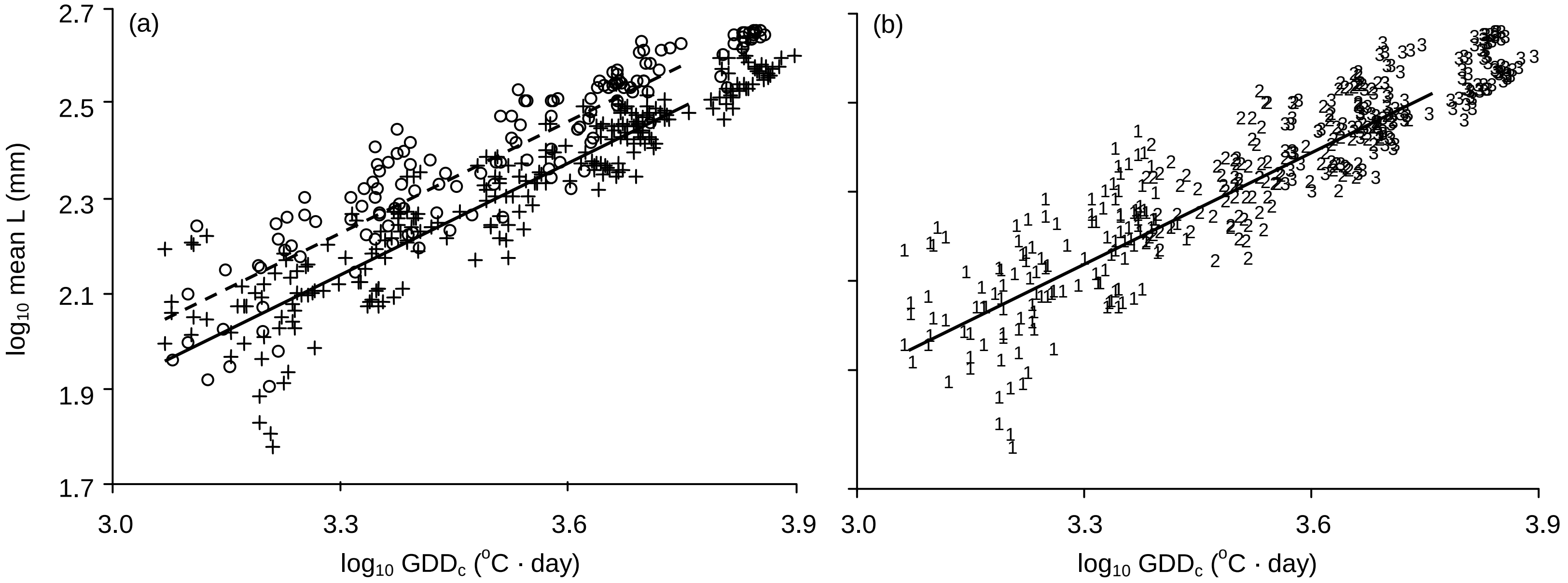

Figure 2.5. Linear ANCOVA models of log-transformed mean total length (log L) of immature walleye (sexes combined) versus log-transformed cumulative annual growing degree-days (GDD$_c$) for 8 collapsed stocks a) with data divided into periods of high ('+' symbols, solid line) and low (open circles, dashed line) density (Figure 2.1e; showing mean relations within a density period) and b) pooled over the entire time series (Figure 2.1c). Numeric symbols in panel b identify estimated calendar ages in years. Points above the 6 000 GDD$_c$ threshold were excluded from analysis because of the potentially confounding effects of maturity.

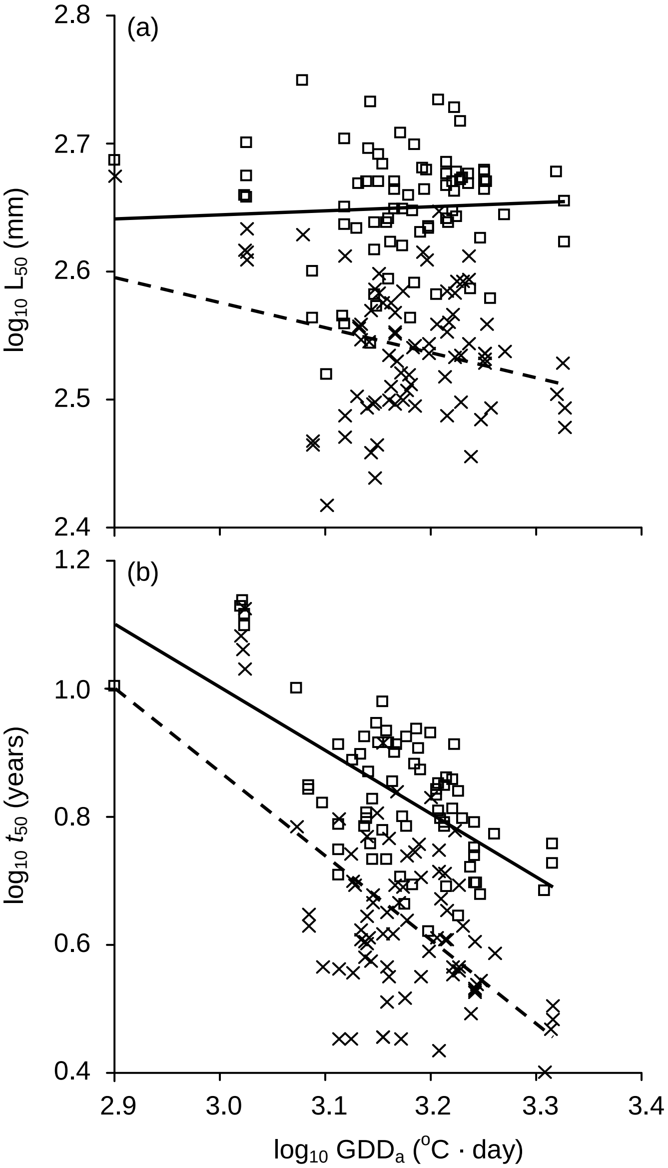

Figure 2.6. Linear regression of a) log total length- (L_{50}) and b) log age-at-50%-maturity (t_{50}) on mean annual growing degree days ($\overline{GDD}_a$) for males ('x' symbols, dashed lines) and females (open squares, solid lines). Maturity data are from Figure 2.3. Regression equations and evidence ratios ($E_{i,j}$) are as follows: log male $L_{50} = -0.20 \cdot \log \overline{GDD}_a + 3.18$, $r^2 = 0.07$, $n = 81$, $E_{i,j} = 1.31$; log female $L_{50} = 0.03 \cdot \log \overline{GDD}_a + 2.54$, $r^2 < 0.01$, $n = 78$, $E_{i,j} = 0.35$; log male $t_{50} = -1.30 \cdot \log \overline{GDD}_a + 4.78$, $r^2 = 0.32$, $n = 78$, $E_{i,j} = 290.18$; log female $t_{50} = -0.99 \cdot \log \overline{GDD}_a + 3.97$, $r^2 = 0.40$, $n = 72$, $E_{i,j} = 891.74$. Evidence ratios measure how much more likely one model is relative to another (Burnham and Anderson 2002, Anderson 2008). In this case, we compared each regression model to a horizontal line that intersected the y-axis at the mean value of log L_{50} or log t_{50} (i.e., a model that assumed no relation with $\overline{GDD}_a$).

Chapter 3
A general, life history-based model for the regional management of walleye (*Sander vitreus*)

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3.1 Abstract

General models of sustainable exploitation are necessary when the number of populations in a region exceeds the capacity to monitor and manage on an individual basis. Here, we present a model of growth and reproduction that combines temperature data with density-dependent life history variation to predict sustainable rates of mortality for walleye (*Sander vitreus*) throughout most of their range. Density-dependence in life history was estimated from 6 populations in which walleye densities have changed dramatically over time. Our model predicted patterns of life history that were in close agreement with empirical data. Overall, our results suggest that populations in the south can sustain more mortality than populations in the north, but that maximum sustainable mortality at any location depends on both the magnitude of density-dependent life history change, and whether adults at low densities allocate energy either to growth or reproduction. Our model establishes benchmarks for sustainable mortality, and provides a framework for refining these benchmarks based on information that is already being collected within existing sampling regimes.

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[3] The co-authors grant permission to include this chapter and its appendix in the thesis, and authorize the use of the thesis by the National Library.

3.2 Introduction

The ability of fish populations to compensate for fishing mortality, and the mechanisms that underlie this compensation, are both well known. In brief, when exploitation reduces the density of a population relative to the carrying capacity of the environment, the resultant increase in per capita food availability tends to promote reproduction and recruitment through increased immature growth and survival, reduced predation risk, reduced age-at-maturity, and increased fecundity or egg size (e.g., Trippel 1995, Rochet 1998, Rochet et al. 2000, Lorenzen and Enberg 2001, Rose et al. 2001).

Much less clear is the magnitude of this compensation and, by extension, how it affects the amount of fishing mortality that a population can sustain. Compensation is difficult to quantify because of inadequate data, issues of scale, the idiosyncrasies of individual populations, and the tendency of population models to propagate errors and uncertainty (reviewed by Rose et al. 2001). These problems are particularly serious for freshwater species that occur in many isolated waterbodies. For example, in Ontario alone, northern pike (*Esox lucius*), walleye (*Sander vitreus*), and lake trout (*Salvelinus namaycush*) are known to occur in at least 6411, 4898, and 2318 waterbodies, respectively (OMNR 1987, 1989, 1990, MacLeod and Wiltshire 2004); directly estimating the ability of each of these populations to sustain fishing mortality is simply not an option.

An alternative to the population-specific approach is to infer the limits of harvest from life history invariants and environmental correlates. For example, because both food availability and temperature affect growth rate (Paloheimo and Dickie 1966), and growth rate can in turn affect age-at-maturity, size-at-age, and longevity (Beverton and Holt 1959), the resiliency of a population to harvest should depend on the latitude, morphometry, and productivity of a lake (e.g., Shuter et al. 1998, Lester et al. 2004a). Furthermore, if such relations between life history, the environment, and resiliency are consistent and predictable, then it is possible to use information from a few well-studied populations to develop generalized models for application to multiple populations or regions and different disturbance scenarios. To date, this generalized approach has been applied to various marine groundfishes (Clark (1991), lake trout (Shuter et al. 1998, Purchase et al. 2005), walleye (Purchase et al. 2005), and others.

In this paper, we use life history information, together with temperature and food availability, to develop a generalized model of maximum sustainable mortality for walleye throughout much of their range. In Canada, the walleye ranks first in value and second in mass among commercial landings of freshwater fishes (DFO 2005), and is the species of choice among recreational fishers, representing nearly one quarter of the combined freshwater and marine catch (DFO 2007). This popularity has contributed significantly to the collapse of many populations (e.g., Colby and Nepszy 1981, Baccante and Colby 1996, Sullivan 2003). These events, while unfortunate, provide a unique opportunity to evaluate intra-population life history variation in an economically important species that is generally too slow-growing, large, and long-lived for laboratory study. In the first part of this study, we used data from the documented collapse of 6 of these populations to quantify the effects of density and temperature on immature growth and maturity. We then incorporated this information into a biphasic model of growth and reproduction (Lester et al. 2004b) to evaluate the effects of these life history responses on net reproductive rate and maximum sustainable mortality.

3.3 Methods

3.3.1 Observed density-dependent changes in immature growth and maturity

The first step in our analysis was to determine a typical response of immature growth and age- and size-at-maturity to population density. We began by identifying 6 populations in which there were large, well-documented changes in walleye density (Table 3.1), and for which sex, age, total length (L), and maturity data were available from either the spring or fall to describe associated life history responses (Table B.1). Using temperature station data, we first estimated (i) the thermal energy that was available for growth and development in each population and year (annual growing degree-day, GDD_a; $^oC/d$), and (ii) the thermal energy that each age class from each population and year had experienced prior to capture (cumulative annual growing degree-day, GDD_c; $^oC/d$) (see Chapter 2 for details). These measures of 'thermal age' are better than 'calendar age' at describing variation in growth and maturity both among (Neuheimer and Taggart 2007, Chapter 2) and within (Chapter 2) fish populations because thermal energy is a common currency that allows for the direct comparison, or even aggregation, of data across multiple years and populations.

To illustrate the advantage of the thermal age approach, consider female walleye from two hypothetical lakes or periods of time that differ only in the amount of thermal energy that was available for immature growth and development. Growth and development in these two groups follow independent trajectories according to calendar age (the conventional length-at-age and age-at-maturity approaches in fish science; Figure 3.1a), but a single trajectory according to thermal age (i.e., L-at-GDD_c and GDD_c-at-maturity; Figure 3.1b). The distance away from the origin that a group of females has moved along this L-GDD_c trajectory depends on the availability of thermal energy (e.g., the length of the growing season). Next, consider females from two lakes or periods of time that differ in both the thermal energy and food that is available for immature growth and development. Under this scenario, both calendar age and thermal age describe independent trajectories of growth and development. However, whereas the trajectories based on calendar age resemble Figure 3.1a—and therefore provide little insight into the relative importance of thermal energy and resource availability—thermal age, by definition, controls for temperature, and therefore implicates resource availability in the between-group differences in both L-at-maturity (Figure 3.1c) and (or) GDD_c-at-maturity (Figure 3.1d).

We estimated the typical density-dependent response of immature growth and maturity to decreased walleye population density as follows. Using probit analysis (Finney 1971, Trippel and Harvey 1991) in SPSS (2007), we first calculated the L- (L_{50}) and GDD_c-at-50%-maturity (GDD_{50}) of both males and females in each population and year for which data were available (Table B.1). Estimates of L_{50} were based on 5 cm length frequency distributions. When published data were available to estimate one of L_{50} or GDD_{50} but not both, we used publication-specific L-age relations to predict one from the other (see Table B.1 for details). Based on information from both unpublished sources and the literature (Chapter 2), we then split the time series of each population into a period when densities were relatively high and a period when densities were relatively low (Table B.1). The mean value of L_{50} and GDD_{50} for both males and females in both periods of density was estimated by first averaging across all years within a period and population, and then across all populations. Because we accounted for variation in temperature both within- and among-populations that had experienced very large changes in density, we interpreted any between-period differences in mean L_{50} and (or) mean GDD_{50} as a density-dependent response.

3.3.2 Modeling adult growth, reproduction, and maximum sustainable mortality

In the second part of our analysis, we used a biphasic model of somatic growth and reproductive investment (Lester et al. 2004b) to convert mean observed changes in L_{50} and GDD_{50} into an estimate of the extent to which walleye can compensate for fishing mortality. We considered mean values of life history change, but also used 95% confidence limits to establish minimum and maximum response scenarios. Each step in the conversion of a response scenario into compensation is described below, and summarized in Figure 3.3. The abbreviation and symbols used here and throughout the text are summarized in Table 3.1. Note that we focused on females under the assumption that males were equally abundant and sperm was not limiting, and, to simplify our calculations, assumed that all females matured at L_{50} and GDD_{50}.

In brief, we established the thermal climate in which growth and development occurred, and then used mean L_{50} and GDD_{50} during the period of high population density to estimate age-specific fecundity (fec_t) and annual instantaneous natural mortality rate (M_{1+}) when the net reproductive rate (R_o) of a typical female walleye was equal to one (i.e., when a population of typical females was replacing itself). For these calculations, we assumed an annual instantaneous fishing mortality rate (F) of zero. We then re-estimated these parameters using mean L_{50} and GDD_{50} during the period of low population density. If $R_o \neq 1$ as a result of this change (i.e., females were over- or under-replacing themselves), we adjusted F until $R_o = 1$. The extent to which F differed from 0 represented the threshold value of F above which a population of typical female walleye would eventually go extinct (F_{ext}).

3.3.2.1 Thermal climate

To convert life history responses into an estimate of F_{ext}, we first had to establish the amount of thermal energy that was available for immature growth and development in each growing season (i.e., GDD_a). Given the natural range of walleye in North America (Colby et al. 1979) and North American climate norms for the period 1971-2000 (NOAA 2002, Environment Canada 2009), walleye can experience as few as 1000 GDD_a near the Arctic coast and as many as 7000 GDD_a near the Gulf of Mexico (see also Colby and Nepszy 1981). For this study, we modelled populations from this northern extreme (1000 GDD_a) to as far south as the Virginias (3000 GDD_a) at intervals of 500 GDD_a. We did not model growth and reproduction further south because of the potential for the inhibition of growth by extreme summertime temperatures (Colby et al. 1979), and (or) behavioural thermoregulation, and because of the potential for region-specific growth-temperature relations as a result of the post-glacial divergence of lineages (Zhao et al. 2008).

3.3.2.2 Lifetime egg production

For each GDD_a scenario, we converted mean GDD_{50} during the period of high density into age-at-50%-maturity (t_{50}) in years by dividing GDD_{50} (the amount of thermal energy that a walleye had to experience before it could mature) by $\mathrm{GDD_a}$ (the amount of thermal energy that was available in an average year):

$$t_{50} = \mathrm{GDD}_{50} / \mathrm{GDD_a}. \qquad 3.1$$

When modelling maturity, it is important to distinguish between the onset of investment in reproduction (i.e., egg production) and first reproduction (i.e., spawning). In this study, L_{50}, GDD_{50}, and t_{50} were estimates of the latter because they were based on maturity data that were generated by assessing the presence or absence of well-developed eggs, either at the end of the growing season or just prior to spawning (Table B.1). Because the energy to develop these eggs was acquired during the previous growing season (Henderson et al. 1996), the GDD and age at which these females began to allocate surplus energy to reproduction is GDD_{50} - GDD_a and t_{50} - 1.

Similarly, L_{50} represented the length of first-time spawning females. However, to estimate female length at t_{50} -1 (L_e), we first had to account for the 'loss' of surplus energy to reproduction in the year leading up to first spawning. Following Charnov et al. (2001), who showed that investment in reproduction is related to both t_{50} -1 and M_{1+}, we used equation (4.5) in Lester et al. (2004b) to estimated M_{1+} as

$$M_{1+} = \ln\left(\frac{1.95}{t_{50} - 1} + 1\right). \qquad 3.2$$

Note that t_{50} - 1 is "T" in Lester et al. (2004b), and that we assumed linear growth through the origin (i.e., "t_1" = 0). This assumption was valid provided that (i) weight increased with the cube of length, (ii) a broad range of prey sizes was available, and (iii) predators did not suppress foraging activity (Lester et al. 2004b).

Using equation (4.6) in Lester et al. (2004b), we then estimated the proportion of total annual surplus energy that was invested in reproduction (i.e. gonads plus all behavioural and metabolic costs associated with reproduction) as

$$g = 1.18 \cdot (1 - \mathrm{e}^{-M_{1+}}). \qquad 3.3$$

Because this parameter represented the proportion of surplus energy that mature females diverted away from adult growth, we could then describe adult growth following Lester et al. (2004b):

$$\mathrm{L}_{\infty} = \frac{3 \cdot \mathrm{L}_e}{(t_{50} - 1) \cdot g}, \tag{3.4}$$

$$k = \ln\left(1 + \frac{g}{3}\right), \tag{3.5}$$

$$t_{\mathrm{o}} = t_{50} - 1 + \frac{\ln\left(1 - \frac{g \cdot (t_{50} - 1)}{3}\right)}{\ln\left(1 + \frac{g}{3}\right)}, \tag{3.6}$$

where L_{∞} is asymptotic length (mm), L_e is the length at which females begin to allocate energy to reproduction (mm), t is age in years, k is the annual rate of deceleration of adult growth (i.e., the von Bertalanffy growth coefficient), and t_{o} is the age in years when L = 0. Note that equation 3.4 combines equations (2.4) and (3.2) in Lester et al. (2004b), and that equation 3.6 was simplified from equation (3.4) in Lester et al. (2004b) by assuming linear growth through the origin.

Provided that (i) weight increases with the cube of length (see Lester et al. 2004b), and (ii) g is constant over a female's reproductive lifetime (see Table 1 in Roff 1983), equations 3.4 to 6 gave a reasonable description of von Bertalanffy growth in an adult fish (equation 3.1 in Lester et al. 2004b):

$$\mathrm{L}_t = \mathrm{L}_{\infty} \cdot (1 - \mathrm{e}^{[-k \cdot (t - t_o)]}), \tag{3.7}$$

where L_t is total length at age-t (mm). Furthermore, because $\mathrm{L}_t = \mathrm{L}_{50}$ when $t = t_{50}$, we substituted equation 3.4 into equation 3.7 and solved for L_e:

$$\mathrm{L}_e = \mathrm{L}_{50} \cdot \frac{g \cdot (t_{50} - 1)}{3 \cdot (1 - \mathrm{e}^{[-k \cdot (t_{50} - t_o)]})}. \tag{3.8}$$

Once L_t and g had been estimated for a given GDD_a, we then proceeded to estimate the lifetime egg production of a typical female walleye in this thermal climate. First, we converted each L_t to body weight using the equation

$$W_t = 9.5 \cdot 10^{-6} \cdot L_t^3 , \tag{3.9}$$

where W_t is weight at age-t (g). This equation was taken from Lester et al. (2000), who found that W_t tended to increase with the cube of L_t in 73 populations of walleye from Ontario. Using a modified version of equation 4.2 in Lester et al. (2004b), we then estimated age-specific fecundity:

$$\text{fec}_t = \frac{0.71 \cdot g \cdot W_t}{2 \cdot w_e} , \tag{3.10}$$

where fec_t is the number of female eggs produced by an age-t female assuming a 1:1 sex ratio, and w_e is the wet mass in grams of an average egg. For all populations, we assumed a w_e of 2.88 x 10^{-3} grams, which is the mean wet egg mass across all 7 populations (1225 to 2145 GDD_a) in Moles et al. (2008; our calculation). We re-scaled g by a factor of 0.71 to account for behavioural and metabolic costs of reproduction, and the inefficient transfer of somatic energy to eggs (Shuter et al. 2005, see also Quince et al. 2008). Finally, we estimated the total number of female eggs produced over the lifetime of a typical female (fec_Σ) as

$$\text{fec}_\Sigma = \sum_{t=t_{50}}^{t_{\max}} \text{fec}_t , \tag{3.11}$$

where $t_{\max}$ is maximum age in years, defined as the number of adult age classes in which individuals made up ≥ 1% of the total adult population according to M_{1+}.

3.3.2.3 Net reproductive rate and first-year mortality

For the high density period, we assumed that a population of typical female walleye in a given temperature environment (i.e., GDD_a) exhibited long-term equilibrium such that, on average, each female produced exactly one daughter over her lifetime. In other words, we assumed that the net reproductive rate (R_o) of each female was 1. To calibrate each population to $R_o = 1$, we determined the instantaneous natural mortality rate of a typical female walleye in her first year of life (M_o) as follows. First, we calculated the number of female offspring that survived to age-*t* as

$$N_t = \mathrm{fec}_{\Sigma} \cdot \mathrm{e}^{-M_o} \cdot \mathrm{e}^{-M_{t-1}} . \qquad 3.12$$

For this calculation, we initially assumed that $M_o = M_{1+}$. We then calculated the probability of female offspring surviving to age-*t* as

$$l_t = \frac{N_t}{\mathrm{fec}_{\Sigma}} , \qquad 3.13$$

and R_o as

$$R_o = \sum_{t=t_{50}}^{t_{\max}} l_t \cdot \mathrm{fec}_t . \qquad 3.14$$

If Ro ≠ 1, we adjusted M_o until the condition $R_o = 1$ was satisfied (Figure 3.3).

3.3.2.4 Maximum sustainable fishing mortality

The final step in our estimate of the extent to which walleye in different climates can compensate for fishing mortality was to re-estimate R_o for each of the mean, minimum, and maximum observed changes in L_{50} and GDD_{50}, and then adjust F until $R_o = 1$ (Figure 3.3). Note that $F = F_{ext}$ when $R_o = 1$. Because total annual instantaneous mortality rate at time t (Z) is equal to $F + M_{1+}$, $R_o = 1$ is also satisfied when $Z = Z_{ext}$ (the highest possible Z that a population of typical female walleye can sustain). F was only applied to walleye ≥ 300 mm. When re-estimating R_o, we assumed that first-year mortality (M_o), egg size (w_e), and the nature of the W_t-L_t relation (equation 3.9) did not change with density; all other parameters were allowed to vary. We also considered two scenarios of reproductive investment: (i) g optimally adapted to M_{1+} ($g[M_{1+}]$) such that it did not vary with F, and (ii) g optimally adapted to total Z ($g[Z]$) such that it was plastic with respect to F.

3.4 Results

3.4.1 Density-dependent changes in immature growth and maturity

We analyzed data from 6 populations of walleye in which densities had changed dramatically over time (Table 3.1). Herein, we focus on results for females because they are relevant to our model. However, for the sake of completeness, and because these data may be useful in the future, results for males are presented in Table 3.1 and Figure 3.2.

Females tended to mature at 417 ±21 mm L and 9418 ±1254 GDD_c when population densities were relatively high, and at 453 ±36 mm L and 7626 ±1502 GDD_c when population densities were relatively low (Table 3.2, Figure 3.2). Thus, in a collapsed walleye population, we can expect females to mature 37 mm larger and 1792 GDD_c earlier. Assuming that growth was linear from the origin to maturity, growth rates of immature females increased 1.3-fold from 0.04 to 0.06 mm/unit GDD_c.

3.4.2 Adult growth, reproduction, and maximum sustainable mortality

We incorporated mean density-dependent changes in the L_{50} and GDD_{50} of female walleye (Figure 3.2) into a biphasic model of growth and reproduction to estimate, over a range of climates (1000 to 3000 GDD_a), the extent to which populations can compensate for fishing mortality (Figure 3.3). To incorporate uncertainty in our estimates, we modeled two scenarios of L_{50} and GDD_{50} response: mean (a 1.3-fold increase in immature growth rate, with females maturing 37 mm larger and 1792 GDD_c earlier) and maximum (+1.7, +65, -3170). Although we also considered a minimum scenario (+1.1, +8, -414), results are not presented here because compensation was negligible (i.e., $F_{ext} \approx 0$).

When F was absent (i.e., population density was high), the relation between t_{50} and GDD_a approximated a power curve (Figure 3.4), with females maturing at age-10 or 11 in the northern edge of their range (1000 GDD_a), and as early as age-4 at 3000 GDD_a. These values of t_{50} represent the number of years that females in different thermal environments took to reach GDD_{50}. Investment in reproduction increased with GDD_a from a low of 0.18 to a high of 0.40 (Figure 3.5). Because g represents a proportional diversion of surplus energy away from somatic growth, growth in length no longer followed a linear trajectory, but instead exhibited von Bertalanffy growth (Figure 3.6). Subsequent egg production per unit body mass was constant across all adult age classes (because both g and w_e were invariant with age for a given GDD_a), but increased linearly with GDD_a from 51 to 137 eggs/g (Figure 3.7). Assuming that all of these eggs were spawned and fertilized, M_o increased with GDD_a (mean scenario: $M_o = 7.88 \cdot GDD_a^{0.034}$; maximum scenario: $M_o = 7.84 \cdot GDD_a^{0.037}$). Thereafter, M_{1+} increased with GDD_a from a low of 0.19/year to a high of 0.50/year (Figure 3.8a).

When F was very high (i.e., population density was very low), L_{50} increased and GDD_{50} decreased according to either the mean or maximum life history response scenario. These changes had a cascading effect on growth and reproduction (Figure 3.3). With respect to t_{50}, females matured 2 to 4 years earlier at 1000 GDD_a, but only one year earlier at 3000 GDD_a (Figure 3.4). Under the $g[M_{1+}]$ strategy (g optimized to M_{1+}, regardless of F), adults grew rapidly (Figure 3.6) but, because both g and w_e did not vary with age for a given GDD_a, continued to produce the same number of eggs per gram (Figure 3.7). Under the $g[Z]$ strategy, (g optimized to Z and therefore varies with F) g increased in all thermal environments, ranging from 0.32 at 1000 GDD_a to 0.71 at 3000 GDD_a (Figure 3.5). This increase in g resulted in an increase in egg production that ranged from 88 to 236 eggs/g (Figure 3.7). Because surplus energy was being invested primarily in gonads (instead of growth), adults exhibited a growth trajectory that was intermediate between the low F and the 'high F, $g[M_{1+}]$' scenarios (Figure 3.6).

The extent to which walleye were able to compensate for F as a result of mean and maximum changes in L_{50} and GDD_{50} varied with GDD_a and, to a lesser degree, whether g was optimized to M_{1+} or Z. Under the most conservative scenario of compensation (mean change, $g[M_{1+}]$), walleye at the northern edge of their range (1000 GDD_a) were able to sustain a Z of 0.31/year (Figure 3.8a), or a F of 0.12/year (Figure 3.8b). At 3000 GDD_a, Z_{ext} and F_{ext} were 0.76 and 0.26, respectively. Under a liberal compensation scenario (maximum change, $g[Z]$), Z_{ext} and F_{ext} were 0.41 and 0.23, respectively, at 1000 GDD_a, and then rose to 0.98 and 0.48, respectively, at 3000 GDD_a (Figure 3.8).

3.5 Discussion

3.5.1 Density-dependent changes in immature growth and maturity

Our combined analysis of 6 walleye populations (1406 to 2411 GDD_a) showed increased growth and earlier maturity in response to low population densities and concomitantly high per capita food availability (Table 3.2, Figure 3.2). Because these results are qualitatively consistent with a wealth of evidence from individual walleye populations (e.g., Anthony and Jorgensen 1977, Chevalier 1977, Colby and Nepszy 1981, Reid and Momot 1985, Muth and Wolfert 1986, Colby et al. 1994, Gangl and Pereira 2003, Schueller et al. 2005) and other fishes (e.g., Trippel 1995, Rochet 1998, Rochet et al. 2000, Lorenzen and Enberg 2001, Rose et al. 2001), we focus on patterns that are relevant to our model and the management of walleye.

On average, the transition from high to low population densities was associated with a large reduction in the time that it took for females to mature (GDD_{50}), but only a small increase in the size at which they matured (L_{50}; Figure 3.2). The invariance of L_{50} relative to GDD_{50} (or t_{50}) is common for walleye (Chapter 2) and among harvested fishes in general (Rochet 1998, Beverton 2002). It is also consistent with life history theory (Roff 1992, Charnov 1993), which predicts a minimum size threshold at which the fitness benefits outweigh the energetic and survival costs associated with maturity. Although this L_{50} threshold varies among populations of walleye, it tends to occur between 332 and 380 mm for males, and between 417 and 470 mm for females (Colby et al. 1979, Rennie et al. 2008, Chapter 2, this study).

Assuming that immature growth trajectories were linear, these changes in GDD_{50} and L_{50} predict a 1.3-fold increase in female growth rates (Figure 3.2). This change is comparable to the 1.2-fold increase reported in Chapter 2, which used an ANCOVA model to compare relations between back-calculated L (sexes combined) and GDD_c among these populations plus two others. Although these results suggest that immature growth rate is a reliable indicator of large density changes when temperature is accurately accounted for, immature growth rate is often difficult to monitor (i) directly because of the size-selective nature of most gear types, and (ii) indirectly because of the effort involved in back-calculating length. On the other hand, GDD_{50} provides a comparable estimate of growth and is relatively easy to monitor within existing sampling regimes (note that t_{50}-based growth estimates will be confounded with temperature; Figure 3.1a).

3.5.2 Adult growth, reproduction, and maximum sustainable mortality

Using only four parameters (GDD_a, L_{50}, GDD_{50}, w_e) and a L-W_t relation, our GDD-based biphasic model accurately predicted walleye growth and reproduction between 1000 and 3000 GDD_a. For example, our conversion of female GDD_{50} to t_{50} across a GDD_a gradient (Figure 3.4) agrees with empirical evidence that populations in the northern mature later than populations south (Colby et al. 1994, Baccante and Colby 1996), and confirms that this evidence was based on data from moderate to heavily exploited populations. Similarly, predicted growth trajectories were in close agreement with data from 342 populations of walleye from Ontario and Quebec (Figure 3.6), with only a slight discrepancy early in life that we attribute to the tendency of (i) gill nets surveys to under-sample walleye <110 mm (i.e., over-estimate length early in life), and (ii) modeled females to mature slightly later than GDD_{50} (e.g., if observed GDD_{50} was 7626 and modelled GDD_a was 2000, then modelled GDD_{50} was 8000).

The accuracy of our life history estimates stems from our use of both the GDD metric, which facilitates among-population analyses by explicitly accounting for temperature effects (Neuheimer and Taggart 2007, Chapter 2), and the biphasic model, which estimates growth by explicitly accounting for the allocation of energy to reproduction (Lester et al. 2004b). The trade-off between growth and reproduction is demonstrated clearly by the behaviour of the biphasic model in the presence of F. Biologically speaking, walleye at low population densities will experience relatively high per capita food availability and have more energy to invest in growth or reproduction. In the model, this increase in surplus energy is represented by a reduction in t_{50} and an increase in immature growth rate (Figure 3.6). If g is optimized to M_{1+} (Figure 3.5), then this energy is allocated to somatic growth such that there is an increase in the adult growth trajectory (Figure 3.6) but no change in relative fecundity (Figure 7). If g is optimized to Z, then adults grow comparatively slowly (Figure 6) and relative fecundity is increased (Figure 3.7).

To determine whether walleye in nature employ a $g[M_{1+}]$ or $g[Z]$ strategy, we compared our results to empirical relations between walleye life history characteristics and GDD_a. For g, this comparison was to published field measures of the gonadosomatic index (the ratio of gonad mass to body mass) that we divided by 0.71 to correct for the higher energy density of gonads relative to soma (Shuter et al. 2005, see also Quince et al. 2008). All 11 of the walleye populations for which observed values of g were available clustered at or below the pattern that was produced by the $g[M_{1+}]$ strategy, with no clear effect of fishing mortality (Figure 3.5). The tendency of observed values to be low relative to predicted values is probably the result of behavioral and metabolic costs of reproduction that are not captured in the gonadosomatic index; accounting for these additional costs would reduce the conversion factor below 0.71 and, ultimately, shift observed data upwards. Although Figure 3.5 suggests tentatively that g is optimized to M_{1+} in walleye, this optimization strategy was not evident in the growth patterns of female walleye from Ontario and Quebec (Figure 3.6). However, much of this ambiguity might stem from the fact that length data were taken from numerous waterbodies; ideally, we would need to conduct careful, within-population analyses that compare adult (i.e., von Bertalanffy) growth parameters between distinct periods of high and low densities.

The $g[M_{1+}]$ strategy was also implied by predicted and observed patterns of relative fecundity (Figure 3.7), although our model appeared to overestimate egg production in general. There are two plausible explanations for or this result. First, interrelationships between g, w_e, and relative fecundity are much more complex in nature than in our model. For example, (i) w_e varies among populations, years, and females (Johnston 1997, Johnston and Leggett 2002, Moles et al. 2008); (ii) there is some evidence for a within-population, density-dependent trade-off with egg number (Baccante and Reid 1988) that has been observed in other fishes (Rijnsdorp et al. 1991, Rochet et al. 2000); and (iii) fecundity patterns are often confounded by greater, and often time-lagged, effects of environmental conditions on growth and the availability of prey (Colby and Nepszy 1981, Baccante and Reid 1988). Thus, whereas our model automatically converted an increase in reproductive energy into an increase in egg number (because w_e was fixed), an entirely different pattern can emerge in the wild. Second, whereas g represents the proportion of surplus energy that a typical adult invests in all aspects of reproduction (i.e., gonads, behaviour, and metabolism), our model ignored behavioural and metabolic costs by assuming that the whole of g was available to invest in eggs ($g[Z]$) or growth ($g[M_{1+}]$). Both of these differences are of little consequence to estimates of Z_{ext} and F_{ext} provided our model accurately estimated the change in the production of age-1 offspring that occurs as a result of changes in L_{50} and GDD_{50}. However, these differences do suggest that predicted and observed relative fecundities are not necessarily equivalent and that any similarities or differences between them should be interpreted with caution.

In the end, our estimates of Z_{ext} and F_{ext} were only mildly sensitive to whether we assumed that g was optimized to M_{1+} or Z (Figure 3.8). This is because of the trade-off between growth and reproduction such that the lifetime egg production of a female that invested in reproduction by growing large ($g[M_{1+}]$) was only slightly less than that of a female that instead invested in reproduction by developing large gonads ($g[Z]$). Estimates of Z_{ext} and F_{ext} were more sensitive to the magnitude of the change in L_{50} and GDD_{50}, which highlights the importance of obtaining accurate measures of these parameters. Our results lend strong support to the F_{ext}-GDD_{a} relation for walleye that was proposed by Baccante and Colby (1996). On the other hand, even our maximum predicted F_{ext}-GDD_{a} relation ($F_{\text{ext}} = 0.0085 \cdot \text{GDD}_{\text{a}}^{0.474}$; Figure 3.8b) might be conservative given that some of the poulations in our analysis were either experiencing exploitation during the ‘high’ period, or not fully collapsed during the ‘low’ period. For example, immature females in Lake Erie doubled in growth rate and matured 4844 GDD_{c} (~2 years) earlier in response to the most dramatic collapse of walleye for which data are available. If this response is typical of all populations, then F_{ext} might exceed our maximum response scenario (line 4 in Figure 3.8b) by ~0.08/year.

Ultimately, F_{ext} will depend on both the amount of thermal energy that a population experiences (GDD_a) and the ability of individuals in that population to grow faster and mature earlier in response to fishing mortality (Figure 3.8b). Across all response scenarios, southern populations of walleye can sustain more fishing mortality than northern populations. This discrepancy stems from the fact that walleye in the north grow more slowly and invest a smaller proportion of their energy in somatic growth; a pattern that argues strongly for strict limits on F in northern populations, particularly in regions with a large number of anglers per lake (e.g., Alberta; Sullivan 2003). Across all values of GDD_a, F_{ext} was lowest under a mean response and $g[M_{1+}]$ scenario, highest under a maximum response and $g[Z]$ scenario, and intermediate between these extremes under the remaining two scenarios (Figure 3.8b). Taken together, our results define a range of F values that are likely to be risk-averse and risk-prone for a particular population or region.

3.5.3 Conclusion

Compensation in walleye is not a question of ‘if’ but of ‘how much’. In this study, we estimated sustainable levels of fishing over a range of climates by incorporating observed, density-dependent changes in immature growth and maturity into a biphasic model of adult growth and reproduction. By focusing on within-population changes in life history while simultaneously accounting for GDD, our approach is an improvement over regional analyses that attempt to quantify density-dependence based on life history differences among populations of varying density, but invariably struggle to account for a myriad of confounding effects (e.g., Sass et al. 2004, Sass and Kitchell 2005). This framework can also be extended to other species, and—provided that attendant changes in water quality, water quantity and food webs are either relatively small or can be accounted for—to alternative climate scenarios (e.g., increased GDD_a).

Given that each lake is physically, chemically, and biologically unique, a generalized approach to fisheries management is bound to result in the over- or under-exploitation of certain populations. To some extent, these errors can be mitigated by refining F_{ext} based on parameter values that are specific to a population or region (although the extrapolation of our results beyond 3000 GDD_a is not recommended). Our model can also be tailored to different lake types by coupling it with a thermal-optical habitat model (Lester et al. 2004a) that estimates maximum sustainable yield (kg/ha/year) based on lake morphometry, water clarity, and GDD_a. This model suggests that, for a given GDD_a, F_{ext} will be lower in lakes that are clear, and (or) either too shallow or too deep to provide suitable benthic habitat. Similarly, F_{ext} can be adjusted to specific predator or prey fields by converting GDD_a to water temperature (Appendix 1 in Lester et al. 2004a; note that GDD_a must be divided by 1000), and then using a bioenergetics model to project growth. However, over- or under-exploitation in certain populations is a necessary compromise in regions in which the resource is too finely divided to manage on a per-population basis. Using just a handful of parameters, our model accurately describes the growth and reproduction of walleye across much of their range, and establishes benchmarks of maximum sustainable fishing mortality.

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3.7 References

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Table 3.1. Walleye populations for which data were available to compare maturity estimates between periods of high and low density. GDD_a = annual growing degree-day (means are from the period 1980-2005). This table was modified from Chapter 2; it does not include Lower Marmion Lake (ID = 5) or Lake Ontario (ID = 6) because maturity data were unavailable for these populations.

Population	ID	Location (lat, long)	Area (ha)	Mean depth (m)	Mean GDD_a	Magnitude of abundance decline	Principal cause(s) of abundance decline
Crooked Pine L.	1	48°47'N, 91°05'W	1 604	6.1	1626	10.43	Recruitment failure
L. Erie (W and W-central basins)	2	41°49'N, 82°38'W	$1.95 \cdot 10^6$	16.6	2411	3319.28	Overexploitation; recruitment failure
Henderson L.	3	48°49'N, 90°18'W	151	2.5	1415	15.44	Experimental overexploitation
L. Huron (Saginaw Bay)	4	43°59'N, 83°29'W	$2.96 \cdot 10^5$	10.1	2349	18.45	Recruitment failure
Savanne L.	7	48°50'N, 90°06'W	364	2.6	1406	4.47	Experimental overexploitation
Shoal L.	8	49°33'N, 95°01'W	25 856	9.1	1710	17.52	Overexploitation

Table 3.2. Between-period differences in the maturity of male and female walleye from the 6 populations in this study. ID numbers correspond to populations in Table 3.1, and ‘high’ and ‘low’ refer to periods of high and low population densities, respectively. Δ = difference (low – high), L_{50} = total length-at-50%-maturity, GDD_{50} = cumulative annual growing degree-days at 50% maturity. See Table B.1 for data sources and related notes.

	Male						Female					
	L_{50} (mm)			GDD_{50} ($^oC/d$)			L_{50} (mm)			GDD_{50} ($^oC/d$)		
ID	High	Low	Δ	High	Low	Δ	High	Low	Δ	High	Low	Δ
1	344	348	4	6408	4083	-2325	441	469	28	9593	7768	-1825
2	358			8669	3467[a]	-5202	391	440	49	10805	5961	-4844
3	383	346	-37	7037	4756	-2281	413	399	-14	7813	6048	-1765
4	383	383	0	9021	5779	-3242	425	501	76	10342	9294	-1048
7	341	314	-27	6753	5769	-984	396	445	49	9802	9102	-700
8		271		4893[a]	4067	-826	433	466	33	8151	7583	-568

[a] The estimate of GDD_{50} for this population was not used to generate Figure 3.2 because the corresponding value of L_{50} could not be estimated.

Table 3.3. Abbreviations, acronyms, and symbols used in this paper.

Abbreviation or symbol	Description
F	annual instantaneous fishing mortality rate
F_{ext}	maximum sustainable F
fec_t	fecundity (number of female eggs) at time t
fec_Σ	lifetime fecundity (number of female eggs)
g	proportion of annual surplus energy allocated to reproduction
$g[M_{1+}]$	g is optimally adapted to M_{1+} only
$g[Z]$	g is optimally adapted to any mortality rate (Z)
GDD_{50}	GDD_c at which 50% of females are mature
GDD_a	annual growing degree-day ($^\text{o}$C/d)
GDD_c	cumulative GDD_a ($^\text{o}$C/d)
k	annual rate of deceleration of growth
l_t	probability of female offspring surviving to age-t
M_o	annual instantaneous natural mortality rate during the first year of life
M_{1+}	annual instantaneous natural mortality rate after the first year of life
N_t	number of female offspring that survive to age-t
R_o	net reproductive rate
t	time in years
t_{50}	age in years at which 50% of females spawn
$t_{50} - 1$	age in years at which 50% of females begin to allocate energy to reproduction
t_{max}	maximum age in years
t_o	age in years when L = 0
L	total length (mm)
L_∞	asymptotic L (mm)
L_{50}	L at which 50% of females spawn
L_e	L at which 50% of females begin to allocate energy to reproduction
L_t	L at time t
w_e	the wet mass (g) of an average egg
W_t	mass at time t (g)
Z	annual instantaneous total mortality rate ($M_{1+} + F$)
Z_{ext}	maximum sustainable Z

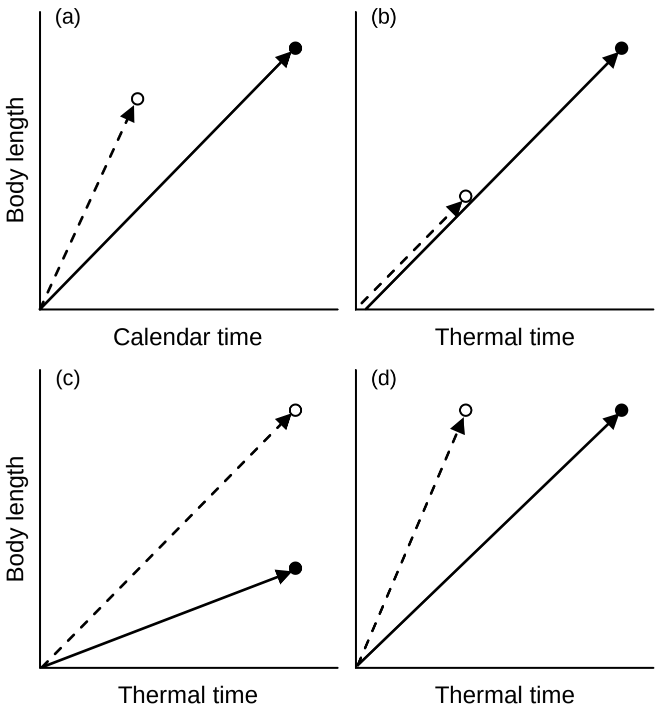

Figure 3.1. Hypothetical relations between body length and time showing growth trajectories (arrows) and points of maturity (circles) during period 1 (solid arrows, filled circles) and period 2 (dashed arrows, closed circle. According to calendar time (a) growth trajectories and points of maturity are different, regardless of whether periods differ in temperature, per capita food availability, or both. Using thermal time (b), growth and maturity fall along the same trajectory if periods differ only in temperature. If periods differ in both temperature and per capita food availability, then growth and maturity follow different trajectories that describe changes in either (c) length-at-maturity (if thermal time-at-maturity is fixed) or (d) thermal time-at-maturity (if length-at-maturity is fixed).

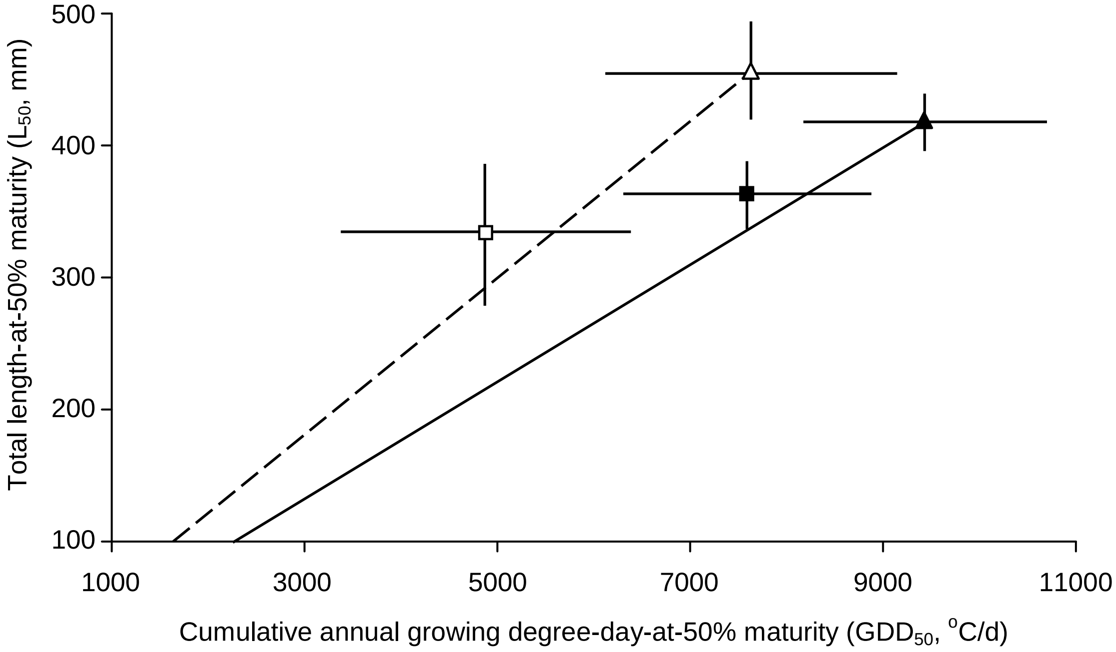

Figure 3.2. The mean total length (L_{50}) and cumulative annual growing degree days (GDD_{50}) at 50% maturity for male (squares, *n* = 4) and female (triangles, *n* = 6) walleye at high (closed symbols) and low (open symbols) population densities. Error bars are 95 %CI. Solid and dashed lines show the growth trajectories of immature females at high and low population densities, respectively, as implied by L_{50} and GDD_{50}.

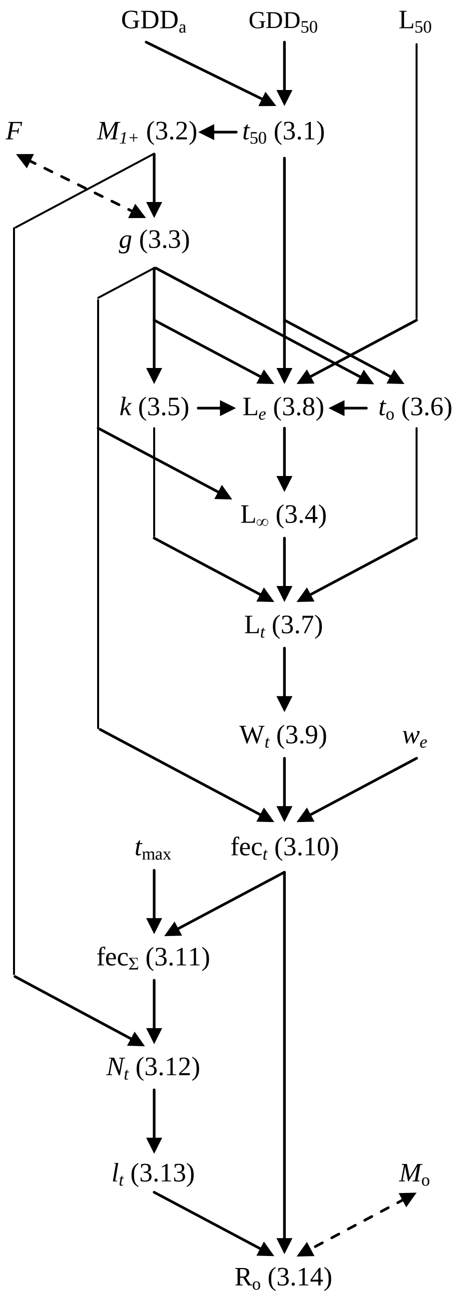

Figure 3.3. Flow diagram for converting $\mathrm{GDD_a}$, $\mathrm{GDD_{50}}$, and $\mathrm{L_{50}}$ into an estimate F_{ext} (the F at which $\mathrm{R_o} = 1$). Using $\mathrm{GDD_{50}}$ and $\mathrm{L_{50}}$ at high population density and a given value of $\mathrm{GDD_a}$, we first adjusted M_o until $\mathrm{R_o} = 1$ at $F = 0$. We then held M_o constant and re-estimated $\mathrm{R_o}$ based on $\mathrm{GDD_{50}}$ and $\mathrm{L_{50}}$ at low population density. If $\mathrm{R_o} \neq 1$ as a result of this change, we adjusted F until $\mathrm{R_o} = 1$. We considered two response scenarios for $\mathrm{L_{50}}$ and $\mathrm{GDD_{50}}$ (mean and maximum) and two strategies of reproductive investment ($g[M_{1+}]$ and $g[Z]$). See text for details. Numbers in parenthesis refer to equations. Symbols are defined in Table 3.3.

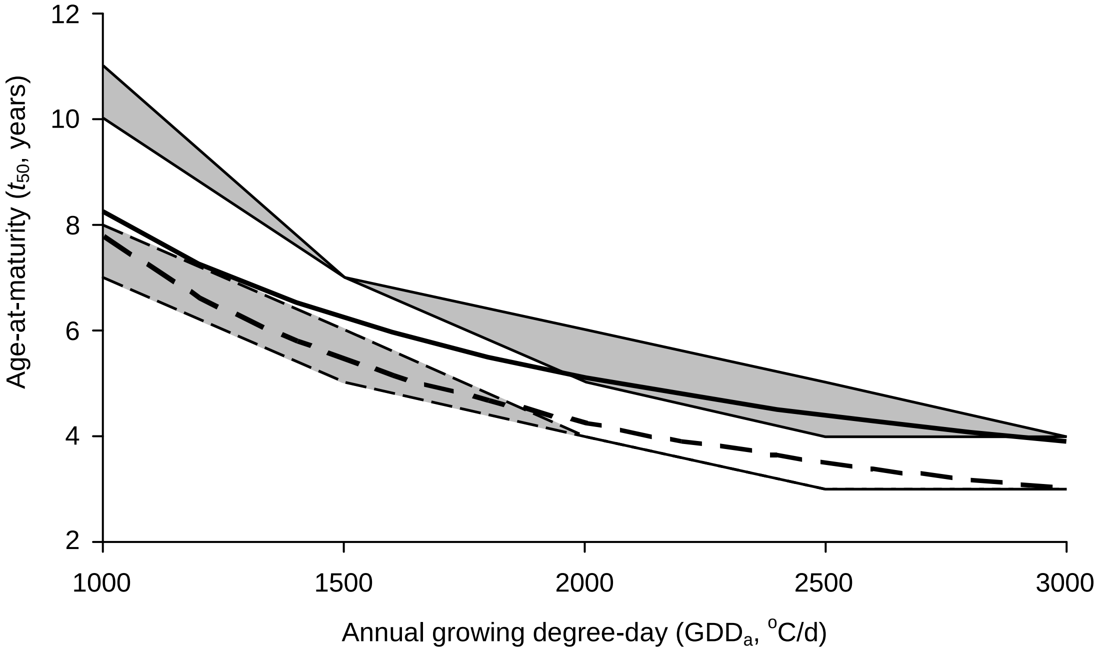

Figure 3.4. Predicted relations between female t_{50} and GDD$_a$ when *F* was absent (thin, solid lines) or present (thin, dashed lines). Shaded areas within a pair of lines define the range of t_{50} values that are predicted by the mean and maximum response scenarios; these lines converge when both response scenarios predict the same t_{50}. Predicted relations can be approximated by the following curves: *F* absent: $t_{50} = 4672.3 \cdot \mathrm{GDD}_a^{-0.886}$, *F* present: $t_{50} = 3867.6 \cdot \mathrm{GDD}_a^{-0.903}$. Thick lines are empirical relations based on data from 11 (Colby et al. 1994; solid line) and 23 (Baccante and Colby 1996; dashed line) populations. See Gangl and Pereira (2003) and Sullivan (2003) for additional data.

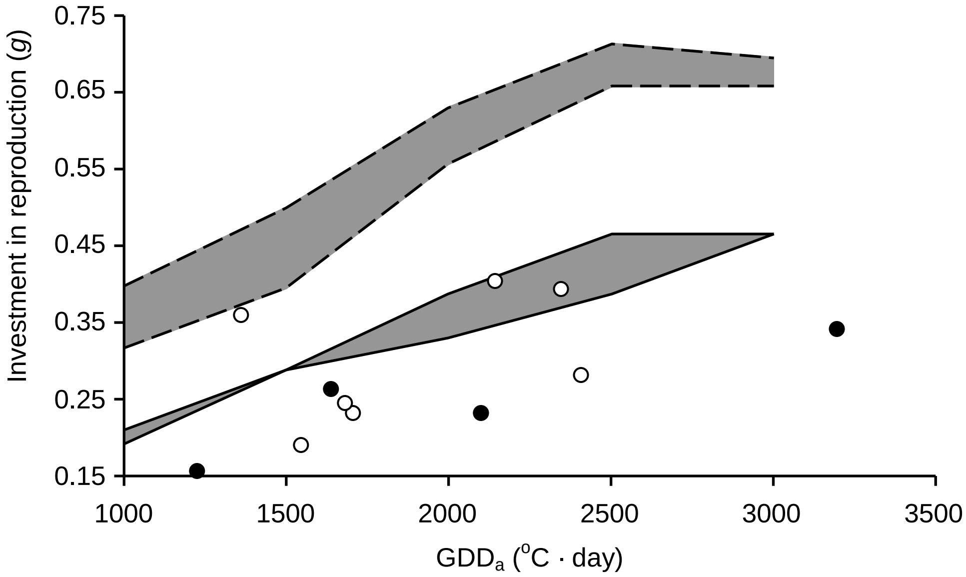

Figure 3.5. Predicted relations between g and GDD_a with g optimized to M_{1+} (thin, solid lines) or Z (thin, dashed lines). Shaded areas within a pair of lines define the range of g values that are predicted by the mean and maximum response scenarios; these lines converge as an artifact of rounding such t_{50} in the absence of F (i.e., M_{1+}; see equation 3.2) is the same for both response scenarios. Predicted relations can be approximated by the following curves: $g[M_{1+}]$: $g = 1.01 \cdot 10^{-3} \cdot GDD_a^{0.769}$, $g[Z]$: $g = 4.15 \cdot 10^{-3} \cdot GDD_a^{0.645}$. Open and closed circles are mean observed gonadosomatic index values from heavily and lightly exploited populations, respectively (Colby et al. 1979, Henderson et al. 1996, Moles et al. 2008), after dividing by 0.71 to correct for the higher energy density of gonads relative to soma. Accounting further for additional behavioral and metabolic costs associated with reproduction would shift these points upwards.

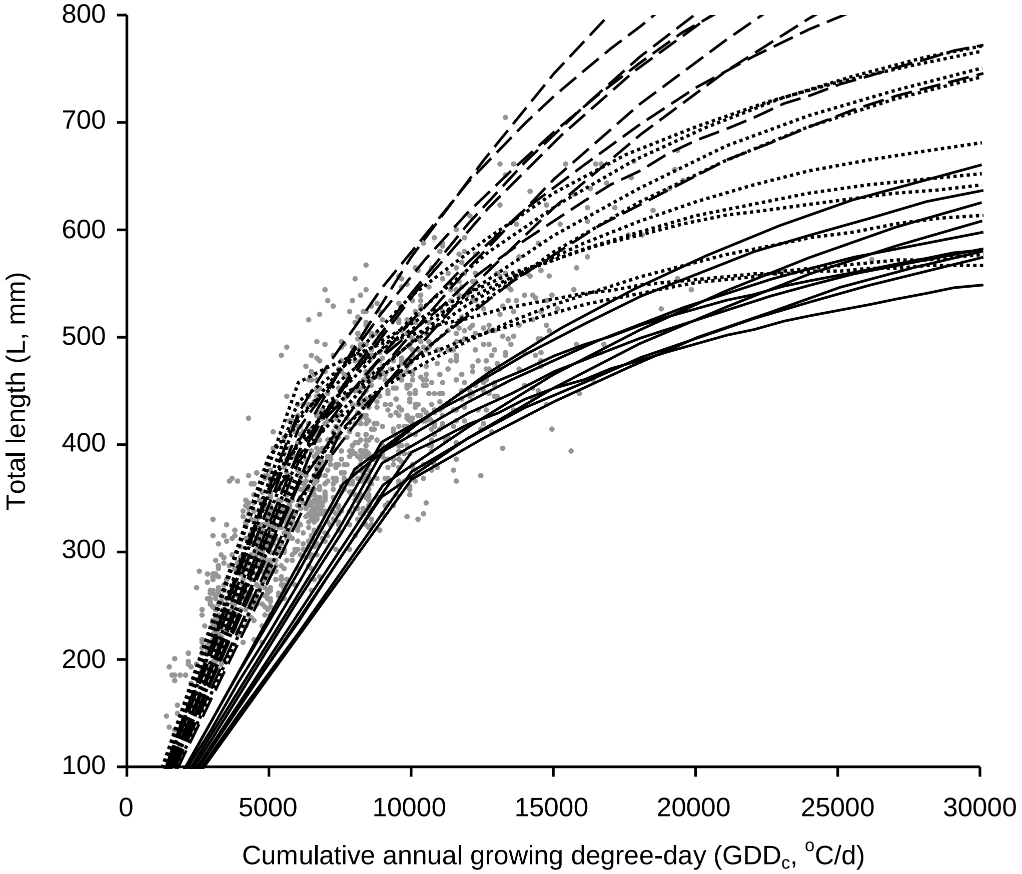

Figure 3.6. Predicted relations between L and GDD$_c$ with *F* absent (solid line), *F* present and *g* optimized to M_{1+} (dashed line), and *F* present and *g* optimized to *Z* (dotted line). Dots are empirical data for female walleye from 342 populations in Ontario and Quebec (Chapter 2).

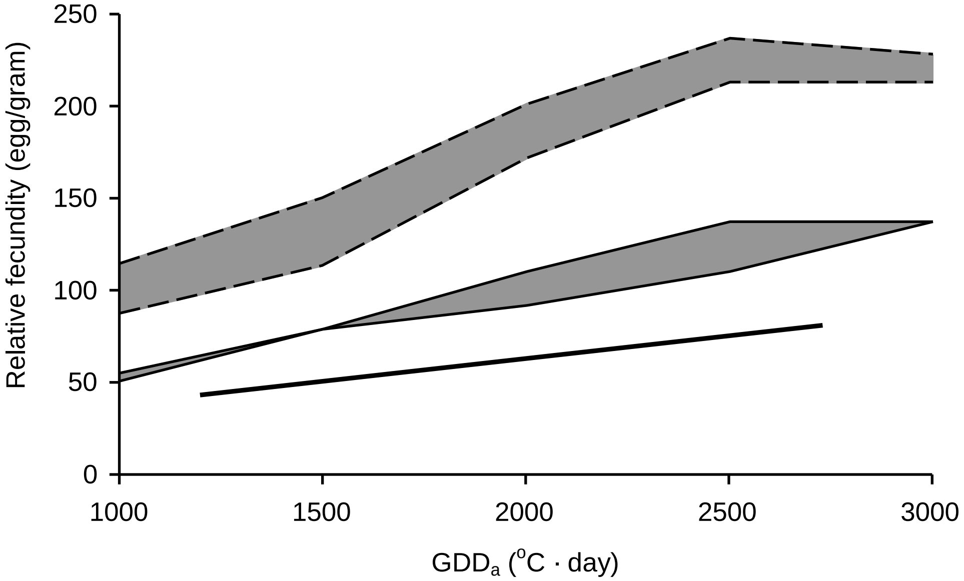

Figure 3.7. Predicted relations between relative fecundity and $\mathrm{GDD_a}$ with g optimized to M_{1+} (thin, solid lines) or Z (thin, dashed lines). Shaded areas within a pair of lines define the range of relative fecundity values that are predicted by the mean and maximum response scenarios; these lines converge as an artifact of rounding such t_{50} in the absence of F (i.e., M_{1+}; see equation 3.2) is the same for both response scenarios. Predicted relations can be approximated by the following curves: $g[M_{1+}]$: relative fecundity = 0.042 · $\mathrm{GDD_a}$ + 14.383, $g[Z]$: relative fecundity = 0.066 · $\mathrm{GDD_a}$ + 41.069. Because our model predicted the production of female eggs (equation 3.10), the values presented here were multiplied by 2 assuming a 1:1 sex ratio. The thick line is an empirical relation based on data from 43 populations (Baccante and Colby 1996).

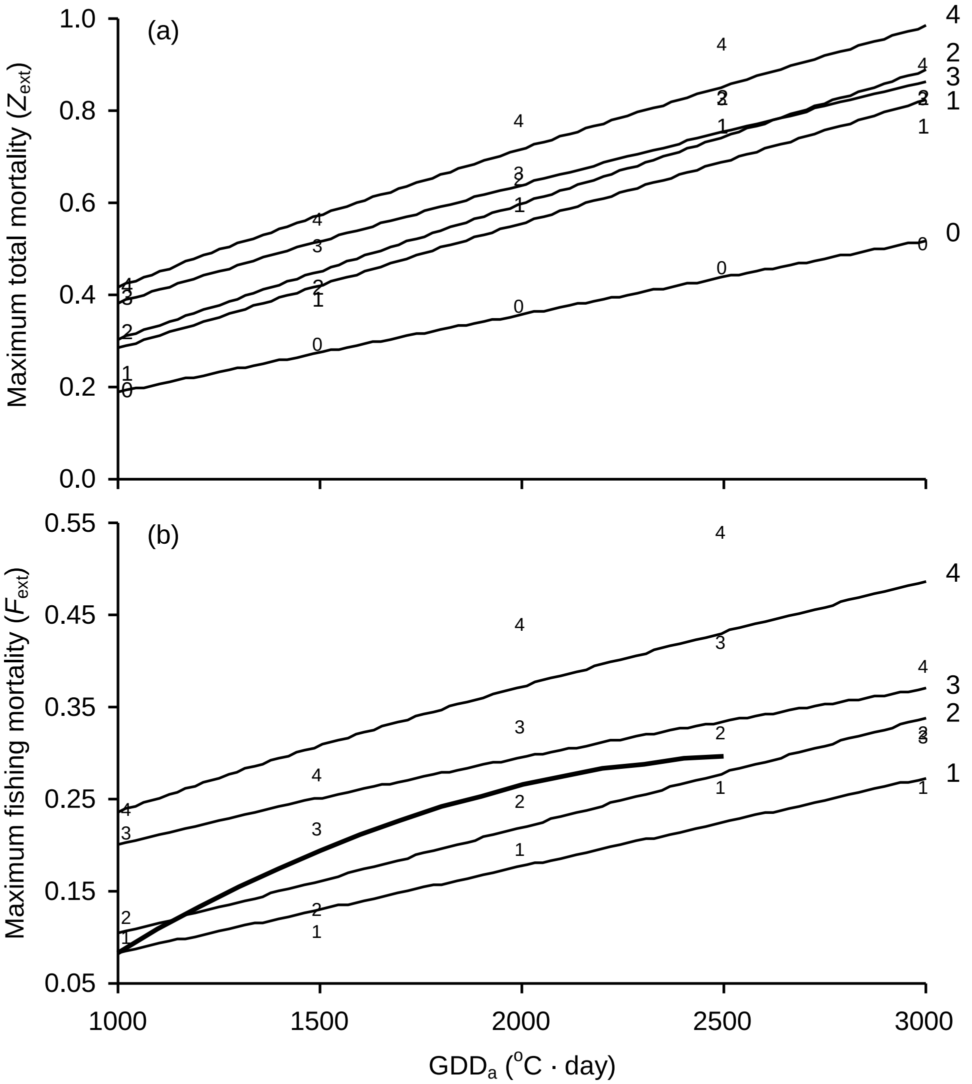

Figure 3.8. Predicted relations between (a) Z_{ext} and (b) F_{ext} and GDD$_a$. Numbers and numbered lines correspond to model results both in the absence of F ($0 = M_{1+}$; panel a only), and for different combinations of life history change and strategies of reproductive investment when F was present: 1 = mean change and $g[M_{1+}]$, 2 = mean change and $g[Z]$, 3 = maximum change and $g[M_{1+}]$, and 4 = maximum change and $g[Z]$. The thick line in panel b is the F_{ext}-GDD$_a$ relation proposed by Baccante and Colby (1996). The upper and lower bounds of Z_{ext} and F_{ext} are given by Z_{ext} upper = $1.87 \cdot 10^{-3} \cdot \text{GDD}_a^{0.783}$, Z_{ext} lower = $3.40 \cdot 10^{-4} \cdot \text{GDD}_a^{0.974}$, and F_{ext} upper = $2.24 \cdot 10^{-3} \cdot \text{GDD}_a^{0.672}$, F_{ext} lower = $6.76 \cdot 10^{-5} \cdot \text{GDD}_a^{1.037}$.

Chapter 4
Evidence for harvest-induced maternal influences on the reproductive rates of fish populations

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4.1 Abstract

Knowledge of the relation between the number of offspring produced (recruitment) and adult abundance is fundamental to forecasting the dynamics of an exploited population. Although small-scale experiments have documented the importance of maternal quality to offspring survival in plants and animals, the effects of this association on the recruitment dynamics of exploited populations are largely unknown. Here, we present results from both a simple population model and a meta-analysis of time series data from 25 species of exploited marine fish that suggest that a population of older, larger individuals has a higher maximum reproductive rate than an equivalent biomass of younger, smaller individuals, and that this difference increases with the reproductive life span of the population. These findings (i) establish an empirical link between population age structure and reproductive rate that is consistent with strong effects of maternal quality on population dynamics, and (ii) provide evidence that extended age structure is important to the sustainability of many exploited fish stocks.

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[4] Venturelli, P.A., Shuter, B.J., and Murphy, C.A. 2009. Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. Proc. R. Soc. Lond. B 276: 919–924. Both the co-authors and the Royal Society grant permission to include this chapter and its appendix in the thesis, and authorize the use of the thesis by the National Library.

4.2 Introduction

The importance of parental quality (both genotypic and phenotypic) to offspring survival has been documented extensively in plants and animals (Bernardo 1996, Rossiter 1996. Mousseau and Fox 1998), and these parental influences on survival are believed to contribute to the dynamics of natural populations (Ginzburg 1998, Fowler 2005). Such an effect of parental quality on population dynamics has been demonstrated convincingly in soil mites (Benton et al. 2005), but empirical evidence from other taxa is both limited and inconsistent (e.g., Erelli and Elkinton 2000, Banks and Powell 2004).

Experiments with fish suggest that offspring survival varies positively with the age, size, and condition of parents, as well as the size and content of gametes (Heath and Blouw 1998, Berkeley et al. 2004, Rideout et al. 2004, Kamler 2005 and references therein), and recent evidence suggests that these relations are relatively consistent across years (Seamons et al. 2007). When parental influences are incorporated into population models, total offspring production (i.e., recruitment) is sensitive to fisheries-induced demographic changes that alter the distribution of ages or sizes within a population (e.g., Forbes and Peterman 1994, Murawski et al. 2001, but see O’Farrell and Botsford 2006). These results are at odds with both prevailing fisheries theory—which assumes that parental quality plays a negligible role in shaping population dynamics—and current management strategies—which largely either ignore population age structure, or promote the harvest of larger individuals (e.g., Myers and Mertz 1998).

The extrapolation of results from experiments to entire populations can be problematic because parental influences might be expressed differently in the wild than in captivity (Bernardo 1996, Chambers and Leggett 1996), or might affect the relative fitness of individual adults (Einum and Fleming 2000) without affecting the reproductive rate of a population (Charlesworth 1980). While the dynamics of exploited fish stocks can behave in ways that are consistent with effects of parental influences on offspring survival (Marteinsdottir and Thorarinsson 1998, Marshall and Frank 1999, Marshall et al. 1999, Hsieh et al. 2006, 2008), direct evidence of this phenomenon is limited to one study of a population of Atlantic cod (*Gadus morhua*) in which recruitment varied positively with the proportion of eggs spawned by older fish (Vallin and Nissling 2000). Indeed, a recent comparison of 29 exploited and unexploited populations of coastal Californian fish yielded little support for the hypothesis that parental influences drive boom-and-bust cycles at low abundance (Anderson et al. 2008).

In this study, we use both a population model and a meta-analysis of data from 25 species of exploited marine fish to show that maternal quality can have strong effects on a population's maximum reproductive rate. We refer to these effects as maternal influences (MI), which acknowledges potential effects of both maternal phenotype (i.e., maternal effects) and genotype. Because maximum reproductive rate relates directly to the maximum rate of exploitation that a population can sustain (Myers et al. 1999), our findings provide insight into failures of past management strategies, and offer a practical remedy by demonstrating that fisheries that promote or protect extended age structure in a stock can be both sustainable and productive.

4.3 The logic of MI on reproductive rate

In fisheries science, stock-recruitment relations (i.e., relations that link offspring abundance to adult abundance, adult biomass, or egg production) are fundamental to determining the dynamics of exploited populations and the sustainability of fisheries (Hilborn and Walters 1992). In this section, we introduce a population model that illustrates how MI on survival can affect the slope at the origin of a stock-recruitment relation (α_o). The symbols and abbreviations used here and throughout the text are summarized in Table 4.1. A complete description of this model is provided in Appendix C.

Consider an age-structured population in which (i) maturity and survival are fixed for ages 1 through L, where L is maximum age; (ii) individuals reproduce once annually from the start of their T^{th} year of life until they die at the end of their L^{th} year, where T is the age-at-maturity; (iii) all age groups exhibit a 1:1 sex ratio; and (iv) demographic effects of density are limited to a linear, positive relation between larval mortality and density that results in a Beverton-Holt (i.e., concave down, positive asymptotic) recruitment relation (Hilborn and Walters 1992) between larval abundance in year t and the abundance of age-1 fish in year t+1 (note that if the recruitment instead followed a Ricker relation, calculations would be more complicated but the result would be the same). As population abundance declines, larval mortality becomes increasingly density-independent, and the slope (α) of the stock-recruitment relation approaches a maximum value (α_o). Finally, assume that egg production per female increases with maternal age (A) according to the equation $f \cdot A^b$ (e.g., Quince et al. 2008a, b), and the density-independent component of egg viability (i.e., MI) increases with A according to the equation $v \cdot A^d$ (e.g., Heath and Blouw 1998), where f and v are >0, and the exponents b and d are ≥0. Because $v \cdot A^d$ often arises from an increase in egg size with A (Heath and Blouw

1998), either (or both) of these expressions is consistent with theoretical and empirical evidence that the ratio of gonadal mass to somatic mass (i.e., reproductive investment) often increases with maternal age (e.g., Quince et al. 2008a, b).

Given these assumptions, it follows that, when population abundance is low,

$$\mathrm{N}_{1,t+1} \approx f \cdot \bar{A}^{d} \cdot v \cdot \bar{A}^{b} \cdot \mathrm{N}^{\mathrm{F}}_{\mathrm{T:L},t} = f \cdot \bar{A}^{d} \cdot v \cdot \bar{A}^{b} \cdot \tfrac{1}{2} \cdot \mathrm{N}_{\mathrm{T:L},t} \qquad 4.1$$

where $\mathrm{N}_{1,t+1}$ is the number of age-1 individuals at the start of year t+1, $\mathrm{N}^{\mathrm{F}}_{\mathrm{T:L},t}$ is the number of spawning females (i.e., females aged T to L) at the start of year t, $\mathrm{N}_{\mathrm{T:L},t}$ is the number of spawning adults at the start of year t, and $\bar{A}$ is the mean age of spawners, sexes combined (see Appendix C). According to this equation, α_o will only depend on $\bar{A}$ if egg production or viability increase with A (i.e., b or d > 0). For example, if exponents b and $d = 0$ (i.e., both egg production and viability are independent of A) then α_o is independent of $\bar{A}$, regardless of whether the spawning population is measured as abundance ($\alpha_o \approx \mathrm{N}_{1,t+1} / \mathrm{N}_{\mathrm{T:L},t} \approx \tfrac{1}{2} \cdot f \cdot v$) or total egg production [$\alpha_o \approx \mathrm{N}_{1,t+1} /(f \cdot \tfrac{1}{2} \cdot \mathrm{N}_{\mathrm{T:L},t}) \approx v$]. If $b > 0$ and $d = 0$ (i.e., egg production increases with A while egg viability remains constant), then α_o is independent of $\bar{A}$ only if the spawning population is measured as total egg production [$\alpha_o \approx \mathrm{N}_{1,t+1} /(f \cdot \bar{A}^{b} \cdot \tfrac{1}{2} \cdot \mathrm{N}_{\mathrm{T:L},t}) \approx v$]. However, if relative fecundity (the number of eggs per unit female body mass, f') does not vary with A or size, then spawning stock biomass (SSB) can also be used to express α_o so that it is independent of $\bar{A}$ [$\alpha_o \approx \mathrm{N}_{1,t+1} /(m[\bar{A}] \cdot \mathrm{N}_{\mathrm{T:L},t}) \approx \tfrac{1}{2} \cdot f' \cdot v$], where $m[\bar{A}]$ is the body mass of an age-$\bar{A}$ spawner. See section 4.4.3 for further discussion of the age- or size-dependence of relative fecundity). Finally, if both b and d >0 (i.e., both egg production and viability increase with A), then α_o depends on $\bar{A}$, even when the spawning population is measured as total egg production [$\alpha_o \approx \mathrm{N}_{1,t+1} /(f \cdot \bar{A}^{b} \cdot \tfrac{1}{2} \cdot \mathrm{N}_{\mathrm{T:L},t}) \approx v \cdot \bar{A}^{d}$].

Another property of this model is that $\bar{A}$ varies directly with both adult survival rate and reproductive life span (RLS = L–T+1) such that the absolute reduction in $\bar{A}$ that results from a fixed reduction in adult survival rate (e.g., as a result of exploitation) is effectively 0 if RLS = 1, but increases rapidly as RLS increases from 1 (see Appendix C and Figure C.1). Therefore, in an exploited, age-structured population in which f' and (or) egg viability increase with A, we expect α_o for a stock-recruitment relation based on SSB to exhibit the following dynamics: (i) α_o during periods of high adult survival is greater than α_o during periods of low adult survival because the former is associated with higher values of $\overline{A}$, and (ii) this difference in values of α_o increases with RLS because the reduction in $\overline{A}$ for a given reduction in survival rate increases with RLS (Figure 4.1).

4.4 Evidence for MI on reproductive rate

4.4.1 Meta-analysis of marine fisheries data

Although our model predicts MI on maximum reproductive rate that increase with reproductive life span (RLS; Figure 4.1), population dynamics in the wild are shaped by a suite of interacting physical and biological factors (Hilborn and Walters 1992, Trippel 1995, Mueter et al. 2007) that could overwhelm MI and limit their relevance to management.

To test for this mechanism in wild populations, we conducted a within-population meta-analysis of published marine stock-recruitment data. We restricted this meta-analysis to populations in which fishing mortality was likely to have contributed to large and consistent changes in SSB by applying the following selection criteria: (i) minimum SSB ≤40% of maximum SSB over the duration of the time series; (ii) SSB exhibiting distinct periods of both growth and decline that each span ≥10 y; (iii) periods of both growth and decline spanning a similar range of SSB; and (iv) fishing mortality (or exploitation rate) significantly higher during the period of SSB decline than during the period of SSB growth (Tables C.1 and C.2). Because fishing mortality in these time series was typically estimated by analyzing the abundance of individual cohorts that were followed over time, high and low fishing mortalities sustained for periods of 10 y or longer were reliable indicators of adult survival and, by extension, the mean age of spawners. Criterion (ii) also ensured a reasonable sample size with which to estimate the stock-recruitment relation for each period, and criterion (iii) controlled for possible confounding effects of density by ensuring that differences in population dynamics did not simply reflect differences in the intensity of density-dependent processes (e.g., life history changes, Allee effects). To avoid confounding effects of viviparity, parental care, and associated characteristics of life-history, we limited our analysis to broadcast spawners that did not change sex with age.

For each population (or region if population-specific data were unavailable), we estimated RLS from published data by subtracting age-at-maturity from maximum age and then adding 1 (Tables C.1 and C.2). For the periods of both growth and decline in a population, we then calculated the slope at the origin of the stock recruitment relation (α_o) by linear analysis of covariance of log recruitment on log SSB with period as a categorical variable. Samples sizes were generally too small (10-39 per period) to assess the normality of residuals via statistic tests, but visual inspection of the distribution of residuals indicated no serious departures from normality. We detected one influential observation in 7 of 39 populations, but the removal of these observations had a negligible effect on the overall result (i.e., Figure 4.2). Following diagnostics, we used the ratio of α_o during the period of population growth to α_o during the period of population decline (α_o^g / α_o^d) as a measure of the difference in maximum reproductive rate between periods. Values of α_o^g / α_o^d were then regressed on values of RLS at both the species and family level (Table C.2).

4.4.2 Meta-analysis results and discussion

We identified 39 marine populations (25 species) in which SSB showed distinct periods of growth and decline that were associated with periods of low and high fishing mortality (i.e., extended and truncated age structure), respectively. All of these populations were located in the north temperate and arctic climatic zones. Consistent with our population model, our meta-analysis of these data suggested that the ratio of α_o during growth to α_o during decline (α_o^g / α_o^d) varied positively and significantly with RLS across both species (Figure 4.2a) and families (Figure 4.2b). Low-RLS species were dominated by salmonids, but two species from two different families (Clupeidae and Engralidae) showed a similar α_o^g / α_o^d response to RLS. Overall, this result suggests that MI on reproductive rate is a general phenomenon among populations of long-lived, marine fishes; independent of SSB, populations that have an extended age structure have higher reproductive rates—and therefore support a higher rate of exploitation—when that structure is preserved.

This result is also consistent with evidence that recruitment can vary with indices of maternal energy reserves (Marshall and Frank 1999, Marshall et al. 1999) or positive effects of maternal age on egg size (Vallin and Nissling 2000) and the timing and duration of spawning (reviewed by Wright and Trippel 2009). Conversely, the absence of this phenomenon among salmonids (data points K-O and 7 in Figure 4.2) is inconsistent with the overwhelming evidence for MI on survival in this taxon (reviewed in Seamons et al. 2007). We propose two mechanisms to explain this discrepancy. First, because the age and size ranges of adults in these populations are relatively narrow, it is unlikely that fisheries differentially selected for reproductively valuable adults (although selection can be strong if these adults are spatially or temporally distributed). Second, our population model predicts relatively small differences in α_o at low values of RLS, even when exploitation is age- or size-selective (see above).

4.4.3 Alternative explanations

A comprehensive evaluation of the importance of MI on survival, relative to other factors that affect the dynamics of individual populations, requires thorough, population-specific analyses that are beyond the scope of this paper. However, we can assess whether alternative explanations are plausible.

First, exploitation often triggers density-dependent life history responses (e.g., early maturation, more eggs per mass of female) that can accelerate population growth rate (Rochet 1998). Results of our meta-analysis are largely independent of these and other density-dependent processes (e.g., cannibalism, Allee effects) because we explicitly controlled for effects of density by ensuring that, for each population, periods of growth and decline spanned a similar range of population densities (i.e., SSB values).

Second, a history of intense exploitation in most of the populations that we included in our analysis might have affected our estimates of both α_o^g / α_o^d and RLS. For example, we probably underestimated RLS in populations where exploitation limited longevity. In addition, lower-than-expected α_o^g / α_o^d values for some intensely-exploited species (e.g., Atlantic cod) might reflect either a shift in age structure from truncated to extremely truncated, or slow rates of population growth as a result of fisheries-induced evolutionary changes in life history (Law 2007 and references therein). Given that these ‘ghosts of exploitation past’ tend to underestimate α_o^g / α_o^d, it seems unlikely to us that they generated a spurious relation with RLS.

Third, long-term climatic conditions (regimes) can dominate the recruitment dynamics of many marine fish stocks by causing persistent and geographically pervasive changes in the carrying capacity of a marine environment (Mueter et al. 2007). However, for climate regimes to explain the positive relation between α_o^g / α_o^d and RLS, they must have coincided closely with periods of relatively high and low fishing mortality, and affected long-lived species more strongly than short-lived ones. We argue that such coincidences are highly unlikely, and instead suggest that the extent to which climate regimes influence population dynamics in ways that are consistent with MI on reproductive rate is more likely to depend on the extent of fisheries-induced age or size truncation. Specifically, if individuals that could contribute the most to recruitment are absent from a population, then that population will be less likely to produce strong year classes when environmental conditions are favourable, and more likely to experience recruitment failure when environmental conditions are poor. Whereas climate regimes determine maximum reproductive rate (α_o), MI determine, via a fisheries-induced demographic shift, the extent to which this maximum is realized.

Finally, our model predicts that if egg production increases disproportionately with female age or length, such that older females produce more eggs per unit body mass (i.e., have a higher relative fecundity; *f'*) than younger females, then egg production alone might explain the positive relation between α_o^g / α_o^d and RLS (note that differences in *f'* among ages are not to be confused with a density-dependent change in *f'* across all ages, which was largely controlled for in our study; see above). An increase in *f'* with age is consistent with both a tradeoff between egg size and number (Roff 1992)—provided that this tradeoff affects older females more than it does younger females—and an increase in reproductive investment with age (Quince et al. 2008a, b). To estimate the extent to which maternal age or length affects *f'* in exploited, north temperate and arctic marine fish populations, we conducted a meta-analysis of published results and data (Table C.3). Of the 25 species examined, 15 (60%) showed a significant (P >0.05) increase in *f'* with age or length in at least one year or population (Table C.3); 9 of 16 (56%) among long-lived species (RLS ≥10 according to Figure 4.2). Across all populations, species, families, and orders, these significant relations explained, on average, 31% ±11 95% CI of the variation in *f'* and predicted a doubling of *f'* (2.2 ±1.1) between observed extremes of age or size (Table C.3). Including the non-significant regressions, maternal age or length explained 17% ±7 of the variation in *f'* and predicted a 1.7 ±0.4 fold increase in *f'* (Table C.3). Therefore, population-specific analyses should consider the importance of age- or length-specific *f'* to recruitment, and use total egg production, rather than SSB, to develop stock-recruitment relations (Rothschild & Fogarty 1989). However, given that (i) predicted increases in *f'* were based on the unlikely assumption that populations were composed of extremes of age or length; and (ii) relations between *f'* and age or length can be absent in many years, populations, and species (Table C.3), these MI on egg production, while potentially influential, are insufficient to explain the observed relation between α_o^g / α_o^d and RLS.

4.5 Management implications

Given that MI on survival (and relative fecundity) can affect the maximum reproductive rates of long-lived, marine fishes, management strategies must recognize that stock-recruitment relations can vary in the absence of meta-population structure and environmental variability (Hilborn and Walters 1992); nonstationarity can also result from fisheries-induced demographic changes in long-lived species. In effect, the shape of any stock-recruitment relation is user-defined; it depends upon the age- or size-classes that a fishery targets, as well as those that it protects. Our evidence for MI on maximum reproductive rate contributes to a growing body of literature that illustrates the complexity of stock-recruitment relations (e.g., Sakuramoto 2005, Minto et al. 2008), and cautions strongly against the continued use of these relations without considering explicitly fisheries-induced demographic changes over time (Marteinsdottir and Thorarinsson 1998).

Management strategies must also recognize that older, larger females are essential to the sustainability of a fishery. Age structure exists, in part, because the strategy of maturing late and spawning over multiple years (i.e., having a relatively long RLS) confers—on older, larger females—an advantage when competing in variable environments for resources that support successful reproduction (Winemiller and Rose 1992, Hsieh et al. 2006); MI on offspring survival stem directly from this advantage. Existing management strategies typically operate to reduce age structure, which undermines the advantages of an extended RLS (Hsieh et al. 2006). In short, forcing an iteroparous species to spawn as if it was semelparous is unsustainable.

We acknowledge that there are conditions (e.g., reproductive senescence) and species (e.g., sex-changing fish) for which parental age does not equate to parental quality, and that further research is needed to determine whether MI on survival is a density-dependent phenomenon that disappears at extremely low densities. However, our study shows that, over a broad range of densities and species of exploited fishes, maximum reproductive rate tends to increase with the mean age or size of spawning adults, a result that stems, in part, from the tendency of older, larger females to produce offspring that are more likely to survive. This result argues strongly for management strategies that not only regulate total mortality, but do so in ways that restore and protect age or size structure—for example, by adopting appropriate size regulations, changing the design and use of fishing gear, or implementing spatially-explicit conservation measures (e.g., marine protected areas). These and other structure-based management strategies are necessary in the face of strong evidence that fisheries-induced demographic changes to age and size structure affect the reproductive rate (this study), stability (Anderson et al. 2008), and evolutionary trajectory (Law 2007 and references therein) of exploited fish stocks. These strategies also provide practical and effective ways of ensuring the sustainability of a fishery in the face of uncontrollable environmental variability (Trippel et al. 1997, Berkeley et al. 2004, Law 2007, Secor 2007, Hsieh et al. 2008).

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Table 4.1. Abbreviations and symbols.

abbreviation or symbol	description
A	maternal age in years.
$\bar{A}$	the mean age of spawners in years (an index of age structure).
b	the exponent of maternal age-specific fecundity.
d	the exponent of maternal age-specific egg viability.
f	fecundity (the number of eggs).
f'	relative fecundity (the number of eggs per unit mass of female).
RLS	reproductive lifespan in years (= L–T+1).
L	maximum age in years.
MI	maternal influences; the effects of maternal quality (both phenotypic and genetic) on offspring survival.
$m[\bar{A}]$	the body mass of a spawner of average age.
N	abundance in numbers (subscripts specify age(s) and time).
SSB	spawning stock biomass (the total mass of all spawning adults).
t	time in years.
T	age-at-maturity in years.
v	egg viability
α	the slope at any point along the stock-recruitment relation (= age-1 abundance at time t+1 divided by a measure of spawning population size such as abundance, SSB, or egg production at time t).
α_o	the slope at the origin of the stock-recruitment relation (an estimate of the maximum reproductive rate that occurs when spawning population size is very small).
α_o^g / α_o^d	the ratio of α_o during the period of population growth to α_o during the period of population decline (an estimate of the difference in reproductive rate between periods of growth and decline).

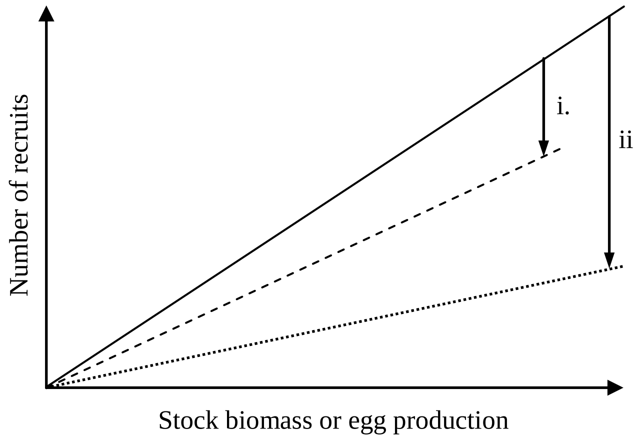

Figure 4.1. Hypothetical stock-recruitment relations showing how MI on survival can affect the slope at the origin (α_o), and how this affect increases with reproductive life span (RLS). When MI are absent, α_o is independent of the mean age of spawners ($\bar{A}$) and describes a single (solid) line. When MI are present, α_o decreases with a decrease in $\bar{A}$. Because the decrease in $\bar{A}$ for a fixed reduction in adult survival rate depends directly on RLS (Figure C.1), the decrease in α_o for a species that has a short RLS will be small (i; dashed line) relative to the decrease in α_o for a species that has a long RLS (ii; dotted line). See text and Appendix C for details.

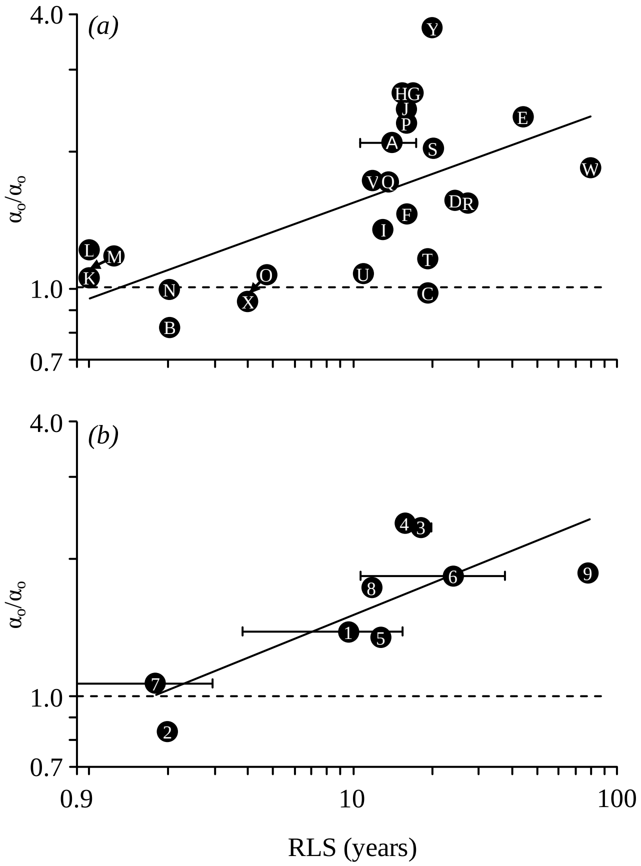

Figure 4.2. Results of a meta-analysis showing the ratio of α_o during growth to α_o during decline (α_o^g / α_o^d) versus reproductive life span (RLS) for (*a*) species ($\alpha_o^g / \alpha_o^d = 0.950 \cdot \mathrm{RLS}^{0.209}$, r^2 = 0.38, n = 25, P = 0.001), and (*b*) families ($\alpha_o^g / \alpha_o^d = 0.878 \cdot \mathrm{RLS}^{0.232}$, r^2 = 0.61, n = 9, P = 0.006). Solid lines were fit by regression analysis. Dashed lines indicate no difference between α_o's (i.e., $\alpha_o^g / \alpha_o^d = 1$). Horizontal error bars are 95 %CI; vertical error bars were not calculated because of the statistical properties of ratios (Atchley et al. 1976). Note that both axes are logarithmic. Letters and numbers refer to species and families, respectively: A = *Clupea harengus* (Atlantic herring), B = *Engraulis encrasicolus* (European anchovy), C = *Gadus macrocephalus* (Pacific cod), D = *Gadus morhua* (Atlantic cod), E = *Hippoglossus stenolepis* (Pacific halibut), F = *Limanda aspera* (yellowfin sole), G = *Merlangius merlangus* (whiting), H = *Melanogrammus aeglefinus* (haddock), I = *Merluccius productus* (North Pacific hake), J = *Micromesistius poutassou* (blue whiting), K = *Oncorhynchus gorbuscha* (pink salmon), L = *O. keta* (chum salmon), M = *O. kisutch* (coho salmon), N = *O. nerka* (sockeye salmon), O = *O. tshawytscha* (chinook salmon), P = *Ophiodon elongates* (lingcod), Q = *Parophrys vetulus*

(English sole), R = *Pleuronectes platessa* (European plaice), S = *P. quadrituberculatus* (Alaska plaice), T = *Pollachius virens* (saithe), U = *Sardinops sagax* (South American pilchard), V = *Scomber japonicus* (chub mackerel), W = *Sebastes alutus* (Pacific Ocean perch), X = *Sprattus sprattus* (European sprat), Y = *Theragra chalcogramma* (Alaska Pollock); 1 = Clupeidae (herring-like fishes), 2 = Engraulidae (anchovies), 3 = Gadidae (cods and haddocks), 4 = Hexagrammidae (greenlings), 5 = Merlucciidae (merluccid hakes), 6 = Pleuronectidae (righteye flounders), 7 = Salmonidae (salmonids), 8 = Scombridae (mackerels), 9 = Scorpaenidae (rockfishes).

Chapter 5

Maternal influences on population dynamics: evidence from an exploited freshwater fish

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5.1 Abstract

We used a field experiment, population modeling, and an analysis of 30 years of data from walleye (*Sander vitreus*; a freshwater fish) in Lake Erie to show that maternal influences on offspring survival can affect population dynamics. We first demonstrate experimentally that the survival of juvenile walleye increases with egg size (and, to a lesser degree, female energy reserves). Because egg size in this species tends to increase with maternal age, we then model these maternal influences on offspring survival as a function of maternal age to show that adult

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[7] The co-authors grant permission to include this chapter and its appendix in the thesis, and authorize the use of the thesis by the National Library.

age structure can affect the maximum rate at which a population can produce new adults. Consistent with this hypothesis, we present empirical evidence that the maximum reproductive rate of an exploited population of walleye was approximately twice as high when older females were abundant as compared to when they were relatively scarce. Taken together, these results indicate that age- or size-based maternal influences on offspring survival can be an important mechanism driving population dynamics, and that exploited populations could benefit from management strategies that protect, rather than target, reproductively valuable individuals.

5.2 Introduction

In most populations, adult females vary in their ability to produce viable offspring. This variation stems, in part, from maternal influences (MI; the combined effect of maternal phenotype and maternal genotype) on offspring survival (see reviews by Roach and Wulff 1987, Mousseau and Dingle 1991, Bernardo 1996, Rossiter 1996, Mousseau and Fox 1998, and others). Because population growth rate depends on the production of new individuals (i.e., recruitment), population dynamics should depend on the extent to which MI affect the survival of offspring. For example, MI are hypothesized to delay or accelerate life history responses to the environment, which can stabilize or destabilize a population, or cause it to cycle (Rossiter 1996, Ginzburg 1998, Kazantseva and Alekseev 2007). Similarly, if older, larger females produce offspring that have a higher survival rate than offspring from younger, smaller females, then population dynamics should depend on population demographics such as adult age or size structure (Forbes and Peterman 1994, Murawski et al. 2001, O'Farrell and Botsford 2006, Lucero 2008, Venturelli et al. 2009). If true, then age- or size-related MI on offspring survival represent a mechanism of population dynamics that, like other demographic characteristics (e.g., density, sex ratio), can be influenced by exploitation (Solemdal 1997).

Despite theoretical support for the effects of this type of MI at the population level, empirical evidence for this phenomenon is very limited. In laboratory populations of soil mites, egg size and maternal age affected population dynamics over many generations (Benton et al. 2005, 2008). Among wild populations of mammals, birds and insects, survival-based MI on population dynamics have been inferred either from MI on the life history and long-term survival of offspring (Albon et al. 1987, Reid et al.2003), or the degree of consistency between observed time series and population models that included MI on survival (e.g., Ginzburg and Taneyhill 1994, Kendall et al. 2005). In wild fishes such as haddock (*Melanogrammus aeglefinus*; Marshall and Frank 1999) and Atlantic cod (*Gadus morhua*; Marteinsdottir and Thorarinsson 1998, Marshall et al. 1999 and others), population dynamics are consistent with MI on offspring survival, but this mechanism has only been demonstrated in one population of Atlantic cod (Cardinale and Arrhenius 2000, Vallin and Nissling 2000). Similarly, although a recent meta-analysis suggests that MI on survival can affect the maximum reproductive rate of populations of long-lived, marine species (Venturelli et al. 2009), differences in relative fecundity (i.e., MI on egg production) could also have contributed to this pattern.

This paper builds on the results of Venturelli et al. (2009) by presenting three concordant lines of evidence that MI on offspring survival can affect a population's maximum reproductive rate. Our study organism was walleye (*Sander vitreus*), a large, freshwater predator that exhibits a periodic life-history (i.e., slow-growing, late-maturing, long-lived, iteroparous, and highly fecund; Winemiller and Rose 1992), and is heavily exploited throughout North America. Maternal influences on survival in walleye are evidenced by positive effects of both maternal age or size (Johnston 1997, Johnston et al. 2007) and egg quality (e.g., egg size, lipid content; Moodie et al. 1989, Czesny and Dabrowski 1998, Johnston et al. 2005, 2007) on the survival of laboratory-reared eggs and larvae. Egg size also tends to have a positive effect on larval size (Moodie et al 1989, Johnston 1997, Johnston et al 2007), which, in turn, influences survival through negative effects on cannibalism, deformities, and starvation (Moodie et al. 1989, Johnston and Mathias 1993, 1996). Because these studies suggest that MI on survival occur later in the life of offspring than has previously been examined, we first report on a large-scale experiment that was designed to quantify MI on the survival of juvenile walleye after two months in naturalized ponds. We then develop a population model to determine whether MI of the magnitude and duration that we observed in the pond experiment can influence population dynamics. Specifically, we model different age-selective harvest strategies to demonstrate that, when juvenile survival increases with maternal age, a population of relatively old adult females will produce new individuals at a consistently higher rate than an equivalent population of young adult females. Finally, we use a 30 year time series of empirical data on the long-term dynamics of the heavily exploited Lake Erie walleye population to show that the presence of older females contributed to a 2-fold increase in the maximum reproductive rate of this population.

5.3 Methods

5.3.1 Pond experiment

We conducted an experiment in naturalized ponds to quantify effects of both maternal and paternal quality on the relative survival of communally-reared, full-sibling offspring. Over 3 nights in April 2002, adult walleye (*n* = 25 males and 25 females) were netted from the Napanee River (44^o12’02” N, 76^o59’08” W), a tributary to the Bay of Quinte, Lake Ontario (Wiegand et al. 2007). Each female was then matched to a male that was selected randomly, without replacement. This matching procedure was repeated 3 times to produce 3 experimental populations, each with 25 unique families of full-sibling offspring (Fig. D.1).

For each parental pair, eggs (40000 eggs ±6500 95%CL) and milt (1.2 ml ±0.2) were mixed as described in Johnston et al. (2005). Fertilized eggs were then pooled by experimental population and incubated in flow-through bell jar hatchery systems at a seasonal photoperiod (15 h light: 9 h dark) and water temperature (8-14°C). At 4-d post-hatch (Day 4), a sample of 300 larvae was taken from each population, euthanized by an overdose of anesthetic, measured for total body length (to the nearest 0.2 mm), and then preserved in 95% ethanol. For this sample, we used non-selective methods to provide as representative a sample as was feasible. On Day 5, a subsample of ~100,000 larvae (estimated volumetrically) from each population was stocked into a separate, fishless, culture pond (Fig. D.1). Each pond was ~0.5 ha in surface area with a maximum depth of ~2 m. To stimulate the production of invertebrate prey, ponds received biweekly treatments of organic fertilization (fermented soybean meal). On Day 66, another representative sample of 300 offspring was taken from each pond, euthanized, measured for fork length (FL; to the nearest 1 mm) and then preserved in 95% ethanol. Parentage assignment of Day 4 and Day 66 offspring was by microsatellite DNA analysis of 7 loci by means of PCR amplification and PAPA 2.0 allocation software (see Appendix D.1.1).

The relative survival rate of offspring of specific sires and dams was estimated by comparing, between the beginning and the end of the experiment, the proportional distribution of offspring among sires or dams within a population and then averaging by sire or dam across the three populations (Appendix D.1.2). For each parent, we obtained the following measures of parental quality (i) age, body length, condition, residual growth rate (percentage deviation around mean size-at-age), and the total lipid content of somatic and liver tissues; (ii) the size (dry mass), total lipid content, and fatty acid profiles of eggs from females; and (iii) the density of sperm in the milt, sperm tail length, and average sperm swimming velocity from males (Appendix D.1.3).

5.3.2 Population modelling

Venturelli et al. (2009) used an analytical model to show that MI on survival can affect the maximum reproductive rate of a population through changes in the mean age of breeding adults. To determine how MI of the magnitude that we observed in our pond experiment might interact with age structure to affect the reproductive rate of a typical population of walleye, we developed a deterministic, density-dependent, stage-within-age matrix projection model (Rose et al. 2003, Murphy 2006; Fig. D.3) in which offspring survival was assumed to increase with maternal age (see below).

Simulations began with the production of offspring by different age classes of mature females and ran until the population equilibrated. The annual contribution of each age class to egg production was calculated by assuming a 1:1 sex ratio and then multiplying the total mass of females in an age class by a constant relative fecundity (egg number per unit body mass). Offspring in their first year of life were modeled daily through 4 stages of development: separately by female age class as eggs (30 d), free swimming larvae (60 d), and early juveniles (90 d), and then as a single group of late (overwintering) juveniles (180 d). Thereafter, age-1 offspring were modeled on an annual (360 d) time-step through to maturity (age-4) and senescence (age-20; Fig. D.3). Additional parameters for length-, mass-, and fecundity-at-age (Table D.6) were assumed to be fixed (i.e., not density-dependent) so that effects of MI on population dynamics could be evaluated in isolation.

Instantaneous rates of natural mortality for each stage were either obtained or derived from the literature (Appendix D.2.1). We incorporated MI into rates of larval and early juvenile mortality by (i) assigning an egg size to each adult female age class, (ii) using these egg sizes to predict daily rates of relative offspring survival (Table 1), and then (iii) subtracting the relative offspring survival rate that was specific to each egg size from the natural mortality rate of larvae and early juveniles (Appendix D.2.2). Thus, offspring mortality during the larval and early juvenile stages declined with maternal age in accordance with the positive relation between egg size and maternal age that is typical of most populations of walleye (Fig. D.4) and other highly fecund, demersal spawning fish (Einum and Fleming 2002). We considered our model to be conservative with respect to likely effects of MI because: (i) we modeled a relation between larval survival and maternal age that reflected a conservative interpretation of the larval survival-egg size relation that was observed in the pond experiment, and (ii) we did not model MI beyond the late juvenile stage, despite evidence that winter mortality decrease with body size in juvenile walleye (e.g., Rose et al. 1999). Finally, natural mortality in the early juvenile stage was further modified via a linear relation between early juvenile mortality and abundance that produced a Ricker-type relation (Hilborn and Walters 1992) between egg production and age-1 abundance (Appendix D.2.3).

To alter the mean age of spawning adults in this population, we added harvest mortality to the natural mortality rate of specific age classes according to three harvest strategies: harvest young (harvest restricted to age classes 2, 3, and 4 in what is typically known as a harvestable or fishable slot), harvest all (all age classes harvested), and harvest old (harvest eliminated each age class in turn beginning with the oldest). We modeled these three strategies because each is an extreme—but not uncommon—form of harvest that affects mean age in a unique way. For each harvest strategy, we generated a relation between the abundance of 1 year-olds and egg production by evaluating the model at equilibrium over a series of incremental increases in fishing mortality. We then estimated the slope at the origin (α_o) of each relation by dividing age-1 abundance by egg production at the point along the relation where egg production was equal to ~0.5 % of unexploited levels. This slope represents a population's maximum reproductive rate, and is related directly to its maximum sustainable exploitation rate (Myers et al. 1999).

5.3.3 Population dynamics in Lake Erie

To evaluate empirical evidence for MI on the maximum reproductive rate of a wild population, we analyzed published data (Appendix D.3.1) on the Lake Erie walleye population from 1947-1976; a period when (i) variation in exploitation rate had produced large, documented changes in the mean age of adult females, and (ii) conditions were relatively similar in terms of invasive species and water quality. The total annual egg production and subsequent recruitment of walleye in Lake Erie from 1947-1976 were estimated using published mark-recapture data, estimates of total harvest and age-specific catch per unit effort, young-of-the-year trawl surveys, age-specific maturity schedules, length- and mass-at-age data, and a relation between relative fecundity (RF, egg number per unit body mass) and body length from 1966 (Appendix D.3.1). Because age-at-maturity, length-at-age, and mass-at-age data were specific to individual years or groups of years, estimates of egg production and recruitment for the period 1947-1976 largely accounted for density-dependent changes in life history.

We analyzed these data as follows. First, to account for environmental effects on recruitment, we incorporated two widely accepted indicators of environmental quality—spring warming rate (ΔT, $^{o}C \cdot g^{-1}$; Shuter et al. 1979) and water level (W, m; Koonce et al. 1996)—into a likelihood-based model selection framework that also included total annual egg production and the mean age of adult females as predictor variables. Because reproduction is a pre-requisite for recruitment, we only considered the 8 linear regression models in which egg production was a variable. According to a small-sample, bias-corrected form of Akaike's Information Criterion (AICc; Anderson 2008), there was strong evidence for two multiple linear regression models: log eggs, ΔT, and W (*adj.* $R^2 = 0.59$, $n = 30$, AICc rank = 1, $w_1 = 0.42$, where w_i is the probability that this model *i* is the best model given the data and the model set), and the full model (log eggs, ΔT, W, and mean age; *adj.* $R^2 = 0.63$, $n = 30$, AICc rank = 2, $w_2 = 0.24$, $\Delta_2 = 1.1$, where Δ_i is the difference in AICc values between the model 1 and model 2). All coefficients for both models were significant at $P \leq 0.03$. Using the full model, we then fixed ΔT and W at mean observed values ($0.21^{o}C \cdot g^{-1}$ ±0.02 and 174.21 m ±0.13, respectively), and predicted four relations between log recruitment and log egg production: one for each of mean age equal to (i) the minimum observed value (3.03 years), (ii) the maximum observed value (4.44 years), (iii) the mean of the 15 smallest observed values (3.29 years ±0.11), and (iv) the mean of the 15 largest observed values (4.01 years ±0.14). The first two of these mean age scenarios establish the range of stock-recruitment relations that are possible given the data, and the last two scenarios identify the mean position of these relations when mean age is below and above the median (3.66 years). Finally, we estimated the α_o of each of these relations by taking the inverse logarithm of their respective intercepts. Lake Erie walleye and environment data for the period 1947-1976 are provided in Table D.7.

5.4 Results and Discussion

5.4.1 Pond experiment

Does the early survival of walleye depend on parental quality? Adult walleye in the pond experiment spanned a range of ages (4 to 20 years) and lengths (455 to 742 mm) that were representative of the source population (T. A. Johnston, unpublished data). Among these adults, measures of gamete quality for both sexes (egg size and lipid content; sperm swimming speed and sperm concentration in the milt) varied approximately 2-fold (Table D.4 and D.5). Offspring survival rates over 62 days also varied among adults such that offspring were more evenly distributed among parents at the beginning of the experiment than at the end (see Tables D.2 and D.3).

Hierarchical partitioning (Mac Nally 2000, Mac Nally and Walsh 2004) based on maternal traits showed that the relative survival of juvenile walleye over two months was influenced most strongly by egg size (Fig. 5.1). Female condition, residual growth, and egg lipid content were also important. According to a AICc, empirical support for multiple linear regression models based on egg size, female condition, residual growth, and egg lipid content was strongest for the model that included only egg size ($w_i = 0.32$, adj. $R^2 = 0.34$); support was also strong for the model that included both egg size and maternal condition ($w_i = 0.15$, adj. $R^2 = 0.39$; Table 5.1). We found little evidence for an effect of paternal quality on offspring survival (Table 5.1; see Appendix D.1.4 and Fig. D.2 for details), and no evidence that either parental size or relative offspring survival rate increased or decreased with spawning day. Regression diagnostics for both univariate and multiple regression models followed Quinn and Keogh (2002).

These results suggest that female walleye exhibit strong MI on juvenile survival under semi-natural field conditions. This finding is consistent with laboratory experiments showing effects of walleye egg size on both hatching success (Johnston 1997) and larval survival up to 13 d post-hatch (Moodie et al. 1989, Johnston et al. 2005). These authors also reported a positive effect of egg size on both larval size (Moodie et al. 1989, Johnston 1997) and feeding success (Moodie et al. 1989). In our experiment, offspring size after 2 mo was related positively to egg size (ln(fork length) = 4.096 + 0.155 x ln(egg size), $r^2 = 0.22$, $n = 25$, $P = 0.017$). Because offspring survival in fish depends on the competitive advantage that body size confers on larger larvae in food-limited environments (Sogard 1997), it is likely that offspring survival in this study was mediated through positive effects of egg size on both offspring size and feeding success. The presence of strong MI on survival into the juvenile stage also corroborates results from rainbow trout and steelhead trout (*Oncorhynchus mykiss*) after 1 year in a hatchery (Herbinger et al. 1995) and 6 months in a stream (Seamons et al. 2004) that show that MI do not necessarily weaken as offspring develop (Bernardo 1996, Chambers and Leggett 1996, Heath and Blouw 1998).

Although egg size and offspring survival were not related to maternal age or size in our sample of 25 females from the Bay of Quinte, the larger sample (*n* = 62) of females that was collected from this population over the period 2002-2004 (Wiegand et al. 2007) showed positive associations between maternal size and both egg size (ANCOVA, $R^2 = 0.34$, $P = 0.002$) and lipid content. These observations are consistent with evidence from other walleye populations that (i) egg size increases with maternal age or size (Fig. D.4; Johnston and Leggett 2002), and (ii) larval survival increases with either maternal age or size (Johnston 1997, Johnston et al. 2007), or with aspects of egg quality that themselves increase with maternal age or size (Moodie et al 1989, Czesny and Dabrowski 1998, Johnston et al 1997). The frequent appearance of associations between maternal age, egg size, and offspring survival in both field and laboratory studies of walleye justify an assessment of the potential influence of such relations on walleye population dynamics.

5.4.2 Population modelling

As outline above, associations between maternal age, egg size, and offspring survival are a common feature of walleye studies. But can MI on offspring survival affect the dynamics of an exploited walleye population? To test this hypothesis, we combined the relation between offspring survival and egg size that was observed in our pond experiment (Table 5.1) with a relation between egg size and maternal age that is typical of walleye populations (Fig. D.4; see Appendix D.2.2 for details). We then incorporated the resultant relation between offspring survival and maternal age into a matrix population model in which maternal age classes were subjected to one of three strategies of harvest: harvest young, harvest all, or harvest old.

Model simulations produced a distinct stock-recruitment relation for each of the three harvest strategies (Fig. 5.2A). These results show that the MI on survival that were observed in our single-season pond experiment are strong enough to affect the dynamics of an exploited population of walleye when these MI scale with maternal age and are applied across all individuals over many seasons. Furthermore, because (i) recruitment over the entire range of egg production was highest when older age classes were protected from harvest, and (ii) the protection of older age classes translated into a 1.2-fold increase in α_o over strategies that either ignore age structure or target older age classes (Fig. 5.2B), we conclude that, when MI increase with maternal age, a population’s maximum reproductive rate will increase with the mean age of adult females.

The relative response of α_o to different harvest strategies was independent of both the strength of density-dependence (see Appendix D.2.3) and our estimate of mortality in the first year of life. However, this relative response was sensitive to the slope of the relation between egg size and maternal age (or FL), which can vary in both time and space in walleye (Fig. D.4; Johnston and Leggett 2002, Wiegand et al. 2007). As the slope of the egg size-maternal age relation increased from 0 (egg sizes equal across all ages) to 0.1 mg dry mass$\cdot$y^{-1} (egg sizes increase with maternal age to a maximum that is typical of walleye in the middle of their range; Johnston and Leggett 2002), harvest-induced changes in α_o increased linearly from 0 to 2-fold. Qualitatively, this result is entirely predictable because the strength of MI on survival in this model depended on the strength of the egg size-age relation; if egg size did not vary with age, then MI were effectively absent from the model. Quantitatively, this result illustrates how the impact of age-based MI on the dynamics of wild population can vary from year to year as a result of known variation in the strength of the egg size-maternal age relation (Johnston and Leggett 2002).

5.4.3 Population dynamics in Lake Erie

Because harvesting tends to remove from a population older, larger individuals (i.e., those individuals that might contribute the most to recruitment), our model predicts that, if MI increase with maternal age or size, then maximum reproductive rate will be lowest when the mean age of adults is low, and highest when the mean age of adults is high (see also Venturelli et al. 2009). However, the extent to which MI on survival affect the dynamics of an actual population will depend on both the strength and consistency of this relation, and the relative influence of many other physical and biological factors (Hilborn and Walters 1992). What evidence is there for MI on maximum reproductive rate in the wild?

Consistent with experimental evidence for strong MI on survival (Table 5.1, Fig. 5.1), as well as model predictions based on the assumption that these MI scale with age (Fig. 5.2), our analysis of published data from an exploited population of walleye in Lake Erie found that (i) recruitment (i.e., offspring survival) tended to be higher when the mean age of adult females was high relative to when it was low (Fig. 5.3), and (ii) the slope at the origin (α_o) of the stock-recruitment relation increased 1.68-fold when the mean age of adult females increased from 3.29 to 4.01 years (comparison of group means), and 2.75-fold when the mean age of adult females increased from 3.03 to 4.44 years (maximum versus minimum values; Fig. 5.3). This positive effect of mean age on recruitment in Lake Erie suggests that MI on survival are related to the mean age of spawners, occur over multiple breeding seasons, and at a magnitude that is sufficient to affect the dynamics of natural populations of walleye. Relative to other exploited fishes, a 1.68-to 2.75-fold difference in α_o is consistent with the results presented in Venturelli et al. (2009), which suggest that MI contributed to a doubling of α_o among long-lived, marine fishes. It is also qualitatively consistent with evidence that recruitment in Baltic cod increases with the relative abundance of older females, which tend to produce eggs that are neutrally buoyant at depths at which temperature, salinity, and oxygen conditions are favorable for survival (Cardinale and Arrhenius 2000, Vallin and Nissling 2000).

With respect to other mechanisms of population dynamics, adult walleye in Lake Erie are not cannibalistic (1 case of cannibalisms in 14 893 adults examined between 1979 and 1994; Madenjian et al. 1996), and our analysis controlled for effects of temperature and water quality. Results are also largely independent of density-dependent processes (e.g., life history changes, Allee effects), first because both curves in Fig. 5.3 cover a similar range of egg production (i.e., population density), and second because we incorporated observed changes in age-at-maturity, length-at-age, and mass-at-age into our estimates of total annual egg production. Inter-annual variation in RF is one exception. Although relations between RF and length can vary annually in fishes (Venturelli et al. 2009), the absence of RF data from years other than 1966 in the period 1947-1976 forced us to assume a constant RF-TL relation in all years (Appendix D.3.1). To determine the sensitivity of our results to this assumption, we used data from 1966 to generate four alternative RF scenarios: (i) a neutral RF relation in which the mean observed RF value (82 $\text{eggs}\cdot\text{g}^{-1}$) was applied to all length classes in all years; (ii) a steep, positive RF relation in which the highest (125 $\text{eggs}\cdot\text{g}^{-1}$) and lowest (45 $\text{eggs}\cdot\text{g}^{-1}$) observed RF values were associated with the largest and smallest females, respectively, in all years; (iii) a steep, negative RF relation in which the highest and lowest observed RF values were associated with the smallest and largest females; and (iv) a density-dependent RF in which the observed slope (0.075) declined linearly to 0 as the estimate of spawning female abundance increased from 0.3 million to 2.7 million individuals. This last scenario was based on evidence in other fishes (e.g., Atlantic cod; Yoneda and Wright 2004) that RF-age relations weaken with increasing density. For each of these scenarios, we repeated our analysis as previously described. We found that α_o increased 1.64 to 1.72 times when the mean age of spawners increased from 3.29 to 4.01 years, and 2.62 to 3.05 times when the mean age of spawners increased from 3.03 to 4.44 years. Because these results are similar to our original estimates of 1.68 and 2.75, we conclude that evidence for MI on maximum reproductive rate in this population was robust to assumptions about the nature of the RF-length relation.

In discussing MI on population dynamics, it is also instructive to highlight several differences between our model and an actual population of walleye. First, our MI-age relation was a necessary simplification of a complex process. In walleye, there is evidence that MI on survival stem from positive effects of maternal quality on spawning time or duration (Zhao et al. 2009), hatching success, and the size of eggs, yolk, and larvae (e.g., Moodie et al. 1989, Johnston 1997, Johnston et al. 2005, 2007, this study). These MI tend to increase with maternal age and (or) size because naïve spawners are often inferior spawners (e.g., Carr and Kaufman 2009), and because optimal egg size often increases with clutch size as a result of density-dependent defects on egg and larval survival (Einum and Fleming 2002, Hendry and Day 2003, Kamler 2005 and references therein). And although senescence dictates that MI are unlikely to persist as wild fish approach maximum age, survival to maximum age in a harvested population is also unlikely (Kamler 2005). The strength of MI on survival are also sure to vary over time and among populations. Therefore, although this study establishes that MI on survival can affect population dynamics, a detailed understanding of the importance of this mechanism to specific populations will require further study. Second, whereas our model assumed fixed, knife-edge maturity at 4 years of age, maturity in Lake Erie walleye was density-dependent, with 4-98% of females in a given year maturing as early as age-3. Because 3 and 4 year-olds together accounted for an average 54% (range 4-100%) of the total annual abundance of adult females, the observed differences in mean age between the maximum and minimum observed values (1.41 years) and the ‘high’ and ‘low’ groups (0.72 years) mask relatively large differences in the distribution of abundance among ages. For example, if we describe the high and low groups in terms of the percentage of adult females that were ‘old’ (i.e., ≥ 5 years of age), it shows that 21% of adult females were old when mean age was high, but only 7% when mean age was low. Finally, we recognize that other factors (e.g., spring warming rate, water level) contribute to the dynamics of wild populations. However, the relative importance of MI on offspring survival stems, not only from its relative effect on recruitment, but also from the fact that it can be managed through exploitation. In other words, managers have little influence over the environment, but they can choose to protect those individuals that are likely to produce the most recruits under both favorable and unfavorable environmental conditions.

5.5 Conclusions

Our results show that juvenile survival in walleye depends on maternal quality (namely egg size), and, for the first time in a species of freshwater fish, that MI on offspring survival can produce relatively large changes in a population's maximum reproductive rate. Together with similar evidence in long-lived marine fishes (Cardinale and Arrhenius 2000, Vallin and Nissling 2000, Venturelli et al. 2009), a soil mite (Benton et al. 2005, 2008), and a pest moth (Kendall et al. 2005), our study confirms that effects of maternal quality on offspring survival can be an important mechanism that should be considered when interpreting (e.g., Kendall et al. 2005, Anderson et al. 2008) and forecasting population dynamics. For example, although total egg production in fish can be a more accurate measure of reproductive potential than adult biomass when RF varies among years or individuals (Marshall et al. 1998), this approach ignores potential effects of MI on the viability of eggs unless it is complimented by information on population structure with respect to those maternal characteristics (e.g., age, size) that correlate with offspring survival (e.g., Marteinsdottir and Thorarinsson 1998).

More generally, our results provide further support for a fundamental change in the way that populations are managed—if certain individuals in a population contribute more to recruitment than others, then these individuals should be a priority of management (e.g., Forbes and Peterman 1994, Marteinsdottir and Thorarinsson 1998, Murawski et al. 2001, Berkeley et al. 2004, Law 2007, Secor 2007, Venturelli et al. 2009). We do not recommend strategies that ignore overall mortality; rather, we recommend additional controls on the distribution of mortality among individuals of varying reproductive value. While it seems obvious to suggest that exploited populations would benefit from strategies that protect rather than target reproductively valuable individuals, many populations are managed as though their dynamics depend solely on population size and extrinsic factors such as climate. Fishing regulations that either ignore age structure or promote the harvest of older individuals through minimum limits on harvestable size (Myers and Mertz 1998) are one example. The selective removal of reproductively valuable individuals through trophy hunting or fishing (Allendorf and Hard 2009) is another. Such strategies must be re-evaluated given increasing evidence that they can erode the reproductive rate of a population through harvest-induced demographic change (Venturelli et al. 2009, this study) and evolution (Allendorf and Hard 2009, Law 2007), and thereby contribute to a reduction in a population's resilience to both environmental variability and exploitation (Berkeley et al. 2004, Law 2007, Secor 2007, Anderson et al. 2008). To this end, we recommend maximum size limits or harvestable slots for recreational fisheries, and changes to gear (e.g., the size and strength of hooks and lines, sorting grids) for commercial fisheries.

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Table 5.1. Multiple linear regression models for which there was strong evidence ($\Delta_i < 2$) that parental traits influenced relative offspring survival rate in the pond experiment.

parent	model	$\log(\hat{\sigma}^2)$	AICc	AICc Rank	Δ_i	w_i	adj R^2
dam	$0.048 \cdot \mathrm{ES} - 0.028$	–4.26	–99.32	1	0.000	0.391	0.34
	$0.045 \cdot \mathrm{ES} + 0.038 \cdot \mathrm{K} - 0.064$	–4.31	–97.95	2	1.561	0.146	0.39
sire	$-0.037 \cdot \mathrm{SD} + 0.072$	–4.03	–93.73	1	0.000	0.178	0.02
	$1.31 \cdot 10^{-4} \cdot 5\mathrm{V} + 0.013$	–4.03	–93.59	2	0.134	0.167	0.00
	$4.32 \cdot 10^{-4} \cdot \mathrm{A} + 0.025$	–4.02	–93.29	3	0.436	0.144	–0.02
	$-0.063 \cdot \mathrm{LL} + 0.054$	–4.02	–93.29	4	0.437	0.143	–0.02

Notes: $n = 25$ dams and 25 sires. Model selection was based on the corrected Akaike's Information Criterion (AICc; Anderson 2008). ES = egg size (mg dry mass), K = condition ($\mathrm{g \cdot mm^{-3} \cdot 10^5}$), EL = egg lipid (proportion of dry mass), SD = log sperm density (millions of $\mathrm{sperm \cdot \mu L^{-1}}$ of milt), 5V = average sperm path velocity (VAP in $\mathrm{\mu m \cdot s^{-1}}$) at 5 s after activation, A = age (years), LL = arcsine square root liver lipid (proportion of dry mass), $\hat{\sigma}^2$ = residual variance, Δ_i = AICc differences, w_i = Akaike weight, adj R^2 = adjusted coefficient of multiple determination.

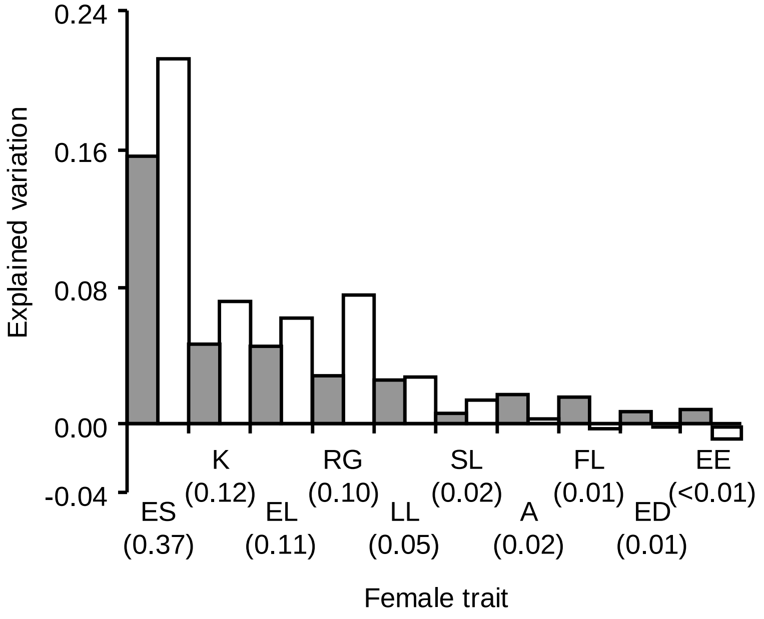

Figure 5.1. Independent (closed bars) and joint (open bars) contributions to the variation in relative offspring survival rate that was explained by each female trait, as determined by hierarchical partitioning. Independent and joint contributions refer to effects that were specific to that trait, and effects that were shared with other traits, respectively. The total (independent + joint) variation explained by each trait is given in parenthesis. ES = egg size (mg dry mass), K = condition ($g{\cdot}mm^{-3}{\cdot}10^5$), EL = egg lipid (proportion of dry mass), RG = residual growth (%), LL = arcsine square root liver lipid (proportion of dry mass), SL = arcsine square root somatic lipid (proportion of dry mass), A = age (years), FL = fork length (mm), ED = arcsine square root egg docosahexaenoic acid (proportion of EL), EE = egg residual eicosapentaenoic:arachidonic acid ratio. See text for details.

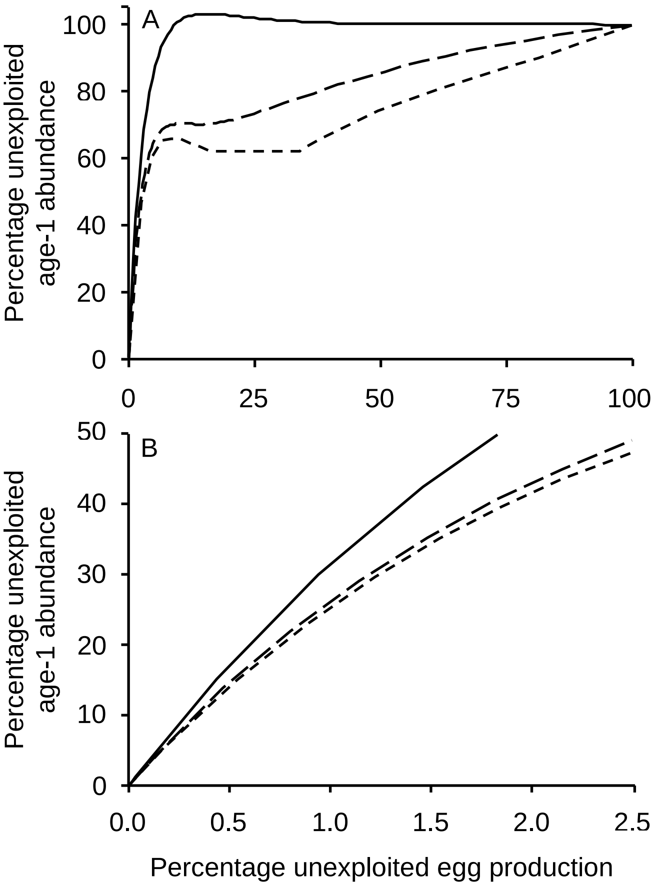

Figure 5.2. Simulated stock-recruitment relations showing MI on recruitment. Egg production and resulting abundance of age-1 recruits (both expressed as a percentage of unexploited levels) are at two scales: (A) over the full range of values, and (B) near the origin (where egg production was low because of high harvest mortality). Each line is from one of three harvest strategies: harvest-young (solid line; ages 2, 3, and 4 harvested), harvest-all (long dashes; all age harvested), and harvest-old (short dashes; age classes eliminated in sequence from oldest to youngest). Any point along a line represents the egg production and corresponding recruitment at equilibrium for a given harvest mortality.

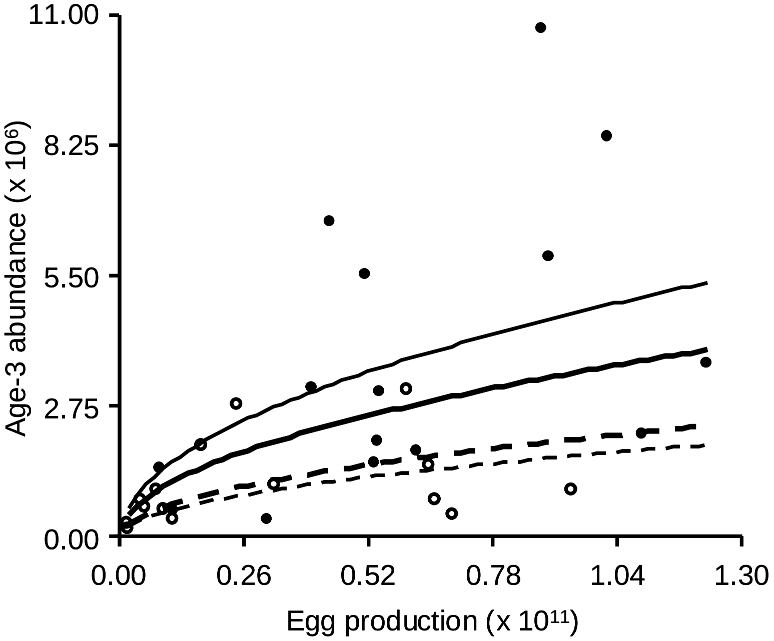

Figure 5.3. The stock-recruitment relation of walleye in Lake Erie from 1947-1976 showing MI on recruitment. Each data point is an estimate of total annual egg production and corresponding age-3 abundance when the mean age of adult females was either above (closed circles) or below (open circles) the median value of 3.66 years. Egg production estimates incorporated density-dependent life history changes, and recruitment estimates are presented here with the effects of spring warming rate (ΔT) and water level (W) removed. Curves were predicted using the multiple linear regression model log recruitment = 0.50 · log egg production + 0.31 · mean age + 6.28 · ΔT + 0.65 · W – 121.36, with ΔT and W fixed at mean observed values of $0.21^{o}C{\cdot}g^{-1}$ and 174.21 m, respectively, and mean age equal to either: minimum observed (3.03 years; thin, dashed line), maximum observed (4.44 years, thin, solid line), mean of values below the median (3.29 years ±0.11; thick, dashed line), and mean of values above the median (4.01 years ±0.14; thick, solid line). The slope at the origin (α_o) of the stock-recruitment relation (10^{-5} age-3 recruits·egg^{-1}) associated with each of these four mean ages was 0.55, 1.52, 0.66, and 1.12, respectively.

Chapter 6
Towards proactive fisheries management

6.1 Summary

Although human activities threaten wild fish stocks in numerous ways (e.g., unintentional by-catch, the introduction of non-native species, fish farms, changes in water quality, pollution, habitat degradation, altered flow regimes, barriers to movement, climate change), fishing mortality remains one of the largest and most immediate threats (Post et al. 2002, Cooke and Cowx 2004, FAO 2006). In this thesis, I combined theory, meta-analysis, field data, experimentation, and modeling to: (i) develop a life history-based framework for estimating sustainable rates of fishing mortality across a thermal gradient (Chapters 2 and 3), and (ii) determine the extent to which population dynamics depend on how this mortality is distributed among individuals of varying reproductive value (Chapters 4 and 5). My study organism was walleye (*Sander vitreus*) a long-lived, freshwater predator that is a management priority throughout much of its North American range (Colby et al. 1979).

A generalized approach to determining sustainable levels of fishing mortality is often necessary when the number of populations of interest in a region exceeds the capacity to monitor and manage them on an individual basis. In Chapters 2 and 3, I estimated maximum sustainable mortality over a range of climates by combining the GDD metric, which facilitates among-population analyses by explicitly accounting for temperature effects (Neuheimer and Taggart 2007, Chapter 2), with the biphasic model, which estimates growth by explicitly accounting for the allocation of energy to reproduction (Lester et al. 2004, Chapters 2 and 3). Using just a handful of parameters (see Chapter 3), this GDD-based model accurately described walleye growth and reproduction (e.g., Baccante and Colby 1996), and established benchmarks of sustainable mortality from the Arctic coast, south to the Virginias (1000 to 3000 GDD/year). Together, these chapters demonstrate that the GDD metric is an effective means of accounting for temperature effects when describing life history variation among hundreds of populations (Chapter 2), and establish a framework for generating life history-based estimates of maximum sustainable mortality that can be tailored to specific populations, regions, climates, or species (Chapter 3).

The sustainability of a particular rate of fishing mortality may depend also on the age or size structure of an exploited population (Forbes and Peterman 1994, Marteinsdottir and Thorarinsson 1998, Murawski et al. 2001, Berkeley et al. 2004, O'Farrell and Botsford 2006, Scott et al. 2006, Lucero 2008); however, empirical evidence for this dependency is limited. In a meta-analysis of 25 species (39 stocks) of exploited marine fishes, I found that populations typically exhibited a 2-fold increase in maximum reproductive rate when their age structure was extended compared to when it was truncated (Chapter 4). I also found that this difference tended to increased with reproductive life span (Chapter 4). I found a similar effect of maternal influences (MI) on population dynamics in a more detailed analysis of walleye in Lake Erie (Chapter 5). These results have important implications for our understanding of the dynamics of exploited populations. First, they suggest that the stock-recruitment relations of long-lived fishes are 'user defined' in that recruitment varies, not only with population density, but with fisheries-induced changes to population age structure. Second, they argue for a fundamental change in the way that populations are managed: if certain individuals in a population contribute more to recruitment than others, then we need controls on how fishing mortality is distributed among individuals of varying reproductive value, in addition to controls on the overall level of fishing mortality itself.

6.2 Looking forward

One of the most exciting aspects of scientific research is that each study raises at least as many questions as it answers. For example, further study is required to determine whether energy allocation to reproduction in walleye and other fishes varies with natural mortality, total mortality, or even adult age (Quince et al. 2008a, b). As outlined in Chapter 3, differentiation among these allocation strategies is possible through within-population analyses that compare adult growth parameters between distinct periods of high and low densities. In addition, because age-at-maturity depends on cumulative temperature, we might ask whether GDD-at-maturity is more informative than age-at-maturity (Chapter 2), and, therefore, more likely to reveal temperature- and density-related trends in maturity patterns both within and among populations (Chapter 3).

The discussion in Chapter 4 presents a summary of data from 25 species of exploited marine fishes that suggests that the assumption that spawning stock biomass is proportional to reproductive potential is valid—or only weakly violated—in many species, populations, and years. This conclusion is inconsistent with individual studies (e.g., Marshall et al. 1998) that attribute the fallibility of stock-recruitment relations to violations of the proportionality assumption. A more thorough analysis would help to identify for which species, populations and years, and under what circumstances (Yoneda and Wright 2004), this assumption is likely to hold.

One of the main conclusions of my research is that fisheries that target long-lived fishes should operate in ways that promote or protect extended age or size structure (Chapters 4 and 5). But advice on how to achieve this goal tends to center on changes to regulations and gear (e.g., Cooke et al. 2005) and the establishment of marine protected areas (e.g., Roberts et al. 2005). While research in these areas is important and should be continued, the impact of this research on a population is ultimately determined by its impact on policy. Because businesses, policymakers, and politicians are inclined to think in terms of dollars and cents instead of fish and eggs, it is essential to determine whether a potential policy alternative is both biologically *and* economically sound—for example, by developing discount rates that reflect more accurately the reproductive value of individuals that remain in the population after harvest. Is a big fish in the water worth two in the net?

Finally, if this thesis has an ‘elephant in the room’ it is fisheries-induced evolution—the idea that a fishery can be a selective agent that favours rapid growth, early maturity, and a short lifespan (Olsen et al. 2004, Jorgensen et al. 2007, Law 2007). Implicit in my analysis of compensation in walleye (Chapters 2 and 3) was the assumption that changes in life history were fully plastic and in no immediate danger of evolving in response to fishing mortality. This assumption should be tested, or at least acknowledged, in light of evidence from other wild fish populations (e.g., Reznick et al. 1990, Haugen and Vøllestad 2001, Quinn et al. 2001, Olsen et al. 2004) and experiments (Conover and Munch 2002) that fishing mortality results in large evolutionary changes in as few as 4 generations when selection is very strong. Similarly, efforts to manage for extended age structure (Chapters 4 and 5) should be evaluated in relation to evolutionary change. Law (2007) argues that policies that protect large fish are less likely to cause deleterious evolutionary change. Provided that fishing mortality is not too high (or too low), the exploitation of younger, smaller fish may also reverse such changes by creating a predator window that favours rapid growth and delayed maturity (but see Ernande et al. 2003).

6.3 Conclusion

This study demonstrates the importance of compensatory life history changes and MI to recruitment in exploited populations of long-lived fish. On the one hand, these findings provide insight into past and present failures. Compensation and longevity likely evolved as ways to maximize fitness in a variable environment (Stearns 1976, Winemiller and Rose 1992, Rose et al. 2001). Fisheries that (i) exploit at a rate that outpaces compensation, and (or) (ii) remove those individuals that contribute the most to recruitment, tend to erode the reproductive capacity of a population and ultimately limit its resilience to both environmental variability and exploitation (Beddington and May 1977, Longhurst 2002, Anderson 2008, this study).

On the other hand, by highlighting the importance of fisheries-induced demographic change to population dynamics, the results of this study demonstrate clearly the benefits of proactive fisheries management. ‘Reactive’ management involves monitoring and reacting to key physical and biological indicators such as size-at-age, prey availability, climate regimes, etc. This approach is a necessary component of any successful management strategy, in part because managers have little influence over the environment. However, ‘proactive’ management strategies acknowledge the role that fisheries play in shaping population dynamics, and therefore adopt policies that are consistent with a species’ inherent capacity for survival. Simply put, the environment cannot be managed, but populations can be managed so as to maximize their resilience to exploitation and environmental variation. Specifically, fisheries must (i) identify the limits of exploitation and stay within those limits (Chapters 2 and 3), and (ii) promote or protect reproductively valuable individuals (Chapters 4 and 5). Although these recommendations are not profound, they stem, in part, from a need to better understand recruitment, both in terms of compensation (Rose et al. 2001) and age or size structure in long-lived species (Berkeley et al. 2004). Furthermore, because these results are rooted in life history theory and principles of population dynamics, they apply generally to any species that is of recreational, commercial or conservation value.

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Appendix A: **Supplementary material for Chapter 2**

Table A.1. Source information and relevant notes for the 8 populations in this study for which there was a large, documented change in abundance.

a) Location, size, and depth

ID	Source(s) and notes(s)
1	Baccante (1989): Fig. 1 and text
2	Henderson and Nepszy (1994): text (mean depth was an area-weighted mean of both basins)
3	Spencer (1997): text
4	Keller et al. (1987): text (area was estimated from Fig. 1)
5	B. Jackson (OMNR, Atikokan Area Office, 108 Saturn Avenue, Atikokan, ON P0T 1C0, unpublished data)
6	Minns, et al. (1986): text
7	Colby and Baccante (1996): text
8	Roos et al. (1981): text

b) Evidence for change in abundance

1	Age-3 (mark-recapture analysis): Frank Amtstaetter (OMNR, Northwest Science and Information, RR#1, 25th Side Road, Thunder Bay, ON P7C 4T9, unpublished data)
2	Age-3+ (catch-at-age analysis): Kutkuhn et al. (1976) and Shuter et al. (1979), but see Chapter 5; Walleye Task Group (2005), Table 8
3	Age-3+ (mark-recapture analysis): F. Amtstaetter (OMNR, Northwest Science and Information, RR#1, 25th Side Road, Thunder Bay, ON P7C 4T9, unpublished data)
4	Commercial yield: Haas and Schaeffer (1992), Fig. 1
5	Index gill net catch per unit effort: B. Jackson (OMNR, Atikokan Area Office, 108 Saturn Avenue, Atikokan, ON P0T 1C0, unpublished data), our calculation
6	Index gill net catch per unit effort: Stewart et al. (1999), Fig. 10.1
7	Adults (mark-recapture analysis): Colby and Baccante (1996), Fig. 1
8	Commercial yield: T. Mosindy (OMNR, Boreal Science Section, Box 5080, 808 Robertson Street, Kenora, ON P9N 3X9, unpublished data)

Table A.1. Continued.

c) Lake productivity

1	No data. Remote and undeveloped lake; anthropogenic change over the period of interest is unlikely
2	Phosphorous levels were high during the low abundance period (1959-1971), but productivity may not have resulted in increased food for walleye because of benthic hypoxia and fish kills associated with extreme eutrophication (Carr and Hiltunen 1965, Sweeney 1993)
3	TDS=40-54 mg/L (*n*=8, 1973-1995) and Secchi depth=1.75-2.50 m (*n*=3, 1981-1986) show no clear change over the period of interest; remote and undeveloped lake (Nunan 1982, Ritchie 1984, Spencer 1997)
4	No data from the high abundance period (1924-1941). The literature suggests that phosphorous control and dreissenid mussels lowered productivity during the low abundance period (1984-1991; Freeman 1974, Bierman et al. 1984, Johengen et al. 1995)
5	Secchi depth=3.23-5.50 m (*n*=5, 1981-2002) indicates lower productivity during the period of low abundance; remote and undeveloped lake (B. Jackson, OMNR, Atikokan Area Office, 108 Saturn Avenue, Atikokan, ON P0T 1C0, unpublished data)
6	Secchi depth=0.9-2.1 m (*n*=23, 1976-1998) indicates higher productivity during the period of low abundance (Jim Hoyle, OMNR, Lake Ontario Management Unit, Glenora Fisheries Station, RR#2, Picton, ON K0K 2T0, unpublished data). But see lake #2.
7	TDS=42-65 mg/L (*n*=5, 1968-1996) indicates lower productivity during the period of low abundance; remote and undeveloped lake (Frank Amtstaetter, OMNR, Northwest Science and Information, RR#1, 25th Side Road, Thunder Bay, ON P7C 4T9, unpublished data; Baccante and Reid 1988; Baccante and Colby 1996)
8	TDS=94-111 mg/L (*n*=26, 1962-2002) and Secci depth=3.24-5.43 m (*n*=11, 1962-2000) show no clear change over the period of interest (Frank DeVries, Water & Waste Dept., City of Winnipeg, 510 Main St., Winnipeg, MB R3B 3M1, unpublished data)

d) GDD

1	T.R. Marshall, unpublished data; Environment Canada (2005): stations 6020383 and 6020379
2	T.R. Marshall, unpublished data; Environment Canada (2005): stations 6136336, 6136335, and 6134190
3	T.R. Marshall, unpublished data; Spencer (1997): Fig. 13
4	Goddard Institute for Space Studies (2005): station 425726370030
5	T.R. Marshall, unpublished data; Environment Canada (2005): stations 6020384 and 6020379
6	T.R. Marshall, unpublished data; Environment Canada (2005): station 6150689
7	T.R. Marshall, unpublished data; Spencer (1997): Fig. 13
8	T.R. Marshall, unpublished data; Environment Canada (2005): station 5031320

Table A.1. Continued.

e) Age and total length

ID	Source
1	Scale samples provided by Frank Amtstaetter, OMNR
2	Parsons (1972): Table 2 (direct measurements); Wolfert (1977): Table 5 (scale back-calculations); Muth and Wolfert (1986): Fig. 1-3 (direct measurements); Madenijan et al. (1996): Table 1 (direct measurements); Zhao (2005): Figure 5, p. 143 (scale back-calculations)
3	Scale samples provided by F. Amtstaetter, OMNR; Reid (1985), Appendix III, Table 3
4	Scale samples provided by D. Fielder, Michigan Department of Natural Resources. Hile (1954): Tables 24 and 25 (scale back-calculations)
5	Scale samples provided by B. Jackson, OMNR
6	Unpublished scale back-calculations provided by J. Casselman, Department of Biology, Queen’s University, Kingston, ON K7L 3N6
7	Scale samples and unpublished scale back-calculations provided by F. Amtstaetter, OMNR, Northwest Science and Information, RR#1, 25th Side Road, Thunder Bay, ON P7C 4T9
8	Scale samples provided by T. Mosindy, OMNR

Note: ID values correspond to populations in Table 1. GDD = growing degree-day, OMNR = Ontario Ministry of Natural Resources, TDS = total dissolved solids.

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Appendix B: **Supplementary material for Chapter 3**

Table B.1. Years for which data were available from both periods in each of the 6 populations in this study to estimate total length (L_{50}) and cumulative annual growing degree-day-at-50%-maturity (GDD_{50}) for both male and female walleye. Sample size (*n*) is for the entire period (not individual years), and ID numbers correspond to populations in Table 3.1.

	Period of high abundance			Period of low abundance			
ID	Year(s)	Male *n* (GDD_{50}, L_{50})	Female *n* (GDD_{50}, L_{50})	Years	Male *n* (GDD_{50}, L_{50})	Female *n* (GDD_{50}, L_{50})	Source(s) and note(s)
1	1982, 1983	484, 485	126, 126	1990, 1998, 2004	146, 146	126, 126	1
2	1927, 1928	829, 829	469, 469	1964-1966	364, na	235, 666	2
3	1980, 2003, 2006	542, 533	438, 440	1981, 1982, 1997	486, 488	518, 480	1, 3
4	1930	536, 683	466, 525	1989-1993	1073, 1073	859, 859	4
7	1979, 1996, 1997, 2001, 2003, 2006	429, 395	518, 468	1980-1984	211, 162	226, 157	1
8	1979, 1980	614, na	386, 378	1981-1988, 1990, 1992-1995, 1997, 1998	4029, 4028	1524, 1524	5

1. F. Amtstaetter, Ontario Ministry of Natural Resources (unpublished data).

2. Deason (1933, Table 5 and Figure 1): standard length was converted to L following Carlander and Smith (1945), and GDD_{50} was estimated from L_{50} via a L-age regression; Wolfert (1969, Table 3 and Figure 1): because almost 100% of males and females were mature at ages-2 and 3, respectively, we assumed that 50% of males and females were mature at ages-1 and 2, respectively.

3. Nunan (1982, Table 12) and Reid (1985, Table 35): L_{50} was estimated from age-at-50%-maturity via L-age regressions.

4. Hile (1954, Tables 47 and 48); D. Fielder, Minnesota Department of Natural Resources (unpublished data).

5. T. Mosindy, Ontario Ministry of Natural Resources (unpublished data).

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Appendix C: **Supplementary material for Chapter 4**

C.1 The logic of MI on reproductive rate

Here, we use a generic population model to demonstrate how egg quantity and egg quality can influence a population's maximum reproductive rate and, by extension, the amount of exploitation that that population can sustain (Myers et al. 1999).

C.1.1 Reproductive rate and quality and quantity of eggs

Consider an age-structured population in which (i) individuals aged 1 through L experience a fixed annual fractional survival rate, *s*; (ii) all individuals die at the end of their L$^{\text{th}}$ year of life; (iii) individuals reproduce once annually, beginning at the start of their T$^{\text{th}}$ year; (iv) all age classes exhibit a 1:1 sex ratio; and (v) the age structure of the population is in equilibrium with these reproductive and survival rates such that abundance in each age class experiences a fixed annual fractional growth rate, λ.

Let $f \cdot A^b$ and $v \cdot A^d$ represent the number and viability of eggs produced, respectively, by a typical spawning female in age-class *i*, where *f* and *v* are >0, and *b* and *d* are ≥0. These functions are consistent with evolutionary theory and empirical evidence that both suggest that overall investment in reproduction (Quince et al. 2008a, b) and maternal influences (Heath and Blouw 1998) increase with maternal age and (or) size for most species of fish. Substituting mean female age ($\overline{A}$) for *i* in these functions gives approximate expressions for the number ($f \cdot \overline{A}^b$) and viability ($v \cdot \overline{A}^d$) of eggs that are produced by a typical mature female in the spawning population.

Taken together, these expressions define a stock-recruitment relation for the population in which the number of age-1 individuals recruiting into the population at the start of year *t* +1 ($\mathrm{N}_{1,t+1}$) is a function of the abundance of spawning females in year *t* ($\mathrm{N}^{\mathrm{F}}_{\mathrm{T:L},t}$, or the abundance of spawners, $\mathrm{N}_{\mathrm{T:L},t}$, because $\mathrm{N}^{\mathrm{F}}_{\mathrm{T:L},t} = ½ \cdot \mathrm{N}_{\mathrm{T:L},t}$), their mean age ($\overline{A}$), and both the number and viability of the eggs that they produce:

$$\mathrm{N}_{1,t+1} = \lambda \cdot \mathrm{N}_{1,t} \approx \mathrm{N}^{\mathrm{F}}_{\mathrm{T:L},t} \cdot f \cdot \overline{A}^b \cdot v \cdot \overline{A}^d = ½ \cdot \mathrm{N}_{\mathrm{T:L},t} \cdot f \cdot \overline{A}^b \cdot v \cdot \overline{A}^d . \qquad \text{C.1}$$

Note that the subscript T:L means “from age-T to age-L”.

If b and $d = 0$ then both egg production and viability are independent of maternal age, equation C.1 simplifies to

$$N_{1,t+1} \approx ½ \cdot N_{T:L,t} \cdot f \cdot v \qquad \text{C.2}$$

and the reproductive rate of the population (α; the slope of the stock-recruitment relation) is independent of adult age structure, regardless of whether the population of spawning adults is measured as abundance ($\alpha \approx N_{1,t+1} / N_{T:L,t} \approx ½ \cdot f \cdot v$) or total egg production $[\alpha \approx N_{1,t+1} /(f \cdot ½ \cdot N_{T:L,t}) \approx v]$.

If $b > 0$ and $d = 0$, then egg production increases with maternal age while egg viability remains constant, equation C.1 simplifies to

$$N_{1,t+1} \approx ½ \cdot N_{T:L,t} \cdot f \cdot \overline{A}^{b} \cdot v, \qquad \text{C.3}$$

and α is only independent of adult age structure when the population of spawning adults is measured as total egg production $[\alpha \approx N_{1,t+1} /(f \cdot \overline{A}^{b} \cdot ½ \cdot N_{T:L,t}) \approx v]$. When egg production per unit female body mass (relative fecundity; *f’*) is independent of female age or size, then spawning stock biomass (SSB) is directly proportional to total egg production, and α is independent of adult age structure when SSB is used to represent adult population size (see thesis section 4.4.3 for a discussion of the age- or size-dependence of *f’*).

Finally, if both b and d are >0, then both egg production and viability increase with maternal age, equation C.1 cannot be simplified, and α depends directly on $\overline{A}$, even when the population of spawning adults is measured as total egg production $[\alpha \approx N_{1,t+1} /(f \cdot \overline{A}^{b} \cdot ½ \cdot N_{T:L,t}) \approx v \cdot \overline{A}^{d}]$.

C.1.2 Maximum reproductive rate, population density, and egg quality

To extend the stock-recruitment relation to include effects of population density, assume that (i) for a time interval of duration h ($h < 1$ year), the instantaneous mortality rate experienced by all individuals at the end of their first year of life, independent of maternal origin, is density-dependent; and (ii) the instantaneous mortality rate at any point in time within the interval *h* equals $\delta + \gamma \cdot N_0$, where N_0 is the number of larvae alive at that point in time.

Given these assumptions, it follows that the population will exhibit a concave down, positive asymptotic curve (i.e., a Beverton-Holt stock-recruitment relation; Beverton and Holt 1957):

$$N_{1,t+1} = \frac{g[\delta,\gamma] \cdot f[N_{\mathrm{T:L},t}, \bar{A}]}{e^{\delta h} \cdot g[\delta,\gamma] + f[N_{\mathrm{T:L},t}, \bar{A}]} \qquad \text{C.4}$$

where $g[\delta,\gamma]$ is maximum recruitment and equals $\delta/[\gamma \cdot (e^{\delta h} - 1)]$, $f[N_{\mathrm{T:L},t}, \bar{A}]$ is the number of larvae at time 1–*h* in year *t* and equals $½ \cdot N_{\mathrm{T:L},t} \cdot (f \cdot \bar{A}^b \cdot v \cdot \bar{A}^d)$, and $e^{\delta h} \cdot g[\delta,\gamma]$ is the half-saturation constant and equals the value of $f[N_{\mathrm{T:L},t}, \bar{A}]$ that will generate recruitment at half of $g[\delta,\gamma]$.

Assume that (i) recruitment is the only demographic process subject to density-dependent regulation; (ii) parameters [*s*, T, L, *f*, *b*, *v*, *d*, *δ*, *γ*] are fixed; and (iii) $s > s_{\min}$, the minimum sustainable survival rate. It follows that, for any initial abundance, the size of the population will tend towards, and eventually reach, an equilibrium in which abundance in each age group is constant and $\lambda = 1$. If this equilibrium population is then subjected to a gradual reduction in *s*, density-dependent effects will keep $\lambda \approx 1$ and, as $s > s_{\min}$, the α based on total egg production $[\alpha \approx N_{1,t+1}/(f \cdot \bar{A}^b \cdot ½ \cdot N_{\mathrm{T:L},t})]$ will approach a maximum value ($\alpha_o \approx e^{\delta d} \cdot v \cdot \bar{A}^d$) that is the slope at the origin of a density-dependent stock-recruitment relation and is equivalent to maximum reproductive rate (Myers et al. 1999). Thus, at low population densities, the α_o of either an egg- or SSB-based stock-recruitment relation will vary directly with $\bar{A}$ as described in section C.1.1 above.

C.1.3 Maximum reproductive rate, population age-structure, and reproductive lifespan

Here, we describe how the mean age of adults ($\bar{A}$) varies with both survival rate (s) and reproductive life span (RLS = L–T+1; the number of lifetime breeding events) in an equilibrium

($\lambda \approx 1$) population. If $\mathrm{N}_{1,t}$ is the abundance of 1-year-olds at the start of year *t*, then the breakdown of adult abundance by age at the start of year *t*+L–1 is

$$\mathrm{N}_{\mathrm{T:L},t+L-1} = s^{\mathrm{T}-1} \cdot \mathrm{N}_{1,t} \cdot \left(1 + s^{1} + s^{2} + \ldots + s^{\mathrm{L}-\mathrm{T}}\right) \qquad \text{C.5}$$

where $s^{\mathrm{T}-1} \cdot \mathrm{N}_{1,t}$ is the number of age-T adults at the start of year *t*+L–1 ($= \mathrm{N}_{\mathrm{T},t+\mathrm{L}\text{-}1}$). From equation C.5, it follows that

$$\overline{A} = \frac{\mathrm{N}_{\mathrm{T},t+\mathrm{L}\text{-}1} \cdot \mathrm{T} + \mathrm{N}_{\mathrm{T},t+\mathrm{L}\text{-}1} \cdot s \cdot (\mathrm{T}+1) + \mathrm{N}_{\mathrm{T},t+\mathrm{L}\text{-}1} \cdot s^{2} \cdot (\mathrm{T}+2) + \ldots + \mathrm{N}_{\mathrm{T},t+\mathrm{L}\text{-}1} \cdot s^{\mathrm{L}-\mathrm{T}} \cdot (\mathrm{T}+\mathrm{L}-\mathrm{T})}{\mathrm{N}_{\mathrm{T},t+\mathrm{L}\text{-}1} + \mathrm{N}_{\mathrm{T},t+\mathrm{L}\text{-}1} \cdot s + \mathrm{N}_{\mathrm{T},t+\mathrm{L}\text{-}1} \cdot s^{2} + \ldots + \mathrm{N}_{\mathrm{T},t+\mathrm{L}\text{-}1} \cdot s^{\mathrm{L}-\mathrm{T}}}$$

$$= \mathrm{T} + \frac{\sum_{i=1}^{\mathrm{RLS}-1} i \cdot s^{i}}{\sum_{i=1}^{\mathrm{RLS}-1} s^{i-1}}. \qquad \text{C.6}$$

Because both of these summations have simple, closed forms

$$\sum_{i=1}^{\mathrm{RLS}-1} i \cdot s^{i} = \left(\frac{1}{1-s}\right) \cdot \left[\frac{1-s^{\mathrm{RLS}}}{1-s} - (\mathrm{RLS}-1)s^{\mathrm{RLS}} - 1\right]$$

and

$$\sum_{i=1}^{\mathrm{RLS}-1} s^{i-1} = \frac{1-s^{\mathrm{RLS}}}{1-s},$$

then equation C.6 becomes

$$\overline{A} = \mathrm{T} + \frac{\left[\frac{1-s^{\mathrm{RLS}}}{1-s} - (\mathrm{RLS}-1)s^{\mathrm{RLS}} - 1\right]}{1-s^{\mathrm{RLS}}} \qquad \text{C.7}$$

Equation C.7 specifies that $\overline{A}$ decreases in response to a reduction in *s*, and that the magnitude of this change increases with RLS (Figure C.1). In other words, the greater a population's RLS, the more age truncation it experiences as a result of additional mortality. Given this result, and those of sections C.11. and C.1.2, the negative impact of a reduction in *s* on maximum reproductive rate (α_o) should also increase with RLS.

C.2 Summary

We have identified two mechanisms by which α_o, the slope at the origin of a stock-recruitment relation, depends directly upon population age-structure when the population of spawning adults is measured as SSB:

(i) egg production per unit female body mass (f') increases with maternal age (but see thesis section 4.4.3); and
(ii) egg viability increases with maternal age.

Therefore, we expect α_o to exhibit the following dynamics in exploited, age-structured populations in which f' and (or) viability increase with maternal age:

(i) α_o during periods of high adult survival is greater than α_o during periods of low adult survival, and

the change in α_o associated with a fixed change in *s* will be higher in populations with longer reproductive life spans [equation A.7 and Figure C.1].

C.3 References

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Table C.1. Species and populations used in the meta-analysis.

(ICES = North International Council for the Exploration of the Sea, NAFO = Northwest Atlantic Fisheries Organization.)

				period		primary source
ID	scientific name	common name	population	growth	decline	
1	*Clupea harengus*	Atlantic herring	Iceland (spring)	1947-1959	1960-1969	1
2			Iceland (summer)	1947-1961, 1972-1995	1962-1971	1
3			Georges Bank & Scotian Shelf (NAFO 4-5)	1967-1970, 1983-1988	1971-1982	1
4			North Sea (ICES IIIa, IV & VIId)	1978-2006	1965-1977	2
5	*Engraulis encrasicolus*	European anchovy	Black Sea	1967-1975, 1991-1993	1976-1990	1
6	*Gadus macrocephalus*	Pacific cod	Bering Sea & Aleutian Islands	1978-1987	1988-2005	3
7	*G. morhua*	Atlantic cod	Baltic Sea (ICES 25-32)	1966-1984	1985-2005	4
8			Celtic Sea (ICES VIIe-k)	1971-1989	1990-2004	5
9			Faroe Plateau (ICES Vb$_1$)	1961-1982	1983-1992, 1996-2005	6
10			Newfoundland Grand Banks (NAFO 3NO)	1976-1989	1965-1975	1
11			Southern coast, Newfoundland (NAFO 3Ps)	1976-1989	1966-1975	1
12			Southern coast, Newfoundland (NAFO 3Ps)	1977-1984, 1995-1999	1985-1994	7
13			Gulf of St Lawrence (NAFO 4T)	1977-1986	1958-1976	8
14	*Hippoglossus stenolepis*	Pacific halibut	Gulf of Alaska	1976-1994	1954-1975	9
15	*Limanda aspera*	yellowfin sole	Bering Sea & Aleutian Islands	1976-1994	1959-1975	10
16	*Merlangius merlangus*	whiting	East Black Sea	1971-1980	1981-1991	1
17	*Melanogrammus aeglefinus*	haddock	Eastern Georges Bank	1974-1978, 1995-2001	1979-1994	11
18	*Merluccius productus*	North Pacific hake	Pacific coast, Canada & U.S.A.	1972-1986	1987-2001	12
19	*Micromesistius poutassou*	blue whiting	Northern ICES	1970-1979	1980-1989	1
20	*Oncorhynchus gorbuscha*	pink salmon	Prince William Sound, Alaska	1960-1969	1945-1954	1
21	*O. keta*	chum salmon	North Alaska Peninsula	1993-2002	1980-1992	13
22	*O. kisutch*	coho salmon	Pacific coast, Oregon	1983-1994	1970-1982	14
23			Skeena River, British Columbia	1951-1977	1978-1995	15
24	*O. nerka*	sockeye salmon	Chignik River, Alaska	1965-1976	1989-2000	16
25	*O. tshawytscha*	chinook salmon	Alaska Peninsula	1971-1982	1983-1993	17
26	*Ophiodon elongates*	lingcod	Pacific coast, U.S.A.	1996-2005	1978-1995	18
27	*Parophrys vetulus*	English sole	Pacific coast, U.S.A.	1994-2005	1972-1993	19
28	*Pleuronectes platessa*	European plaice	Western English Channel (ICES VIIe)	1976-1988	1989-2004	20
29	*P. quadrituberculatus*	Alaska plaice	East Bering Sea	1971-1983	1984-1995	21

Table C.1. Continued

				period		primary
ID	scientific name	common name	population	growth	decline	source
30	*Pollachius virens*	saithe	Norwegian Sea (ICES VI)	1963-1974	1975-1992	1
31			North Sea, Norwegian Sea (ICES IIIa, IV & VI)	1960-1973, 1994-2004	1975-1993	22
32			Northeastern Arctic (ICES I & II)	1960-1969, 1995-2004	1972-1994	23
33	*Sardinox sagax*	South American pilchard	Pacific coast, California	1967-1989	1951-1966	24
34	*Scomber japonicus*	chub mackerel	Northeastern Pacific	1967-1982	1935-1966	25
35	*Sebastes alutus*	Pacific Ocean perch	Bering Sea & Aleutian Islands	1978-1999	1963-1977	26
36			Gulf of Alaska	1983-2005	1963-1981	27
37			Goose Island Gully, British Columbia	1978-1988	1963-1977	1
38	*Sprattus sprattus*	European sprat	Black Sea	1958-1979	1979-1993	1
39	*Theragra chalcogramma*	Alaska Pollock	Bogoslof Island region, Alaska	1977-1983, 1994-2006	1984-1993	28

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Table C.2. Characteristics of populations used in the meta-analysis.

(Unless otherwise indicated, α-growth and α-decline were estimated from recruitment abundance and spawning stock biomass, and mean F was calculated from fishing mortality rate. The hypothesis that F was higher during the period of SSB decline than during the period of SSB growth was tested using a one-tailed *t*-test evaluated at alpha = 0.05. RLS = reproductive life span in years, α-growth and α-decline = the slopes at the origin of the stock-recruitment relation during population growth and decline, respectively, $\alpha_{g:d}$ = the ratio of α-growth to α-decline, F = fishing mortality rate, *P* = probability).

					mean F (95%CI)		
ID	RLS	α-growth[a]	α-decline[a]	α_g/α_d	growth	decline	*P*
1	16	0.94	$3.39 \cdot 10^{-1}$	2.78	0.089 (0.05)	0.983 (0.33)	$2.87 \cdot 10^{-6}$
2	15	$5.05 \cdot 10^{2}$	$2.84 \cdot 10^{2}$	1.78	0.304 (0.08)	0.983 (0.21)	$9.95 \cdot 10^{-9}$
3	16	$5.32 \cdot 10^{3}$	$2.31 \cdot 10^{3}$	2.30	0.330 (0.13)	0.859 (0.13)	$1.04 \cdot 10^{-5}$
4	9	$3.81 \cdot 10^{4}$	$2.55 \cdot 10^{4}$	1.49	0.420 (0.06)	1.049 (0.17)	$6.62 \cdot 10^{-11}$
5	2	0.54	$6.59 \cdot 10^{-1}$	0.82	0.383 (0.06)	0.674 (0.17)	0.004
6	19	$1.02 \cdot 10^{7}$	$1.06 \cdot 10^{7}$	0.97	0.102 (0.03)	0.221 (0.02)	$1.26 \cdot 10^{-7}$
7	26	$4.29 \cdot 10^{4}$	$1.74 \cdot 10^{4}$	2.28	0.867 (0.09)	1.010 (0.10)	0.021
8	26	$9.42 \cdot 10^{-2}$	$1.28 \cdot 10^{-1}$	0.74	0.633 (0.07)	0.905 (0.04)	$2.34 \cdot 10^{-7}$
9	26	$6.10 \cdot 10^{4}$	$3.13 \cdot 10^{4}$	1.95	0.442 (0.04)	0.613 (0.06)	$7.57 \cdot 10^{-6}$
10	24	$3.31 \cdot 10^{4}$	$1.03 \cdot 10^{5}$	0.32	0.316 (0.06)	0.745 (0.15)	$3.60 \cdot 10^{-6}$
11	24	$6.78 \cdot 10^{3}$	$7.34 \cdot 10^{3}$	0.92	0.544 (0.06)	0.680 (0.13)	0.024
12	24	$4.45 \cdot 10^{3}$	$3.43 \cdot 10^{3}$	1.29	0.108 (0.03)[d]	0.207 (0.06)[d]	0.002
13	25	$9.73 \cdot 10$	$3.09 \cdot 10$	3.14	0.270 (0.03)[d]	0.370 (0.04)[d]	0.002
14	44	$2.14 \cdot 10$	9.13	2.35	0.144 (0.01)[d]	0.271 (0.02)[d]	$4.35 \cdot 10^{-10}$
15	16	$8.45 \cdot 10^{4}$	$5.83 \cdot 10^{4}$	1.45	0.091 (0.01)	0.491 (0.16)	$5.69 \cdot 10^{-6}$
16	17	$1.14 \cdot 10$	4.30	2.65	0.137 (0.08)	0.404 (0.22)	0.022
17	16	$8.69 \cdot 10^{6}$	$3.27 \cdot 10^{6}$	2.66	0.140 (0.02)[d]	0.273 (0.03)[d]	$5.49 \cdot 10^{-7}$
18	13	$7.04 \cdot 10^{13}$	$5.27 \cdot 10^{13}$	1.34	0.060 (0.01)	0.088 (0.03)	0.030
19	16	$5.26 \cdot 10^{8}$	$2.15 \cdot 10^{8}$	2.44	0.040 (0.04)	0.234 (0.04)	$6.45 \cdot 10^{-7}$
20	1	3.96[b]	3.80[b]	1.04	1.220 (0.19)[d]	1.910 (0.31)[d]	0.001
21	1	$6.88 \cdot 10^{4}$[b]	$5.76 \cdot 10^{4}$[b]	1.20	0.136 (0.04)[d]	0.504 (0.08)[d]	$1.12 \cdot 10^{-7}$
22	1	$4.26 \cdot 10$[b]	$8.34 \cdot 10$[b]	0.51	0.420 (0.11)[d]	0.755 (0.05)[d]	$3.85 \cdot 10^{-6}$
23	1	$1.11 \cdot 10^{3}$[b]	$6.50 \cdot 10^{2}$[b]	1.70	0.553 (0.03)[d]	0.700 (0.03)[d]	$9.51 \cdot 10^{-8}$
24	2	$1.07 \cdot 10$[b]	$1.08 \cdot 10$[b]	0.98	0.556 (0.08)[d]	0.687 (0.05)[d]	0.007
25	4	$9.85 \cdot 10^{3}$	$1.02 \cdot 10^{4}$	0.97	1.208 (0.34)[d]	2.563 (0.42)[d]	$3.51 \cdot 10^{-5}$
26	16	$8.94 \cdot 10^{3}$	$3.80 \cdot 10^{3}$	2.35	0.035 (0.02)[d]	0.116 (0.02)[d]	$1.78 \cdot 10^{-5}$
27	14	$1.34 \cdot 10^{5}$	$7.87 \cdot 10^{4}$	1.70	0.050 (0.01)[d]	0.127 (0.01)[d]	$2.85 \cdot 10^{-10}$
28	27	$3.80 \cdot 10^{2}$	$2.47 \cdot 10^{2}$	1.54	0.500 (0.03)	0.596 (0.03)	$3.49 \cdot 10^{-5}$
28	20	$3.43 \cdot 10^{3}$	$1.71 \cdot 10^{3}$	2.01	0.012 (0.01)	0.048 (0.02)	$5.50 \cdot 10^{-5}$
30	19	$1.15 \cdot 10$	8.89	1.29	0.297 (0.05)	0.407 (0.07)	0.044
31	19	$7.46 \cdot 10^{3}$	$6.45 \cdot 10^{3}$	1.16	0.352 (0.03)	0.581 (0.06)	$4.69 \cdot 10^{-9}$
32	19	$1.59 \cdot 10^{4}$	$1.56 \cdot 10^{4}$	1.02	0.225 (0.03)	0.536 (0.03)	$6.76 \cdot 10^{-8}$
33	11	$5.57 \cdot 10^{-2}$[c]	$5.18 \cdot 10^{-2}$[c]	1.08	0.022 (0.02)[d]	0.364 (0.08)[d]	$2.32 \cdot 10^{-7}$

Table C.2. Continued.

ID	RLS	α-growth[a]	α-decline[a]	$\alpha_{g/}\alpha_d$	mean F (95%CI) growth	mean F (95%CI) decline	*P*
34	12	$1.14 \cdot 10^{2}$	$6.63 \cdot 10$	1.71	0.040 (0.01)	0.378 (0.05)	$1.43 \cdot 10^{-11}$
35	79	$3.60 \cdot 10^{4}$	$1.83 \cdot 10^{4}$	1.97	0.043 (0.01)	0.276 (0.05)	$5.52 \cdot 10^{-12}$
36	79	$3.70 \cdot 10^{2}$	$2.10 \cdot 10^{2}$	1.77	0.066 (0.02)	0.339 (0.07)	$1.41 \cdot 10^{-10}$
37	79	$9.45 \cdot 10^{-1}$	$5.34 \cdot 10^{-1}$	1.77	0.035 (0.01)	0.150 (0.04)	$5.42 \cdot 10^{-5}$
38	4	3.48	3.71	0.94	0.098 (0.03)	0.394 (0.10)	$1.26 \cdot 10^{-7}$
39	20	$1.24 \cdot 10^{-2}$	$3.34 \cdot 10^{-3}$	3.71	0.003 (0.01)	0.198 (0.13)	$9.70 \cdot 10^{-5}$

[a] units of recruitment abundance and spawning stock biomass vary among populations, [b] recruitment abundance and spawner abundance, [c] number of larvae per square meter and spawner abundance, [d] annual exploitation rate (%).

Table C.3. A summary of published information on relations between relative fecundity (*f*′) and maternal age or size in exploited populations of north temperate and arctic marine fishes.

(Information for this analysis were taken from the text or tables, or digitized from figures in the publications listed. Because some figures were difficult to digitize, sample sizes (*n*) associated these figures are sometimes slightly less than the *n* in original publications. Regression equations were used to predict *f*′ over the range of ages or sizes observed. Note that a hump-shaped relation between *f*′ and maternal age or size is not necessarily indicative of reproductive senescence, as this shape can also result from older, larger females sacrificing egg number for egg size. An effect of age or size on *f*′ was estimated as the ratio of maximum to minimum predicted *f*′. To estimate the mean effect of female age and size on either the coefficient of determination (r^2) or the *f*′ ratio, we first averaged values based on length and age within a year, and then averaged among years within a population, populations within a species, species within a family, families within an order, and orders within the class Actinopterygii. We found no evidence that r^2 or the *f*′ ratio increased with reproductive life span (RLS) at any taxonomic level (regression results not shown). Blank cells indicate that data were unavailable. FL = fork length, ICES = North International Council for the Exploration of the Sea, NAFO = Northwest Atlantic Fisheries Organization, *P* = probability, *r* = correlation coefficient, r_a^2 = adjusted r^2, SM, = somatic mass, TL = total length, TM = total mass.)

					predictor			*f*′		
scientific name	common name	population	RLS	year(s)	variable	unit	range	unit	range	statistical test
Atheresthes stomias	arrowtooth flouder	Gulf of Alaska	20	1993	FL	mm	480–829	eggs/g SM	178–394	regression
Boops boops	bogue	Atlantic coast, Portugal	4	1987–1989	TL	mm	145–365	eggs/g TM	408–1458	regression
			"	"	Age	years	1–10	"	"	"
Clupea harengus	Atlantic herring	Baltic Sea (ICES 29)	13	1988, 1991	TL	mm		eggs/g TM		correlation
		Iceland (summer)	15	1999, 2000	TL	cm	25–39	eggs/g SM	200–880	regression
Coryphaena hippurus	common dolphinfish	Western Mediterranean	4	1990, 1991	FL	mm	65–117	eggs/g SM	71–1977	regression
Cynoscion nebulosus	spotted weakfish	Atlantic coast, South Carolina	6	1998–2000	TL	mm	272–530	eggs/g SM	205–1372	regression
Dexistes rikuzenius	Rikuzen flounder	Pacific coast, Japan	10	2000, 2001	Age	years	1–8	oocytes/g SM	843–2009	regression
Engraulis encrasicolus	European anchovy	Southwestern Adriatic Sea	4	1993	TL	mm	119–171	eggs/g SM	271–584	regression
Gadus morhua	Atlantic cod	Atlantic coast, Scotland	21	1969, 1970	Age	years	3–8	oocytes/g predicted SM		regression
			"	2002, 2003	"	"	2–6	"	265–1226	"

Table C.3. Continued from the right of page 134.

result	r	r^2	r_a^2	n	P	predicted f' range	f' ratio	source	notes
$f' = 0.300 \cdot \mathrm{FL} + 89.868$	0.61	0.37	0.31	12	0.036	234–339	1.45	1 (figure 7)	our regression
$f' = -0.041 \cdot \mathrm{TL}^2 + 20.966 \cdot \mathrm{TL} - 1557.391$	0.75	0.57	0.55	75	<0.001	621–1123	1.81	2 (table 1)	our regression
$f' = -17.180 \cdot \mathrm{Age}^2 + 180.59 \cdot \mathrm{Age} + 633.856$	0.57	0.33	0.31	75	<0.001	797–1107	1.39	"	"
f' was not correlated with TL				78				3 (text p. 70)	*n*: sum of all shoals and years
$f' = 590.3 - e^{11.9 - 0.2295 \cdot \mathrm{TL}}$		0.57		451	<0.001	116–571	4.94	4 (figure 10)	
$f' = -0.364 \cdot \mathrm{FL} + 154.109$	0.21	0.04	-0.04	14	0.470	130–111	0.85	5 (table 2)	batch fecundity; our regression
$f' = 0.944 \cdot \mathrm{TL} + 239.343$	0.26	0.07	0.06	113	0.006	496–740	1.49	6 (figure 5)	our regression
$f' = -31.355 \cdot \mathrm{Age}^2 + 317.203 \cdot \mathrm{Age} + 820.381$	0.53	0.28	0.24	41	0.002	1106–1622	1.47	7 (figure 7)	our regression
$f' = -0.213 \cdot \mathrm{TL} + 466.220$	0.05	<0.01	-0.01	72	0.705	441–430	0.97	8 (table 4)	batch fecundity; our regression
$f' = 652.6 \cdot \mathrm{Age}^{0.005}$		<0.01		69	0.969	656–659	1.00	9 (table 3)	
$f' = 296.8 \cdot \mathrm{Age}^{0.613}$		0.29		50	<0.001	582–1062	1.82	"	

Table C.3. Continued from the bottom of page 134.

					predictor			f'		
scientific name	common name	population	RLS	year(s)	variable	unit	range	unit	range	statistical test
Gadus morhua	Atlantic cod	Baltic Sea (ICES 25)	26	1987	TL	cm	32–104	eggs/g TM		residual regression
			"	1988	"	"	27–76	"		"
			"	1989	"	"	37–62	"		"
			"	1990	"	"	35–68	"		"
			"	1991	"	"	38–87	"		"
			"	1992	"	"	41–98	"		"
			"	1996	"	"	36–84	"		"
			"	1998	"	"	35–91	"		"
			"	1999	"	"	26–126	"		"
			"	2000	"	"	28–108	"		"
		Iceland	20	1995	TL	cm	67–125	eggs/g TM	199–1192	regression
			"	1996	"	"	57–133	"	342–1325	"
			"	1997	"	"	66–128	"	50–1241	"
			"	1998	"	"	59–129	"	50–1117	"
			"	1999	"	"	59–133	"	300–1233	"
			"	2000	"	"	62–131	"	182–1167	"
		Northeastern Arctic	22	1986	TL	cm	55–135	eggs/g TM	226–688	regression
			"	1988	"	"	50–122	"	220–715	"
			22	1987	TL	cm	50–86	eggs/g TM		correlation
			"	1991	"	"	50–127	"		"
		North Sea (inshore)	21	1969, 1970	Age	years	3–5	oocytes/g predicted SM		regression
			"	2002, 2003	"	"	2–8	"	269–1400	"
		North Sea (offshore)	"	"	"	"	2–6	"	211–1182	"
Glyptocephalus cynoglossus	witch flounder	Northwestern Atlantic (NAFO 3L)	18	1974–1977	TL	cm	44–63	eggs/g TM	128–663	regression
			"	"	Age	years	11–23	"	"	"
			18	1993–1998	TL	cm	35–61	eggs/g TM	111–740	regression
		Northwestern Atlantic (NAFO 3LNO)	18	1993–1998	TL	cm	35–61	"	119–828	"
		Northwestern Atlantic (NAFO 3NO)	18	1974–1977	TL	cm	42–65	eggs/g TM	137–671	regression
			"	"	Age	years	8–22	"	"	"
			18	1993–1998	TL	cm	30–58	eggs/g TM	93–852	regression
Hippoglossoides platessoides	American plaice	Atlantic coast, Scotland	19	1954	TL	cm	15-31	eggs/g SM	797–1807	regression

Table C.3. Continued from the right of page 136.

result	r	r^2	r_a^2	n	P	predicted f' range	f' ratio	source	notes
TL did not explain residual variation in the fecundity-total mass relation				64	>0.400			10 (table 2, text p. 1911)	
"				115	>0.700			"	
"				65	>0.300			"	
"				104	>0.800			"	
"				77	>0.200			"	
"				43	>0.800			"	
"				91	>0.800			"	
"				40	>0.500			"	
"				65	>0.400			"	
"				94	>0.800			"	
$f' = 4.8 \cdot \mathrm{TL} + 91.2$		0.20			<0.001	413–691	1.67	11 (figure 7, table 5)	
$f' = 4.6 \cdot \mathrm{TL} + 184.7$		0.23			<0.001	447–796	1.78	"	
$f' = 5.5 \cdot \mathrm{TL} - 8.4$		0.14			<0.001	354–696	1.96	"	
$f' = 8.3 \cdot \mathrm{TL} - 200.2$		0.38			<0.001	289–870	3.01	"	
$f' = 4.5 \cdot \mathrm{TL} + 258.6$		0.19			<0.001	524–857	1.63	"	
$f' = 5.1 \cdot \mathrm{TL} + 168.6$		0.21			<0.001	485–834	1.73	"	
$f' = 1.685 \cdot \mathrm{TL} + 271.577$	0.31	0.09	0.07	48	0.035	364–499	1.37	12 (figure 3), 13 (text p. 310)	our regression
$f' = 3.026 \cdot \mathrm{TL} + 139.437$	0.56	0.31	0.29	45	0.001	291–509	1.75	"	"
f' was not correlated with TL				23	>0.500			13 (text p. 311)	
"				8	>0.500			"	
$f' = 561.2 \cdot \mathrm{Age}^{0.097}$		<0.01		52	0.752	624–656	1.05	9 (table 3)	
$f' = 357.8 \cdot \mathrm{Age}^{0.607}$		0.20		109	<0.001	545–1264	2.32	"	
$f' = 138.8 \cdot \mathrm{Age}^{1.075}$		0.50		47	<0.001	292–953	3.26	"	
$f' = 61.663 \cdot \mathrm{TL}^{0.405}$	0.08	0.01	-0.01	63	0.558	285–330	1.16	14 (figure 2, 5, 8)	our regression
$f' = -8.306 \cdot \mathrm{Age} + 463.335$	0.16	0.03	0.01	63	0.205	372–273	0.73	"	"
f' was independent of TL				41				14 (text p. 1763)	
"				177				"	
$f' = 0.921 \cdot \mathrm{TL}^{1.506}$	0.37	0.14	0.13	103	<0.001	256–495	1.93	14 (figure 2, 5, 8)	our regression
$f' = 5.094 \cdot \mathrm{Age} + 272.133$	0.11	0.01	0.00	103	0.250	323–405	1.25	"	"
$f' = 0.232 \cdot \mathrm{TL}^{1.841}$	0.48	0.23	0.22	107	<0.001	198–422	2.14	"	"
$f' = 50.385 \cdot \mathrm{Age}^{0.644}$	0.39	0.15	0.14	107	<0.001	192–369	1.92	"	"
f' was independent of TL				131				15 (text p. 1763)	
$f' = 4.759 \cdot \mathrm{TL} + 1146.464$	0.07	0.01	0.00	117	0.464	1218–1294	1.06	16 (table 30)	our regression

Table C.3. Continued from the bottom of page 136.

					predictor			f'		
scientific name	common name	Population	RLS	year(s)	variable	unit	range	unit	range	statistical test
Hippoglossoides platessoides	American plaice		19	1954	Age	years	2–5	eggs/g SM	797–1807	regression
		Northwestern Atlantic (NAFO 3LNO)	19	1993–1998	TL	cm	24–67	eggs/g TM	117–1077	regression
		Northwestern Atlantic (NAFO 3Ps)	"	"	"	"	26–72	"	78–1071	"
Hoplostethus atlanticus	orange roughy	Northeastern Atlantic	100	2002	SL	mm	362–528	eggs/g TM	10–65	regression
Limanda ferruginea	yellowtail flounder	Northwestern Atlantic (NAFO 3LNO)	8	1993–1998	TL	cm	30–54	eggs/g TM	182–7263	regression
		Northwestern Atlantic (NAFO 3Ps)	"	"	"	"	30–50	"	340–8349	"
Malostus villosus	capelin	Barents Sea	9	1997	TL	mm	111–162	eggs/g SM	49–115	regression
Melanogrammus aeglefinus	haddock	Atlantic coast, Scotland	14	1986, 1987	Age	years	2–6	eggs/g TM		
		North Sea	14	1976	TL	cm	30–47	eggs/g SM	223–701	regression
			"	1977	"	"	22–44	"	208–635	"
			"	1978	"	"	26–45	"	210–802	"
			"	1976	Age	years	2–5	"	223–701	"
			"	1977	"	"	2–6	"	208–635	"
			"	1978	"	"	2–8	"	210–802	"
Melanogrammus aeglefinus	haddock	Northwestern Atlantic (Grand Bank)	13	1957	TL	cm	38–64	eggs/g SM	145–1468	regression
			"	1958	"	"	39–53	"	262–1116	"
			"	1960	"	"	36–54	"	109–1193	"
Pleuronectes platessa	European plaice	Atlantic coast, Scotland	27	1956	TL	mm	305–566	eggs/g TM	178–400	regression
			"	1957	"	"	327–438	"	136–402	"
			"	1956	Age	years	4–10	"	178–400	"
			"	1957	"	"	3–10	"	136–402	"
		Celtic Sea (Bristol Channel)	25	1990	TL	mm	244–413	eggs/g SM	168–439	regression
			"	1990	Age	years	2–7	"	"	"
		Celtic Sea (Irish coast)	"	1991	TL	mm	285–455	"	136–457	"
			"	"	Age	years	3–8	"	"	"
		Irish Sea (Cumbrian coast)	25	1995	SM	g		eggs/g TM		regression

Table C.3. Continued from the right of page 138.

result	r	r^2	r_a^2	n	P	predicted f' range	f' ratio	source	notes
$f' = 12.514 \cdot \text{Age} + 1209.854$	0.05	<0.01	-0.10	116	0.594	1235–1272	1.03	16 (table 30)	our regression
f' was independent of TL				606				15 (table 1, text pp 1763, 1766)	
"				358				"	
$f' = 0.074 \cdot \text{SL} - 2.100$	0.23	0.05	0.04	61	0.075	25–37	1.50	17 (figure 2, 3)	our regression
f' was independent of TL				444				15 (table 1, text pp 1763, 1766)	
"				102				"	
$f' = 0.709 \cdot \text{TL} - 25.136$	0.58	0.33	0.32	64	<0.001	54–90	1.67	18 (figure 2, 3)	our regression
f' increased with age and then plateaued				447		278–493	1.77	19 (figure 5)	predicted range and ratio are from age-2 vs age-3+ mean
$f' = -2.557 \cdot \text{TL}^2 + 198.065 \cdot \text{TL} - 3306.375$	0.44	0.20	0.17	67	0.001	334–529	1.58	20 (appendix table 1, 2)	our regression
$f' = 3.164 \cdot \text{TL} + 365.821$	0.17	0.03	0.01	41	0.273	435–505	1.16	"	"
$f' = -1.404 \cdot \text{TL}^2 + 106.903 \cdot \text{TL} - 1458.936$	0.35	0.12	0.11	119	0.001	371–576	1.55	"	"
$f' = -66.355 \cdot \text{Age}^2 + 504.795 \cdot \text{Age} - 417.589$	0.40	0.16	0.13	67	0.004	327–550	1.68	"	"
$f' = 0.600 \cdot \text{Age} + 464.376$	0.01	<0.01	-0.03	41	0.977	466–468	1.00	"	"
$f' = -24.001 \cdot \text{Age}^2 + 215.346 \cdot \text{Age} - 70.830$	0.32	0.10	0.09	119	0.002	264–406	1.54	"	"
$f' = 0.403 \cdot \text{TL}^{1.910}$	0.49	0.24	0.23	92	<0.001	419–1135	2.71	21 (figure 2, 3)	our regression
$f' = 0.123 \cdot \text{TL}^{2.234}$	0.46	0.22	0.18	22	0.029	441–875	1.98	"	"
$f' = 0.016 \cdot \text{TL}^{2.782}$	0.60	0.37	0.35	52	<0.001	342–1056	3.09	"	"
$f' = 0.133 \cdot \text{TL} + 203.872$	0.17	0.03	0.00	31	0.350	244–279	1.14	22 (appendix)	our regression
$f' = 0.537 \cdot \text{TL} + 60.338$	0.24	0.06	0.03	31	0.188	236–295	1.25	"	"
$f' = 1.910 \cdot \text{Age} + 248.024$	0.07	0.01	-0.04	24	0.748	256–267	1.04	"	"
$f' = -6.688 \cdot \text{Age}^2 + 82.502 \cdot \text{Age} - 23.767$	0.38	0.14	0.08	31	0.117	163–230	1.41	"	"
$f' = 0.082 \cdot \text{TL} + 271.22$	0.04	<0.01	-0.04	25	0.836	291–305	1.05	23 (table 1)	our regression
$f' = 15.685 \cdot \text{Age} + 239.891$	0.20	0.04	0.00	25	0.328	271–350	1.29	"	"
$f' = 0.958 \cdot \text{TL} - 91.778$	0.66	0.44	0.41	23	0.001	181–344	1.90	"	"
$f' = 47.009 \cdot \text{Age} + 8.494$	0.69	0.47	0.45	23		149–385	2.57	"	"
$f' = 0.059 \cdot \text{SM} + 230.40$		0.03	0.02	95				24 (table 6)	
$f' = 12.514 \cdot \text{Age} + 1209.854$	0.05	<0.01	-0.10	116	0.594	1235–1272	1.03	"	"
f' was independent of TL				606				15 (table 1, text pp 1763, 1766)	
"				358				"	
$f' = 0.074 \cdot \text{SL} - 2.100$	0.23	0.05	0.04	61	0.075	25–37	1.50	17 (figure 2, 3)	our regression
f' was independent of TL				444				15 (table 1, text pp 1763, 1766)	
"				102				"	
$f' = 0.709 \cdot \text{TL} - 25.136$	0.58	0.33	0.32	64	<0.001	54–90	1.67	18 (figure 2, 3)	our regression

Table C.3. Continued from the bottom of page 138.

					predictor			*f*′		
scientific name	common name	Population	RLS	year(s)	variable	unit	range	unit	range	statistical test
Pleuronectes platessa	European plaice	Irish Sea (Liverpool Bay)	25	1995	SM	g		eggs/g TM		regression
		Irish Sea, west	"	"	"	"		"	"	"
		Irish Sea (Cardigan Bay)	"	"	"	"		"	"	"
		North Sea	25	1982	TL	mm	284–613	eggs/g SM	121–381	regression
			"	1983	"	"	259–649	"	115–390	"
			"	1984	"	"	260–588	"	90–340	"
			"	1985	"	"	286–547	"	80–353	"
			"	1982	Age	years	3–19	"	121–381	"
			"	1983	"	"	3–18	"	115–390	"
			"	1984	"	"	3–18	"	90–340	"
			"	1985	"	"	3–16	"	80–353	"
Reinhardtius hippoglossoides	Greenland halibut	North Atlantic (ICES XIVb)	13	1997	TL	cm	63–110	eggs/g SM	6–21	regression
Salmo salar	Atlantic salmon	Barents Sea (River Teno)	8	1994–1998	TL	cm		eggs/kg TM		regression
Sardina pilchardus	European pilchard	Aegean Sea	6	2000–2001	SM	g	10–26	eggs/g TM		intercept test
		Ionian Sea	"	"	"	"	7–24	"		"
Scomber japonicus	chub mackerel	Izu Islands, Japan	11	1993	FL	mm	329–393	eggs/g SM	32–250	regression
		Pacific coast, California	12	1985	FL	mm	300–340	eggs/g SM	53–315	regression
Sebastes melanops	black rockfish	Pacific coast, Oregon	23	1995–1998	Age	years	6–16	eggs/g SM	170–315	parallel lines multiple linear regression
Solea solea	common sole	English Channel (ICES VIId)	25	1991	TL	mm	260–440	eggs/g SM	129–1416	regression
			"	"	Age	years	2–19	"	"	"
		English Channel (ICES VIIe)	"	"	TL	mm	312–500	"	372–884	"
		Irish Sea (ICES VIIa)	"	"	"	"	282–411	"	465–1169	"
			"	"	Age	years	3–10	"	"	"
		North Sea (ICES IVb east)	"	"	TL	mm	258–481	"	666–1422	"
			"	"	Age	years	3–12	"	"	"
		North Sea (ICES IVb west)	"	"	TL	mm	241–456	"	371–1005	"
			"	"	Age	years	3–19	"	"	"
		North Sea (ICES IVc)	"	"	TL	mm	248–456	"	651–1504	"
			"	"	Age	years	3–15	"	"	"

Table C.3. Continued from the right of page 140.

result	r	r^2	r_a^2	n	P	predicted f' range	f' ratio	source	notes
$f' = 0.203 \cdot \mathrm{SM} + 170.09$		0.31	0.29	42				24 (table 6)	
$f' = 0.197 \cdot \mathrm{SM} + 112.54$		0.37	0.36	46				"	
$f' = 0.059 \cdot \mathrm{SM} + 181.73$		0.15	0.13	43				"	
$f' = 0.059 \cdot \mathrm{TL} + 218.916$	0.07	<0.01	-0.01	102	0.507	236–255	1.08	25 (appendix)	our regression
$f' = 0.100 \cdot \mathrm{TL} + 184.622$	0.13	0.02	0.01	153	0.103	210–249	1.18	"	"
$f' = 0.169 \cdot \mathrm{TL} + 145.148$	0.24	0.06	0.05	129	0.007	189–244	1.29	"	"
$f' = 0.198 \cdot \mathrm{TL} + 133.974$	0.22	0.05	0.04	104	0.026	191–242	1.27	"	"
$f' = 0.247 \cdot \mathrm{Age} + 244.898$	0.02	<0.01	-0.01	102	0.884	246–250	1.02	"	"
$f' = 1.822 \cdot \mathrm{Age} + 213.677$	0.12	0.02	0.01	153	0.133	219–246	1.12	"	"
$f' = 1.575 \cdot \mathrm{Age} + 205.164$	0.09	0.01	0.00	127	0.316	210–233	1.11	"	"
$f' = 2.556 \cdot \mathrm{Age} + 196.59$	0.13	0.02	0.01	104	0.181	204–237	1.16	"	"
$f' = 0.098 \cdot \mathrm{TL} + 5.980$	0.32	0.11	0.10	100	0.001	12–18	1.38	26 (figure 3, 5)	our regression
$\log(f') = -0.358 \cdot \log(\mathrm{TL}) + 9.143$		0.03	0.00	46	0.298			27 (table 2)	
The intercept of the f'-SM relation was not significantly different from 0					>0.050			28 (text p. 21)	batch fecundity
"					"			"	"
$f' = -0.293 \cdot \mathrm{FL} + 266.545$	0.09	0.01	-0.08	14	0.774	170–151	0.89	29 (table 4)	batch fecundity; our regression
$f' = 0.130 \cdot \mathrm{FL} + 129.349$	0.02	<0.01	-0.09	13	0.935	168–173	1.03	30 (table 7)	batch fecundity; our regression
$f' = 357.7 + 17.5 \cdot \mathrm{Age} - 106.5 \cdot \mathrm{stage}$		0.27		166	<0.001	371–552	1.49	31 (figure 9)	stage refers to prefertilization and fertlized eggs; *f'* was estimated from the latter
$f' = 1.994 \cdot \mathrm{TL} + 75.445$	0.36	0.13	0.11	49	0.011	594–953	1.60	32 (appendix 1)	our regression
$f' = 172.716 \cdot \mathrm{Ln(Age)} + 478.564$	0.35	0.12	0.10	49	0.014	598–987	1.65	"	"
$f' = 0.026 \cdot \mathrm{TL} + 585.369$	0.01	<0.01	-0.03	33	0.957	593–598	1.01	"	"
$f' = 1.269 \cdot \mathrm{TL} + 412.603$	0.23	0.05	0.02	29	0.221	770–934	1.21	"	"
$f' = 23.442 \cdot \mathrm{Age} + 682.411$	0.17	0.03	0.00	29	0.390	753–917	1.22	"	"
$f' = 0.819 \cdot \mathrm{TL} + 702.787$	0.26	0.06	0.04	40	0.112	914–1097	1.20	"	"
$f' = 11.857 \cdot \mathrm{Age} + 931.175$	0.17	0.03	0.00	40	0.291	967–1073	1.11	"	"
$f' = 1.650 \cdot \mathrm{TL} + 64.039$	0.53	0.28	0.26	45	<0.001	462–816	1.77	"	"
$f' = 351.185 \cdot \mathrm{Age}^{0.285}$	0.54	0.29	0.28	45	<0.001	480–813	1.69	"	"
$f' = 0.849 \cdot \mathrm{TL} + 707.530$	0.24	0.06	0.04	55	0.074	918–1095	1.19	"	"
$f' = 9.469 \cdot \mathrm{Age} + 951.822$	0.10	0.01	-0.01	55	0.456	980–1094	1.12	"	"

Table C.3. Continued from the bottom of page 140.

					predictor			f'		
scientific name	common name	Population	RLS	year(s)	variable	unit	range	unit	range	statistical test
Solea solea	common sole	Northeastern Atlantic, Bay of Biscay (ICES VIIIa)	25	1991	TL	mm	287–471	eggs/g SM	365–918	regression
			"	"	Age	years	3–19	"	"	"
		Northeastern Atlantic, Portugese coast (ICES IXa)	"	"	TL	mm	290–475	"	349–776	"
Spondyliosoma cantharus	black seabream	Adriatic Sea	10	1994	TL	cm	19–34	eggs/g SM	454–1155	regression
			"	"	Age	years	2–7	"	"	"
Tanakius kitaharai	willowy flounder	Pacific coast, Japan	7	2003, 2004	Age	years	2–8	oocytes/g TM		ANOVA
Theragra chalcogramma	Alaska pollock	Strait of Georgia, British Columbia	15	1980, 1981	FL	cm	32–67	oocytes/g TM	530–830	
Trachurus symmetricus	Pacific jack mackerel	Pacific coast, California	27	1991	FL	mm	382–540	eggs/g SM	47–172	regression

Table C.3. Continued from the right of the above section of table.

result	r	r^2	r_a^2	n	P	predicted f' range	f' ratio	source	notes
$f' = 0.978 \cdot \text{TL} + 253.557$	0.37	0.14	0.11	39	0.020	534–714	1.34	32 (appendix 1)	our regression
$f' = 23.442 \cdot \text{Age} + 682.411$	0.17	0.03	-0.01	39	0.390	753–1128	1.50	"	"
$f' = 0.937 \cdot \text{TL} + 183.474$	0.37	0.14	0.11	33	0.034	455–628	1.38	"	"
$f' = 25.665 \cdot \text{TL} + 38.377$	0.71	0.50	0.49	59	<0.001	526–911	1.73	33 (table 1)	our regression
$f' = 385.697 \cdot \text{Ln(Age)} + 173.566$	0.65	0.42	0.41	59	<0.001	441–924	2.10	"	"
f' increased and then decreased with age				58	<0.050	1022–1245	1.22	34 (figure 5)	predicted range and ratio based on age class means
f' decreased with FL								35 (text p. 340)	
$f' = 0.120 \cdot \text{FL} + 59.735$	0.13	0.02	-0.01	33	0.463	106–124	1.18	36 (table 4)	our regression

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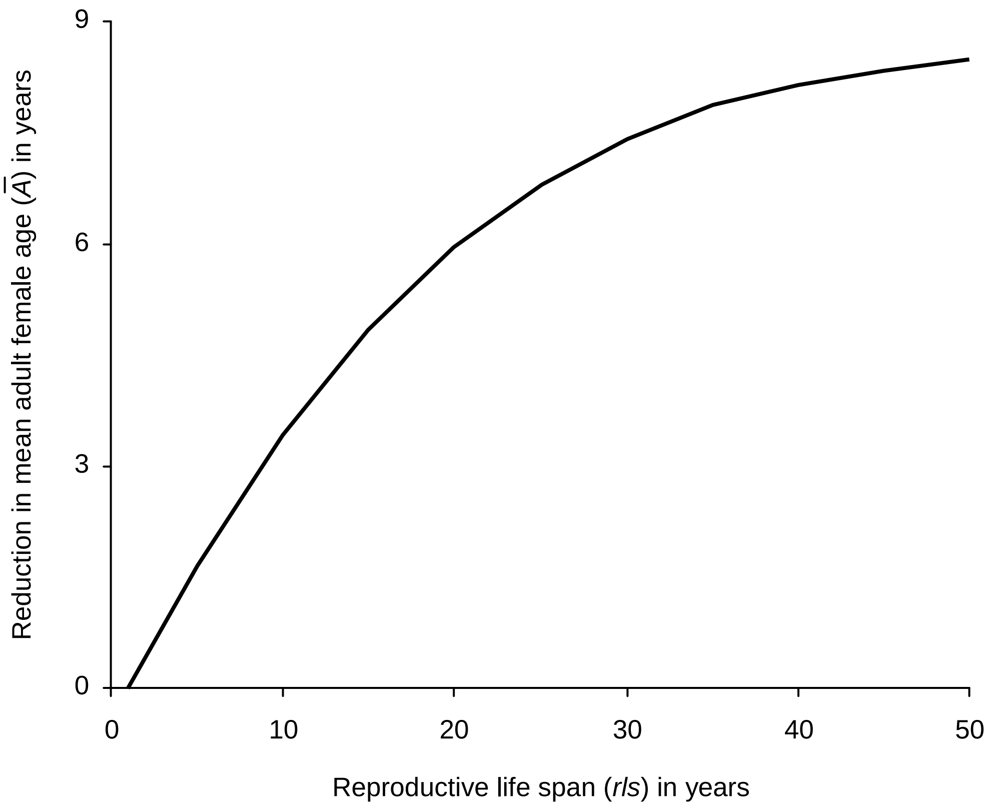

Figure C.1. The reduction in the mean age of adult females ($\overline{A}$) with reproductive life span (RLS) according to equation C.2 and a change in survival (*s*) from 0.9 to 0.2. Population growth rate (λ) was set to 1 so that age structure was stable and the entire reduction in $\overline{A}$ was due to the change in *s*.

Appendix D: **Supplementary material for Chapter 5**

D.1 Additional material related to the pond experiment

D.1.1 Parentage assignment

Offspring sampled from each population on Days 4 and 66 post-hatch were genotyped and assigned to one of 25 parental pairs for each population by matching their microsatellite DNA genotypes with those of the potential parental pairs (Estoup et al. 1998, Johnston et al. 2005). Seven loci were used as described below, six of which were previously published — Svi 4, Svi 17 and Svi 33 from Borer et al. (1999), and Svi 2, Svi 7, and Svi 16 from Eldridge et al. (2002) — with the seventh locus comprising primers redesigned for locus Svi 26 (Borer et al. 1999) using sequences of the flanking region (Genbank Accession Numbers G36965).

Using a DNeasy® (QIAgen, Germany) kit, DNA was extracted from whole offspring and from either the liver or muscle tissue of parents. Six of the seven microsatellites were optimized for a LICOR 4200 automatic sequencer, whereas data for locus Svi 26 were collected using autoradiographic (P^{33}) methods. Amplification for all loci was done in a Biometra T-Gradient Cycler in 10-µL reactions of 1x QIAgen PCR buffer containing 15 mM $MgCl_2$, 0.75 mM of each dNTP, 0.3 µM of each primer (with the forward primer tagged with a 700- or 800-IR dye, or end-labeled with P^{33}) and 0.1 U of Taq DNA polymerase (QIAgen). Thermocycling conditions for six of the seven loci were similar to those previously published, while for Svi 26 we used: 94.0°C for 3 min, then 35 cycles of 94.0°C for 30 s, 62.0°C for 30 s, 72.0°C for 40 s, with a final extension at 72.0°C for 10 min. For microsatellites analyzed on the LICOR 4200, alleles were electrophoresed with commercial standards (Licor 50-350 bp size standards 4200-44 and 4200-44B), and the amplicons were sized using GENE IMAGR 4.05 software (Scanalytics, USA). Svi 26, alleles were sized by including end-labeled amplicons of known size in the electrophoresis of the PCR products, which were subsequently exposed to Biomax MR (Kodak, USA) autoradiographic film.

Characteristics of the loci for the sample of parent fish are summarized in Table D.1. All loci were in H-W equilibrium, and there was no evidence at any locus for null alleles, allelic dropout, or large steps in allele size. The final set of 1,614 offspring analyzed included all samples yielding high molecular weight DNA that reliably amplified, and had missing data at no more than two loci; 765 larvae and 849 juveniles met these criteria, for population samples of 257, 250, and 258 for larvae, and 279, 281, and 289 for juveniles, respectively.

Breeders that are related to each other can complicate parentage assignment; therefore we used GenAlEx 6.2 (Peakall and Smouse 2006) to estimate pairwise relatedness (*r*) between the 25 male and 25 female parents used in our study, where *r* is the arithmetic average of two reciprocal relatedness estimates (Lynch and Ritland 1999). With the caveat that estimates of pairwise relatedness display very large sampling variances (Lynch and Ritland 1999), three groups of comparisons gave the following results: (i) for 300 pairwise comparisons of males, average r = -0.010, range = -0.136 to 0.213, number of values ≥ 0.125 = 5; (ii) for 300 pairwise comparisons of females, average r = -0.013, range = -0.132 to 0.317, number of values ≥ 0.125 = 10; (ii) for 625 pairwise comparisons of males and females, average r = -0.009, range = -0.155 to 0.282, number of values ≥ 0.125 = 22. These data suggest that the adults in the pond experiment were from a relatively large, outbred population, and that complications due to having highly genetically similar adults in our experiment should be minimal, especially since our assignments are to breeding pairs, not to individual male or female parents. Of the 22 male-female pairs with $r \geq 0.125$ (equivalent to first cousins), 3 actually occurred in our design (e.g., 4% of the 75 crosses made). These 3 pairs had an average *r* of 0.143, with one pair in each experimental population.

Offspring were assigned to one of 25 parental pairs in each population with PAPA 2.0 software (Duchesne et al. 2002), using the input option of sexed, structured parental files. Initial parental simulations in PAPA followed by trial assignments of offspring showed that a subset of 4 loci (Svi7, Svi17, Svi26a, Svi33) used with the default non-uniform error model of ± 2 offsets (specified in PAPA as focal allele transmission probabilities of 0.002, 0.008, 0.980, 0.008, 0.00) were predicted to allocate 99+% of offspring to parental pairs with 99+% correctness.

In the production runs of PAPA, offspring with missing values for >2 loci at 7 locus genotypes or >1 locus of 4 locus genotypes were ignored. Subsequent assignment success was 97% averaged across the three larval populations and 96% across the juvenile populations (Tables D.2 and D.3). These included a small number of larvae (6) and juveniles (7) that were identified as ‘ambiguous’ in the 4 locus PAPA analysis, all of which were resolved by reference to full 7 locus genotypes. The remaining 3-4% of samples could not be reliably resolved using the full 7 locus genotypes; these samples were four times more likely to contain missing data than assigned individuals and presumably also contained errors from a variety of sources including mislabeling during collection or processing, data entry, allele sizing, or other lab and data processing procedures. A sample of individuals that were independently amplified and scored by different lab workers suggested that allele sizing error due to molecular lab methods alone was under 0.5% (e.g., 1400 alleles from 100 individuals could include 7 alleles that were scored incorrectly). A variety of other checks validated the basic patterns of family assignment results. Thus, similar results were obtained using PAPA with a different, but almost equally efficient, set of 4 loci. We also conducted a larger set of simulations in which equal numbers of 'pseudo-offspring' were generated from parental pairs outside of PAPA; these were accurately assigned by PAPA, with no tendency for any parental pairs to receive more or fewer offspring than expected by chance, as might happen if PAPA assignments were biased, e.g., because certain parents had several alleles that were particularly common in the population (Enright 2004).

D.1.2 Derivation and calculation of relative offspring survival rate

In this section, we describe the relative rate of offspring survival for each female parent (OS_f). We used the same procedure to derive and calculate a relative offspring survival rate for each male parent (OS_m).

First, we assumed that there was a baseline, instantaneous mortality rate (Z) that applied to all offspring over a given life stage, and that this life stage had a duration = t. Baseline survival of offspring of female k at time t (N_t^k) was therefore

$$N_t^k = N_0^k \cdot \exp(-Z \cdot t) \qquad \text{D.1}$$

where N_0^k is the number of offspring of female k that are alive at time 0. We assumed that female k influenced the survival of her offspring by partially offsetting Z. Therefore, equation D.1 becomes

$$\begin{aligned} N_t^k &= N_0^k \cdot \exp(-(Z - OS_f^k) \cdot t) \\ &= N_0^k \cdot \exp(-Z \cdot t + OS_f^k \cdot t) \qquad \text{D.2} \end{aligned}$$

where OS_f^k refers to the relative survival rate of the offspring of female k. By definition, $0 \le OS_f^k \le Z$.

In our breeding population, let

n = the number of breeding females,

N_0^i = the number of offspring of female i at time 0, and

N_0^T = the total number of offspring in the population at time 0

$$= \sum_{i=1}^{n} N_0^i \, . \tag{D.3}$$

The proportion of all offspring at time 0 that belonged to female k is therefore

$$P_0^k = \frac{N_0^k}{N_0^T} \, , \tag{D.4}$$

and the proportion of all offspring that were alive at time t that belonged to female k is therefore

$$P_t^k = \frac{N_0^k \cdot \exp(-Z \cdot t + OS_f^k \cdot t)}{\sum_{i=1}^{n} N_0^i \cdot \exp(-Z \cdot t + OS_f^i \cdot t)}$$

$$= \frac{N_0^k \cdot \exp(-Z \cdot t)}{N_0^T \cdot \exp(-Z \cdot t)} \cdot \frac{\exp(OS_f^k \cdot t)}{\sum_{i=1}^{n} P_0^i \cdot \exp(OS_f^i \cdot t)}$$

$$= \frac{P_0^k \cdot \exp(OS_f^k \cdot t)}{\sum_{i=1}^{n} P_0^i \cdot \exp(OS_f^i \cdot t)} \tag{D.5}$$

and thus,

$$\ln\left(\frac{P_t^k}{P_0^k}\right) = (OS_f^k \cdot t) + \ln\left(\frac{1}{\sum_{i=1}^{n} P_0^i \cdot \exp(OS_f^i \cdot t)}\right) . \tag{D.6}$$

Because t is the same for all females,

$$\ln\left(\frac{1}{\sum_{i=1}^{n} P_0^i \cdot \exp(OS_f^i \cdot t)}\right)\Bigg)$$

is a common additive constant (C) embedded in each expression of equation D.6, and we can write

$$\ln\left(\frac{P_t^k}{P_0^k}\right) = (OS_f^k \cdot t) + C \, . \tag{D.7}$$

Because $OS_f^k \cdot t > 0$, equation D.7 will reach a minimum when $OS_f^k \cdot t = 0$, an operational estimate of C ($\hat{C}$; survival in the absence of MI) can be derived directly from the observed minimum value of equation D.7 such that

$$\hat{C} = \min\left\{ \ln\left(\frac{P_t^k}{P_0^k} \right) \right\}. \qquad \text{D.8}$$

We therefore estimated the maternal influence of female k as:

$$\hat{O}S_f^k \cdot t = \ln\left(\frac{P_t^k}{P_0^k} \right) - \hat{C}. \qquad \text{D.9}$$

In effect, $\hat{O}S_f^k$ is a measure of OS_f relative to the female whose offspring exhibited the greatest reduction in relative abundance over the time period of interest. P_0^k and P_t^k were calculated using parentage data from Days 4 and 66, respectively. We expressed the number of offspring of female k in a population as the proportion of the total number of offspring that were assigned parentage in that population, and then averaged across populations. We divided $\hat{O}S_f^k$ by 62, the number of days in our experiment, to create a daily rate that was then incorporated into our matrix model.

D.1.3 Determination of parental traits

Each parent was measured (FL to the nearest 1 mm) and weighed (wet tissue mass to the nearest 10 g) as described previously (Wiegand et al. 2007). Because the slope of the log somatic mass on log FL relation did not differ significantly from 3 in either females (2.99 ±1.76 95%CL, t_{23} = 0.085, P = 0.933) or males (3.30 ±1.59, t_{23} = 1.76, P = 0.092), body condition was estimated as Fulton's K:

$$K = \left(\frac{\text{total mass}}{FL^3} \right) \cdot 10^5, \qquad \text{D.10}$$

where 10^5 is a scaling factor that brings the mean K close to 1.0. Adult age (years) was determined from thin (360 µm ±30), transverse sections of sagittal otoliths, or acetate replicas (Casselman and Gunn 1992). An index of relative growth one year prior to spawning was calculated as the percent difference between an individual's FL at age of capture and a standardized FL that was estimated by fitting a von Bertalanffy growth curve to the mean size-at-age data of walleye up to age 18 y from 9 populations, with sexes weighted equally (J. M.

Casselman, unpublished data). Prior to analysis, index values were centered on zero by converting them to a residual about the overall mean, expressed as a percentage.

Total lipid content of eggs, and somatic and liver tissues, as well as egg fatty acid profiles, were determined as described by Wiegand et al. (2004, 2007). Total lipid content was expressed as a proportion of tissue dry mass (g lipid·g^{-1} dry tissue). Because some lipid proportions were <0.2, these data were arcsine square root transformed prior to analysis to normalize the distribution of residuals. Egg fatty acid profiles were developed from the 28 fatty acids that were most prominent in the chromatograms, including the essential fatty acids DHA, eicosapentaenoic acid (EPA), and arachidonic acid (AA; reviewed in Wiegand et al. 2004). DHA was arcsine square root transformed prior to analysis to normalize the distribution of residuals. Because the importance of EPA to the development and survival of young walleye depends upon the relative concentration of AA (reviewed in Wiegand et al. 2004), raw EPA data were converted to residuals around the EPA on AA regression prior to analysis. For each sire, we measured sperm density (sperm·μL^{-1} of milt), sperm tail length (µm), and average sperm swimming velocity (µm·s^{-1}; average path velocity, VAP) at 5 and 10 s after sperm activation (see Casselman et al. 2006 for details). Sperm density was log-transformed prior to analysis to normalize the distribution of residuals.

D.1.4 Paternal influences on offspring survival

With respect to paternal influences, hierarchical partitioning revealed that relative offspring survival was influenced most strongly by sperm concentration in the milt, sperm velocity at 5 s after activation, paternal age, and liver lipid content (Fig. D.2). However, empirical support for multiple linear regression models based on any combination of these traits was weak (Table 5.1). This result was not changed when we repeated our analysis after correcting for effects of females (P. A. Venturelli, unpublished data).

D.2 Additional material related to the population model

D.2.1 Natural mortality

Instantaneous mortality rates for walleye eggs (0.15·d^{-1}; Rose et al. 1999), and for age-1 and older walleye (0.22·y^{-1}; Shuter and Koonce 1977), were obtained from the literature. A daily instantaneous mortality rate of 0.01 in the intervening stages (larvae, and early and late juveniles) was based on an indirect estimate of mortality in the first year of life as follows. First, we estimated from the literature (Myers et al. 1999) that the maximum annual reproductive rate of walleye is 8 new spawners per spawner. Assuming that all walleye mature at age-4 and spawn monogamously, this rate is equivalent to four age-4 spawners per spawning female or, assuming an annual instantaneous mortality rate of 0.22 (Shuter and Koonce 1977), 32 age-1 offspring per spawning female. Because the maximum annual reproductive rate of walleye was estimated from an overexploited (i.e., age-truncated) population (Myers et al. 1999), we then used mean age-4 fecundity (125,000 eggs; Table D.6) as an estimate of offspring that were initially produced by a single spawning female. A loss of 124,968 offspring in the first year of life corresponded to a daily mortality rate of 0.02, or 0.01 after allowing for a daily egg mortality of 0.15 in the first 30 d of life (Rose et al. 1999). The probability of surviving a time-step and remaining in the same life stage (P), and the probability of surviving a time-step and moving to the next life stage (G) were then calculated from both the mortality rate and duration of each life stage (equations 6.97 and 6.98 in Caswell 2000).

D.2.2 Maternal influences

MI were incorporated into the larval and early juvenile stages by subtracting from the daily natural instantaneous mortality rate (0.01) a daily rate of relative offspring survival ($\hat{O}S_f^k$; see Appendix D.1.2) that was specific to each age class of adult females (Table D.6). We incorporated MI into the model in three steps. First, we estimated FL-at-age using data from walleye captured in spring in the Bay of Quinte, Lake Ontario, Ontario, Canada (this study; T. A. Johnston, unpublished data). Second, we used data from 31 populations of walleye (Johnston and Leggett 2002; T. A. Johnston, unpublished data) to predict egg size (ES) from FL. We focused on ES because empirical support was highest for the $\hat{O}S_f^k$-ES model (Table 5.1). We focused on FL because (i) it is a better indicator of maturation (i.e., the onset of egg production) than age (Lester et al. 2000), and (ii) egg size-FL relations are less variable than ES-age relations in both time and space (Johnston and Leggett 2002). We then used the ES model from Table 5.1 to predict $\hat{O}S_f^k$ that increased with adult age. Because this approach produced a much smaller range in egg sizes (0.88 to 0.97 mg dry mass) than was observed in the pond experiment (Table D.4), we modeled a smaller range in $\hat{O}S_f^k$ (0.017 to 0.022·d^{-1}) than was observed in the pond experiment (Table D.4). Given also that we did not apply these MI beyond the late juvenile stage, despite evidence that winter mortality decrease with body size in juvenile walleye (e.g., Rose et al. 1999), our simulations represent a fairly conservative estimate of MI on population dynamics.

D.2.3 Density dependence

We incorporated density-dependence into the early juvenile stage because both predation and competition for resources are highly density dependent at the onset of exogenous feeding (Cowan et al. 2000). We allowed early juvenile mortality to vary positively with density:

$$Z' = Z \cdot (\lambda \cdot \rho_{\mathrm{c}} + 1), \qquad \text{D.11}$$

where λ is a parameter that defines the sensitivity of natural mortality (Z) to the number of individuals at the start of (day 90) and during (days 120 and 150) the early juvenile stage (ρ_{c}). This equation produced a Ricker stock-recruitment relation (Hilborn and Walters 1992); because we were interested in model behaviour close to the origin, results did not change when we used a Beverton-Holt relation. Similarly, the value of λ was arbitrary and did not affect the relative response of population dynamics to different harvest strategies because λ determined the ‘scale ratio’ of the stock-recruitment relation (i.e., how ‘big’ or ‘small’ it was), not its shape.

D.3 Additional material related to the analysis of Lake Erie walleye

D.3.1 Estimates of egg production and recruitment

Walleye data from Lake Erie during the period 1947-1976 were from Kutkuhn et al. (1976) and Shuter et al. (1979) unless otherwise noted. We estimated recruitment (age-3 abundance) by estimating the age-distribution of walleye in each year. Abundance-at-age estimates for 1947-1969 were derived from mark-recapture data, annual estimates of total harvest and catch per unit effort at age, and trawl surveys of young-of-the-year. Abundance-at-age estimates for 1970-1976 were derived by combining abundance estimates of cohorts alive in 1969 with forward projections of annual estimates of young-of-the-year abundance from trawl surveys.

To estimate total annual egg production, we first divided abundance-at-age by 2, which gave the distribution of females assuming a 1:1 sex ratio. We then (i) estimated the fraction of mature females in each age class by means of age-specific maturity schedules, (ii) assigned a mean length to each age class by means of length-at-age data, and (iii) converted length to mass by means of published mass-at-length regressions (Parsons 1972, Wolfert 1977, Muth and Wolfert 1986). Because these published relations were based on information from specific years or groups of years, they largely accounted for documented, density-dependent changes in age-at-maturity, and length- and mass-at-age from 1947-1976. We then calculated the biomass of mature females in each age class by multiplying abundance-at-age by age-specific mass. To estimate the number of eggs produced by each age class, we used data from Lake Erie in 1966 (Wolfert 1969) to predict relative fecundity (RF; eggs per g female) from total length (TL; RF = 39.38 eggs·g^{-1} + 0.075 x TL, $r^2 = 0.20$, $n = 78$, $P < 0.0001$), and then multiplied RF by mature female biomass. Finally, we estimated total annual egg production by summing egg production across all age classes.

D.4 References

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Table D.1. Characteristics of seven dinucleotide repeat microsatellite loci used for parentage analysis, summarized using GenAlEx 6.2 (Peakall and Smouse 2006). Sample size is 50, including the 25 male and female breeders used in the study.

Locus	H_o	H_e	No. alleles	Allele size range (bp)	H-W *P*	F
Svi2	0.880	0.835	8	124-154	0.82	-0.054
Svi7	0.760	0.750	7	174-192	0.25	-0.013
Svi16	0.920	0.906	20	230-284	0.74	-0.015
Svi17	0.660	0.680	8	122-138	0.87	0.029
Svi26a	0.940	0.829	17	268-312	0.57	-0.134
Svi33	0.800	0.840	11	103-123	0.79	0.047
Svi4L	0.740	0.737	9	226-248	0.40	-0.004
Overall	0.814 ± 0.04	0.797 ± 0.03	11.4	-	0.89	-0.020 ± 0.02

Notes: H_o = observed heterozygosity; H_e = expected heterozygosity; allele sizes are number of base-pairs; H-W *P* is probability of departure from Hardy-Weinberg equilibrium (not significant for any locus); F is the fixation index. Averages are ± SE.

Table D.2. Results of the pond experiment showing the distribution of larval and juvenile offspring and the variation in reproductive success among female walleye in populations 1, 2, and 3.

	Larvae (time 0) distribution					Juveniles (time t) distribution				
dam	1	2	3	P_0^k	CV	1	2	3	P_t^k	CV
1	4	3	6	0.02	33.53	2	2	3	0.01	26.16
2	34	25	11	0.09	49.30	22	4	13	0.05	69.46
3	8	12	16	0.05	32.94	8	5	14	0.03	52.30
4	0	2	0	0.00	173.21	2	3	0	0.01	91.15
5	2	5	4	0.01	43.54	1	2	7	0.01	97.71
6	29	22	13	0.09	37.30	36	15	8	0.07	74.48
7	10	15	11	0.05	24.83	4	12	9	0.03	47.52
8	7	16	0	0.03	106.23	9	16	9	0.04	33.89
9	13	12	13	0.05	2.02	17	36	28	0.10	34.27
10	5	17	16	0.05	53.55	3	62	49	0.14	81.06
11	4	6	8	0.02	32.94	20	0	3	0.03	140.38
12	8	21	19	0.07	45.08	4	47	20	0.09	90.47
13	5	4	8	0.02	35.09	4	1	9	0.02	87.48
14	4	3	0	0.01	88.48	5	2	9	0.02	66.98
15	5	7	12	0.03	43.98	16	3	12	0.04	64.80
16	1	9	9	0.03	73.29	3	7	16	0.03	78.11
17	1	0	11	0.02	152.07	0	3	12	0.02	126.04
18	11	4	7	0.03	46.32	1	2	9	0.01	110.14
19	27	12	16	0.07	40.76	27	25	12	0.08	37.51
20	26	8	22	0.07	49.20	11	2	3	0.02	92.68
21	4	0	8	0.02	100.00	6	9	5	0.02	29.45
22	20	15	9	0.06	37.21	53	16	5	0.09	102.50
23	0	3	5	0.01	93.16	5	0	1	0.01	131.94
24	15	16	15	0.06	6.42	10	2	3	0.02	87.38
25	8	3	12	0.03	57.55	2	1	9	0.01	109.88
assigned	251	240	251			271	277	268		
analyzed	257	250	258			279	281	289		
% assign.	97.67	96.00	97.29			97.13	98.58	92.73		
mean no.	10.04	9.60	10.04			10.84	11.08	10.72		
variance	95.12	52.33	32.79			160.72	250.41	102.13		
CV	97.14	75.36	57.03			116.95	142.82	94.27		

Notes: To estimate from these data the survival rate of the offspring of a given female (OS_f^k), we calculated the natural logarithm of the ratio of P_t^k to P_0^k. We then estimated *relative* survival ($\hat{O}S_f^k$) by subtracting from each value of OS_f^k the smallest observed value of OS_f^k (equation D.9). We converted $\hat{O}S_f^k$ to a daily rate by dividing by 62, the number of days in our experiment.

Table D.3. Results of the pond experiment showing the distribution of larval and juvenile offspring and the variation in reproductive success among male walleye in populations 1, 2, and 3.

	Larvae (time 0)					Juveniles (time t)				
	distribution					distribution				
dam	1	2	3	P_0^k	CV	1	2	3	P_t^k	CV
1	4	25	16	0.06	72.07	2	2	3	0.01	26.16
2	0	3	11	0.02	120.25	2	4	14	0.02	97.71
3	8	2	6	0.02	56.02	8	3	13	0.03	63.60
4	34	12	0	0.06	110.80	22	5	0	0.03	128.87
5	2	22	11	0.05	87.81	1	15	9	0.03	83.26
6	7	5	13	0.03	48.43	9	2	8	0.02	60.34
7	10	16	4	0.04	62.18	4	16	7	0.03	67.77
8	29	15	0	0.06	97.45	36	12	9	0.07	78.26
9	13	17	8	0.05	37.83	17	62	3	0.10	111.76
10	8	12	16	0.05	32.94	4	36	49	0.11	78.71
11	4	21	13	0.05	69.15	20	47	28	0.12	42.21
12	5	6	19	0.04	76.71	3	0	20	0.03	140.98
13	5	3	12	0.03	69.61	4	2	12	0.02	89.28
14	1	4	0	0.01	126.44	3	1	9	0.02	96.99
15	5	9	8	0.03	30.16	16	7	9	0.04	44.77
16	4	7	9	0.03	37.57	5	3	16	0.03	88.65
17	1	4	16	0.03	111.93	0	2	12	0.02	138.70
18	26	0	7	0.04	122.31	11	3	9	0.03	54.91
19	27	8	11	0.06	65.25	27	2	12	0.05	91.95
20	11	12	22	0.06	39.21	1	25	3	0.04	136.84
21	4	3	9	0.02	58.84	6	1	5	0.01	66.53
22	0	0	12	0.02	173.21	5	9	9	0.03	29.95
23	15	3	8	0.03	68.44	10	0	5	0.02	99.63
24	20	16	5	0.06	56.70	53	2	1	0.07	159.45
25	8	15	15	0.05	32.99	2	16	3	0.03	110.24
assigned	251	251	240	251		271	277	268		
analyzed	257	257	250	258		279	281	289		
% assign.	97.67	97.67	96.00	97.29		97.13	98.58	92.73		
mean no.	10.04	10.04	9.60	10.04		10.84	11.08	10.72		
variance	95.12	95.12	52.33	32.79		160.72	250.41	102.13		
CV	97.14	97.14	75.36	57.03		116.95	142.82	94.27		

Notes: To estimate from these data the survival rate of the offspring of a given female (OS_m^k), we calculated the natural logarithm of the ratio of P_t^k to P_0^k. We then estimated *relative* survival ($\hat{O}S_m^k$) by subtracting from each value of OS_m^k the smallest observed value of OS_m^k (equation D.9). We converted $\hat{O}S_m^k$ to a daily rate by dividing by 62, the number of days in our experiment.

Table D.4. Maternal traits and relative offspring survival rate of Lake Ontario walleye in the pond experiment.

dam	A	FL	K	RG	SL	LL	ES	EL	ED	EE	$\hat{OS}_f^k$
1	11	700	0.97	136.1	0.160	0.183	0.96	0.393	0.186	1.42	0.010
2	13	695	1.05	129.5	0.207	0.144	0.95	0.368	0.166	1.41	0.011
3	11	676	0.94	131.4	0.214	0.150	0.87	0.384	0.198	1.26	0.015
4	11	652	1.01	126.7	0.294	0.146	1.18	0.405	0.190	1.46	0.034
5	11	668	1.03	129.8	0.204	0.149	1.09	0.362	0.212	1.39	0.019
6	12	671	1.04	127.4	0.265	0.166	1.00	0.376	0.183	1.42	0.019
7	7	570	1.10	128.5	0.251	0.113	1.05	0.372	0.146	2.31	0.014
8	8	625	0.93	134.3	0.195	0.133	1.12	0.399	0.155	1.84	0.026
9	11	697	1.14	135.5	0.201	0.169	1.08	0.381	0.173	1.44	0.032
10	8	621	1.10	133.4	0.200	0.149	1.09	0.391	0.184	1.36	0.038
11	10	655	0.99	130.9	0.174	0.124	0.91	0.409	0.155	1.61	0.024
12	9	646	1.02	133.4	0.259	0.165	1.05	0.383	0.209	1.36	0.026
13	8	587	1.00	126.1	0.198	0.095	1.13	0.386	0.163	2.35	0.017
14	6	554	1.05	132.5	0.224	0.115	1.11	0.375	0.156	1.94	0.033
15	20	725	1.05	125.4	0.147	0.187	0.84	0.365	0.198	1.27	0.024
16	10	707	0.99	141.2	0.270	0.146	0.97	0.379	0.181	1.63	0.025
17	6	512	0.94	122.5	0.231	0.092	1.17	0.388	0.134	2.77	0.024
18	9	671	0.90	138.5	0.238	0.188	1.02	0.375	0.208	1.30	0.010
19	7	545	1.11	122.9	0.312	0.084	0.97	0.383	0.149	2.24	0.023
20	4	503	1.05	142.2	0.293	0.139	0.92	0.395	0.145	2.70	0.000
21	16	742	1.05	132.5	0.246	0.186	1.04	0.387	0.198	1.33	0.028
22	12	691	1.18	131.2	0.229	0.134	1.01	0.401	0.179	1.36	0.028
23	13	711	0.95	132.4	0.238	0.186	0.82	0.400	0.192	1.41	0.015
24	12	711	1.00	135.0	0.099	0.221	0.75	0.356	0.210	1.23	0.002
25	4	500	0.99	141.3	0.269	0.147	0.76	0.378	0.203	1.31	0.010
min.	4	500	0.90	122.5	0.099	0.084	0.75	0.356	0.134	1.23	0.000
max.	20	742	1.18	142.2	0.312	0.221	1.18	0.409	0.212	2.77	0.038
ave.	10	641	1.02	132.0	0.225	0.148	0.99	0.384	0.179	1.64	0.020

Notes: A = age (y), FL = fork length (mm), K = condition ($g \cdot mm^{-3} \cdot 10^5$), RG = residual growth (%), SL = somatic lipid (proportion of dry mass), LL = liver lipid (proportion of dry mass), ES = egg size (mg dry mass), EL = egg total lipid (proportion of dry mass), ED = egg docosahexaenoic acid (proportion of total egg fatty acid), EE = egg eicosapentaenoic:arachidonic acid ratio, $\hat{OS}_f^k$ = relative offspring survival rate among dams. Some traits were transformed prior to analysis (Appendix D.1.3).

Table D.5. Paternal traits and relative offspring survival rate of Lake Ontario walleye in the pond experiment.

sire	A	FL	K	RG	SL	LL	SD	TL	5V	10V	$\hat{\mathrm{O}}\mathrm{S}_{\mathrm{m}}^{\mathrm{k}}$
1	9	575	1.10	110.6	0.207	0.227	15.4	29.78	120.9	122.6	0.000
2	17	624	1.24	100.1	0.236	0.272	11.5	31.05	147.6	121.5	0.036
3	5	518	1.05	103.9	0.249	0.109	17.2	34.63	147.4	126.1	0.037
4	14	598	1.03	94.1	0.176	0.241	13.7	32.35	72.2	98.3	0.022
5	9	528	1.21	101.1	0.266	0.280	13.0	32.19	134.0	123.1	0.024
6	10	583	1.11	106.5	0.227	0.205	16.9	34.43	129.4	100.1	0.026
7	5	456	1.01	96.0	0.184	0.234	11.9	33.18	116.3	85.8	0.028
8	11	647	1.16	115.6	0.288	0.211	12.9	31.91	130.7	117.8	0.034
9	10	641	1.15	103.6	0.291	0.390	11.7	31.30	124.0	109.7	0.042
10	16	621	1.14	104.1	0.161	0.268	12.2	30.01	124.7	104.6	0.045
11	13	561	1.18	98.9	0.201	0.171	11.8	33.06	127.5	116.9	0.045
12	11	579	0.97	98.3	0.197	0.181	12.9	31.79	126.8	98.7	0.026
13	12	641	1.41	112.8	0.355	0.120	10.5	29.73	135.9	113.7	0.029
14	9	551	1.16	102.2	0.204	0.218	13.4	28.99	142.0	104.9	0.045
15	9	541	1.00	101.0	0.151	0.148	14.4	29.00	131.5	93.1	0.036
16	7	541	1.08	96.7	0.208	0.144	13.6	28.56	141.4	85.3	0.033
17	4	455	1.16	95.9	0.254	0.190	14.8	30.25	150.7	104.1	0.024
18	18	685	1.13	98.3	0.104	0.207	12.9	30.50	143.5	78.8	0.025
19	15	638	1.19	105.9	0.206	0.399	20.0	31.09	140.9	122.5	0.028
20	8	572	1.20	100.3	0.269	0.308	17.3	30.89	141.1	96.0	0.023
21	14	615	1.38	103.4	0.320	0.186	12.1	29.59	145.1	91.6	0.026
22	12	634	1.11	106.0	0.254	0.207	17.4	29.24	130.3	62.1	0.041
23	9	594	1.26	104.8	0.271	0.206	13.8	31.20	118.1	42.3	0.022
24	14	638	1.09	114.2	0.203	0.214	13.9	30.53	na	na	0.035
25	11	584	1.09	101.1	0.270	0.156	16.4	30.85	133.1	88.4	0.020
min.	4	455	0.97	94.1	0.104	0.109	10.5	28.56	72.2	42.3	0.000
max.	18	685	1.41	115.6	0.355	0.399	20.0	34.63	150.7	126.1	0.045
ave.	11	585	1.14	103.0	0.230	0.220	14.1	31.04	131.5	100.3	0.030

Notes: A = age (y), FL = fork length (mm), K = condition ($\mathrm{g \cdot mm^{-3} \cdot 10^{5}}$), RG = residual growth (%), SL = somatic lipid (proportion of dry mass), LL = liver lipid (proportion of dry mass), SD = sperm density (millions of sperm·μL^{-1} of milt), TL = average sperm tail length (µm), 5V = average path velocity (VAP in $\mu m \cdot s^{-1}$) at 5 s after activation, 10V = VAP at 10 s after activation, $\hat{\mathrm{O}}\mathrm{S}_{\mathrm{m}}^{\mathrm{k}}$ = relative offspring survival rate among sires, na = data not available. Some traits were transformed prior to analysis (Appendix D.1.3).

Table D.6. Age-specific parameters used in the stage-within-age matrix projection model.

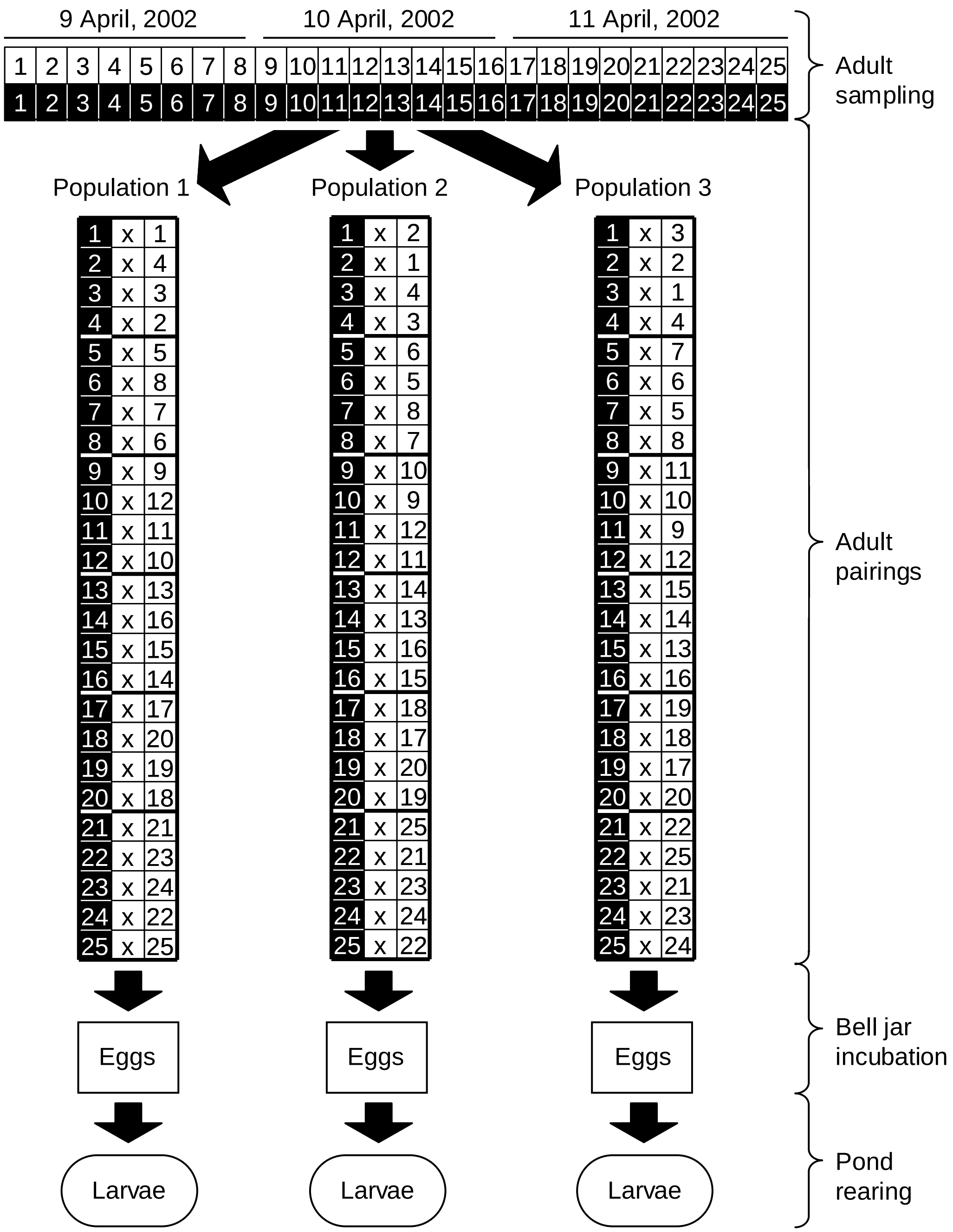
parameter	model	r^2	Notes
FL	$359.60 \cdot A^{0.247}$	0.93	pre-maturation growth was linear
M	$542.33 \cdot A^{0.782}$	0.91	pre-maturation growth was linear
RF	$78.644 \cdot M - 0.262$	0.20	Mature walleye only
ES	$0.234 \cdot \ln(FL) - 0.57$	0.13	Mature walleye only
OS_f	$0.057 \cdot ES - 0.033$	0.41	Mature walleye only

Notes: Parameter values for fork length (FL, mm), mass (M, g), age-at-maturity (4 years), and maximum age (20 years) were estimated by regression using data from walleye captured in the Bay of Quinte, Lake Ontario (Ontario, Canada) each spring from 2002-2005 (this study; T. A. Johnston, unpublished data). The relation for relative fecundity (RF, eggs·g^{-1} M) was derived from data in Wolfert (1969), and the relation for egg size (ES, mg dry mass) was based on data from 31 populations of walleye (Johnston and Leggett 2002; T. A. Johnston, unpublished data). Values of relative offspring survival rate ($\hat{O}S_f^k$) for each female were estimated from both egg size (ES) and FL (see Appendix D.2.2 for details). A = age (years). r^2 = coefficient of determination.

Table D.7. Lake Erie walleye and environment data, 1947-1976.

Year	ΔT	W	$\overline{A}$	TEP	R
1947	0.19	173.99	4.18	8.79 x 10^{10}	5.67 x 10^{6}
1948	0.19	174.09	4.39	1.02 x 10^{11}	5.20 x 10^{6}
1949	0.21	174.31	4.44	5.12 x 10^{10}	6.10 x 10^{6}
1950	0.22	174.50	4.21	6.21 x 10^{10}	2.98 x 10^{6}
1951	0.23	174.32	4.12	5.39 x 10^{10}	2.98 x 10^{6}
1952	0.27	174.26	3.84	5.41 x 10^{10}	7.10 x 10^{6}
1953	0.18	174.34	4.04	5.31 x 10^{10}	1.20 x 10^{6}
1954	0.21	174.09	3.79	4.39 x 10^{10}	5.42 x 10^{6}
1955	0.28	174.03	3.36	6.47 x 10^{10}	2.91 x 10^{6}
1956	0.19	173.81	3.89	4.00 x 10^{10}	1.29 x 10^{6}
1957	0.21	173.83	3.31	6.59 x 10^{10}	4.30 x 10^{5}
1958	0.17	174.08	3.59	6.96 x 10^{10}	2.10 x 10^{5}
1959	0.24	174.08	3.31	2.47 x 10^{10}	3.33 x 10^{6}
1960	0.17	173.89	3.89	3.07 x 10^{10}	1.10 x 10^{5}
1961	0.24	173.73	3.43	9.46 x 10^{9}	4.10 x 10^{5}
1962	0.29	173.59	3.08	5.97 x 10^{10}	3.59 x 10^{6}
1963	0.20	173.68	3.70	8.42 x 10^{9}	5.60 x 10^{5}
1964	0.32	173.87	3.61	1.63 x 10^{9}	5.30 x 10^{5}
1965	0.36	174.03	3.06	1.12 x 10^{10}	1.97 x 10^{6}
1966	0.10	174.19	3.63	4.64 x 10^{9}	1.70 x 10^{5}
1967	0.13	174.36	3.27	5.31 x 10^{9}	2.40 x 10^{5}
1968	0.12	174.24	3.03	3.23 x 10^{10}	3.20 x 10^{5}
1969	0.24	174.31	3.69	1.10 x 10^{10}	9.70 x 10^{5}
1970	0.31	174.46	3.29	7.72 x 10^{9}	5.28 x 10^{6}
1971	0.21	174.91	3.14	1.84 x 10^{9}	5.80 x 10^{5}
1972	0.20	174.85	3.07	1.70 x 10^{10}	4.02 x 10^{6}
1973	0.17	174.78	3.12	9.43 x 10^{10}	1.27 x 10^{6}
1974	0.19	174.75	3.96	8.94 x 10^{10}	9.50 x 10^{6}
1975	0.21	174.46	3.73	1.22 x 10^{11}	5.05 x 10^{6}
1976	0.14	174.54	4.30	1.09 x 10^{11}	1.31 x 10^{6}

Notes: ΔT = spring warming rate (^{o}C·g^{-1}, Shuter et al. 1979), W = water level (m, Koonce et al. 1996), $\overline{A}$ = mean age of adult females (years), TEP = total annual egg production (number), R = recruitment (age-3 abundance).



Population 1	Population 2	Population 3
1 x 1	1 x 2	1 x 3
2 x 4	2 x 1	2 x 2
3 x 3	3 x 4	3 x 1
4 x 2	4 x 3	4 x 4
5 x 5	5 x 6	5 x 7
6 x 8	6 x 5	6 x 6
7 x 7	7 x 8	7 x 5
8 x 6	8 x 7	8 x 8
9 x 9	9 x 10	9 x 11
10 x 12	10 x 9	10 x 10
11 x 11	11 x 12	11 x 9
12 x 10	12 x 11	12 x 12
13 x 13	13 x 14	13 x 15
14 x 16	14 x 13	14 x 14
15 x 15	15 x 16	15 x 13
16 x 14	16 x 15	16 x 16
17 x 17	17 x 18	17 x 19
18 x 20	18 x 17	18 x 18
19 x 19	19 x 20	19 x 17
20 x 18	20 x 19	20 x 20
21 x 21	21 x 25	21 x 22
22 x 23	22 x 21	22 x 25
23 x 24	23 x 23	23 x 21
24 x 22	24 x 24	24 x 23
25 x 25	25 x 22	25 x 24

Figure D.1. Experimental design showing the set-up and treatment of 3 populations, each with full-sib offspring from 25 unique parental matches. Numbered cells represent individual adult walleye (black = males, white = females). Boxes within a population identify groups of males and females that were matched at similar times to minimize effects of storage on the viability of gametes. Hatching was complete by 2 May (Day 0). Larvae were sampled on 6 May (Day 4), stocked into ponds one day later, and re-sampled on 7 July (Day 66).

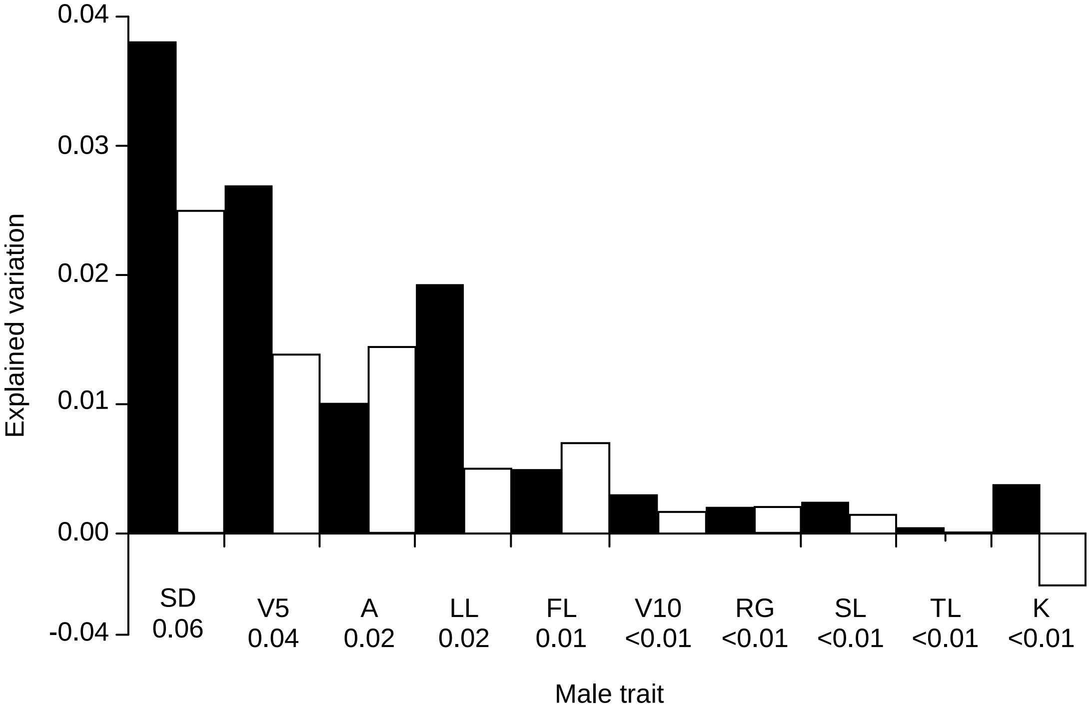


Figure D.2. Independent (closed bars) and joint (open bars) contributions to the variation in relative offspring survival rate that was explained by each male trait, as determined by hierarchical partitioning. Independent and joint contributions refer to effects that were specific to that trait, and effects that were shared with other traits, respectively. The total (independent + joint) proportion of variation explained by each trait is given in parentheses. SD = log sperm density (sperm·µL^{-1} of milt), RG = residual growth (%), V10 = average curvilinear sperm swimming velocity (VAP in µm·s^{-1}) at 10 s after activation, LL = arcsine square root liver lipid, SL = arcsine square root somatic lipid, A = age (y), TL = sperm tail length (µm), FL = fork length (mm), K = condition (g·mm^{-3}·10^{5}), V5 = VAP at 5 s after activation (µm·s^{-1}).

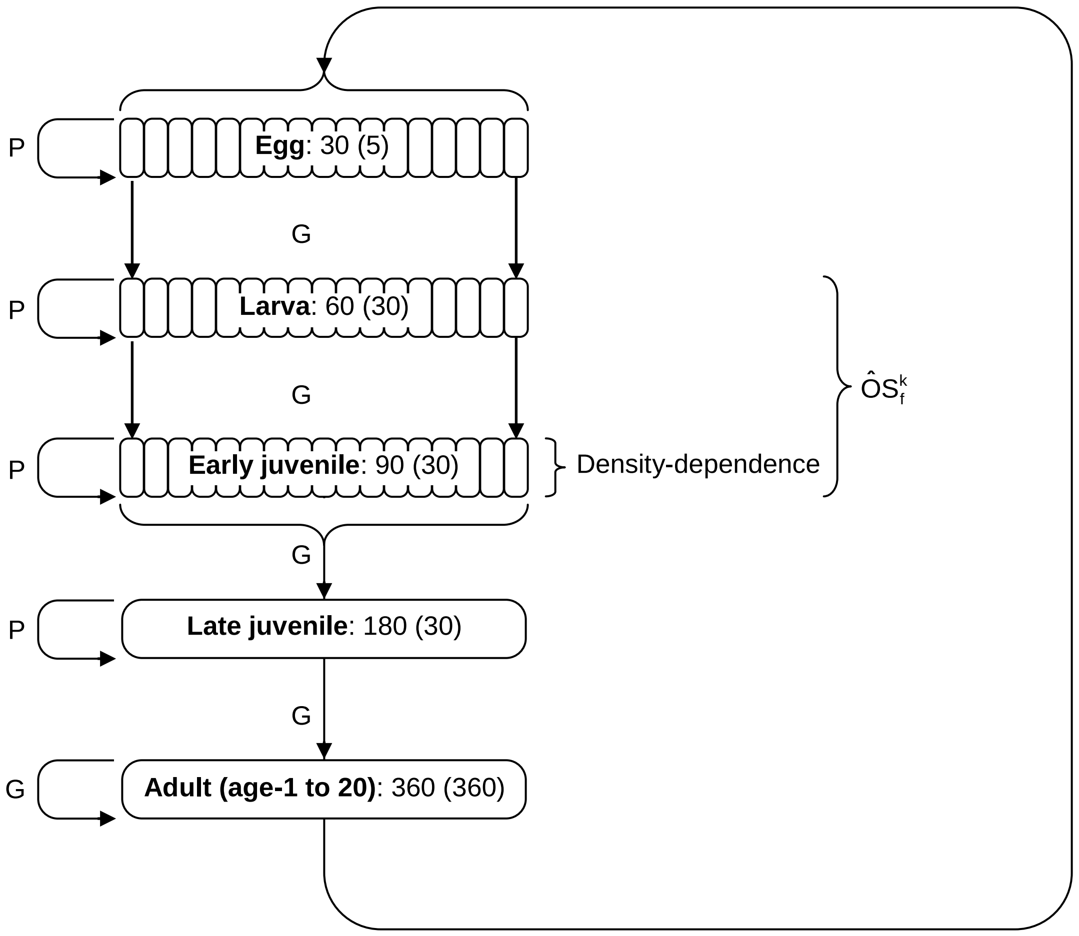


Figure D.3. Movement diagram of the stage-within-age matrix projection model. Egg, larva (free-swimming), early juvenile (piscivorous), late juvenile (overwintering), and adult lifestages are represented by boxes. Offspring from female age-classes 4-y to 20-y were modeled as separate groups through the egg, larva, and early juvenile life stages; thereafter, they were modeled as a single cohort. Numbers after colons are stage durations, with stage time-steps in parentheses, both in days. Mortality in the early juvenile stage was density-dependent. Mortality in the larva and early juvenile stages included relative offspring survival rates ($\hat{\text{O}}\text{S}_{\text{f}}^{\text{k}}$) that were specific to mature female age classes. P = the probability of surviving a time-step and remaining in the same life stage, and G = the probability of surviving a time-step and moving to the next life stage (Caswell 2002). Within a stage, P and G did not vary among groups of offspring. Model structure and parameters were based on the biology of walleye, but are qualitatively similar to those of any harvestable fish species with a periodic life-history (Winemiller and Rose 1992).

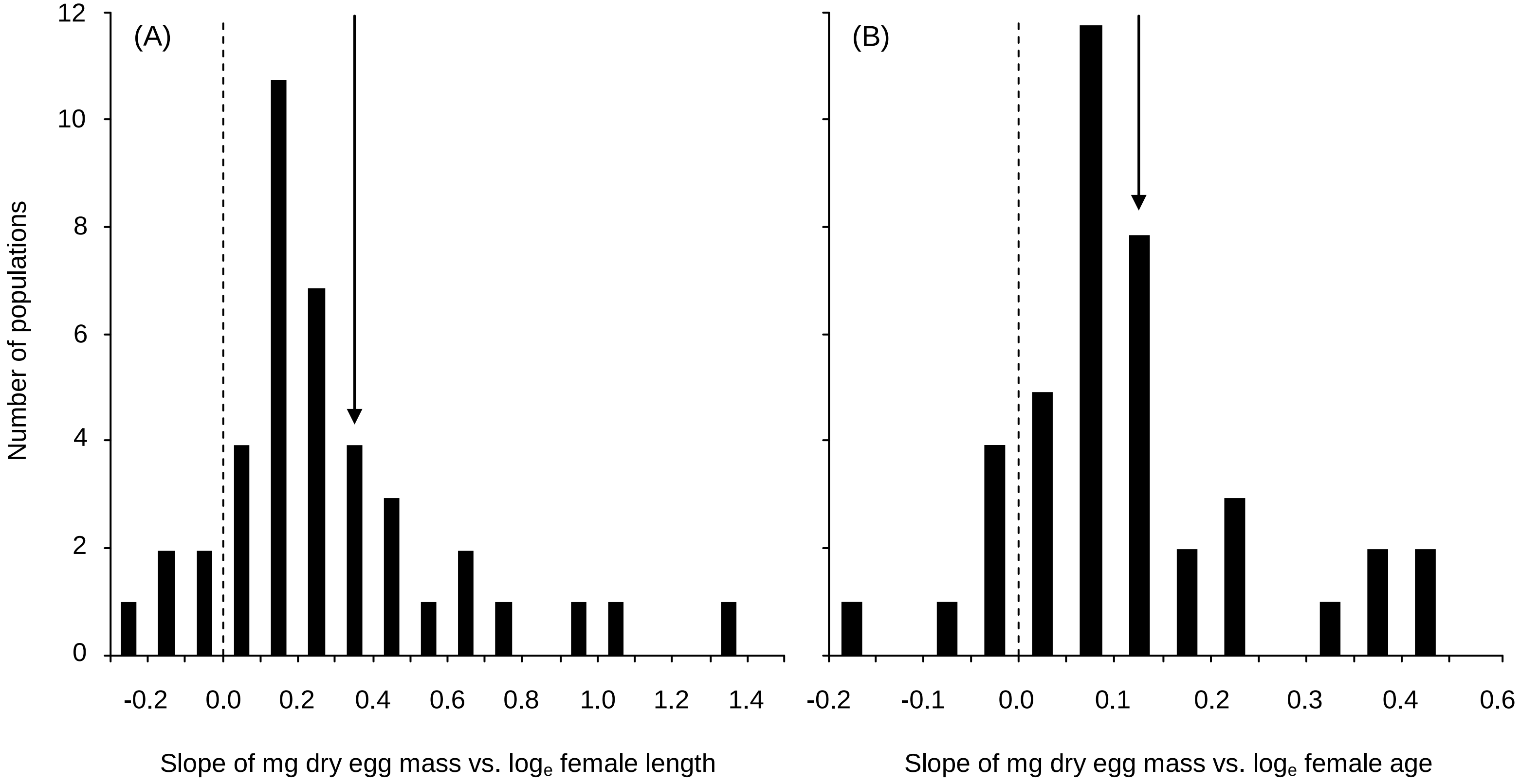
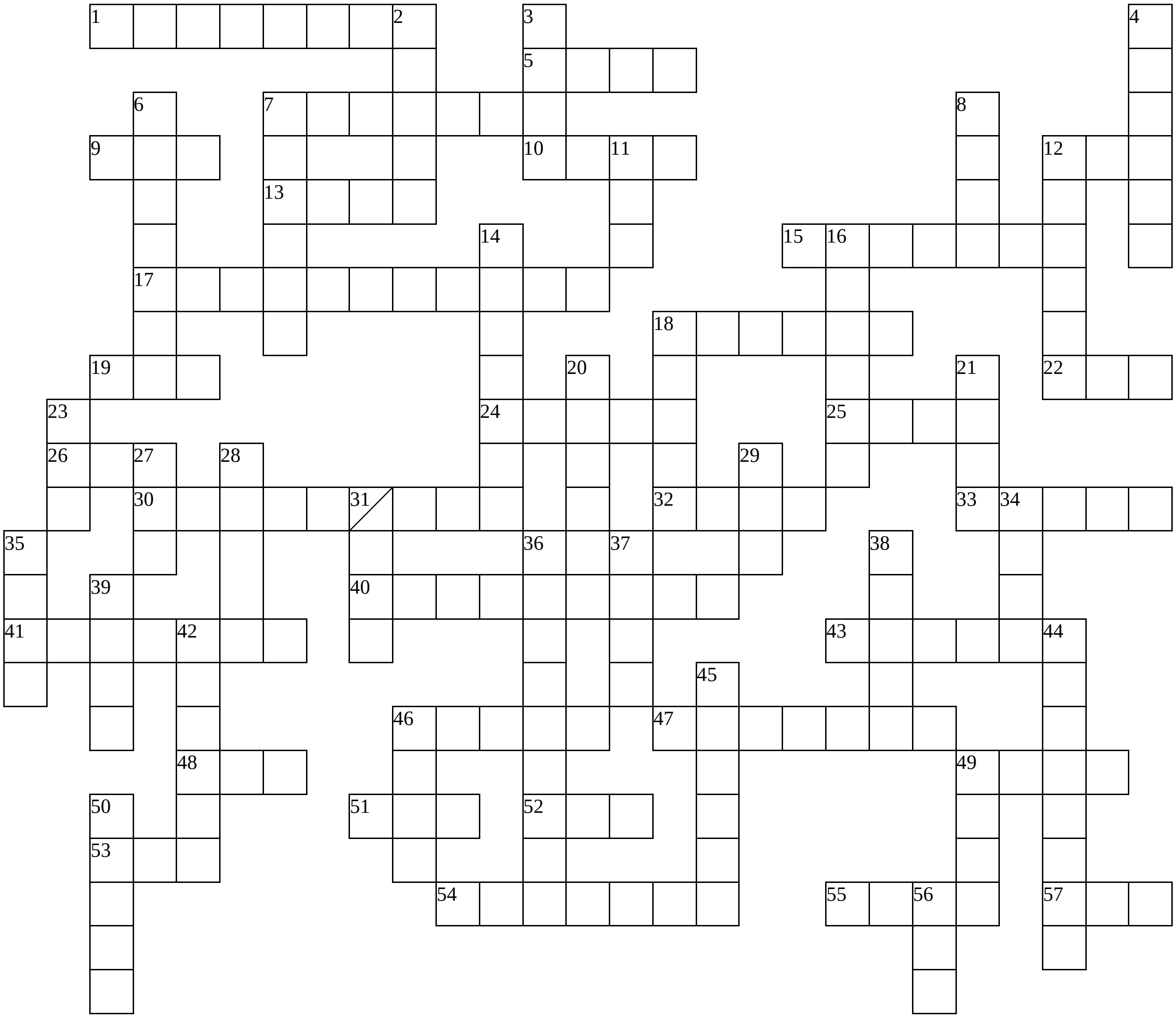


Figure D.4. The distribution of the slope of relations between egg mass (mg dry mass) and (A) log$_e$ female fork length (mm), and (B) log$_e$ female age (years) for 41 walleye populations. Data are from Johnston and Leggett (2002; 34 populations) and T. A. Johnston (unpublished data; 7 populations). Dashed lines identify a slope of 0, and arrows denote the mean slope across all populations.

Appendix E: **Keywords**



ACROSS
1 New individuals
5 Max. reproductive ___
7 *Alma matter*
9 Famous gadid
10 Most acknowledged
12 Part of MI
13 Great lake
15 Exploit
17 Spawns more than once
18 Age group
19 Post-doc inst.
22 Department acronym
24 'Goal' model
25 ___-analysis
26 Temperature index (acronym)
30 Number of eggs
32 Once around the sun
33 Fish population
40 M, F, or Z
41 External external
43 Walleye genus
46 Representation
47 Author's middle name
48 Acknowledgements page
49 Ontario gill net survey
51 Lipid
52 Employer of 24 Across and 4 Down
53 Degree granted
54 Concentration
55 Helen of Committee
57 Model selection metric

DOWN
2 Rise over run
3 Become larger
4 Toronto street or supervisor
6 Internal external
7 Strong hypothesis
8 ___ history
11 No. of adult yrs (acronym)
12 Ripen
14 Steward of Shoal Lake
16 'Hydra' supervisor
18 Walleye Synopsis author
20 Female gametes
21 Saginaw and Quinte
23 Get older
27 FOC acronym
28 Structure for aging
29 Part of ANCOVA
31 Fisher. ind. ___
34 *t*
35 Information
36 'Aging' co-author
37 Actinopterygia, to most
38 Release 20 Down and 50 Down
39 Crooked ___ Lake
42 An interval of time
44 Remainder
45 Radical or tubular synonym
46 Hateful average?
49 Limited at high density
50 Male gametes
56 Part of MDNR

Solution on next page

		R	E	C	R	U	I	T	S			G														S
									L			R	A	T	E											H
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			I	T	E	R	O	P	A	R	O	U	S						B					U		
			N			Y					S				C	O	H	O	R	T				R		
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	E		F	E	C	U	N	D	E/I	T	Y		S		Y	E	A	R				S	T	O	C	K
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T	R	I	P	P	E	L			L			S		S					S	A	N	D	E	R		
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				I	V				E			L				A						F	W	I	N	
		S		O				F	A	T		M	N	R		R						O		D		
		P	H	D					N			A				L						O		U		
		E								D	E	N	S	I	T	Y			R	O	D	D		A	I	C
		R																			E			L		
		M																			P					