Intra-Specific Life History Variation of Great Lakes Fishes: Environmental and Fisheries-Induced Selection

by

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Abstract

Life history traits are important determinants of fish population dynamics and may provide insight as to how populations will respond to current and future environmental conditions and stressors. However, given that most life history traits respond to both genetic and environmental processes, it is difficult to elucidate processes underlying life history trait variation. Through a combination of methodologies, I considered intra-specific variation of important life history traits, i.e., maturation, growth and egg size, for two fish in the Great Lakes: lake whitefish (*Coregonus clupeaformis*) and walleye (*Sander vitreus*). Abundance of both lake whitefish and walleye stocks have fluctuated across spatial and temporal scales, due to harvest, habitat degradation, and ecosystem changes. Using several analytic methods (age and length at 50% maturity, age-specific maturity ogives, and probabilistic maturation reaction norms), I demonstrated that spatial and temporal variation of maturation schedules for lake whitefish and walleye could be partitioned into plastic (changes in maturation schedules due to different growth rates) and potential adaptive variation (selection-induced changes in maturation schedules). For example, after accounting for different growth rates, lake whitefish in three Upper Great Lakes (lakes Michigan, Huron, and Superior) expressed intrinsically different maturation schedules, apparently corresponding to relative levels of natural and fishing mortality. Further, to investigate potential fishing-induced selection on maturation schedules and growth, I developed a generalized eco-genetic individual-based model

(IBM). By running simulations with various harvest scenarios, I demonstrated that selectively harvesting large fish might impose selection that favored slow growth rates and early maturation schedules, leading to unsustainable fisheries. Conversely, harvesting small fish might achieve sustainability by promoting fast growing and delayed maturity. Moreover, I showed significant variation in egg size among five walleye stocks in the Great Lakes region, and that such inter-stock egg size variation appeared to correspond to quality (e.g., primary production) of spawning habitats. Collectively, this research demonstrates that life history variation is attributable to both genetic and plastic factors and that both environmental and anthropogenic processes can influence life history expression. Thus, effective fisheries management must account for both ecological and evolutionary consequences on life history variation.

Chapter I

Introduction

Introduction

Intra-specific life history variation reflects interactions of genetic and environment processes among individuals and populations. Understanding variation of key life history traits (that influence fitness of a population) could help elucidate population dynamics in response to current and future environmental conditions. Herein, I focus on intra-specific variation of two important life history traits, maturation and egg size, for two fish in the Great Lakes: lake whitefish (*Coregonus clupeaformis*) and walleye (*Sander vitreus*). Both traits are essential to determination of population growth rates, and are thus important for assessing stock resilience under a varying environment including anthropogenic induced perturbations. Further, there is considerable evidence that these traits vary among con-specific fish stocks, suggesting that differential local effects may in part contribute to expression of these traits in specific environments.

Variation in these life history traits may reflect both genetic variability and phenotypic plasticity. Although these traits tend to be highly plastic, several studies have shown that average heritability (h^2~ 0.2-0.3; Roff 1992; Law 2000) for life history traits could be high enough to react to genetic selection. Further, empirical data suggest that even with a relatively low heritability many life history traits are able to evolve (Heath et al. 2003 for egg size; Swain et al. 2007 for growth rates; Reznick et al. 2005 for maturation schedules). Moreover, traits may co-vary, due to either genetic or phenotypic correlation, upon local selection factors. Thus, selection that acts on one trait may induce changes in multiple traits.

A well-known example of evolutionary life history variation is countergradient variation in growth rates demonstrated by Conover and Schultz (1995) and Conover (1998). The authors suggest that latitudinal adaptation of growth rates of conspecific fish stocks may correspond to differential size-dependent winter mortality rates, i.e., severe winter at high latitudes may impose selection that favors fast growth rates. If life history variation can be shaped by natural mortality, then it is likely that anthropogenic activities (e.g., fisheries operation) could also induce evolutionary changes in these traits. Fisheries harvest imposes selection (mortality) at much higher intensity than most natural mortality sources, and is often selective--based on body size, age, or location. Furthermore, it is interesting to investigate potential fisheries-induced selection on life history parameters because it often counteracts natural selection (Carlson et al. 2007). In the long term, the evolutionary consequences of fishing could negatively affect sustainability (Jørgensen et al. 2007).

Variation in maturation schedules and egg size

For a given fish species, maturation schedules (age and size at which fish reach maturity) and egg size vary widely among individuals and across different stocks. Such variation may be attributed to genetic variability (G), environmentally-induced phenotypic plasticity (E), and interactions between these components (GxE). For example, using a common garden experiment McDermid et al. (2007) demonstrated that lake trout (*Salvelinus namaycush*) display genetic distinctness in egg size, growth rates, and age and length at maturity, as well as phenotypic plasticity in age at maturity and growth.

Because both maturation schedules and egg size are vital to the resilience of a fish population (Stearns 1992; Trippel 1995), it is important to understand variation and directions of changes in these traits in order to manage fishery resources effectively. In fact, maturation of fishes has been used as a surrogate to monitor fish population dynamics (Trippel 1995, M. Cardinale 1999). However, because variation of egg size and maturation is often highly plastic, and simultaneously determined by environmental and genetic processes, it is often difficult to find clear trends in these traits in relation to extrinsic factors.

Changes in fish maturation schedules or egg size may affect lifetime reproductive success of individual fish and the productive capacity of populations. When everything else is equal, a shift towards early maturation may lead to a shorter generation time and increased lifetime egg production (Jensen 1981). However, owing to trade-offs between growth and reproduction and between current and future reproduction (Roff 1983; Stearns 1992), early maturation may lower lifetime reproductive output and thus impair population growth (Heino 1998). Furthermore, for many species, offspring fitness tends to be positively correlated with age or size of parents, whereby precocious spawners may contribute little to population recruitment. Similarly, egg size could have significant effects on population productivity. Egg size could influence fitness of both offspring and females (Stearns 1992; Berkeley et al. 2004), i.e., while offspring fitness tends to increase with egg size, due to the trade-off between egg size and egg number, female fecundity may decrease with egg size. Consequently, for a population with a particular environmental and genetic background, selection may favor an optimal egg size.

Effects of size-selective fisheries mortality on maturation and growth variation

Many studies have shown that fishery exploitation may induce changes in maturation schedules (e.g., Spangler et al. 1977; Diana 1983; Stokes et al. 1993). Recent studies suggest that such fishing-induced effects may occur through plastic and genetic processes (e.g., Trippel 1995; Law 2000). Fishing increases mortality of a population and reduced population density may lead to a decrease in the intensity of intra-specific competition. Thereby, individual fish may grow faster and mature earlier and at larger size. In addition, fishing may affect life history patterns, either by increasing overall mortality rates or through a size-dependent selective process. Life history theory predicts that elevated mortality rates selects for early maturation schedules (Stearns 1992). Further, as most fishing gears are size-selective, removal of large (or old) fish may induce a selection force that favors early maturation and maturation at small size. Similarly, size-selective mortality may select for slower genetically-determined growth rates, whereby fish that grow slowly may be less vulnerable to fisheries.

Empirical data have shown that many commercially-harvested stocks display shifts in age and size at maturity toward earlier maturation and smaller size-at-age over time (e.g., summarized in Jørgensen et al. 2007). This is consistent with the hypothesis that fishing may induce genetic changes in maturation and growth despite relatively low heritability levels (Law 2000). While simultaneous environmental effects could interact with fishing-induced changes of growth and maturation schedules, several studies suggest that size-selective mortality by fishing still could cause conspicuous effects. A noteworthy study by Rijnsdorp (1993) showed that temporal decreases in length and age at maturity for female North Sea plaice (*Pleuronectes platessa*) could not be fully explained by concurrent changes in juvenile growth; the unexplained trend in maturation schedules may be attributable to genetic changes. Similarly, using statistical analyses Sinclair et al. (2002a, 2002b) showed strong effects by size-selective fishing mortality on size-at-age of adult Atlantic cod (*Gadus morhua*) when accounting for the effects of population density and temperatures. Moreover, the trends for small size-at-age of adult cod did not reverse after closure of fisheries (Sinclair et al. 2002b), suggesting that size-selective mortality by fishing could have decreased genetic variability for growth expression (also see Smith et al. 1991).

Given numerous indications of potential fishing-induced life history evolution, it is important to elucidate and account for such effects in fisheries management (Jørgensen et al. 2007). Notwithstanding studies based on model simulations or under specific laboratory environments, there is currently limited clear evidence of causal relationships between fishing and genetic changes (Hutchings and Fraser 2008). Hence, future studies that provide linkages between size-selective fishing mortality and genetic dynamics in natural systems will be critical to address evolutionary implications in fisheries management (Kuparinen and Merilä 2007).

Partitioning plasticity and genetic variation in maturation

Due to the complex nature of genetic and environmental interactions, it can be challenging to dissect causes of life history variation. For example, a common measure of maturation schedules (age and length at 50% maturity, hereafter referred as A_{50} and L_{50}) can not distinguish variation due to phenotypic plasticity and genetic variability (Heino et al. 2002). Thus, it may be misleading to diagnose spatial and temporal trends in maturation processes using A_{50} and L_{50}, unless the environmental conditions and the sampling protocols are relatively constant across space and over time.

By accounting for phenotypically plastic responses of maturation to growth, the probabilistic maturation reaction norm (PMRN) approach overcomes this limitation; it can be used to diagnose population-level adaptive variation in maturation (Dieckmann and Heino 2007). PMRNs are based on theoretical maturation reaction norms (MRN, Stearns and Koella 1986; Stearns 1992) that characterize the plastic maturation processes as a genetically-based function expressed in different environmental conditions (e.g., growth rates). For a population, a PMRN describes the probability of maturation for immature individuals of given age, length, body condition, etc. (Heino et al. 2002), such that if two populations have distinct (e.g., $P<0.05$) age-specific PMRN estimates, their maturation schedules would likely be genetically distinct. Several studies have applied PMRN approaches to demonstrate plastic and genetic variation in maturation schedules of several marine and freshwater fishes (e.g., Grift et al. 2003; Olsen et al. 2004; Dunlop et al. 2005).

Dissertation chapters

In the Great Lakes region, lake whitefish and walleye constitute long-standing economically valuable fishery resources. Due to a number of reasons (e.g., overfishing, habitat degradation, and/or competition or predation with exotic species), harvest production and abundances of many Great Lakes lake whitefish and walleye stocks fluctuated, and some stocks dramatically declined during the mid-20th century. Stock-specific mean age and length at maturity are highly variable, and the mean ages at maturity of the most intensively exploited lake whitefish and walleye stocks (lake whitefish in Lake Michigan and walleye in western Lake Erie) have continued to decline (but lengths at maturity were variable; Parsons 1972; Muth and Wolfert 1986; Taylor et al. 1992; Muth and Icks 1993).

While there is clear conspecific inter-stock variation in maturation schedules of Great Lakes lake whitefish and walleye stocks, the underlying mechanisms of this variation (e.g., genetic vs. plastic bases) have not been fully evaluated. Furthermore, although previous studies demonstrate early maturation and increased growth and fecundity in exploited lake whitefish and walleye stocks (Henderson et al. 1983; Baccante and Reid 1988; Taylor et al. 1992), it is unclear whether such changes were plastic or genetic responses. To ensure the sustainability of lake whitefish and walleye fishery resources, information regarding the potential long-term effects of fishing on maturation schedules should be assessed and used to inform management decisions.

Similarly, to promote fisheries sustainability we must understand the factors that affect recruitment variability. Several studies suggest that egg size may be pivotal to fitness of offspring for walleye, whereby post-hatching growth and survival rates tend to increase with egg size (Johnston 1997; Johnston et al. 2007). However, the realized effects of egg size on offspring fitness may depend on habitat quality (Einum and Fleming 1999); e.g., the effects of egg size on larval growth and survival may be more pronounced in a relatively poor growth environment. Walleye are widely distributed in

North American, utilize different spawning habitats, and display a wide range of egg size variation across stocks. However, relatively little research has quantified inter-stock variation in egg size in relation to early life habitat quality (but see Johnston and Leggett 2002).

My objectives are to 1) investigate spatial and temporal variation of maturation (for lake whitefish and walleye) and egg size (for walleye) among con-specific fish stocks, and 2) understand the mechanisms through which plastic and genetic changes in maturation and growth may influence dynamics of fish in the Great Lakes region. The five research chapters (chapters II-VI) in my dissertation address these issues. Chapters II and III present statistical analyses of maturation schedules for lake whitefish and walleye stocks in the Great Lakes region. I used three maturation indices to measure maturation schedules: A_{50} and L_{50}, age-specific maturation ogives (the length cutoff at which fish for given age has 50% chance to be mature), and PMRNs. These maturation indices together provide implications for potential adaptive and plastic variation in maturation schedules. In Chapters IV and V, I developed and used an individual-based modeling (IBM) approach to evaluate fishing-induced plastic and evolutionary effects on maturation, growth, and harvest productivity. Lastly, Chapter VI presents an evaluation of potential adaptive and plastic variation of egg size among five walleye stocks across the Great Lakes region. Together, these chapters demonstrate that applications of evolutionary theory should benefit long-term fisheries management.

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Chapter II

Spatial and temporal variation of maturation schedules of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes

Abstract

Fish maturation schedules can vary greatly among systems and over time, reflecting both plastic and adaptive responses to ecosystem structure, physical habitats, and mortality (natural and fishing). We examined maturation schedules of commercially exploited lake whitefish *Coregonus clupeaformis* in the Laurentian Great Lakes (lakes Michigan, Huron, and Superior) by estimating ages and lengths at 50% maturity, age-specific maturity ogives (age-specific probability of being mature), and midpoints of probabilistic maturation reaction norms (PMRNs; a metric that accounts for plastic effects of growth and mortality). Collectively, these estimates indicated significant variation in maturation schedules between sexes (i.e., males tend to mature at younger ages and shorter lengths than females) and among systems (midpoints of lake-sex-age-specific estimates of PMRNs were smallest for Lake Michigan fish, intermediate for fish in the main basin of Lake Huron, and largest for fish in Lake Huron's Georgian Bay and Lake Superior). Temporally, recent increases in age at 50% maturity in lakes Huron and Michigan may primarily reflect plastic responses to decreased growth rates associated with ecosystem changes. As plastic and adaptive changes in maturation schedules of fish stocks may occur simultaneously and require different management considerations, we recommend the concomitant analysis of multiple maturation indices.

Introduction

Maturation schedules constitute key demographic attributes for fisheries management. Intra-specific variation in maturation of fish might reflect both plastic (e.g., variable maturation schedules due to changes in growth or mortality rates) and adaptive (e.g., selection-induced changes in maturation schedules) responses to various environmental factors (Law 2000). Further, widespread anthropogenic activities (e.g., fishery exploitation) have likely increased the force of genetic selection on life history traits (Stokes et al. 1993; Laikre and Ryman 1996). It is important to understand if intra-specific temporal and spatial variation in maturation schedules of fish stocks is adaptively determined, as 1) maturation schedules influence yield and recruitment potential (Jensen 1981), 2) selection-induced variation in life history traits may be difficult to reverse (Conover and Munch 2002), and 3) as suggested by Olsen et al. (2004) for cod *Gadus morhua*, rapid changes in genetically determined maturation schedules may be an indicator of imminent stock collapse.

Lake whitefish *Coregonus clupeaformis* (hereafter whitefish) constitute important commercial fisheries in the Laurentian Great Lakes and numerous inland lakes (Healey 1975; Ebener 1997). Whitefish maturation schedules are known to vary dramatically among populations (e.g., Beauchamp et al. 2004). For instance, several authors have suggested that whitefish from exploited stocks grow faster, mature at younger ages and smaller sizes, and potentially have higher fecundity than whitefish from unexploited stocks (Healey 1975, 1978, 1980). Henderson et al. (1983) suggested that such changes in maturation schedules of an exploited stock might be a compensatory response (i.e., increased growth rates due to decreased population density), and Taylor et al. (1992)

suggested that in addition to exploitation effects, latitudinal variation might influence size and age at maturation for Great Lakes whitefish stocks.

Many Great Lakes whitefish stocks are genetically distinct (Imhof et al. 1980; Ihssen et al. 1981; Ebener 1997), but it is unclear if such genetic variation leads to differences in maturation schedules (via genetic and environmental interactions). Intra-specific variation of maturation schedules of whitefish have been measured using traditional methods, i.e., age and length at 50% maturity (e.g., Beauchamp et al. 2004). However, such estimates cannot distinguish between plastic and genetic variation, i.e., these metrics do not adequately account for the effects of growth and mortality on maturation schedules (Heino et al. 2002).

A method to estimate probabilistic maturation reaction norms (PMRN) was developed based on the maturation reaction norm concept (Stearns and Koella 1986) to account for plastic effects of growth and mortality when depicting a population's maturation schedule (Heino et al. 2002; Barot et al. 2004a; Dieckmann and Heino 2007). PMRNs (usually expressed as a midpoint [at which probability of maturing = 0.5] with 95% confidence interval [C.I.]) represent individual variability within a population, and characterize an intrinsic population-level expression of probability of maturation under different growth rates (Figure. 1; Dieckmann and Heino 2007; Kraak 2007). Changes in growth rates (through either plastic or adaptive effects; Dieckmann and Heino 2007) may cause shifts in maturation schedules of a population with no changes to the underlying PMRN, whereas selection (via genetic or environmental factors) that alters frequency of genotypes that influence maturation schedules may alter a population's PMRN (Ernande et al. 2004; Dunlop et al. 2007). The concept of PMRN has been successfully applied to evaluate spatial and temporal variation of maturation schedules of various fish stocks (e.g., plaice *Pleuronectes platessa*, Grift et al. 2003; smallmouth bass *Micropterus dolomieu*, Dunlop et al. 2005).

In this study, we aimed to evaluate spatial and temporal variation in maturation schedules of whitefish in the three Upper Great Lakes (lakes Michigan, Huron, and Superior) using three indices: 1) age and length at 50% maturity, 2) midpoints of age-specific maturity ogives, and 3) age-specific PMRN midpoints. The Upper Great Lakes represent interesting systems to evaluate subtle, intra-specific variation in maturation schedules because they are large, inter-connected water bodies where whitefish stocks may inter-mix, and environmental and anthropogenic factors may influence maturation schedules of whitefish in relatively similar ways (i.e., there would likely be greater differences in environmental and anthropogenic factors between the Great Lakes and inland lakes). Nonetheless, within these three Great Lakes whitefish experience distinct physical habitats, food web structures, and exploitation intensities (Nalepa et al. 2005; Ebener et al. 2005). As these features strongly influence size- and age-specific growth and mortality rates, it is likely that whitefish experience different selection pressures (both natural and artificial selection) among lakes.

We hypothesize that compared to fish in the other lakes, Lake Superior whitefish mature relatively late due to their historically slow growth rates (Taylor et al. 1992) caused by low water temperatures, short growing seasons, and potentially low food supply due to relatively low primary production (Barbiero and Tuchman 2001). While whitefish growth rates in lakes Michigan and Huron have historically been higher, these rates have recently declined, likely due to both density-dependent effects (commercial catch data suggest that during recent years whitefish abundance has increased, while size at age and condition of whitefish have declined; Mohr and Ebener 2005; Schneeberger et al. 2005) and decreasing density of an important prey, *Diporeia* spp. (a high caloric-content amphipod, whose decline during the 1990s coincided with the invasion and spread of zebra mussels *Dreissena polymorpha*; Pothoven et al. 2001; Pothoven and Nalepa 2006). Further, whitefish in lakes Michigan and Huron have likely experienced more intense (relative to Lake Superior), but variable size-specific mortality related to sea lamprey *Petromyzon marinus* predation (Ebener et al. 2005) and fisheries harvest (Baldwin et al. 2002; Mohr and Ebener 2005; Schneeberger et al. 2005).

Materials and methods

Data

We analyzed two types of datasets (from three sources; Table 1) which contain information on total length, sex, and maturation status of whitefish: 1) fishery-independent biological survey data from the Michigan Department of Natural Resources (MDNR) and Ontario Ministry of Natural Resources (OMNR) and 2) commercial catch and assessment data from Chippewa Ottawa Resource Authority's (CORA) Inter-Tribal Fisheries and Assessment Program (ITFAP).

The MDNR biological surveys were conducted annually in each lake whitefish management unit (Figure 2) in Lake Michigan during Apr. to Oct. 1989-1993 using commercial trap nets (114.3 mm stretched mesh; Schneeberger et al. 2005) and in Lake Superior during May to Oct. 1971-1996 using mostly large mesh gillnets (114.3 mm stretched mesh) and, less frequently, graded mesh gillnets (38.1 to 114.3 mm mesh in

12.7 mm increments). OMNR surveys (1979-2005) were primarily conducted in Aug. (Georgian Bay) and June and Sept. (southeast region [OH3 and OH4/5] of the main basin of Lake Huron; Figure 2), using multi-panel index gillnets (38.1 to 127.0 mm mesh in 12.7 mm increments; Cottrill and Speers 2005; Mohr and Ebener 2005). Although commercial trap net sites within each Lake Michigan management unit were randomly chosen, both agencies conducted surveys at relatively constant sites over time (e.g., OMNR surveys sampled three fixed sites in Georgian Bay and two locations in the main basin of Lake Huron; Figure 2). Sample sizes and seasonal distributions of samples varied among the three lakes (Table 1), e.g., Lake Michigan data included a relatively high proportion of fish samples from fall (Sept.-Oct.). Both agencies aged fish using scales, and determined sex and maturity status of fish by internal examination of gonads. Scale aging may be biased for old (age > 7 yrs), slow growing whitefish (i.e., individuals with unidentifiable annuli), but is generally accurate for young fish (age ≤ 7 years) from exploited, fast growing populations (Mills and Beamish 1980; Mills et al. 2004).

The ITFAP data were primarily derived from fish sampled from tribal commercial catches using large mesh gillnets (≥ 114-mm stretched mesh) or trap nets in the 1836-ceded waters of lakes Michigan, Huron, and Superior (Figure 2; Ebener et al. 2005). These data were primarily collected from May to Nov. during 1980-2003 (similar seasonal distributions among lakes; Table 1), based on protocols that involved sampling 0.25-0.5% of total yields from each gear and management unit (Ebener et al. 2005). Due to small sample sizes of immature fish in the commercial catches, a small proportion (23, 29, and 6% of samples from Lakes Michigan, Huron, and Superior, respectively) of ITFAP data was derived from whitefish assessment surveys (gear types included graded mesh survey gillnets of 50.8 to 152.4 mm stretched mesh in 12.7 mm increments, electrofishing, trap nets, and seines). These assessment surveys were conducted at six sites near each of three designated ports per lake (M.P. Ebener, personal communication). While pooling data collected by different sampling gears may bias length and age distributions, the effect of gear bias was minimized when estimating PMRN midpoints (described below) because this analytic procedure facilitates analyses of biased length and age distributions (Heino et al. 2002; Barot et al. 2004a, 2004b). All of the ITFAP samples from both commercial catches and assessment programs were aged using scales. While sex of mature fish was determined via external examination during the spawning season (Oct. and Nov.), sex of immature fish and sex and maturity status of fish sampled during non-spawning seasons were internally examined by experienced research crews (Ebener 2005).

We used both types of data (i.e. biological survey data and ITFAP data) collected over 6 months (May to Oct.) to compare maturation schedules of whitefish among the three Great Lakes. Moreover, the large spatial coverage of OMNR survey data allowed us to examine spatial variation in maturation schedules within Lake Huron (Georgian Bay versus main basin; Figure 2). The inclusion of data collected over a 6 month period could lead to potential biases related to: 1) seasonal variation in size at age and 2) the differential ability to identify mature fish during various months. However, because means of size-at-age for age 3 and older fish were not correlated with month of capture, we believe that biases related to growth of fish over the six-month period of data collection were likely minimal (an assumption borne by our results; see Discussion). In addition, mature fish were collected throughout the sampling season. And, the large

ITFAP dataset allowed us to conduct analyses based on subsets of fish collected during Aug. to Oct. We found that estimates of age-specific maturity ogive and PMRN midpoints based on data from Aug. to Oct. were either not significantly different or slightly smaller than estimates based on data from May to Oct. More importantly, spatial and temporal patterns of all maturation indices were qualitatively consistent when comparing these two temporal ranges of data (see Supplemental material Table S1, Figure S1).

To compare temporal changes in maturation schedules within each lake, we aggregated cohort-specific data into two groups: fish born during or before 1990 (pre-1990 cohorts), and fish born after 1990 (post-1990 cohorts). Data availability precluded us from analyzing temporal trends by annual cohort. Further, Dieckmann and Heino (2007) suggest that year to year variation in estimates of PMRNs can be relatively high, and thus some temporal aggregation may be appropriate. The year (1990) for division of data was chosen such that temporal subsets had approximately equal fish samples, and because the year 1990 approximates the time when zebra mussels became established and subsequently altered Great Lakes ecosystems (Mills et al. 1993; Nalepa et al. 1998). Temporal changes were determined by comparing maturation indices (see below) estimated from the two subsets. MDNR survey data were not used for temporal analyses because of insufficient temporal coverage.

Analysis

We estimated three indices of whitefish maturation schedules by sex, lake, and over time: 1) age and length at 50% maturity, 2) midpoints of age-specific maturity ogives, and 3) midpoints of PMRNs. We first estimated age (A_{50}) and length (L_{50}) at 50% maturity, i.e., the age and length at which 50% of the fish population is mature (see Beauchamp et al. 2004 for detailed formula for estimation). For each sex-lake- and time-specific dataset, we fitted a logistic regression on data with maturity status (0 = immature; 1 = mature) as binary response and fish age or length as a predictor. The A_{50} and L_{50} were subsequently calculated by dividing the negative intercepts by the slopes of estimated logistic curves. The 95% C.I. of the A_{50} and L_{50} estimates were estimated using bootstrap techniques (Manly 1997). We randomly selected fish samples with replacement to generate 1,000 sets of data, each of equivalent sample size as the original dataset, and we fitted logistic regression on each of 1,000 bootstrapped datasets to generate 1,000 A_{50} and L_{50} estimates. The 95% C.I. of A_{50} or L_{50} was calculated as the sorted 25th (lower bound) and 975th (upper bound) values of the 1,000 bootstrap estimates. Statistical differences among A_{50} and L_{50} estimates (e.g., among lakes or between time periods) were evaluated by comparing the 95% C.I.

The second method for estimating maturation schedules involved fitting midpoints of age-specific maturity ogives (hereafter age-specific maturity ogives; Heino et al. 2002). This method was similar to estimating L_{50}, but the length at which probability of being mature = 0.5 was estimated separately for each age class ($L_{50,a}$; *a* indexes for age). Specifically, we partitioned data by lake, sex, and age and then fitted a logistic regression on each of the subsets with maturity status as response and length as a predictor:

$$\mathrm{logit}(o_a) = \ln(\tfrac{o_a}{1-o_a}) = \beta_0 + \beta_1 \times L_a \qquad (1)$$

Where o_a is the maturity ogive for age a, and L_a is length of fish at age a. $L_{50,a}$ was calculated by dividing the negative intercept by the slope of age-specific maturity ogive (o_a) in step (1). The 95% C.I.s of $L_{50,a}$ were estimated using the bootstrap techniques described above.

The third method for estimating maturation schedules was the approach developed by Barot et al. (2004a, 2004b) to estimate midpoints of PMRNs. After estimating age-specific maturity ogives (equation 1), we then estimated the age-specific probability of maturing (*m*):

$$m(L_a) = \frac{o_a(L_a) - o_{a-1}(L_a - \Delta L)}{1 - o_{a-1}(L_a - \Delta L)} \qquad (2)$$

Where o_a and o_{a-1} are derived from the logistic regressions fitted in the previous step. ΔL is the mean length increment from age *a-1* to age *a* (i.e., $\overline{L_a} - \overline{L_{a-1}}$). Probability of maturing (*m*) described the fraction of fish that was immature at age *a-1* and then grew in length (ΔL) to mature at age *a*. It should be noted that the validity of applying equation (2) to estimate the probability of maturing depends on the assumption that immature and mature individuals have the same age-specific growth and mortality rates (Barot et al. 2004a, 2004b). Growth rates of whitefish decrease with increasing size (i.e., growth rates approximate von Bertalanffy growth; Mills et al. 2004). This decrease in growth may be in response to maturity, and thus our analysis could have violated the above assumption.

However, Barot et al. (2004 a, 2004b) demonstrated that this method might be robust even when this assumption is violated.

The probability of maturing (m) usually increased with length from zero to one and had a sigmoid shape. We followed Barot et al.'s (2004a) procedures to estimate the length at which $m(L_a) = 0.5$ (i.e., $Lp_{50,a}$; p indexes for PMRNs) by fitting a logistic regression with $m(L_a)$ as the response and length (L_a) as a predictor. The $Lp_{50,a}$ was calculated by dividing the negative intercept by the slope of the logistic regression (equations [3] and [4]):

$$\operatorname{logit}(m(L_a)) = \beta_0 + \beta_1 \times L_a \tag{3}$$

$$Lp_{50,a} = -\frac{\beta_0}{\beta_1} \tag{4}$$

The 95% C.I.s of $Lp_{50,a}$ were estimated using bootstrap techniques. We generated 1,000 bootstrapped datasets of age a and age $a-1$ (each of equal sample size as the original dataset), and then generated 1,000 estimates of $Lp_{50,a}$ (using equations 1-4). The 95% C.I. of $Lp_{50,a}$ was given as the sorted 25th (lower bound) and 975th (upper bound) value of $Lp_{50,a}$ estimates.

All three methods for estimating maturation schedules involve fitting a logistic regression on data of binary responses. As no exact statistical test exists for evaluating goodness of fit for this type of statistical model, we judged model fit by using a deviance-based test (at $\alpha = 0.05$) as well as visual inspection. In the results we only report estimates of all three maturation metrics generated from valid statistical models based on these criteria.

Results

Age and length at 50% maturity

The age (A_{50}) and length (L_{50}) at 50% maturity varied between sexes and among the three Great Lakes. In general, female whitefish had significantly greater A_{50} and L_{50} than males in all three lakes based both on survey and ITFAP data (Table 2A-B). Among lakes, A_{50} and L_{50} of both sexes were generally lower for fish in Lake Michigan than in lakes Superior and Huron (Table 2A-B). Differences between lakes Huron and Superior were less consistent, e.g., based on survey data A_{50} estimates for both sexes were greater in Lake Superior than Lake Huron, but ITFAP data suggested the opposite pattern. Finally, based on OMNR survey data A_{50} tended to be lower but L_{50} was significantly greater for fish in Georgian Bay than in the main basin of Lake Huron (Table 2A).

Within-lake temporal changes were evident for both A_{50} and L_{50} values (Table 3A-B). Most noteworthy, based on both survey and ITFAP data A_{50} values in lakes Huron and Michigan increased significantly from pre-1990 to post-1990 cohorts. On the other hand, there were no significant changes in A_{50} values for Lake Superior, and temporal trends of L_{50} values were inconsistent (Table 3A-B).

Age-specific maturity ogives

Estimates of age-specific maturity ogives ($L_{50,a}$) differed significantly between sexes (females > males) and among lakes at younger ages (e.g., age ≤ 6). However, at older ages the inter-lake differences tended to be insignificant based on comparison of 95% C.I.s (C.I.s of estimates for older ages are relatively large due to fewer immature fish at older ages; Figures 3a, 3b, 4a, 4b). Inter-lake comparisons were possible when age-specific $L_{50,a}$ and 95% C.I. were estimable for >1 lake. Based on survey data, $L_{50,a}$ estimates for Lake Michigan fish (for both sexes) were significantly lower than for lakes Huron and Superior (Figures 3a, 3b). Further, $L_{50,a}$ estimates for the main basin of Lake Huron tended to be lower than both Georgian Bay and Lake Superior. There were, however, no significant differences between Georgian Bay and Lake Superior.

Based on ITFAP data, $L_{50,a}$ estimates for age 5-6 males and age 4-6 females were significantly lower in Lake Michigan than in the other lakes (Figures 4a, 4b). While differences between lakes Huron and Superior were less pronounced, age 4 female $L_{50,a}$ was significantly greater for Lake Superior than Lake Huron (Figure 4b).

Temporal changes in $L_{50,a}$ estimates were minimal. However, based on OMNR survey data $L_{50,a}$ estimates for age 4-5 males in Lake Huron's main basin and age 4 males in Georgian Bay increased significantly from pre-1990 to post-1990 cohorts (see Supplemental material Figure S2). Also, based on ITFAP data, $L_{50,a}$ estimates for age-5 females in Lake Michigan decreased significantly from pre-1990 to post-1990 cohorts while no significant temporal changes were observed in the other lakes (see Supplemental material Figure S3).

PMRN

Estimated age-specific PMRN midpoints ($Lp_{50,a}$) were significantly greater for females than males. Spatially, significant variation in $Lp_{50,a}$ among lakes was observed for both sexes (for age 3-4 males and age 4 females), based on both survey (Figures 3c, 3d) and ITFAP data (Fig. 4c, 4d). For both sexes, survey-based $Lp_{50,a}$ estimates showed that compared to fish in lakes Huron and Superior, Lake Michigan fish matured at smaller lengths for a given age (Figures 3c, 3d). Further, $Lp_{50,a}$ estimates for both males and females in the main basin of Lake Huron were smaller than estimates for Georgian Bay, and there were no significant differences in $Lp_{50,a}$ estimates between fish in Georgian Bay and Lake Superior (Figures 3c, 3d). While patterns were qualitatively similar based on ITFAP data, only $Lp_{50,a}$ for age 4 females differed significantly among lakes (Figures 4c, 4d).

Based on OMNR survey data, $Lp_{50,a}$ estimates for age 4 males in both the main basin of Lake Huron and Georgian Bay increased from pre- to post-1990 cohorts (Figures 5a, 5c). However, estimates for females in the main basin did not change significantly (Figure 5b). Further, based on ITFAP data there were no significant temporal changes in estimates of $Lp_{50,a}$ for fish of either sex in any of the lakes (Figure 6).

Discussion

We demonstrate that maturation schedules of Upper Great Lakes lake whitefish vary sexually, spatially, and temporally. Simultaneous analyses of two types of data (survey and ITFAP data) using three methods (age and length at 50% maturity [A_{50} and L_{50}] and midpoints of age-specific maturity ogives [$L_{50,a}$] and PMRNs [$Lp_{50,a}$]) suggest that: 1) intrinsic variation in maturation schedules exists between sexes (i.e., females tend to mature at older ages and larger sizes than males); 2) whitefish of both sexes in the three Great Lakes and within Lake Huron have distinct maturation schedules, with Lake Michigan fish maturing at smaller lengths for given ages than fish in the other two Great Lakes; and 3) age at 50% maturity increased significantly from pre-1990 to post-1990 cohorts in lakes Michigan and Huron (but not Lake Superior), but these temporal shifts appear to be primarily plastic responses to dramatic ecosystem changes.

Sexual variation

Our findings of delayed maturation schedules of female whitefish are consistent with predictions based on life history theory. In general, energetic costs for reproduction are higher for female fish, and both female fecundity and egg size (and thus likely egg viability) increase with size of female whitefish (Ihssen et al.1981). Given that there is likely a tradeoff between reproductive and somatic growth, delayed maturation may increase overall lifetime reproductive success. Thus, female whitefish maturation schedules may have evolved to maximize lifetime reproductive capacity by delaying maturation (as seen in several salmonid species; e.g., Fleming and Gross 1994). On the other hand, male whitefish have seemingly low reproductive costs (i.e., minor tradeoff between reproduction and somatic growth), and, therefore, one might expect that male whitefish should mature at relatively small sizes and early ages.

Spatial variation

Across-lake variation in age-specific PMRN midpoints suggests that through adaptive processes whitefish in the Great Lakes may express intrinsically different maturation schedules in response to long term variable conditions among lakes, e.g., relatively high adult mortality and/or juvenile growth rates may select for early maturation schedules (Stearns 1992). Delayed maturation schedules of whitefish in Lake Superior may in part be attributable to slow growth and relatively low mortality rates (Z

= 0.5-0.7; Ebener et al. 2005). Although information on life histories of whitefish in Georgian Bay is relatively scarce, whitefish in the southern main basin of Lake Huron and throughout Lake Michigan may have experienced relatively similar selection pressures on maturation schedules, with fish in both systems likely experiencing relatively high adult mortality (Lake Michigan, Z = 0.8-0.9; Lake Huron, Z = 0.8; Ebener et al. 2005) due to a combination of intensive harvesting, sea lamprey related mortality, and other sources of natural mortality.

Across system difference in maturation schedules also likely reflect plastic responses to variation in mortality rates and differences in habitats and community structure among the three Great Lakes. For example, the harvest of a large proportion of a population may affect maturation schedules of whitefish through a compensatory response (i.e., maturation at younger ages and larger size due to increased growth rates at lower population density; Jensen 1981).

Our analysis suggested that whitefish maturation schedules differ between Lake Huron's main basin and Georgian Bay (i.e., two large, distinct basins in the same lake). It is quite possible that local adaptations also lead to within-lake differences in whitefish maturation schedules at much finer spatial scales. Such differences likely exist because of 1) the large geographic extent and heterogeneous habitats of the Great Lakes, 2) spatially variable selection pressures within these lakes (Taylor et al. 1992), and 3) potential reproductive isolation among sub-stocks.

Temporal variation

Large increases in age at 50% maturity of whitefish from pre-1990 to post-1990 cohorts in lakes Michigan and Huron coupled with only minor shifts in estimated age-specific maturity ogive and PMRN midpoints may reflect primarily plastic, temporal changes in whitefish maturation schedules in response to dramatic, within-lake ecosystem changes. Several authors have suggested that recruitment and harvest production of whitefish in both lakes increased from the 1960s to mid 1990s as a result of sea lamprey control (Eshenroder and Burnham-Curtis 1999), decreased predation on early life stages (by alewife *Alosa pseudoherangus* and rainbow smelt *Osmerus mordax*), low inter-specific competition (e.g., with other Coregonines; Ebener 1997), and favorable climatic conditions (Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993). More recently (during the 1980s to 1990s), growth rates (as indicated by mean length- and weight-at-age) and body condition of whitefish have declined in lakes Michigan and Huron, likely reflecting both intra-specific density-dependent effects and diet shifts to energetically-unfavorable prey (due to severe declines in high caloric-content *Diporeia* spp.; Pothoven et al. 2001; Mohr and Ebener 2005; Pothoven and Nalepa 2006). Decreased growth rates of whitefish in the two lakes likely led to upward shifts in the age structure of mature fish (i.e., higher A_{50} estimates as reported in our study and elsewhere; Mohr and Ebener 2005). Interestingly, as opposed to lakes Michigan and Huron, whitefish growth rates in Lake Superior have not declined (Schorfharr and Schneeberger 1997; perhaps because *Diporeia* spp. densities have remained stable in this system; Scharold et al. 2004; Dermott et al. 2005; Nalepa et al. 2006), and in turn we found no significant temporal variation in A_{50} estimates for Lake Superior whitefish.

Temporal changes in age-specific estimates of maturity ogive and PMRN midpoints within lakes were minimal. Several authors have suggested that long-term size-selective fishery harvest may lead fish to evolve earlier age and smaller size at maturation (Stokes et al. 1993; Rochet et al. 2000; Olsen et al. 2004). While it is quite possible that Great Lakes whitefish have evolved in such a manner, we analyzed data that cover a short period relative to the history of commercial fishing (in Lake Michigan commercial fishing began in the 1840s; Wells and McLain 1973), and thus our temporal analyses may not be able to sufficiently evaluate this hypothesis.

It should be noted, however, that survey-based estimates of PMRN midpoints for Lake Huron male fish did change from pre-1990 to post-1990 cohorts. Relative to temporal trends in fisheries pressure, Lake Huron's ecosystem structure changed dramatically from the pre-1990 to post-1990 time periods (e.g., decline of *Diporeia* spp. after invasion of zebra mussels). Thus, this shift suggests that temporal variation in ecosystem characteristics may induce not only plastic, but also rapid adaptive changes in maturation schedules.

Analytical and data considerations

Our conclusions regarding temporal and spatial variation in both plastically and intrinsically determined maturation schedules are based on comparisons between traditional coarse indices of fish maturation schedules (A_{50} and L_{50}) and more sensitive measures (age-specific maturity ogive and PMRN midpoints; Heino et al. 2002; Barot et al. 2004a, 2004b). We suggest that these different types of indices are complementary and can collectively provide insight as to both plastic and adaptive trends in maturation schedules. The age and length at 50% maturity metrics provide a relatively quick and simple index of maturation schedules. However, these estimates are sensitive to sampling biases (e.g., gear selectivity, different time of sampling, etc.) as well as growth and mortality rates of a fish stock (Heino et al. 2002). Further, on their own these indices provide limited insight as to whether variation in maturation schedules is primarily dependent on plastic or adaptive processes. Conversely, midpoints of age-specific maturity ogives and PMRNs are age-specific estimates for maturation schedules, and thus are relatively unbiased by factors that alter age distributions alone. While PMRN indices are useful for comparing spatial and temporal patterns in adaptively determined maturation schedules, these indices do not allow evaluation of non-genetically determined, plastic variation of maturation schedules. We recommend that fisheries agencies should assess maturation schedules of fish stocks via these different maturation metrics in order to identify plastic and adaptive changes in maturation schedules that may occur simultaneously and require different management considerations.

In evaluating age-specific PMRN midpoints, it is important to consider the underlying assumption of such estimates, i.e., length-at-age is the primary determinant of individual maturation. Several authors have accepted this assumption and used estimates of PMRN midpoints to compare intra-specific genetically determined maturation schedules across space and time (Grift et al. 2003; Olsen et al. 2005; Dunlop et al. 2005). A noteworthy study by Dunlop et al. (2005) compared maturation schedules of two distinct smallmouth bass populations from a common source population, and revealed that while these two populations had very different maturation schedules their age-specific PMRN length midpoints were not significantly different, thereby demonstrating the utility of this approach. Nonetheless, while length-at-age is a useful proxy of whole lifetime growth, it is clear that a variety of factors contribute to timing of maturation (Marshall and McAdam 2007; Wright 2007).

Recent studies demonstrate that using additional or different explanatory variables (e.g., weight, condition, or temperatures) to estimate PMRN midpoints may better encapsulate plastic effects on maturation (e.g., three-dimensional PMRNs; Grift et al. 2007; Kraak 2007). For instance, it is possible that weight-at-age and condition strongly influence PMRN midpoints for Great Lakes whitefish. Mature whitefish in inland lakes are known to express facultative spawning due to insufficient energy intake for maturation (Kennedy 1953). Consequently, it is possible that whitefish in poor body condition in lakes Michigan and Huron will not spawn during successive years (Pothoven et al. 2001; Pothoven and Nalepa 2006) which may affect precision of estimates of PMRN midpoints. To explore the effects of weight-at-age on age-specific maturation of whitefish, we analyzed MDNR and OMNR survey data and estimated midpoints of PMRNs with weight (instead of length) as a predictor. These analyses suggested that PMRN metrics based on weight reveal qualitatively similar spatial and temporal patterns as estimates based on length (see Supplemental material Figures S4, S5).

While inter-lake differences in PMRN estimates may suggest adaptive variation in maturation schedules among stocks, such adaptive maturation schedules could be induced by other processes which may be partially genetically determined. For example, recent studies suggest that growth rates could vary genetically within and between populations (Conover and Munch 2002; Walsh et al. 2006). As a result, variation in maturation schedules could have been genetically influenced via maturation, growth, or correlated growth-maturation heritance. Nonetheless, Dieckmann and Heino (2007) suggested that population-level PMRN estimates are likely unaffected by heritable growth or correlated growth-maturation heritance provided that growth variation is primarily environmentally determined. Given that whitefish display highly plastic growth (Healey 1975, 1980; Henderson et al. 1983), it is likely that intra-specific genetic variation in growth has minimal biasing effects on PMRN estimates.

We analyzed data collected by different agencies during slightly different times of year. While the use of such variable data could introduce biases in our analyses, we believe that our conclusions regarding spatial and temporal variation of whitefish maturation schedules are at least qualitatively robust. As an example, the seasonal distributions of survey data varied among lakes (higher proportion [58%] of fish collected in fall in Lake Michigan than in lakes Huron [30%] and Superior [25%]). These seasonal distributions would suggest that age-specific maturity ogive and PMRN estimates for Lake Michigan could be positively biased (due to additional growth during summer and fall). However, we observed the opposite, i.e., sex-age-specific estimates of maturity ogives and PMRNs were smallest for Lake Michigan fish, suggesting that the magnitude of differences in lake-specific maturation schedules were large enough to overcome differences in time of collection.

It is also noteworthy that we analyzed two types of data (OMNR and MDNR survey data and ITFAP data) which yielded quantitatively different results, e.g., we found that some survey-based estimates of lake-time-sex-specific A_{50}, L_{50}, $L_{50,a}$ and $Lp_{50,a}$ were significantly greater than ITFAP-based estimates. Collection of these two types of data involved different agencies, time periods, sampling gear, as well as locations within the lakes (Figure 2). Because age-specific maturity ogive and PMRN estimates are robust to different sampling procedures (Heino et al. 2002), we believe that differences in maturation indices between the two types of data primarily reflect agency biases, including the possibility that different agencies sample different whitefish sub-stocks within a lake. Most importantly, despite these differences both types of data led to the same qualitative conclusions regarding spatial and temporal patterns of whitefish maturation schedules, suggesting that maturation schedules do indeed differ among Great Lakes whitefish stocks and that recent within-lake shifts in maturation schedules are primarily attributable to plastic processes.

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Table 2.1. Data sources (Michigan Department of Natural Resources [MDNR], Ontario Ministry of Natural Resources [OMNR], and Chippewa-Ottawa Resource Authority's [CORA] Inter-Tribal Fisheries and Assessment Program [ITFAP]) and their temporal and spatial extent. OMNR Lake Huron survey data are separated by main basin (MB) and Georgian Bay (GB).

Data sources	Lake	Year	N	Proportion of data in		
				May-June	July-Aug.	Sept.-Oct.
MDNR (Survey data)	L. Michigan	1989-1993	2,954	0.23	0.19	0.58
	L. Superior	1971-1996	2,026	0.17	0.58	0.25
OMNR (Survey data)	L. Huron (MB)	1979-2005	13,294	0.43	0.04	0.53
	L. Huron (GB)	1979-2005	11,033	< 0.01	0.99	< 0.01
CORA (ITFAP data)	L. Michigan	1980-2003	13,915	0.23	0.26	0.51
	L. Huron	1980-2003	15,430	0.20	0.16	0.64
	L. Superior	1980-2003	10,909	0.27	0.28	0.45

Table 2.2. Age (A_{50}, yr) and length (L_{50}, mm) at 50% maturity with (95% C.I. in parentheses) of male and female lake whitefish among the three Upper Great Lakes based on survey (A) and ITFAP data (B). Estimates for Lake Huron based on OMNR survey data are separated by main basin (MB) and Georgian Bay (GB).

A

Lake	Male			Female		
	N	A_{50}	L_{50}	N	A_{50}	L_{50}
L. Michigan	1,546	2.8 (2.7, 2.9)	412 (407, 415)	1,408	3.5 (3.4, 3.5)	456 (452, 461)
L. Huron (MB)	6,952	4.2 (4.1, 4.3)	445 (442, 447)	6,342	4.9 (4.8, 5.0)	484 (481, 487)
L. Huron (GB)	5,999	4.0 (3.9, 4.1)	493 (489, 497)	5,034	4.5 (4.5, 4.6)	538 (533, 543)
L. Superior	1,044	5.3 (5.1, 5.4)	470 (463, 477)	982	5.9 (5.7, 6.1)	505 (497, 512)

B

Lake	Male			Female		
	N	A_{50}	L_{50}	N	A_{50}	L_{50}
L. Michigan	7,187	2.9 (2.7, 3.0)	410 (407, 412)	6,728	3.4 (3.3, 3.5)	412 (409, 415)
L. Huron	9,009	4.2 (4.1, 4.3)	415 (413, 417)	6,421	5.1 (5.1, 5.2)	429 (427, 431)
L. Superior	5,790	3.9 (3.8, 4.0)	414 (407, 419)	5,119	4.5 (4.4, 4.6)	437 (432, 441)

Table 2.3. Temporal variation (pre- vs. post-1990 cohorts) in age (A_{50}, yr) and length (L_{50}, mm) at 50% maturity (with 95% C.I. in parentheses) of male and female lake whitefish based on OMNR Lake Huron survey data (A) in the main basin (MB) and Georgian Bay (GB) and ITFAP data (B) in the three Upper Great Lakes.

A

Sex	Lake Huron	Pre-1990 cohorts			Post-1990 cohorts		
		N	A_{50}	L_{50}	N	A_{50}	L_{50}
M	MB	4,902	3.6 (3.5, 3.7)	443 (440, 445)	2,050	5.5 (5.4, 5.7)	450 (445, 456)
	GB	3,385	3.7 (3.6, 3.7)	483 (479, 488)	2,614	4.7 (4.6, 4.8)	519 (510, 530)
F	MB	4,428	4.4 (4.3, 4.5)	489 (486, 492)	1,914	5.8 (5.6, 5.9)	466 (461, 472)
	GB	2,728	4.3 (4.2, 4.4)	532 (527, 538)	2,306	5.1 (4.9, 5.3)	558 (544, 574)

B

Sex	Lake	Pre-1990 cohorts			Post-1990 cohorts		
		N	A_{50}	L_{50}	N	A_{50}	L_{50}
M	Michigan	4,388	2.7 (2.4, 2.9)	415 (411, 420)	2,799	4.1 (3.9, 4.3)	406 (403, 409)
	Huron	3,697	2.5 (2.2, 2.9)	412 (406, 417)	5,312	5.3 (5.2, 5.3)	416 (414, 418)
	Superior	2,946	3.9 (3.7, 4.1)	413 (402, 421)	2,844	4.0 (3.8, 4.1)	418 (411, 424)
F	Michigan	4,003	3.1 (2.8, 3.2)	429 (425, 433)	2,725	4.3 (4.1, 4.4)	403 (399, 406)
	Huron	2,455	4.2 (4.0, 4.4)	444 (440, 449)	3,966	5.7 (5.7, 5.8)	425 (422, 428)
	Superior	2,639	4.6 (4.4, 4.7)	426 (415, 434)	2,480	4.6 (4.5, 4.7)	446 (441, 451)

Figure captions

Figure 2.1. Two hypothetical probabilistic maturation reaction norms (PMRNs). The two straight lines represent fast (e.g., with a steeper slope) and slow growth trajectories. The solid and dashed curves represent probability of maturing = 0.5 and 95% C.I., respectively, at given age and size. The two PMRNs depict distinct population-level maturation schedules in response to different growth rates, i.e., the intersection of growth trajectories and PMRNs represent onset of maturation at given age and size.

Figure 2.2. Sampling areas of 1) CORA-ITFAP data from commercial catches and assessment programs in 1836-ceded waters (outlined with black thick lines), 2) OMNR biological surveys in Georgian Bay and southeast of main basin (including the central [OH3] and southern regions [OH4/5]) of Lake Huron (in dark gray), and 3) MDNR biological surveys in lake whitefish management units in lakes Superior and Michigan (in light gray). OMNR surveys were conducted at fixed sites (shown in open circles) within Lake Huron, whereas MDNR surveys were at sites randomly chosen within the MDNR lake whitefish management units.

Figure 2.3. Midpoints of age-specific maturity ogives ($L_{50,a}$; male [a] and female [b]) and PMRNs ($Lp_{50,a}$; male [c] and female [d]) for lake whitefish *Coregonus clupeaformis* in lakes Michigan, Huron (main basin and Georgian Bay), and Superior based on MDNR (in 1971-1996) and OMNR (in 1979-2005) survey datasets. Error bars represent 95% C.I. The labels of numbers represent significant inter-lake variation of age-specific estimates based on 95% C.I., i.e., if the 95% C.I. of two lakes do not overlap, they are labeled with different numbers. To facilitate visual inspection, estimates for lakes Michigan, Huron-main basin and Superior are slightly offset along the x-axis. Black diamonds, Lake Michigan; gray squares, Lake Huron main basin; gray circles, Lake Huron Georgian Bay; open triangles, Lake Superior. The norms of $L_{50,a}$ and $Lp_{50,a}$ for a given lake are shown by connecting age-specific estimates with lines in different patterns.

Figure 2.4. Midpoints of age-specific maturity ogives ($L_{50,a}$; male [a] and female [b]) and PMRNs ($Lp_{50,a}$; male [c] and female [d]) for lake whitefish *Coregonus clupeaformis* in lakes Michigan, Huron, and Superior based on ITFAP (in 1980-2003) datasets. Error bars represent 95% C.I. The labels of numbers represent significant inter-lake variation of age-specific estimates based on 95% C.I.; e.g., C.I. of a lake labeled with “1,2” overlaps with C.I. of lake “1” and C.I. of lake “2” while C.I.s of lakes “1” and “2” do not overlap. To facilitate visual inspection, estimates for lakes Michigan and Superior are slightly offset along the x-axis. Black diamonds, Lake Michigan; gray squares, Lake Huron; open triangles, Lake Superior. The norms of $L_{50,a}$ and $Lp_{50,a}$ for a given lake are shown by connecting age-specific estimates with lines in different patterns.

Figure 2.5. Temporal (pre-and post-1990 cohorts) patterns (based on OMNR survey data, 1979-2005) of midpoints of PMRNs ($Lp_{50,a}$) of male (a) and female (b) lake whitefish *Coregonus clupeaformis* in Lake Huron’s main basin and males (c) in Georgian Bay.

Error bars represent 95% C.I. The labels of numbers represent significant temporal variation of age-specific estimates based on 95% C.I. To facilitate visual inspection, estimates for pre-1990 cohorts are slightly offset along x-axis. Black diamonds, pre-1990 cohorts; open diamonds, post-1990 cohorts. The norms of $Lp_{50,a}$ for pre- and post-1990 cohorts are shown by connecting age-specific estimates with lines in different patterns.

Figure 2.6. Temporal (pre-and post-1990 cohorts) patterns (based on ITFAP data, 1980-2003) of midpoints of PMRNs ($Lp_{50,a}$) of male (left column) and female (right column) lake whitefish *Coregonus clupeaformis* in lakes Michigan (a,d), Huron (b,e), and Superior (c,f). Error bars represent 95% C.I. To facilitate visual inspection, estimates for pre-1990 cohorts are slightly offset along x-axis. Black diamonds, pre-1990 cohorts; open diamonds, post-1990 cohorts. The norms of $Lp_{50,a}$ for pre- and post-1990 cohorts are shown by connecting age-specific estimates with lines in different patterns.

Figure 2.1

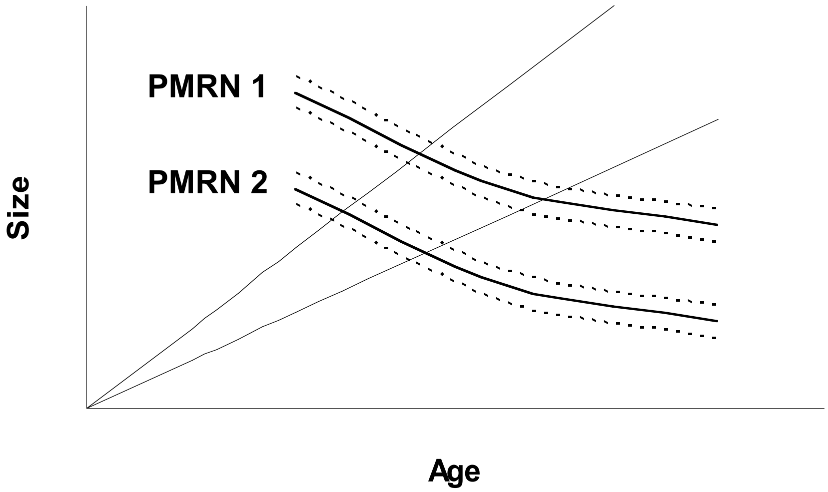
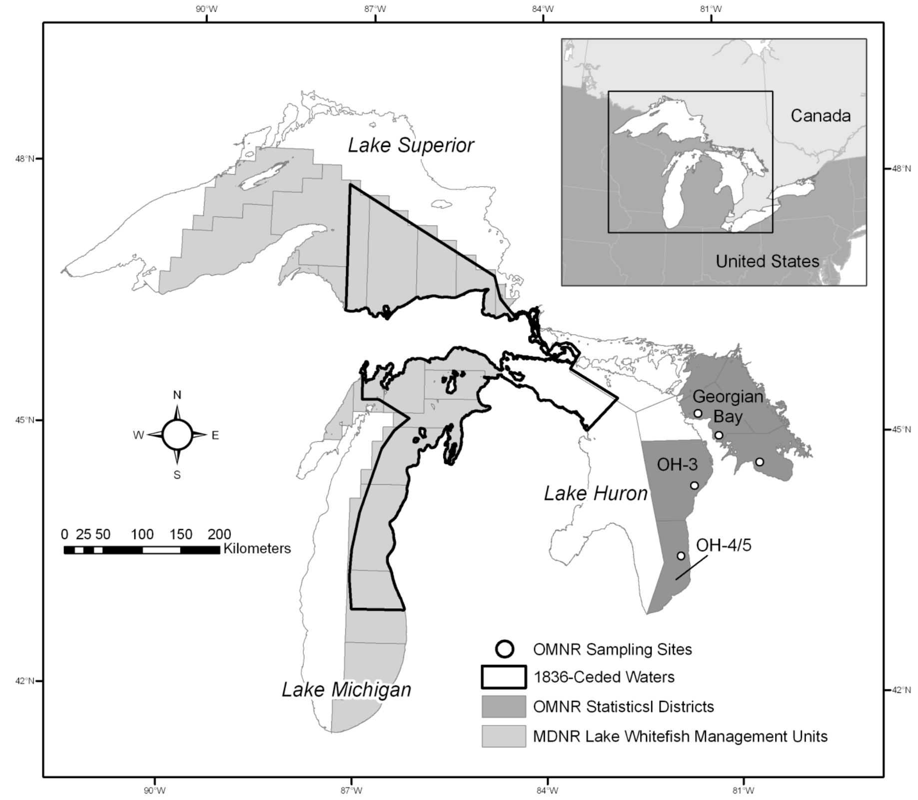


Figure 2.2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84°W
81°W
48°N
45°N
42°N
Canada
United States
Lake Superior
N
W
E
S
Georgian Bay
OH-3
OH-4/5
Lake Huron
Lake Michigan
0 25 50 100 150 200
Kilometers
OMNR Sampling Sites
1836-Ceded Waters
OMNR Statisticsl Districts
MDNR Lake Whitefish Management Units

Figure 2.3

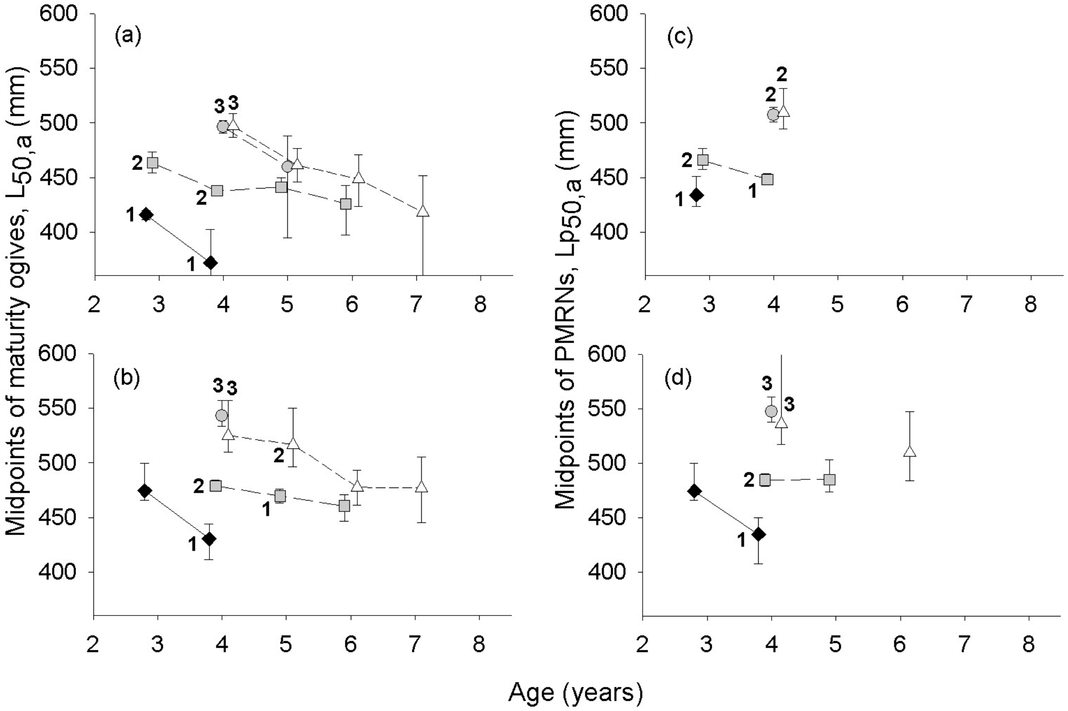
(a)
(b)
(c)
(d)
Midpoints of maturity ogives, $L_{50,a}$ (mm)
Midpoints of PMRNs, $Lp_{50,a}$ (mm)
Age (years)
600
550
500
450
400
2
3
4
5
6
7
8
1
2
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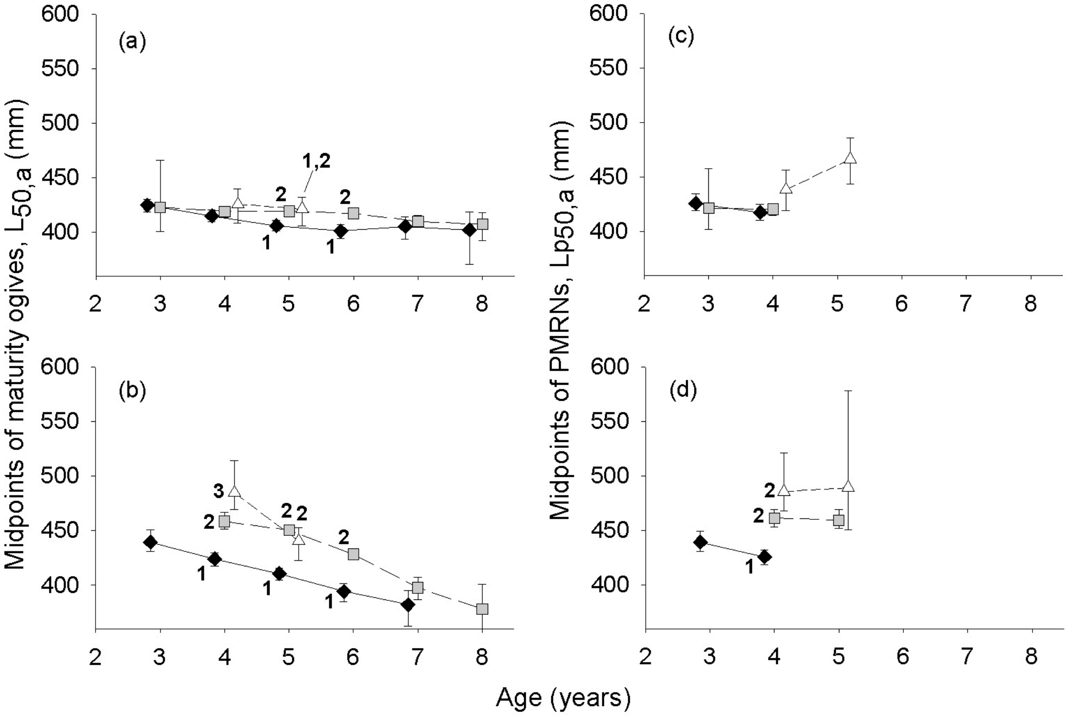
Figure 2.4



(a)
(b)
(c)
(d)
Midpoints of maturity ogives, L50,a (mm)
Midpoints of PMRNs, Lp50,a (mm)
Age (years)
600
550
500
450
400
2
3
4
5
6
7
8
1,2
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2
1
1
3
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2 2
2
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2
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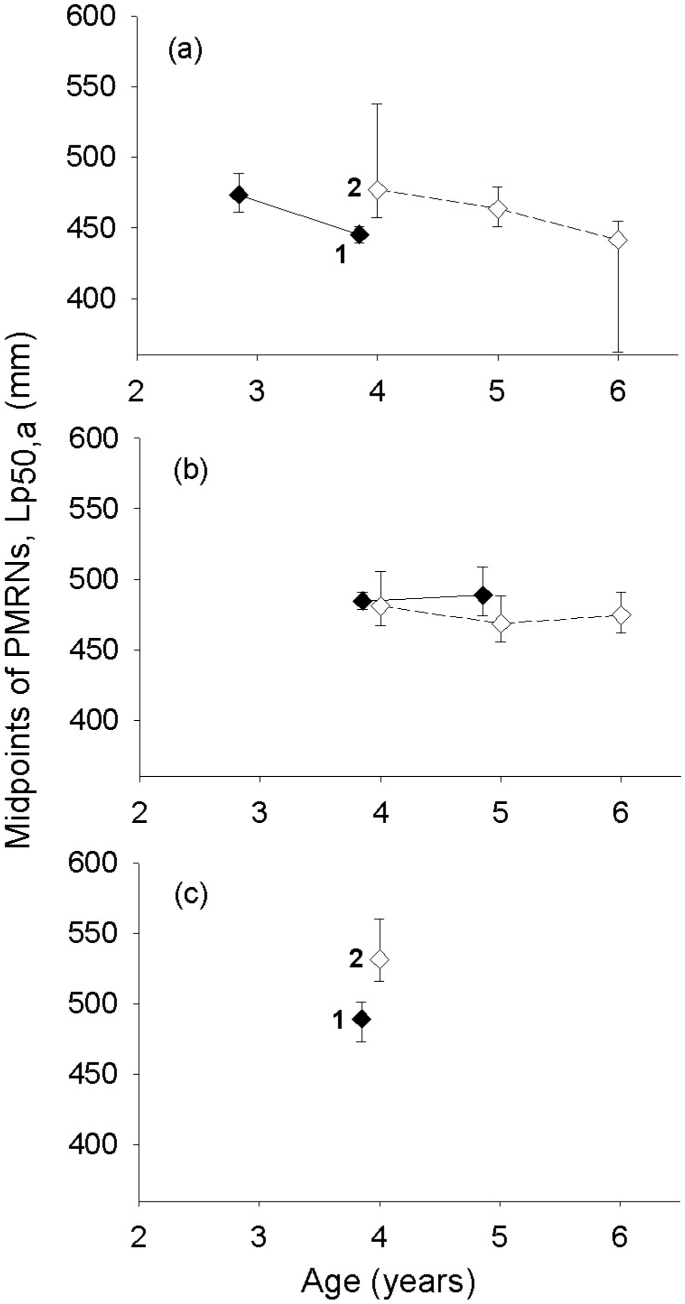
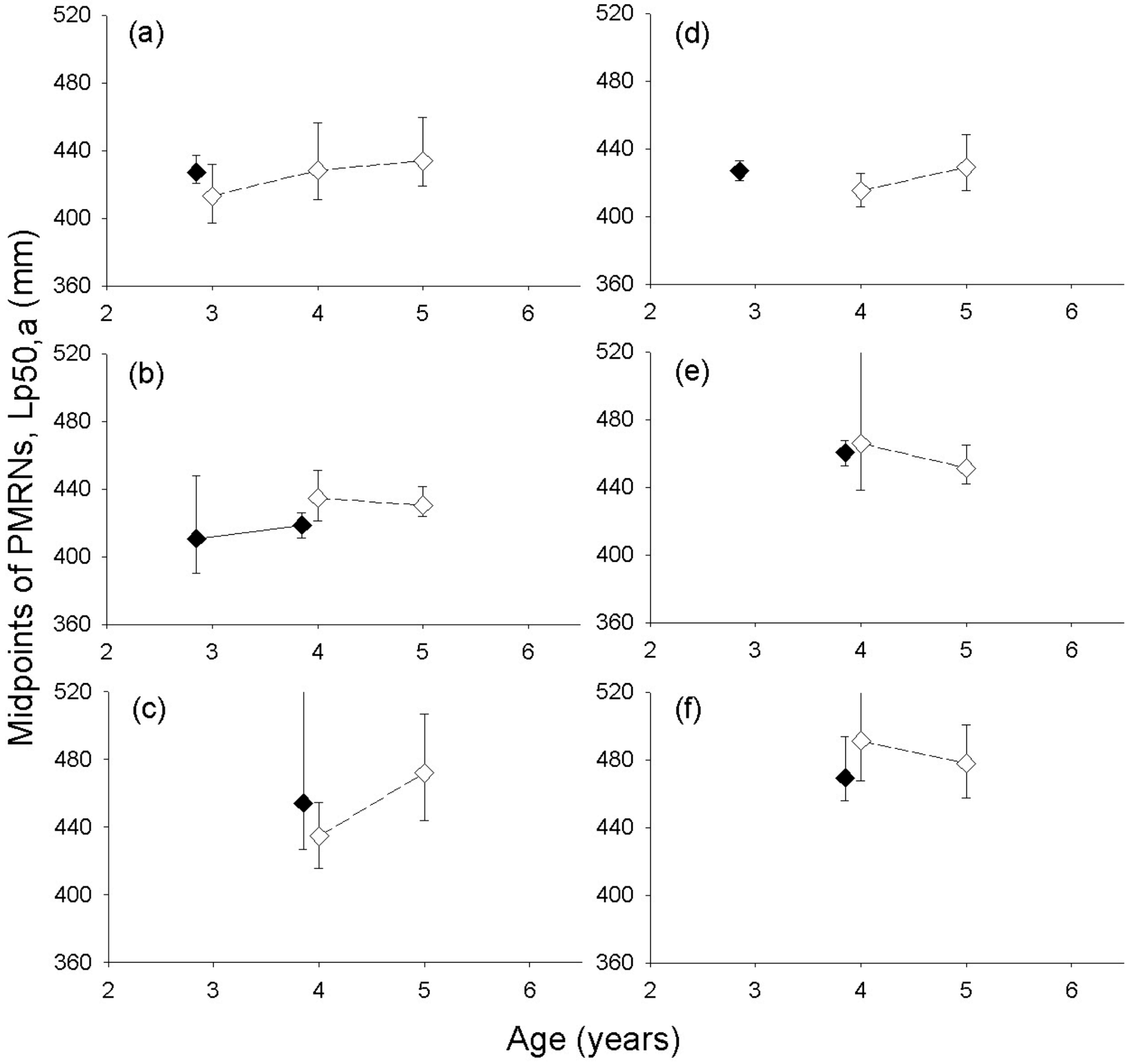
1

Figure 2.5



Midpoints of PMRNs, Lp50,a (mm)
Age (years)
(a)
(b)
(c)
1
2
600
550
500
450
400
2
3
4
5
6

Figure 2.6


(a)
(b)
(c)
(d)
(e)
(f)
520
480
440
400
360
2
3
4
5
6
Midpoints of PMRNs, Lp50,a (mm)
Age (years)

Supplemental material

Table S1. Age (A_{50}, yr) and length (L_{50}, mm) at 50% maturity (with 95% C.I. in parentheses) of male and female lake whitefish among the three Upper Great Lakes based on ITFAP data in Aug.-Oct., 1980-2003.

Lake	Male			Female		
	N	A_{50}	L_{50}	N	A_{50}	L_{50}
Michigan	4,676	2.5	395	4,164	2.9	408
		(2.1, 2.8)	(390, 400)		(2.6, 3.2)	(402, 413)
Huron	6,743	3.4	405	4,385	4.5	419
		(3.2, 3.5)	(402, 409)		(4.3, 4.6)	(415, 423)
Superior	3,607	3.9	408	2,853	4.8	447
		(3.7, 4.0)	(399, 416)		(4.7, 4.9)	(440, 453)

Figure S1. Midpoints of age-specific maturity ogives ($L_{50,a}$; male [a] and female [b]) and PMRNs ($Lp_{50,a}$; male [c] and female [d]) for lake whitefish *Coregonus clupeaformis* in lakes Michigan, Huron, and Superior based on ITFAP datasets in Aug.-Oct., 1980-2003. Error bars represent 95% C.I. The labels of numbers represent significant inter-lake variation of age-specific estimates based on 95% C.I.; i.e., if the 95% C.I. of two lakes do not overlap, they are labeled with different numbers. To facilitate visual inspection, estimates for lakes Michigan and Superior are slightly offset along the x-axis. Black diamonds, Lake Michigan; gray squares, Lake Huron; open triangles, Lake Superior. The norms of $L_{50,a}$ and $Lp_{50,a}$ for a given lake are shown by connecting age-specific estimates with lines in different patterns.

Figure S2. Temporal (pre-and post-1990 cohorts) patterns (based on OMNR survey data, 1979-2005) of midpoints of age-specific maturity ogives ($L_{50,a}$) of male (a) and female (b) lake whitefish *Coregonus clupeaformis* in Lake Huron's main basin and males (c) in Georgian Bay. Error bars represent 95% C.I. The labels of numbers represent significant temporal variation of age-specific estimates based on 95% C.I. To facilitate visual inspection, estimates for pre-1990 cohorts are slightly offset along x-axis. Black diamonds, pre-1990 cohorts; open diamonds, post-1990 cohorts. The norms of $L_{50,a}$ for pre- and post-1990 cohorts are shown by connecting age-specific estimates with lines in different patterns.

Figure S3. Temporal (pre-and post-1990 cohorts) patterns (based on ITFAP data, 1980-2003) of midpoints of age-specific maturity ogives ($L_{50,a}$) of male (left column) and female (right column) lake whitefish *Coregonus clupeaformis* in lakes Michigan (a, d), Huron (b, e), and Superior (c, f). Error bars represent 95% C.I. The labels of numbers represent significant temporal variation of age-specific estimates based on 95% C.I. To facilitate visual inspection, estimates for pre-1990 cohorts are slightly offset along x-axis. Black diamonds, pre-1990 cohorts; open diamonds, post-1990 cohorts. The norms of $L_{50,a}$ for pre- and post-1990 cohorts are shown by connecting age-specific estimates with lines in different patterns.

Figure S4. Weight-based midpoints of age-specific maturity ogives ($W_{50,a}$; male [a] and female [b]) and PMRNs ($Wp_{50,a}$; male [c] and female [d]) for lake whitefish *Coregonus clupeaformis* in lakes Michigan and Huron (main basin and Georgian Bay) based on MDNR (1989-1993) and OMNR (1979-2005) survey datasets. Error bars represent 95% C.I. The labels of numbers represent significant inter-lake variation of age-specific estimates based on 95% C.I. To facilitate visual inspection, estimates for lakes Michigan and Huron-Georgian Bay are slightly offset along the x-axis. Black diamonds, Lake Michigan; gray squares, Lake Huron main basin; gray circles, Lake Huron Georgian Bay. The norms of $W_{50,a}$ and $Wp_{50,a}$ for a given lake are shown by connecting age-specific estimates with lines in different patterns.

Figure S5. Temporal (pre-and post-1990 cohorts) patterns (based on OMNR survey data, 1979-2005) of weight-based midpoints of age-specific maturity ogives ($W_{50,a;}$ left column) and PMRNs ($Wp_{50,a;}$ right column) of male (a, d) and female (b, e) lake whitefish *Coregonus clupeaformis* in Lake Huron's main basin and males (c, f) in

Georgian Bay. Error bars represent 95% C.I. The labels of numbers represent significant temporal variation of age-specific estimates based on 95% C.I. To facilitate visual inspection, estimates for pre-1990 cohorts are slightly offset along x-axis. Black diamonds, pre-1990 cohorts; open diamonds, post-1990 cohorts. The norms of $W_{50,a}$ and $Wp_{50,a}$ for pre- and post-1990 cohorts are shown by connecting age-specific estimates with lines in different patterns.

Figure S1

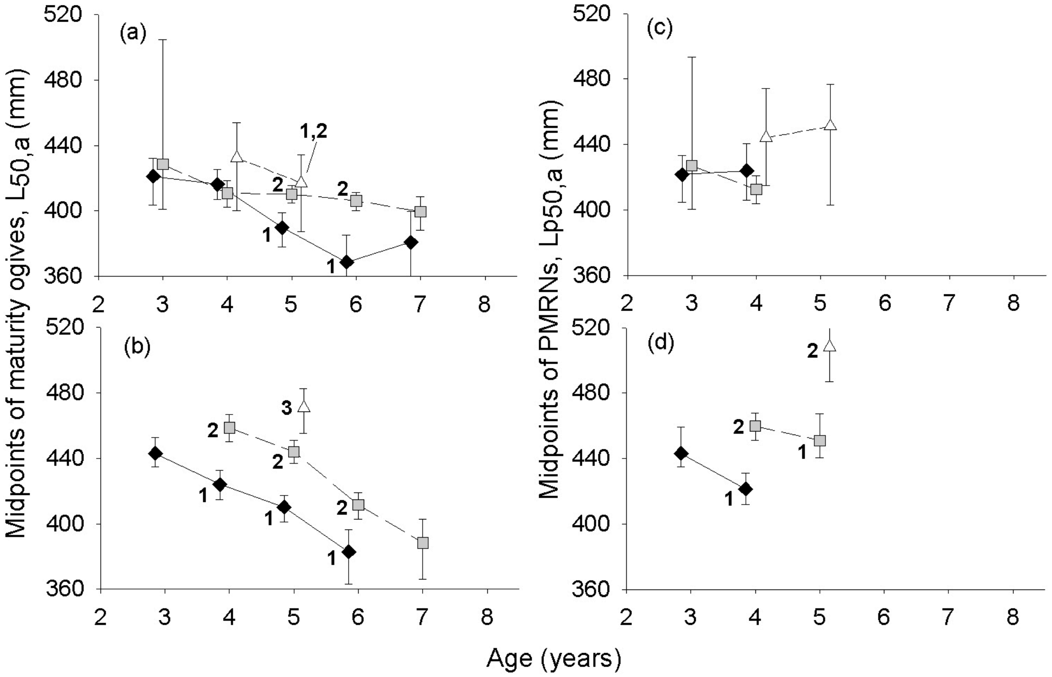

(a)
(b)
(c)
(d)
Midpoints of maturity ogives, L50,a (mm)
Midpoints of PMRNs, Lp50,a (mm)
Age (years)
520
480
440
400
360
2
3
4
5
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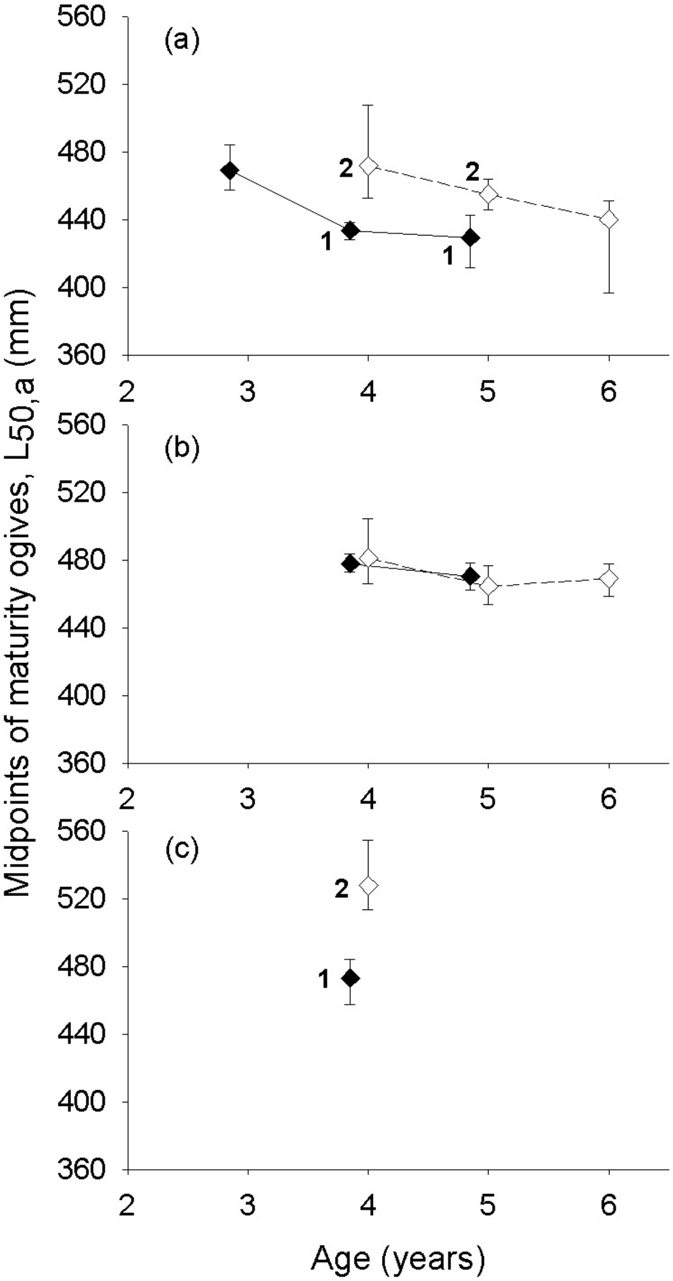
Figure S2


Midpoints of maturity ogives, L50,a (mm)
(a)
(b)
(c)
560
520
480
440
400
360
2
3
4
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6
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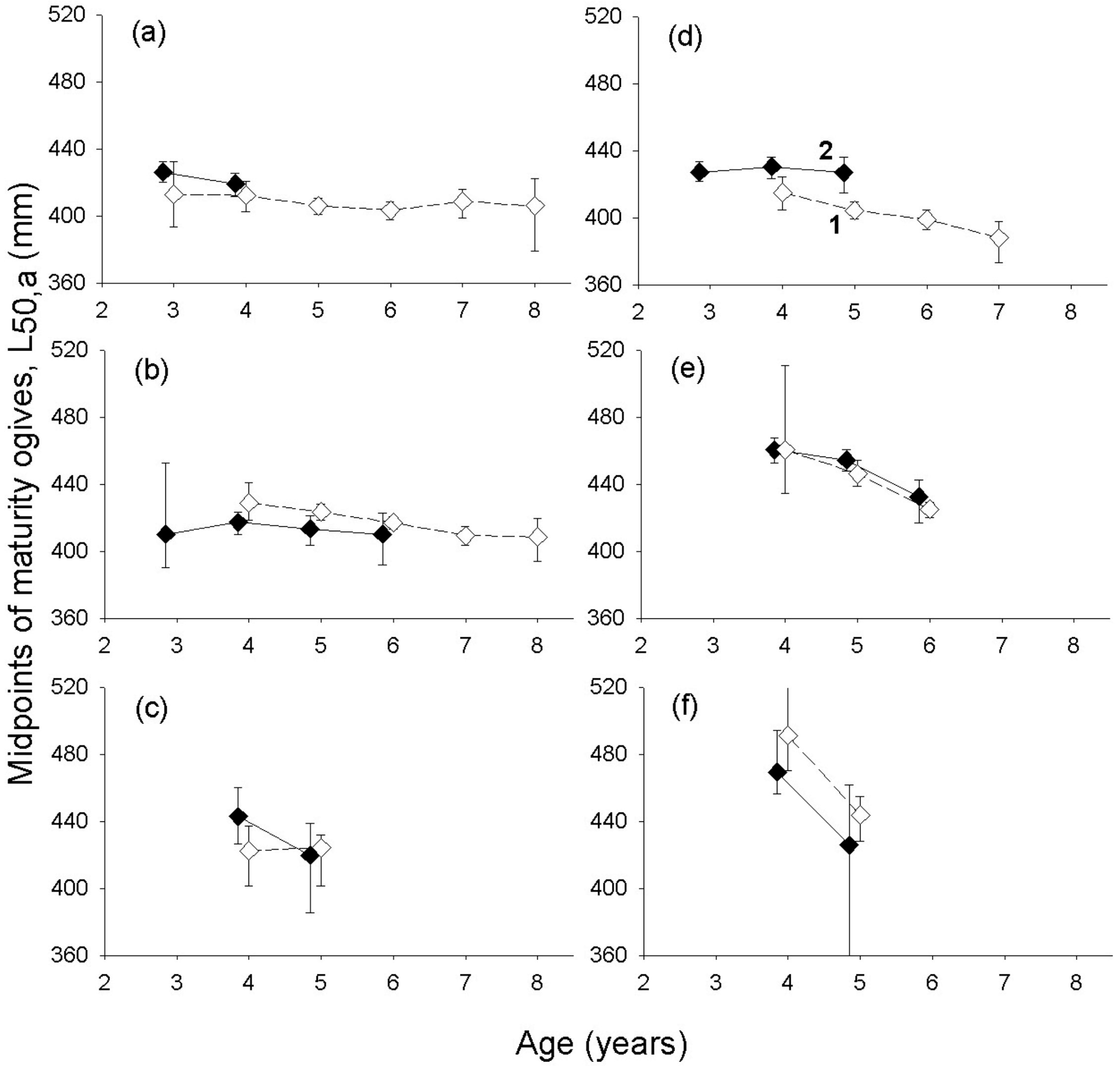
2
2
1
2
Age (years)

Figure S3



(a)
(b)
(c)
(d)
(e)
(f)
2
1
520
480
440
400
360
2
3
4
5
6
7
8
Midpoints of maturity ogives, L50,a (mm)
Age (years)

Figure S4

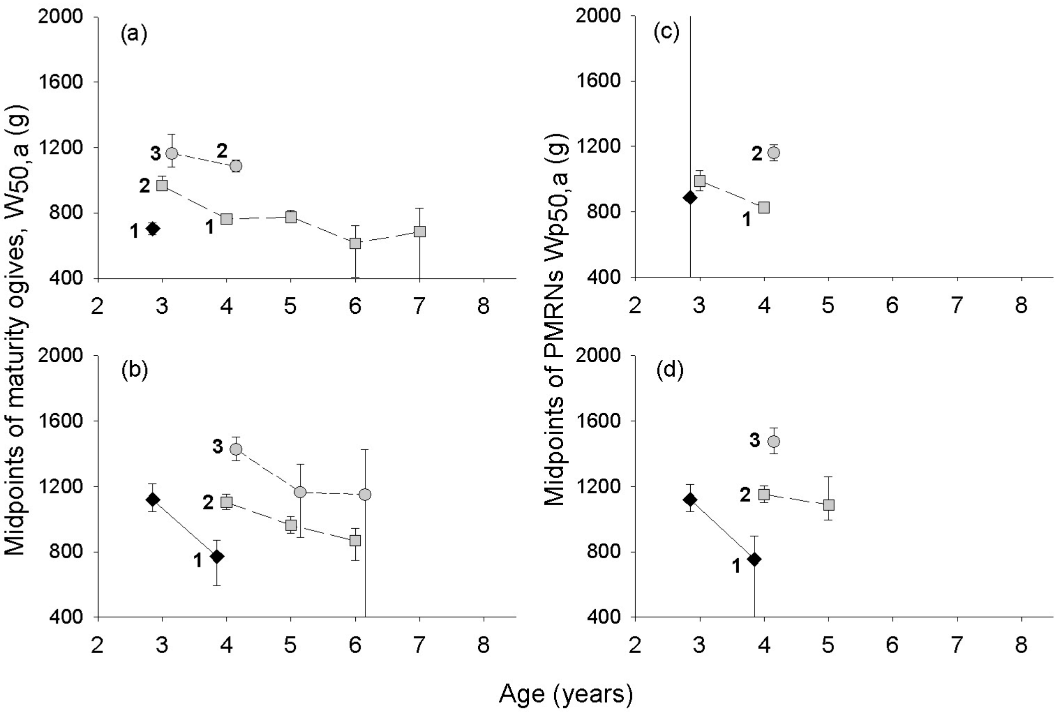
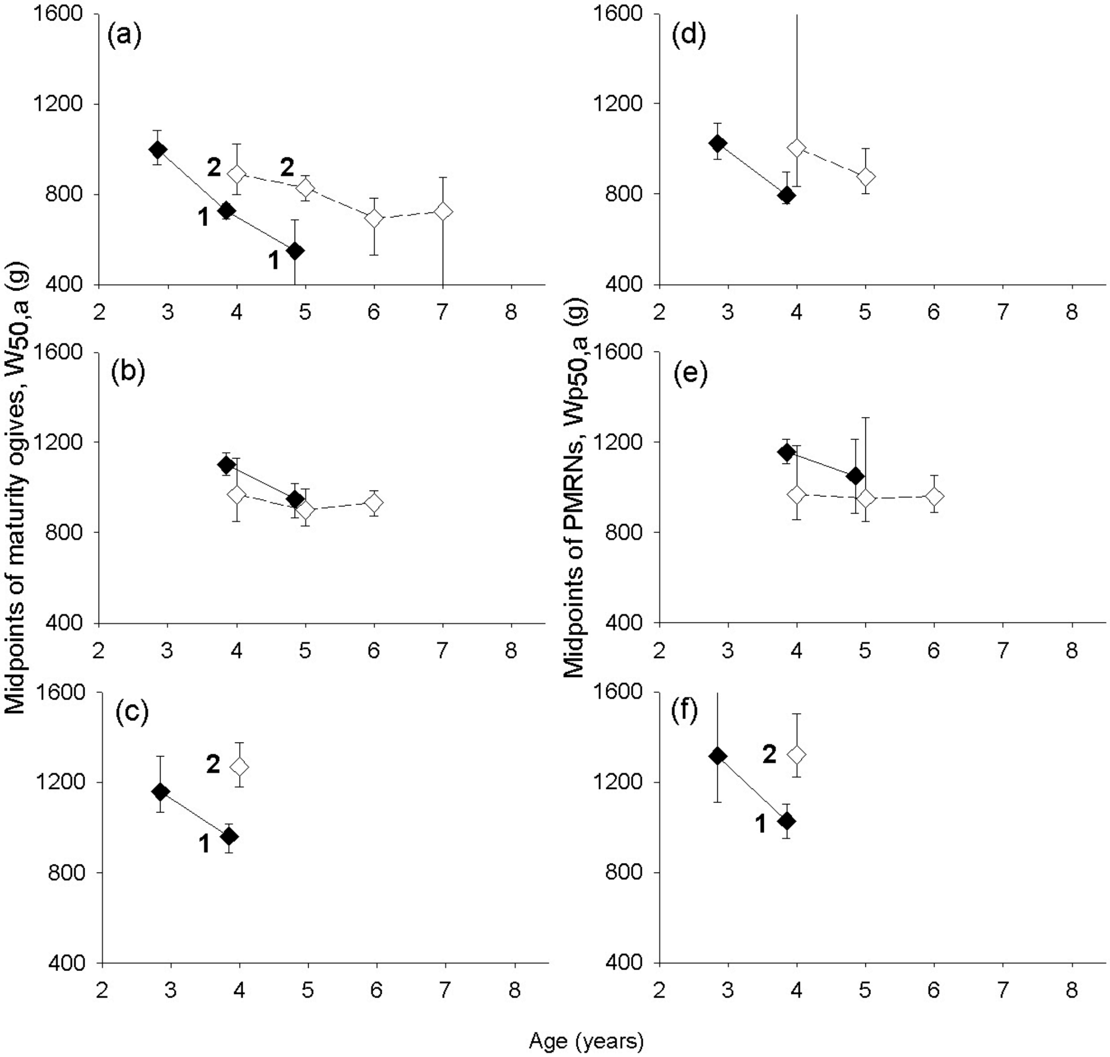

(a)
(b)
(c)
(d)
Midpoints of maturity ogives, W50,a (g)
Midpoints of PMRNs Wp50,a (g)
Age (years)
2000
1600
1200
800
400
2
3
4
5
6
7
8
1
2
3

Figure S5


(a)
(b)
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(d)
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(f)
1600
1200
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4
5
6
7
8
1
2
Midpoints of maturity ogives, W50,a (g)
Midpoints of PMRNs, Wp50,a (g)
Age (years)

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Chapter III

Sampling effects and inter-stock variation of maturation schedules of walleye: maturity ogives versus probabilistic maturation reaction norms

Abstract

Although variation in fish maturation schedules are influenced by both plastic and adaptive processes, commonly used maturation indices (e.g., age and length at 50% maturity) do not facilitate discrimination between plastic and adaptive variation in maturation. More recently, several researchers have employed probabilistic maturation reaction norms (PMRNs) to help discriminate between plastic and adaptive variation in maturation schedules. PMRNs represent the probability that a fish of a certain length and age will mature in the following year. To quantify inter-stock plastic and adaptive variation in maturation schedules and to evaluate sensitivity of maturation indices to sampling-induced biases, we quantified spatial and temporal variation of walleye *Sander vitreus* maturation schedules in Lake Erie, Lake Huron's Saginaw Bay, and Oneida Lake using 1) age and length at 50% maturity, 2) midpoint of age-specific maturation ogives (age specific length cut-offs at which probability of maturity = 0.5), and 3) midpoints of PMRNs (age-specific length cut-offs at which probability of maturing in the following year = 0.5). Our findings suggest that while sampling month, gear, and agency effects can bias estimates of age and length at 50% maturity, midpoints of PMRN estimates appear to be more robust to gear and month effects (but sensitive to biases relating to agency effects). Nonetheless, PMRN estimates are suggestive of potential adaptive variation in maturation schedules among walleye stocks and over time. For instance, Oneida Lake walleye (who grew at relatively slow rates) matured at a smaller size for a given age (smaller midpoints of PMRNs) than the other stocks. Temporally, walleye in the western basin of Lake Erie matured at a larger size in recent years (increasing midpoints of PMRNs). Our study highlights the necessity to monitor maturation schedules using multiple maturation indices and the need to account for sampling-induced biases when comparing maturation schedules.

Introduction

Maturation schedules (e.g., age and size at maturity) constitute important life history traits for fish, directly affecting fitness (e.g., number of offspring that survives to reproduce) at both individual and population levels (Stearns 1992; Trippel 1995) and influencing a fish stock's sustainable harvest potential. Intra-specific comparisons of maturation schedules among stocks allow for gauging of the current status and relative sustainability of multiple fish stocks. In fact, such inter-stock variation in maturation schedules is well documented (e.g., lake whitefish *Coregonus clupeaformis*; Taylor et al. 1992; lake trout *Salvelinus namaycush*; McDermid et al. 2007) and likely reflects both phenotypic plasticity (e.g., variation in maturation schedules induced by changes in growth rates) and local adaptation (e.g., variation in maturation schedules shaped by genetic selection with respect to factors such as size-selective mortality; Trippel 1995; Law 2000). Discrimination between adaptive and plastic variation in maturation schedules can be insightful, because whereas an adaptive maturation schedule is intrinsic to a stock and may be difficult to reverse (Olsen et al. 2005), plastically-determined maturation schedules may readily respond to management actions.

It is, however, difficult to distinguish plastic and adaptive changes in maturation schedules as these changes may occur simultaneously and have different magnitudes and directions (Law 2000). While most previous studies investigating spatial and temporal variation in maturation schedules have relied on estimates of age (A_{50}) and length (L_{50}) at 50% maturity, several authors suggest that these estimates are sensitive to biases related to gear selectivity and variation in growth and mortality rates (Heino et al. 2002; Dunlop et al. 2005). Thus, these indices are not suitable for distinguishing between plastic and selection-induced changes in maturation schedules. More recently, several studies have estimated midpoints of probabilistic maturation reaction norms (PMRNs; i.e., the length cut-offs at which probability of maturing = 0.5 for given ages) to characterize maturation schedules while accounting for the effects of growth and mortality rates (Heino et al. 2002; Dunlop et al. 2005; Dieckmann and Heino 2007). Such studies have demonstrated both within-stock temporal variation and across-stock spatial variation in adaptively-determined maturation schedules (e.g., decreased age and size at maturity is favored under size-selective fisheries; Grift et al. 2003; Olsen et al. 2004, 2005). Theoretically, PMRN estimates should be relatively robust to gear-induced estimation biases (Dieckmann and Heino 2007), as compared to A_{50} and L_{50} estimates which are highly sensitive to such biases. However, the potential for assessment methods (e.g., collection gear, time of assessment) to bias PMRN estimates has not been fully evaluated for most fish species.

Herein, we present a study to document within-stock temporal variation and across-stock spatial variation of maturation schedules of walleye from throughout the Laurentian Great Lakes region, including the western (WB), central (CB), and eastern basins (EB) of Lake Erie, Saginaw Bay of Lake Huron, and Oneida Lake. These ecosystems have all historically supported important walleye fisheries (Forney 1977; Schneider and Leach 1977; Fielder 2002), with variable harvest and management practices. Presently, walleye are harvested by both commercial and sport fisheries in Lake Erie (Knight 1997), but solely by anglers in Saginaw Bay and Oneida Lake (VanDeValk et al. 2002; Fielder and Thomas 2006). Previous research suggests that walleye in these lakes are genetically distinct (Billington and Hebert 1988; Billington et al. 1992; McParland et al. 1999), but the genetic distinctiveness across Lake Erie stocks is somewhat equivocal (Merker and Woodruff 1996; Strange and Stepien 2007). It is clear that these stocks display variable maturation schedules, growth, and mortality rates; e.g., while walleye in Oneida Lake have relatively low growth and mortality rates and mature at relatively old ages (Forney 1977; He et al. 2005), Lake Erie walleye experience much higher mortality rates and display intermediate growth rates and relatively early onset of maturation (Colby and Nepszy 1981; Wang 2003). Growth rates of walleye in Saginaw Bay have historically been high, but have declined in recent years (Fielder and Thomas 2006).

In this study, we quantify spatial and temporal inter-stock variation in maturation schedules of walleye by estimating 1) age and length at 50% maturity, 2) the age specific length cut-offs at which the probability of a fish being mature is 0.5 (hereafter referred to as the midpoints of age-specific maturation ogives; ogives are the probability of being mature for given ages; Barot et al. 2004a, 2004b), and 3) the age specific length cut-offs at which the probability of maturing the following year is 0.5 (hereafter referred to as the midpoints of PMRNs). In a previous study, we demonstrate that these maturation indices provide complementary information for identifying potential plastic and potential adaptive variation in maturation schedules of fish (Wang et al. in press). Our objectives were 1) to evaluate sensitivity of these maturation indices to potential confounding factors (as our data were obtained from multiple agencies which conducted surveys using different gears and during different months; see the Methods section) and 2) to identify if these walleye stocks display intrinsically different maturation schedules across space and over time.

Methods

Data

We analyzed fisheries-independent survey data (including total length, sex, age, and maturation state) of individual walleye collected in fall (from late August to November) by five assessment programs in three lakes (Figure 1; Table 1): Ohio Department of Natural Resources (ODNR; western and central basins [WB and CB] of Lake Erie), Ontario Ministry of Natural Resources (OMNR; WB, CB, and eastern basin [EB] of Lake Erie), New York State Department of Environmental Conservation (NYSDEC; EB of Lake Erie), Michigan Department of Natural Resources (MDNR; Saginaw Bay [SB] of Lake Huron), and Cornell University (CU; Oneida Lake). While all five programs conducted surveys during spring and fall, only fall open-lake surveys target both mature (i.e., fish that will spawn next year) and immature fish (i.e., fish that will not spawn next year). Information relating to both maturity states is necessary to quantify population level maturation indices. All programs internally examined sex and maturation state of fish (e.g., whether a fish will or will not spawn in the following spring) and used consistent within-programs methods for determining age (e.g., using otoliths, scales, or dorsal spines). While sex and maturation state of most walleye collected in fall can be identified by inspecting gonads (Forney 1965; Goede and Barton 1990; Henderson et al. 1996), there may be relatively high uncertainty in maturity identification during early fall (A. Cook, unpublished data). Note, that all ages reported herein are fall ages, and actual spawning would take place when fish are one year older.

The sampling protocols used by each assessment program were generally consistent over time but varied among agencies. The ODNR surveys (September-October 1978-2006) in WB and CB were located at seven fixed sites and each year approximately fifty additional sites were selected using a stratified random method (ODW 2006; Figure 1). At all sites, suspended multifilament gillnets (13 panels [dimension = 30.5 * 1.8 m, graded stretched mesh sizes ranged from 51 to 127 mm in 6mm increments] in random order) were set over night. In addition, at the seven fixed sites suspended and bottom monofilament gillnets (12 panels [dimension = 15.2 * 1.8 m, stretched mesh sizes ranged from 32 to 76mm in 6mm increments and from 76 to 127 mm in 12 mm increments] in random order) were also used (ODW 2006). Monthly distributions of samples were consistent between WB and CB but varied by gear; 38% (WB) and 24% (CB) of catches by monofilament gillnets were in September while the majority (96% and > 99% in WB and CB, respectively) of catches by multifilament gillnets was in October.

OMNR (1989-2006) used monofilament suspended and bottom gillnets at sites randomly selected within WB, CB, and EB (Figure 1). Each gillnet set was comprised of 3 small (dimension = 15.2 * 1.8 m mesh sizes = 32, 38, and 44 mm) and 9 (dimension = 30.5 * 1.8 m mesh sizes = 51, 57, 64, 70, 76, 89, 102, 114, and 127 mm) or 11 large (mesh sizes = 140 and 152 mm were added in 1993 and years after) panels of nets set in random order. During 1989-1990 and 1999-2001, additional gangs of nets were set in EB. Each year the inter-basin surveys initiated in EB (late August [24% of samples] to early September [73%] when the thermocline was present), continue to WB (September [86%] to October [14%]), and finished in CB following fall turnover (late September [15%] to October [85%]; A. Cook, unpublished data).

The spatial coverage of NYSDEC surveys was generally consistent over time (1981-2006), but sampling methods changed in 1993. From 1981 to 1992, NYSDEC conducted surveys in EB at 24 fixed nearshore stations (depths varied from 5.5 to 11 m) using bottom multifilament gillnets (8 panels [dimension = 15.2 * 1.8 m graded stretch mesh sizes ranged from 38 to 127mm mesh in 13mm increments]). Since 1993, NYSDEC has employed sampling procedures similar to ODNR and OMNR. The post-1993 sites were selected using a stratified random approach and sampled with monofilament gillnets (14 panels [dimension = 15.2 * 1.8 m] of nets set in random order; stretched mesh sizes ranged from 32 to 152 mm in 9 mm increments). Both suspended and bottom gillnets were set during 1993-1995, while only bottom gillnets were set during 1996-2006. Moreover, since 2005 the largest mesh panel (152 mm mesh) has not been employed to minimize likelihood of net damage (Einhouse et al. 2005).

MDNR surveys in SB have been conducted at nine fixed sites throughout the bay since 1989 (Fielder and Thomas 2006). The agency has employed two overnight sets of multifilament gillnets per site (each net with 11 panels [30.5 * 2 m stretched mesh sizes = 38, 51, 57, 64, 70, 76, 83, 89, 102, 114, and 127mm]).

Lastly, CU surveys were conducted using a variety of methods including 14 m and 5.5 m opening bottom trawls, trapnets, and electrofishing surveys. Trawling surveys targeted sites throughout the lake (for more details see Rudstam et al. 2004).

Analysis

To compare variation in maturation schedules among walleye stocks, we estimated three types of maturation metrics with bootstrapped 95% confidence intervals (C.I.): 1) age (A_{50}) and length (L_{50}) at 50% maturity, 2) midpoints of age-specific maturation ogives ($L_{50,a}$; *a* indexes for age), and 3) midpoints of PMRNs ($Lp_{50,a}$), using analytic procedures described in Barot et al. (2004a, 2004b) and Wang et al. (in press). Estimation procedures for these three metrics were similar but involved differential grouping of data. For example, all three metrics involved fitting a logistic regression (e.g., using length or age as a predictor with binary maturation state [0 = immature; 1 = mature] as the response variable). This was then used to estimate the length cut-offs (or age in the case of A_{50}) at which probability of maturity = 0.5. Specifically, A_{50} and L_{50} were estimated by pooling all samples of a sex within a stock (as walleye express sexual dimorphism; Henderson and Morgan 2002), while $L_{50,a}$ was estimated by grouping only samples of a given age-sex-stock group. Following the fitting of a logistic regression for age-specific maturation ogives, $Lp_{50,a}$ was estimated in two steps. First, we calculated the age-specific probability of maturing as the ratio of 1) the probability of an immature individual at age *a*-1 being mature at age *a* and 2) the probability of being immature at age *a*-1 (estimated based on the average growth increment from age *a*-1 to age *a*). Second, we fit a logistic regression (with length of age *a* as a predictor and probability of maturing as the response variable) to estimate $Lp_{50,a}$ (Barot et al. 2004a, 2004b; Wang et al. in press). Moreover, we only reported indices estimated via valid logistic regression models based on both a deviance-based test (at $\alpha = 0.05$) and visual inspection of fit. Statistical inferences were based on comparison of the 95% C.I.'s, i.e., two estimates varied significantly if their 95% C.I.'s do not overlap.

Exploration of sampling biases: Using Lake Erie survey data, we performed a series of analyses to explore how differences in sampling and analytical methods may impact estimates of maturation metrics. In particular, we evaluated variation in maturation indices due to 1) month of sampling, 2) gear type, and 3) agency effects. Month of sampling might affect the ability to accurately identify maturation state and observed length distributions. That is, as walleye grow relatively fast in fall (e.g., when water temperatures are bioenergetically favorable; Kitchell et al. 1977; Kershner et al. 1999), size differences over a one-month period (September-October) may be noticeable. Different sampling gear may bias observed age and length distributions due to gear selectivity. And, discrepancies in estimates from various agencies may result from differences in sampling procedures, including sampling different locations and agency-specific biases in assessing age, length, and maturation state.

To evaluate effects of these factors, we selected comparable subsets of data. We used ODNR monofilament gillnet data (1992-1995) from WB and CB, respectively, to evaluate sensitivity of maturation indices to month of sampling (September vs. October). With respect to gear (multi- vs. mono-filament gillnets), we analyzed ODNR data collected in October 1992-2006 in WB and CB, respectively. Finally, to consider agency effects, we analyzed monofilament gillnet data collected in 1) September 1991-2006 in WB (ODNR vs. OMNR), 2) October 1989-2006 in CB (ODNR vs. OMNR), and 3) September 1989-2006 in EB (OMNR vs. NYSDEC). Tagging studies suggest that during fall walleye are recaptured throughout each of the basins independent of tagging locations (Wang et al. 2007), and recent genetic analyses indicate that genetic variation of walleye within a basin is limited (Strange and Stepien 2007). Thus, we would expect that fall collections by different agencies within basin would target similar walleye, and that resulting differences in maturation indices would primarily result from agency-specific methodological differences and not from collection of different walleye sub-stocks.

Spatial and temporal variation: To evaluate spatial and temporal variation of maturation indices, we combined data from all gear types collected during September-October 1989-2006, but (based on the evaluation of sensitivity of maturation indices to potential biasing factors; see the Results section) we did not combine data across assessment agencies. While A_{50} and L_{50} estimates are likely sensitive to size-biases introduced by collection gear, PMRN estimates should be robust to such biasing factors (Heino et al. 2002; Dieckmann and Heino 2007). To explore temporal variation in maturation indices, we aggregated fish by estimated year classes into two approximately equal groups. While data of either temporal group might be disproportionately represented by certain strong year classes, there were insufficient data to estimate separate maturation indices for each annual cohort. We estimated and evaluated changes in maturation indices for each temporal group.

Results

Sensitivity of maturation indices to month of sampling, gear, and agency

Estimates of A_{50} and L_{50} appear to be sensitive to sampling month, gear, and agency (Table 2). While female A_{50} and L_{50} did not vary by sampling month or gear, one L_{50} estimate (CB) and multiple A_{50} estimates for males varied significantly by month and gear (Table 2A-B). Further, all estimates of A_{50} and L_{50} for both sexes varied significantly when comparing across assessment programs even when controlling for gear and month of capture (Table 2C).

In contrast, estimates of sex-age-specific $L_{50,a}$ and $Lp_{50,a}$ appeared to be relatively robust to month and gear related sampling biases. For example, $L_{50,a}$ and $Lp_{50,a}$ for age 3 females in WB did not vary significantly between September and October (Figure 2a-b). Moreover, while one $L_{50,a}$ estimate varied by gear (age 1 males in CB), no $Lp_{50,a}$ estimates varied by gear type (Figure 2c-d). However, some sex-age-specific $L_{50,a}$ and $Lp_{50,a}$ estimates based on data from the same systems but different agencies were significantly different (Figure 2e-f).

Among-stock variation in maturation indices

Estimates of A_{50} and L_{50} for both male and female walleye varied significantly among systems and assessment programs, but patterns were not necessarily consistent (Table 3). For example, whereas male A_{50} estimates were relatively small for WB-ODNR, CB-ODNR, and CB-OMNR and relatively large for WB-OMNR and EB-OMNR, female A_{50} estimates displayed dissimilar spatial patterns (Table 3). Further, despite of significant sensitivity of A_{50} and L_{50} with respect to agencies, these indices for males tended to be large in EB and SB relative to WB and CB. The spatial variation in A_{50} and L_{50} for females was less pronounced and differed from the pattern of these indices for males. Lastly, L_{50} for both sexes were relatively small for Oneida Lake (Table 3).

Sex-age-specific estimates of $L_{50,a}$ and $Lp_{50,a}$ also varied significantly among system-agency units (Figure 3). However, spatial patterns of $L_{50,a}$ and $Lp_{50,a}$ estimates were not consistent across ages. For example, while both maturation indices ($L_{50,a}$ and $Lp_{50,a}$) for age 1 males were relatively large for SB and small for WB-OMNR, the spatial pattern of these same indices for age 2 males reversed (Figure 3a-b). Similarly, both indices for females showed inconsistent and somewhat ambiguous (perhaps confounded by sensitivity of the indices to agency effects) spatial patterns across ages; $L_{50,a}$ for age 2 of CB-ODNR significantly varied from that of EB-OMNR, but $L_{50,a}$ and $Lp_{50,a}$ for age 3 did not vary between the two system-agency units (Figure 3c-d). Further, while the $L_{50,a}$ and $Lp_{50,a}$ estimates for age 1 males varied conspicuously between WB and CB based on OMNR data, between-basin differences in these indices based on ODNR data were much smaller or not significant (Figure 3a-b). Despite such inconsistent patterns, two trends were particularly noticeable; 1) spatial variation in $L_{50,a}$ and $Lp_{50,a}$ estimates for males was more pronounced than for females, and 2) while norms estimated for Lake Erie and SB tended to intersect, $L_{50,a}$ or $Lp_{50,a}$ estimates for Oneida Lake were relatively low and distinct from the other stocks (Figure 3a, c, and d).

Within-stock temporal variation in maturation indices

While agency-related biases confounded interpretation of cross-stock variation in maturation indices, there is no indication that biases should confound interpretation of within-stock temporal patterns. Significant and variable temporal changes in A_{50} and L_{50} were detected for most stocks (Table 4). While most male estimates tended to increase over time or remain unchanged, both indices for CB-OMNR males decreased. On the other hand, female A_{50} estimates tended to decrease or remain unchanged. While all female L_{50} estimates changed significantly over time, the direction of change varied among system-agency units (Table 4).

Some temporal changes in sex-age-specific $L_{50,a}$ and $Lp_{50,a}$ estimates were also evident, and trends (increasing or decreasing) were generally consistent between sexes and among age classes (Figure 4). Age-specific $L_{50,a}$ and $Lp_{50,a}$ estimates increased significantly for males and females in WB (based on both ODNR and OMNR data; Figure 4a-d). On the other hand, changes in $L_{50,a}$ and $Lp_{50,a}$ estimates for CB (based on ODNR data) and EB (based on NYSDEC data) were not significant (Figure 4e-h). And, while age 2 male $L_{50,a}$ estimates for Oneida Lake increased over time, other sex-age-specific $L_{50,a}$ and $Lp_{50,a}$ estimates for Oneida Lake did not change significantly over time (Figure 4i-j).

Discussion

By quantifying maturation schedules of walleye stocks via three types of maturation indices, we demonstrate that: 1) A_{50} and L_{50} estimates are relatively sensitive to biases related to sampling procedures (including agency related issues); 2) $L_{50,a}$ and $Lp_{50,a}$ are less sensitive to biases related to sampling time and gear, but are also influenced by agency-specific sampling-related biases; and 3) after accounting for age and length, walleye stocks appear to display intrinsically different maturation schedules (e.g., variation in $Lp_{50,a}$) among systems and over time. Standard assessments over time suggest that within-system temporal changes in PMRN midpoints are indicative of adaptive changes. Further, while across-agency sampling biases confound interpretation of spatial variation of PMRN midpoints, the congruency of life history expectations as well as magnitude and consistency of across-system differences in PMRNs are suggestive of adaptive variation.

The great sensitivity of A_{50} and L_{50} estimates to sampling biases suggests that it may be inappropriate to use these indices to quantify spatial and temporal variation in walleye maturation schedules when data collection involves various methods and assessment programs. Similarly, agency-related biases when estimating midpoints of age-specific maturation ogives and PMRNs may confound interpretation of spatial variation. That is, we can not unequivocally distinguish between intrinsic variation in walleye maturation schedules and agency effects. The mechanisms underlying agency differences in estimates of maturation schedules are unclear. It is possible that by sampling in different areas within a basin of Lake Erie, agencies are collecting walleye from different sub-stocks. However, EB and WB are fairly small basins which walleye readily move throughout (Wang et al. 2007). Alternatively, such agency-related bias may result from uncertainty in identifying maturation state of walleye during fall. Mature walleye in Lake Erie start developing gonads during August to October (Henderson et al. 1996), and it is possible that some walleye that will spawn in the spring may be evaluated as immature during September surveys. While misidentification of maturation state for walleye could be reduced by using spring survey data, lack of immature fish in spring samples would preclude this analysis. We believe that while misidentification of maturation state may be relatively pronounced for walleye, such misidentification may be minor for surveys which take place more immediate to spawning time.

Uncertainty in identifying walleye maturation state and sex of young fish during fall could have strong impact on maturation indices. For example, while females generally mature at older ages and larger lengths than males for a given walleye population (Henderson and Morgan 2002), based on OMNR data in Lake Erie EB and WB (where data were collected during early to mid-fall), the A_{50} and L_{50} estimates for males appear to be inflated and L_{50} for females are relatively small. Furthermore, such uncertainty in data quality also may have confounded the within-agency across-basin variation in PMRN estimates. We found that PMRN estimates varied conspicuously between WB and CB based on OMNR data but not ODNR data. Given that monthly distributions of ODNR samples were approximately equal in both basins but varied across basins for OMNR data, it is possible that between-basin variation in PMRNs based on OMNR data was inflated due to difference in time of sampling. While we could have avoided this bias by only using October data, the combination of samples from

September and October was in many cases necessary to achieve a sufficient sample size for PMRN analysis (Barot et al. 2004a, 2004b).

By accounting for the effects of growth and mortality rates, spatial and temporal variation in midpoints of PMRNs may identify adaptive responses among walleye stocks and over time. Further, comparison between PMRNs and A_{50} and L_{50} indices may inform the role of plasticity in maturation schedules (e.g., significant variation in A_{50} and L_{50} but not $Lp_{50,a}$). Thus, different maturation indices are complimentary. While potential biases related to agency-specific assessment methods preclude robust interpretation of across-agency spatial variation in PMRN estimates, we believe it is appropriate to consider within-system-agency temporal variation of our results.

While A_{50} and L_{50} for females in EB-NYSDEC decreased over time, insignificant changes in the $Lp_{50,a}$ for age 3 females suggest that such temporal changes may be a plastic response (e.g., A_{50} and L_{50} but not PMRNs were sensitive to temporal changes in length-at-age of fish). Moreover, although growth rates did not change (ODW 2006), $L_{50,a}$, and $Lp_{50,a}$ for WB fish showed significant signs of temporal increases, suggesting that fish matured at larger lengths for a given age in recent year classes. Such temporal trends in walleye maturation schedules differ from those of many commercial fishes (e.g., several commercially harvested Atlantic cod *Gadus morhua* stocks were observed to express decreases in midpoints of PMRNs over time; Olsen et al. 2004). Several authors suggest that intensive (e.g., commercial) size-selective harvest may induce decreases in midpoints of PMRNs for a fish stock (e.g., Stokes et al. 1993; Law 2007). While the selection experienced by walleye in Lake Erie may not be comparable to that for other commercially-harvested species, we believe that it is possible that present management of

Lake Erie walleye may have factored in the observed temporal PMRN patterns. Harvest of walleye in Lake Erie has involved defining quota for whole-lake annual catches based on long-term monitoring of spawning and recruitment status (GLFC Press Releases 2008). Such proactive adjustments of harvest intensity may have contributed towards an increase in midpoints of PMRNs for WB walleye.

Spatially, the across-agency variation of walleye maturation schedules must be considered with the caveat that such variation may be due to intrinsic variation among stocks, agency-related assessment biases, or both. Nonetheless, variation of maturation schedules among these walleye stocks do appear to correspond to variation in their life history traits. Prior to 2004, walleye in Saginaw Bay expressed relatively fast juvenile growth rates (e.g., mean length for age 1 in SB = 350 mm while mean length age 1 in WB = 300 and in CB and EB = 330 mm, respectively; Fielder et al. 2000; Fielder and Thomas 2006; OMNR data in this study), and consistent with these growth patterns, estimated midpoints of PMRNs suggest that males in Saginaw Bay mature at relatively early ages (e.g., at age 2) and large sizes. Conversely, walleye in Oneida Lake experience relatively slow juvenile growth (mean length for age 1 = 170 mm; He et al. 2005) and low mortality rates, and walleye in this system appear to mature at relatively small sizes, even at older ages. Interestingly, patterns of PMRN estimates for walleye across Lake Erie basins do not correspond to differences in their life history traits. EB walleye grow relatively fast and experience low mortality rates as compared to WB walleyes (Wang 2003; A. Cook unpublished data). However, age-specific PMRN estimates for males were greater in WB than in EB and among-basin variation for females was not significant. This disparity between maturation schedules and other life history traits of

Lake Erie walleye suggests that 1) these stocks may have experienced complex local selection pressures, 2) adaptive variation in maturation schedules of these walleye stocks is not fully characterized by PMRN estimates (see below), and/or 3) agency-related assessment biases obscure the depiction of intrinsic maturation schedules (including uncertainty in identifying maturity state during fall surveys).

In addition to assessment-related biases, other factors may also confound interpretation of length-based PMRN patterns. For example, stocks may potentially mix among inter-connected systems. While we used fall survey data to ensure inclusion of both juvenile and adult fish, among-basin or between-lake movements of walleye imply that it is possible that some fish collected in WB, CB, EB and SB were not residents of these systems. However, tag-recapture studies suggest that during fall most fish occupy their natal system (Fielder and Thomas 2006; Wang et al. 2007). Further, while estimation of PMRNs involves controlling for length and age, several authors suggest that as length and age do not fully account for plastic variation, it may be inappropriate to interpret variation in PMRN estimates as indicative of genetically distinct maturation schedules (Kraak 2007; Marshall and McAdam 2007). Recent studies show that weight or condition may serve as additional explanatory variables for estimating PMRNs (Grift et al. 2007; Wright 2007). Indeed, condition could have an important effect on maturation processes of walleye (Henderson and Nepszy 1994; Henderson et al. 1996; Henderson and Morgan 2002). At the individual-level, onset of maturation of female walleye begins during early fall when visceral fat is replenished, and gonadal development during fall and winter depends on the amount of available visceral fat (Henderson et al. 1996). As a result, PMRN estimates might better represent adaptive variation in maturation schedules by incorporating information on weight or condition. However, because 1) length and weight are often correlated and 2) adding more explanatory variables may introduce additional assumptions and measurement error (as suggested by Dieckmann and Heino 2007), we believe that the spatial or temporal variation in length-based PMRN estimates would likely be consistent with the weight-based estimates (as shown by Wang et al. in press).

In conclusion, variation in age and length at maturation has direct implications for management of walleye (Henderson and Nepszy 1994, Henderson et al. 1996, Madenjian et al. 1996). Furthermore, to ensure sustainability of fisheries, it is useful to monitor and understand the role of adaptive versus plastic effects on maturation traits (Law 2007). Based on our results, we suggest that interpretation of variation in maturation schedules based solely on age and length at 50% maturity would be inappropriate as 1) these indices are unsuitable for informing adaptive changes and 2) these estimates are sensitive to sampling protocols and agencies. We recommend using multiple maturation indices (e.g., age and length at 50% maturity and PMRN estimates) which collectively help to reveal both adaptive and plastic variation. Finally, in large systems where stock assessment and fisheries management involves different agencies, we recommend that agencies consider adopting similar survey protocols when possible and conduct experimental surveys to evaluate agency- and sampling-induced biases related to estimation of age and maturation state.

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Table 3.1. Sources, spatial and temporal extent, gear types, and sample sizes (N) of data analyzed in this study. ODNR, Ohio Department of Natural Resources; OMNR, Ontario Ministry of Natural Resources; NYSDEC, New York State Department of Environmental Conservation; MDNR, Michigan Department of Natural Resources; CU, Cornell University; WB, CB, and EB, western, central, and eastern basins; SB, Saginaw Bay; Multi- and mono-GN, multifilament and monofilament gillnet; TW, trawl; TP, trap net; EF, electrofishing.

Data sources	Lake	Year	Month	Gear	N
ODNR	Lake Erie (WB)	1978-2006	Sep-Oct	Multi-GN	32,678
	Lake Erie (WB)	1992-2006	Sep-Oct	Mono-GN	4,039
	Lake Erie (CB)	1981-2006	Sep-Oct	Multi-GN	14,824
	Lake Erie (CB)	1990-2006	Sep-Oct	Mono-GN	2,648
OMNR	Lake Erie (WB)	1990-2006	Sep-Oct	Mono-GN	17,433
	Lake Erie (CB)	1989-2006	Sep-Oct	Mono-GN	13,053
	Lake Erie (EB)	1989-2006	Aug-Oct	Mono-GN	2,386
NYSDEC	Lake Erie (EB)	1981-2006	Sep-Oct	Mono-GN	8,969
MDNR	Lake Huron (SB)	1989-2006	Sep	Multi-GN	5,318
CU	Oneida Lake	1961-2005	Oct-Nov	TW, TP, EF	3,793

Table 3.2. Estimated age (A_{50}) and length (L_{50}) at 50% maturity with 95% C.I. (in parentheses) for male and female walleye by A: month of sampling (Sep. vs. Oct., based on ODNR monofilament gillnet data from the western basin [WB] of Lake Erie, 1992-1995), B: gear types (multi- vs. mono-filament gillnets, based on ODNR data from WB and central basin [CB], October, 1992-2006), and C: agencies (based on monofilament gillnet data from WB [ODNR vs. OMNR using data in September 1991-2006], CB [ODNR vs. OMNR using data in October 1989-2006], and eastern basin [EB; OMNR vs. NYSDEC using data in September 1989-2006] of Lake Erie).

A

Month	Lake	Male			Female		
		N	A_{50}	L_{50}	N	A_{50}	L_{50}
Sep	WB	787	1.4 (1.3, 1.4)	333 (329, 338)	703	2.8 (2.6, 3.0)	447 (437, 460)
Oct	WB	559	1.1 (1.0, 1.2)	331 (326, 337)	349	2.6 (2.5, 2.8)	457 (447, 467)
Sep	CB	291	1.4 (1.1, 1.6)	341 (332, 349)	288	2.4 (2.1, 2.7)	441 (425, 455)
Oct	CB	498	1.2 (1.1, 1.2)	339 (332, 346)	460	2.6 (2.4, 2.7)	462 (454, 470)

B

Gear	Lake	Male			Female		
		N	A_{50}	L_{50}	N	A_{50}	L_{50}
Multi-GN	WB	7,614	1.0 (0.9, 1.0)	326 (323, 328)	4,666	2.5 (2.5, 2.5)	464 (462, 466)
Mono-GN	WB	1,244	1.0 (1.0, 1.1)	327 (324, 331)	889	2.5 (2.4, 2.6)	458 (452, 463)
Multi-GN	CB	4,756	0.9 (0.8, 0.9)	323 (319, 328)	4,151	2.5 (2.5, 2.6)	470 (468, 472)
Mono-GN	CB	862	1.2 (1.1, 1.2)	342 (337, 347)	803	2.5 (2.4, 2.6)	464 (458, 470)

C

Agency[a]	Lake	Male			Female		
		N	A_{50}	L_{50}	N	A_{50}	L_{50}
ODNR	WB	796	1.4 (1.3, 1.4)	333 (329, 337)	709	2.8 (2.6, 3.0)	446 (436, 458)
OMNR	WB	3,625	2.3 (2.3, 2.4)	403 (400, 407)	5,235	2.5 (2.5, 2.6)	420 (417, 422)
ODNR	CB	958	1.2 (1.1, 1.2)	344 (339, 349)	904	2.5 (2.4, 2.6)	463 (457, 469)
OMNR	CB	4,265	0.9 (0.9, 1.0)	324 (320, 328)	3,553	2.3 (2.3, 2.3)	454 (451, 456)
OMNR	EB	566	2.8 (2.5, 3.1)	439 (430, 448)	774	2.3 (2.1, 2.5)	436 (428, 443)
NYDEC	EB	2,078	1.8 (1.7, 1.8)	377 (373, 380)	1,077	3.1 (2.9, 3.5)	464 (458, 471)

[a] See Table 1.

Table 3.3. Estimated age [A_{50}] and length [L_{50}] at 50% maturity with 95% C.I. (in parentheses) for male and female walleye by lake system and agency. All estimates were based on combined-gear data collected during September-October, 1989-2006.

Lake-agency[a]	Male			Female		
	N	A_{50}	L_{50}	N	A_{50}	L_{50}
WB-ODNR	13,219	1.0 (1.0, 1.0)	329 (328, 331)	7,739	2.5 (2.5, 2.5)	459 (458, 461)
WB-OMNR	4,254	2.2 (2.1, 2.3)	395 (392, 398)	5,645	2.5 (2.4, 2.6)	419 (417, 423)
CB-ODNR	7,758	1.0 (1.0, 1.1)	332 (329, 335)	6,792	2.5 (2.5, 2.5)	465 (463, 466)
CB-OMNR	5,072	1.0 (1.0, 1.0)	328 (324, 331)	4,534	2.3 (2.3, 2.3)	449 (446, 451)
EB-OMNR	581	2.7 (2.4, 3.0)	436 (427, 444)	828	2.3 (2.1, 2.5)	434 (426, 441)
EB-NYSDEC	2,078	1.8 (1.7, 1.8)	377 (373, 380)	1,077	3.1 (2.9, 3.5)	464 (458, 472)
SB	2,747	1.7 (1.6, 1.7)	383 (379, 386)	2,171	2.5 (2.5, 2.6)	455 (448, 460)
Oneida Lake	928	1.9 (1.8, 2.1)	327 (323, 331)	885	3.3 (3.2, 3.4)	383 (380, 387)

[a] see Table 1.

Table 3.4. Estimated age [A_{50}] and length [L_{50}] at 50% maturity with 95% C.I. (in parentheses) for male and female walleye in each lake-agency unit by temporal groups. The temporal groups for each lake-agency unit were defined by dividing data into two approximately equal subsets based on estimated year-classes.

Lake-agency[a]	Year-classes	Male			Female		
		N	A_{50}	L_{50}	N	A_{50}	L_{50}
WB-ODNR	pre-1990	11,313	0.8 (0.7, 0.8)	318 (315, 320)	6,799	2.4 (2.4, 2.5)	455 (453, 457)
	post-1990	8,716	1.0 (1.0, 1.1)	328 (326, 330)	5,878	2.5 (2.5, 2.5)	461 (459, 463)
WB-OMNR	pre-1997	2,798	1.9 (1.9, 2.0)	379 (376, 383)	2,765	2.5 (2.4, 2.6)	427 (422, 431)
	post-1997	1,456	2.7 (2.5, 2.8)	420 (413, 428)	2,880	2.5 (2.4, 2.6)	415 (410, 419)
CB-ODNR	pre-1990	3,844	0.9 (0.8, 1.0)	335 (331, 339)	3,319	2.5 (2.5, 2.6)	463 (460, 465)
	post-1990	5,214	1.1 (1.0, 1.1)	329 (327, 332)	4,645	2.5 (2.5, 2.6)	469 (467, 471)
CB-OMNR	pre-1997	2,005	1.3 (1.2, 1.3)	349 (345, 353)	2,230	2.3 (2.2, 2.3)	440 (435, 444)
	post-1997	3,067	0.8 (0.8, 0.9)	312 (305, 319)	2,304	2.3 (2.3, 2.3)	455 (451, 458)
EB-NYSDEC	pre-1993	1,529	1.9 (1.7, 2.0)	382 (376, 387)	794	3.4 (3.1, 3.8)	479 (471, 488)
	post-1993	1,397	1.8 (1.7, 1.8)	375 (371, 379)	890	2.8 (2.7, 2.9)	460 (453, 466)
SB	pre-1993	1,522	1.5 (1.4, 1.5)	384 (379, 389)	1,035	3.0 (2.9, 3.1)	496 (491, 502)
	post-1993	1,225	1.8 (1.7, 1.8)	383 (378, 387)	1,136	2.2 (2.1, 2.3)	428 (419, 437)
Oneida Lake	pre-1985	852	2.0 (1.9, 2.1)	315 (311, 317)	993	3.3 (3.2, 3.4)	369 (366, 372)
	post-1985	880	1.9 (1.8, 2.1)	327 (323, 331)	885	3.3 (3.2, 3.4)	383 (381, 386)

[a] see Table 1.

Figure List

Figure 3.1 Map of study area, including western (WB), central (CB) and eastern basins (EB) of Lake Erie, Saginaw Bay of Lake Huron, and Oneida Lake. WB, CB, and EB were surveyed by multiple agencies, i.e., WB and CB surveys involved OMNR and ODNR, and EB surveys involved OMNR and NYSDEC. While ODNR conducted surveys at seven fixed sites (black dots) and additional randomly selected sites, all other Lake Erie agencies used a stratified-random sampling procedure. See Table 1 for agency acronyms.

Figure 3.2. Comparison of midpoints (with 95% C.I.) of age-specific maturation ogives ($L_{50,a}$; left column) and probabilistic maturation reaction norms (PMRN; $Lp_{50,a}$; right column) by: 1) month of sampling (a and b; Sep vs. Oct, comparisons were based on age 3 western basin [WB] female estimates [open diamonds], ODNR monofilament gillnet data in WB, 1992-1995); 2) gear types (c and d; multi- vs. monofilament gillnets, based on estimates of age 1 male in WB [black diamonds] and CB [black squares] and age 3 females in WB [open diamonds], October, 1992-2006, ODNR data); 3) agencies (e and f; ODNR vs. OMNR comparisons were on estimates of age 1 males in CB [black squares] and age 3 females in WB [open diamonds]; OMNR vs. NYSDEC comparisons were on estimates of age 2 males [black triangles] and age 3 females in EB [open triangles]). Evaluation of agency effects were based on monofilament gillnet data from the WB (September 1991-2006), CB (October 1989-2006), and EB (September 1989-2006). Significantly different midpoints are indicated by different numbers.

Figure 3.3. Midpoints (with 95% C.I.) of age-specific maturation ogives ($L_{50,a}$; male [a] and female [c]) and probabilistic maturation reaction norms (PMRN; $Lp_{50,a}$; male [b], and female [d]) for walleye from various systems, collected by different agencies (see Table 1). Significantly different midpoints are indicated by different numbers. To facilitate visual inspection, estimates for a given age are slightly offset along the x-axis. Black diamonds: WB-ODNR, black squares: WB-OMNR, open diamonds: CB-ODNR, open squares: CB-OMNR, gray squares: EB-OMNR, gray circles: EB-NYSDEC, crosses: SB, dotted triangles: OL.

Figure 3.4. Temporal trends of midpoints (with 95% C.I.) of age-specific maturation ogives ($L_{50,a}$; left column) and probabilistic maturation reaction norms (PMRN; $Lp_{50,a}$; right commune) for walleye from various systems, collected by different agencies: WB-ODNR (a and b); WB-OMNR (c and d); CB-ODNR (e and f); EB-NYSDEC (g and h); Oneida Lake (i and j). Black diamonds: pre-cutoff-year classes, open diamonds: post-cutoff-year classes. Temporal groups per lake-agency unit were defined by dividing data into two approximately equal subsets based on estimated year-classes (i.e., individuals born before or after year indicated for division; see Table 4). Age-specific estimates to the left and right of vertical dotted lines are for males and females, respectively.

Figure 3.1

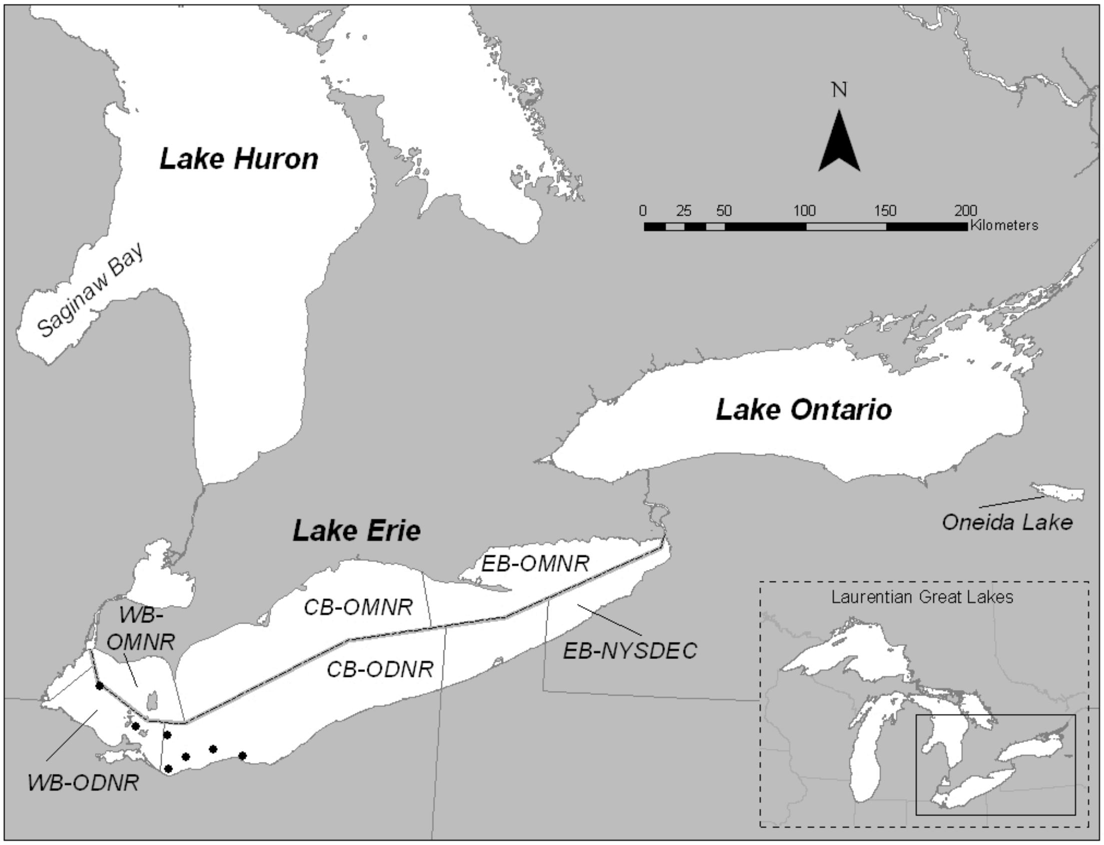

Lake Huron
Saginaw Bay
N
0 25 50 100 150 200
Kilometers
Lake Ontario
Oneida Lake
Lake Erie
EB-OMNR
CB-OMNR
WB-
OMNR
CB-ODNR
EB-NYSDEC
WB-ODNR
Laurentian Great Lakes

Figure 3.2

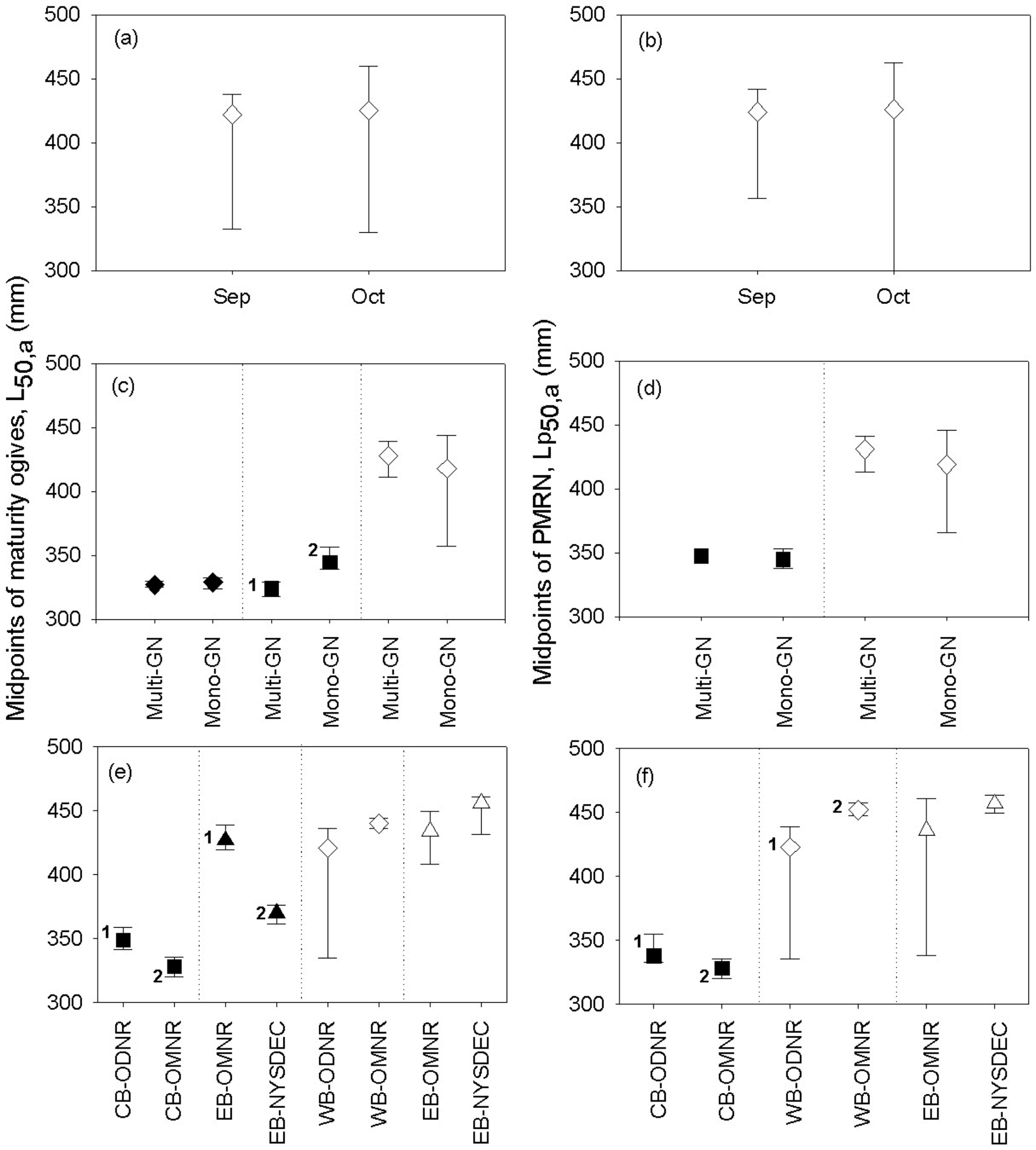
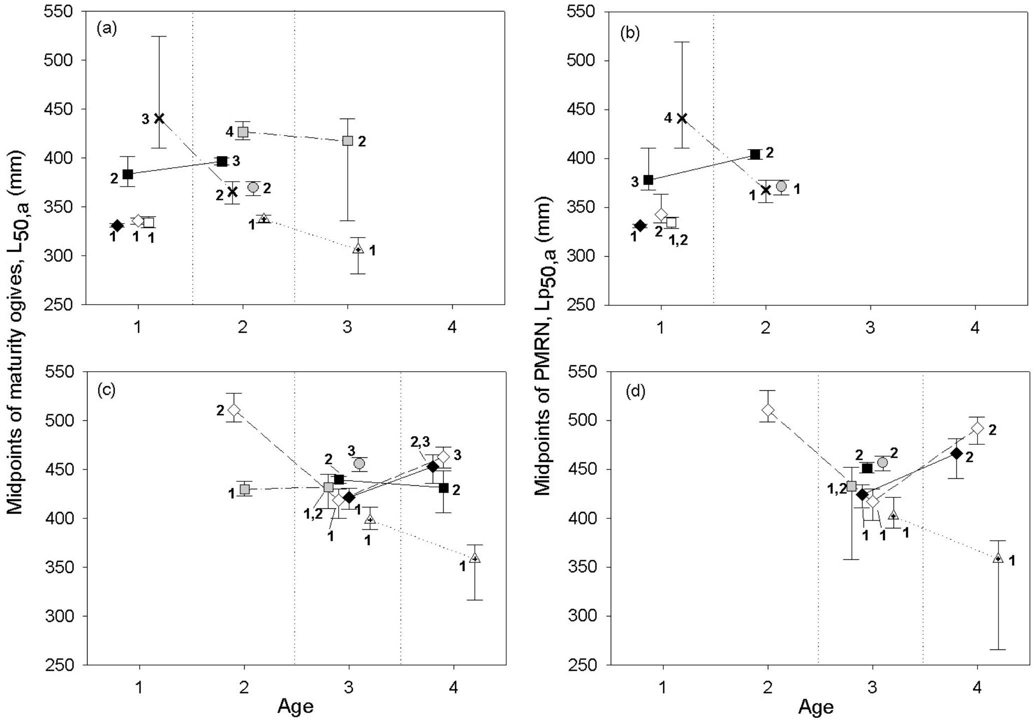
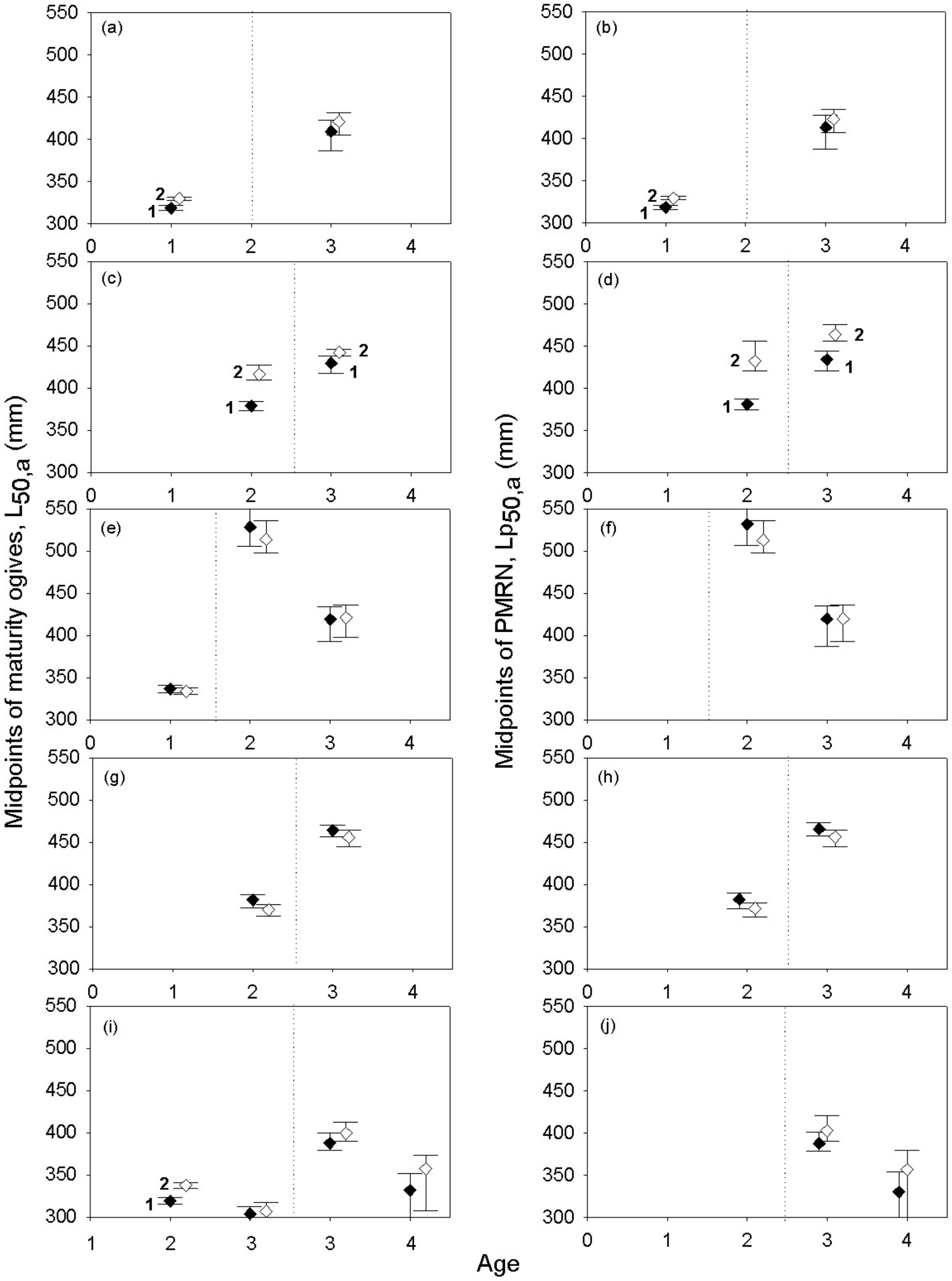

(a)
(b)
(c)
(d)
(e)
(f)
Midpoints of maturity ogives, $L_{50,a}$ (mm)
Midpoints of PMRN, $Lp_{50,a}$ (mm)
300
350
400
450
500
Sep
Oct
Multi-GN
Mono-GN
1
2
CB-ODNR
CB-OMNR
EB-OMNR
EB-NYSDEC
WB-ODNR
WB-OMNR

Figure 3.3



(a)
(b)
(c)
(d)
Midpoints of maturity ogives, L50,a (mm)
Midpoints of PMRN, Lp50,a (mm)
Age
250
300
350
400
450
500
550
1
2
3
4
1,2
2,3

Figure 3.4


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
1
2
550
500
450
400
350
300
0
1
2
3
4
Midpoints of maturity ogives, $L_{50,a}$ (mm)
Midpoints of PMRN, $Lp_{50,a}$ (mm)
Age

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Chapter IV

A generalized individual-based model of ecological and evolutionary effects on fish growth and maturation schedules

Abstract

Eco-genetic individual-based models involve tracking the ecological dynamics of simulated individual organisms that are in part characterized by heritable parameters. We developed a generalized eco-genetic individual-based model to explore ecological and evolutionary effects on fish growth and maturation schedules. Our model is flexible and allows for exploration of the effects of heritable growth rates (based on von Bertalanffy growth patterns), heritable maturation schedules (based on maturation reaction norm concepts), or both, on individual and population traits. With rather simple ecological tradeoffs and over a relatively short time period (less than 200 simulation years), simulated male and female fish evolve differential genetic growth and maturation. Resulting patterns of genetically determined growth and maturation are influenced by mortality rate and density dependent processes. Further, maturation and growth parameters interact to mediate the evolution of one another. We suggest that our model can be extended to consider other processes (e.g., size selective fisheries harvest).

Introduction

There is increasing evidence that genetic selection occurs at a time scale relevant to population dynamics and fisheries management (e.g. Hendry et al. 2000; Conover and

Munch 2002). Further, ecological processes (e.g. intra-specific competition, interacting species dynamics) can influence genetic selection and phenotypic expression within a population. These linkages between ecology and evolution are particularly relevant for fisheries management. Fish are generally selectively harvested based upon individual traits such as size, behavior, and location. Such selective harvesting can alter the genetic composition of the population and affect mean life history traits including, growth rates and maturation schedules (Stokes et al. 1993; Heino 1998; Law 2000; Conover and Munch 2002; Heino and Godø 2002). In turn, as these traits have strong influence on a fish stock's harvest potential, effective management of fisheries for sustainable yields and genetic diversity requires consideration of both short and long term impacts (including both ecological and genetic effects) on fish growth and maturation schedules.

As individual phenotypic expression (e.g., growth, age or size at maturity) is a function of both individual genetics and environmental (both biotic and abiotic) interactions it can be quite difficult to predict and discriminate between ecological versus genetic changes in life history traits. Most fish species are phenotypically plastic and temporal and spatial trends in life history trait values generally do not arise due to genetic selection alone. For instance, while size-selective harvest may select for early maturing genotypes, such harvest may also increase per capita food availability (by decreasing population size) thereby increasing individual growth rates and perhaps decreasing mean age at maturity. Thus, a trend of decreasing age at maturity coincident with increasing fishing pressure may arise from genetic selection, release from compensatory density dependent suppression of growth, or both.

Quantitative fish population models which take into account genetic inheritance represent a potentially useful tool to consider the evolutionary impacts of size-selective fisheries harvest (e.g., Martínez-Garmendia 1998; Jager 2001; Dunlop et al. 2007). In particular, models which depict life history traits as phenotypically plastic and density-dependent and which represent the inherent trade-offs between current and future growth and reproduction (i.e., Eco-genetic models, Dunlop et al. 2007) should prove particularly insightful for evaluating the relative importance of genetic and ecological effects on fish life history traits and stock productivity. In addition to constructing, parameterizing and applying such models for specific fish populations, we believe it is beneficial to evaluate the consequences of certain model approaches and assumptions on qualitative and quantitative model predictions.

Herein, we present a generalized eco-genetic individual-based model to consider the evolution of genotypes describing growth and maturation schedules and consequences for fish population dynamics and individual phenotypic expression. While the model is generalized, it is loosely based on two, similar-sized freshwater North American fish species, lake whitefish (*Coregonus clupeaformis*) and walleye (*Sander vitreus*). These two species can be classified as periodic and display high across-system variation in growth and maturation schedules. We use this model to explore phenotypic expression and genotypic evolution. Further, we consider consequences of growth and maturation schedule genotypes evolving separately versus concurrently and the effects of stochastic and density dependent factors.

Model Overview

Our model is multi-generational and tracks the simulated population at annual time steps. Although the model describes individual-level fish dynamics, the model actually tracks 'super-individuals' with each super-individual potentially representing a multitude of individual fish (e.g., Scheffer et al. 1995). This approach is useful as it does not necessitate the elimination of simulated fish whenever there is a mortality event (mortality simply causes a reduction in the number of individuals represented by a super-individual), thereby allowing for efficient simulation of large populations. In addition to the number of individual fish (NI) represented by a super-individual, other individual-level (i.e., I-state) variables include: sex (binary), age (years), maturation status (binary), total length (mm), somatic weight (g), gonadal weight (g) and heritable growth and maturation parameters. Each year individual fish grow, potentially mature, and experience some mortality. Between annual time steps (y and $y+1$), mature individuals reproduce. The resulting new individuals (which are characterized by heritable growth and maturation parameters obtained from reproductively successful adults) enter the population as age 1 fish at the beginning of annual time step, $y+2$.

Maturation

Individual fish can become mature at age 2 and older, and once an individual becomes mature it remains mature throughout its life. The maturation process is modeled via a maturation reaction norm (MRN) approach (Heino et al. 2002a; Heino et al. 2002b; Barot et al. 2004a; Barot et al. 2004b; Olsen et al. 2004). Each individual is characterized by 18 pairs of heritable maturation values and means of each pair determine an individual's 18 maturation parameters ($M_{1\text{-}18}$; $M_{1\text{-}8}$ and $M_{10\text{-}17}$ relate to maturation of age 2-9 males and females, respectively; M_9 and M_{18} relate to maturation of age $\geq$10 males and females, respectively). Each maturation parameter represents the minimum length an immature individual must reach to mature at a given age. For example, assume an immature four-year-old female's twelfth maturation parameter (M_{12}) is 500-mm. If this individual is to mature at the end of the year, she must grow to at least 500-mm. While this discrete representation of MRNs requires tracking a multitude of individual maturation parameters (as opposed to a linear function, e.g., Dunlop et al. (2007), or some other parameter-sparse function of age), it does not require us to presuppose the form of MRNs and allows each parameter to only directly influence maturation for a single age.

Growth

The model tracks growth of two tissue types (somatic and gonadal) of equal energy density, i.e., growth of gonads occurs at a direct cost to growth of soma. Spawning occurs at the end of each year, and consequently at the beginning of a year, individuals' gonads weigh 0-g. Individual growth rates are dependent on population abundance and individual size, sex and heritable growth parameters. Our growth model is an integration of von Bertalanffy and biphasic growth models (Quince et al. 2008a, 2008b). Each individual is characterized by 12 pairs of heritable growth values and means of each pair determine an individual's 12 growth parameters ($X_{1\text{-}12}$). These growth parameters can take values between 0 and 1 (6 parameters relate to growth of males, $X_{1\text{-}6}$, and females, $X_{7\text{-}12}$, respectively). These parameters, in turn, determine an individual's intrinsic somatic growth rate (K) and maximum length (L_{max}). We assume a negative relationship between

K and L_{max} and that these variables can take a defined range of values, i.e., for an individual male:

1) $$K_i = 0.3(X_1 + X_2) + 0.05(X_3 + X_4 - 1.0)$$

2) $$L_{\max,i} = 874 - 252(X_1 + X_2) + 30(X_5 + X_6 - 1.0).$$

That is, if all growth parameters ($X_{1\text{-}6}$) equal 0.5, then $K_i = 0.3$ and $L_{max,i} = 622$-mm.

We assume an expected, exponential relationship between fish length (L, mm) and somatic weight (W_S, g):

3) $$W_S = aL^b$$

where a=0.00003 and b=3.0. Further, we assume the expected gonadal weight (W_G, g) to be a proportion (PROP) of expected somatic weight:

4) $$PROP = \frac{c}{1 + de^{-fL}}$$

with different parameter values for males (c=0.03; d=4.0; f=0.008) and females (c=0.15; d=20.0; f=0.01).

Each year, we calculate a mature individual's total growth potential (GP_T, g) as the sum of potential somatic growth (GP_S, g) and gonadal growth (GP_G, g). We assume that annual growth potential is a function of an individual's length. A mature individual's length is expected to increase (ΔL) as a function of its length at the beginning of a year (L_t):

5) $$\Delta L = (L_{\max} - L_t) \times (1 - e^{-K}) .$$

Thus, the potential somatic growth for a mature individual is,

6) $$GP_S = a(\Delta L + L_t)^b - aL_t^b ,$$

and its potential gonadal growth is,

7) $$GP_G = PROP \times (a(\Delta L + L_t)^b) .$$

Total realized growth (GR_T, g) is then calculated by multiplying an individual's total growth potential (GP_T) by a term (ADJ) which encapsulates density dependent and stochastic processes:

8) $$ADJ = \frac{CC + \varepsilon}{\sum W_i N_i} ,$$

where CC is population carrying capacity (2×10^{11} g), W_i and N_i are the somatic weight and number of individuals represented by super-individual i, respectively, and ε is a random normal variable (from -1.5×10^{11} to $+1.5\times10^{11}$ g) representing inter-annual growth variation. To bound potential growth rates, ADJ can take values between 0.25 and 2.5.

GR_T is then partitioned between somatic and gonadal growth. First, we compare the sum (W_{S+G}, g) of an individual's expected somatic weight (W_S, i.e., given its length at the beginning of the year) and gonadal weight (W_g, i.e., given its length at the beginning of the year) versus it new total weight (W_T, g), i.e., the sum of its actual weight at the beginning of the year (W_A, g) and GR_T. If $W_T \geq W_{S+G}$, then we calculate an individual's new somatic weight ($W_{S(t+1)}$, g), gonadal weight before spawning ($W_{G(')}$, g), and length ($L_{(t+1)}$) as:

9) $$W_{S(t+1)} = \frac{W_T}{1 + PROP},$$

10) $$W_{G(')} = W_T - W_{S(t+1)},$$

11) $$L_{(t+1)} = \left(\frac{W_{S(t+1)}}{a}\right)^{1/b}.$$

If $W_T < W_{S+G}$, then

12) $$L_{t+1} = L_t.$$

Further, if $W_T \leq W_S - W_G$,

13) $$W_{S(t+1)} = W_T\,,$$

14) $$W_{G(')} = 0\,.$$

On the other hand, if $W_{S+G} > W_T \geq W_S$,

15) $$W_{S(t+1)} = W_T - W_G\,,$$

16) $$W_{G(')} = W_G\,.$$

Finally, if $W_S > W_T > W_S - W_G$,

17) $$W_{S(t+1)} = W_S - W_G\,,$$

18) $$W_{G(')} = W_T - \left(W_S - W_G\right).$$

Individuals which are immature at the beginning of a year can either remain immature or become mature during the year. Thus, we initially calculate growth of immature individuals identical to growth of mature individuals. If resulting L_{t+1} exceeds the relevant MRN parameter, then the individual becomes mature (i.e., $W_{S(t+1)}$ and $W_{G(')}$ are calculated as above). Otherwise, the individual remains immature,

19) $$W_{S(t+1)} = W_T ,$$

20) $$W_{G(')} = 0 ,$$

21) $$L_{(t+1)} = \left(\frac{W_{S(t+1)}}{a} \right)^{1/b} .$$

Mortality

Mortality is depicted as a random process and includes both size-independent, natural mortality and size-dependent, fishing mortality. Initially, to evaluate model behavior we only include natural mortality and set Z (instantaneous total mortality) to 0.5 year^{-1}. Each year, the number of individuals represented by a super-individual is reduced by a random number drawn from a binomial distribution (p = 1-e^{-Z}; n = number of individuals represented by a super-individual).

Reproduction

If the population contains at least one mature male and female fish, then reproduction occurs between annual time steps (*y* and *y+1*), and the resulting new individuals enter the population as age 1 fish at the beginning of annual time step, *y+2*. The number of new individuals (R) entering the population is a function of the population's viable egg production (S_{EP}; i.e., the sum of all female super-individuals' egg production; EP_i) and follows a Ricker-type stock recruitment curve:

22) $$R = a \times S_{EP} \times e^{-bS_{EP}} \times \varepsilon ,$$

where a= 0.008, b=5.5×10^{-12}, and ε is a log-normally distributed random variable with a mean of 1.0. Each year, R is divided amongst 1,000 new super-individuals. If $R \leq 10^3$, then each new super-individual represents 1 fish. Similarly, if $R \geq 10^9$, then each new super-individual represents 10^6 fish. The parents for these new super-individuals are drawn from pools of mature female and male fish as a function of individuals' egg and milt production. The probability that an individual mature female will be the mother for a given new super-individual is simply the proportion of the population's total egg production contributed by the individual (i.e., EP_i/ S_{EP}), and the probability that an individual mature male will be the father for a given new super-individual is simply the proportion of the population's total milt production contributed by the individual.

A female super-individual's egg production (EP_i) is calculated as a function of its $W_{G('),i}$, NI_i, proportion of viable eggs (V_i), and mean egg weight (E_i; g),

23) $$EP_i = \frac{NI_i \times W_{G('),i} \times V_i}{E_i} .$$

We assume that E_i increases with female age (A_i) to a maximum of 0.035422-g,

24) $$E_i = 0.0005 A_i^{1.5},$$

and that V_i increases with E_i (V_i=1.0 when E_i = 0.035422-g),

25) $$V_i = 150 E_i^{1.5}.$$

A male super-individual's milt production (MP_i) is calculated in a similar manner, but we assume that for males V_i=1.0, and thus,

26) $$MP_i = NI_i \times W_{G('),i}.$$

Again, new super-individuals enter the model as immature, either male or female (0.5 probability) age-1 fish each representing R/1,000 individuals. Further, each new super-individual is in part characterized by its heritable growth and maturation parameters. Based on Mendalian inheritance, for each maturation and growth parameter an individual receives one random heritable value from both its mother and father. Parameter expression is based on co-dominance (i.e., each parameter is expressed as the mean of paired values). Initial gonadal weight is by definition 0 g (i.e., immature fish), and initial length and somatic weight are calculated based on an individual's inherited growth parameters.

Simulations

We apply the model to simulate a series of potential conditions. Our simulations can be grouped into four general categories: 1) neither maturation nor growth parameters are heritable, 2) only maturation parameters are heritable, 3) only growth parameters are heritable, and 4) both growth and maturation parameters are heritable. The initial population consists of 5,000 super-individuals, with sex and age assigned randomly. The number of individuals initially represented by each super-individual is determined as a function of age and annual mortality rate. For simulations with heritable maturation parameters, initial parameter values for each super-individual are drawn from a normal distribution with a mean of 400-mm and a standard deviation of 300-mm (bounded by 150 and 750-mm). Similarly, for simulations with heritable growth parameters, initial parameter values for each super-individual are drawn from a uniform distribution with a mean of 0.5 and a maximum and minimum of 0.1 and 0.9999, respectively.

For baseline simulations with no heritability of maturation or growth, we set M_{1-18}=400-mm and X_{1-12}=0.5, respectively. We also explore the effects of the magnitude of fixed maturation parameters on inheritance patterns of growth patterns, and vice versa, by running simulations with M_{1-18} set at 300 or 500-mm and X_{1-12} set at 0.3 or 0.7. Similarly, to explore the effects of mortality rate on inheritance patterns, we ran simulations with Z=0.3, 0.5, or 0.7. We run all of our simulations assuming that recruitment and carrying capacity vary stochastically from year to year. Then we repeat simulations assuming that recruitment is deterministic (ε=0; recruitment is solely a function of spawner stock size) and carrying capacity is fixed. Finally, to explore the effects of density dependence on inheritance patterns we repeat all simulations with density dependent effects removed from the model. That is, we assume that growth is deterministic and independent of population size (i.e., ADJ=1.0; a super-individual's growth is solely a function of its growth parameters) and recruitment is deterministic. Each simulation tracks the population for 200 years, and we extract population-level information at 20 year intervals. For each set of conditions, we run ten replicate simulations, thereby accounting for stochastic effects.

Results

Heritable maturation and growth parameters clearly influenced both population level phenotypic expression (Figures 1 and 2) and genetic variation (Figures 3-6). With density dependent processes and stochastic effects included in simulations, there was a high degree of variation in phenotypic expression across simulations (Figure 1). With deterministic recruitment and fixed carrying capacity, phenotypic expression across simulation types was less variable (Figure 2). Genotypic evolution was similar under deterministic and stochastic recruitment and carrying capacity. Thus, herein we only present genotypic variation under deterministic recruitment and carrying capacity (Figures 3-6). As such, in comparing simulations with no inheritance, inherited maturation parameters, inherited growth parameters and both inherited maturation and growth parameters there was no clear difference across simulation types in mean population size or recruitment (Figure 1 a-b). On the other, mean length at age varied among these different simulation types (Fig 1 c-d).

Selection on maturation parameters appeared to differ among males and females and was most dramatic for parameters corresponding to younger ages (Figure 3). Since a mature super-individual remains mature until it is removed from the simulation, there is likely limited selection pressure exerted on maturation parameters corresponding to older ages. Selection on maturation parameters corresponding to younger ages led to a decrease in mean M_i values. Decreases in mean M_i values were most pronounced during initial simulation years, but continued to year 200. Further, decreases in mean M_i values were more dramatic for males than females.

Selection on maturation parameters was also mediated by intrinsic growth and mortality rates. For simulations with slow initial growth (i.e., relatively low X_i values [low K_i and high $L_{max,i}$] and low mortality resulting in high density dependent growth suppression), decreases in mean M_x values were more evident for parameters corresponding to ages >2 years.

Similar to selection on maturation parameters, selection on growth parameters differed among males and females, was more evident during initial simulation years, and continued to the end of simulations (Figure 4). In general, males evolved to grow quicker during young ages (increased mean K_i) at the expense of maximum attainable size (decreased mean $L_{max,i}$), and females evolved in the opposite direction. However, when the threshold size to mature was set sufficiently high (i.e., 500 mm), mean $L_{max,i}$ evolved to increase and K_i decreased for both sexes.

Mean maturation and growth parameters arising in simulations in which both M_i and X_i were heritable tended to differ slightly from simulations in which only one type of parameter was heritable (Figure 5; compare Figure 6 with Figures 3 and 4). At the end of simulations, mean M_i corresponding to young ages tended to not vary much between simulations with only heritable maturation parameters versus simulations with both heritable growth and maturation parameters. Conversely, on simulation year 200 mean

K_i tended to be slightly less in simulations with both heritable growth and maturation parameters as compared to simulations with only heritable growth parameters.

To explore the effects of density dependence on inheritance patterns, we repeated all simulations with density dependent effects removed from the model. Not surprisingly, inter-simulation variation in population level phenotypic expression was lower for density independent simulations (compare Figures 1-2 and 7). Further, it is noteworthy that by simulation end total population size and recruitment were at a higher level when only growth or both growth and maturation parameters were heritable, than when only maturation, or neither type of parameters were heritable (Figure 7).

Under density independent conditions, mean heritable parameters differed from corresponding density dependent simulations (compare Figures 3 and 8 and Figures 4 and 9). Moreover, for density independent simulations with identical conditions, inter-simulation variation of mean heritable parameters tended to be slightly lower than for corresponding density dependent simulations (Figures 5, 8-9). However, for density independent simulations with relatively high mortality rates, inter-simulation variation in heritable traits was greater than for corresponding density dependent simulations. When density dependent processes cannot compensate for high mortality or low initial growth rates, the number of reproducing super-individuals is very low and hence some random drift can strongly influence mean heritable parameters.

Discussion

Eco-genetic individual based models are a potentially useful tool for considering how environmental and genetic processes may interact to shape phenotypic expression of fish populations. Our simulation results demonstrate how a plethora of ecological factors may impact plastic growth and maturation schedules. For instance, the magnitude of mortality rates may have strong influence on the genetic components of growth rate and maturation schedules. Moreover, density dependent processes may feedback and mediate factors which exert selection pressure on growth rate and maturation schedules.

Some past attempts to incorporate inheritance into fish IBMs have not simultaneously considered genetic and ecological processes (e.g., Martínez-Garmendia 1998; Jager 2001). Martínez-Garmendia's (1998) model of cod evolution assumes that both size-at-maturity and growth rates are individually fixed, thus ignoring environmental effects and density-dependence. Jager's (2001) model of white sturgeon (*Acipenser transmontanus*) includes a more realistic genetic module and considers both genetic and environmental components as determinates of individual age at maturity. However, this environmental component is assigned randomly at birth and there is no population-level feedback to influence individual growth or age at maturity (i.e. density-dependence is largely ignored). Not accounting for ecological processes can compromise predictions on the direction and magnitude of genetic selection. For instance, Gårdmark et al. (2003) demonstrate that the selective harvesting of large individuals in a population will not necessarily favor earlier maturation if there is simultaneous natural predation directed towards small individuals.

Several recent studies have highlighted the potential for rapid evolutionary changes in genetically determined maturation schedules (e.g., Olsen et al. 2004) and growth rates (e.g., Conover and Munch 2002) of fish. However, relatively few studies have simultaneously focused on both heritable growth and maturation. This trend also holds for eco-genetic fish models, which have primarily focused on either growth or maturation (e.g., Martínez-Garmendia 1998; Jager 2001; Dunlop et al. 2007). Our simulations suggest that when size at maturation is fixed and growth rates are partially genetically determined, the maturation length threshold has potentially strong influence on the genetic component of growth. Similarly, when growth parameters are fixed and maturation parameters are heritable, fixed growth parameters exert strong selection on genetically-determined maturation length thresholds. Simulations allowing for simultaneous selection on both growth and maturation parameters facilitate continuous co-selective feedback of these two life history traits.

Anthropogenic activities (e.g., fisheries harvest) have the potential to not only impact fish populations through demographic (e.g., changes in age-specific abundance) and ecological (e.g., changes in individual growth) processes, but may also play a role in altering the genetic makeup of fish stocks. Several studies have drawn attention to the notion that growth and maturation schedules are in part genetically determined, and that size-selective fisheries harvest can play a significant role in altering a fish population's growth and maturation genotypes (Stokes et al. 1993; Heino 1998; Law 2000; Conover and Munch 2002; Heino and Godø 2002). In turn, as these traits have strong influence on a fish stock's harvest potential, it is important to consider both short and long term impacts (including genetic effects) of size-selective harvest on fish growth and maturation schedules. Eco-genetic models provide a mechanism to explore these various impacts of size-selective fishing. Herein, we focus on developing a generalized eco-genetic model and explore how various factors influence model behavior. An obvious next step involves using our eco-genetic model to explore the impacts of size-selective fishing on genetically determined growth and maturation schedules and resulting stock productivity (Wang and Höök et al. in review).

While several authors have used eco-genetic models to evaluate selective pressures on specific fish populations (e.g., Dunlop et al. 2007), our model is generalized. Ultimately, the development of species- and stock-specific models could be beneficial. However, we suggest that for many populations the ecological and genetic understanding necessary to develop a realistic stock-specific eco-genetic model is lacking. For instance, while maturation and growth rate may be partially genetically determined the number and type of genes which exert control on these traits are less clear. Herein, we use relatively simple and naïve genetic models in part because the basis for assuming something more complex is lacking. Similarly, many of the tradeoffs and potential costs which select for appropriate maturation and growth genotypes (e.g., tradeoff between somatic and gonadal growth; energy exerted during spawning; relationship between egg viability and female age and size; behavioral hierarchy of spawning) are insufficiently understood to incorporate into a stock-specific model.

It is manifest that important life history traits of many fish populations are partially genetically determined, and there is a growing recognition of the need for fisheries managers to consider short-term evolutionary processes. Eco-genetic models are a potentially useful tool for considering how environmental and genetic processes may interact to shape phenotypic expression of fish populations. Our simulations demonstrate the potential influence of ecological factors (mortality rate, density-dependent growth) and the interactive effects of growth and maturation on the inheritance of these two life-history traits. We suggest that our model can be extended to consider other processes (e.g., size selective fisheries harvest), but we caution that detailed predictions for specific fish stocks are unlikely to be quantitatively meaningful without a more thorough understanding of key ecological and genetic processes.

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Figures

Figure 4.1. Population level phenotypic expression for 40 simulations with stochastic recruitment and carrying capacity and including density dependent growth (black, no inheritance; red, inherited maturation parameters; green, inherited growth parameters; blue, inherited growth and maturation parameters): a) total population size, b) number of age 1 individuals, c) mean total length of age 2 super-individuals and d) mean total length of age 10 super individuals.

Figure 4.2. Population level phenotypic expression for 40 simulations with deterministic recruitment, fixed carrying capacity and including density dependent growth (black, no inheritance; red, inherited maturation parameters; green, inherited growth parameters; blue, inherited growth and maturation parameters): a) total population size, b) number of age 1 individuals, c) mean total length of age 2 super-individuals and d) mean total length of age 10 super individuals.

Figure 4.3. Evolution of maturation parameters for males (left) and females (right) in simulations with inherited maturation and fixed growth parameters and including density dependent growth: a) mean (from 10 separate simulations) maturation reaction norms (MRNs) for 40 year intervals, b) mean MRNs in year 200 of 30 simulations with different fixed growth parameters (X_i), and c) mean MRNs in year 200 of 30 simulations with different mortality rates (Z).

Figure 4.4. Evolution of growth parameters for males (left) and females (right) in simulations with inherited growth and fixed maturation parameters including density dependent growth: a) mean (from 10 separate simulations) initial growth rate (K) and maximum attainable length (L_{max}) for 40 year intervals, b) mean K and L_{max} in year 200 of 30 simulations with different fixed maturation parameters (M_i), and c) mean K and L_{max} in year 200 of 30 simulations with different mortality rates (Z).

Figure 4.5. Evolution of age 3 maturation reaction norm (MRN; a) and initial growth rate (K; b) for simulations with either inherited maturation or growth parameters (black lines) versus simulations with both inherited maturation and growth parameters (red lines). Each plot presents mean results for 20 separate simulations.

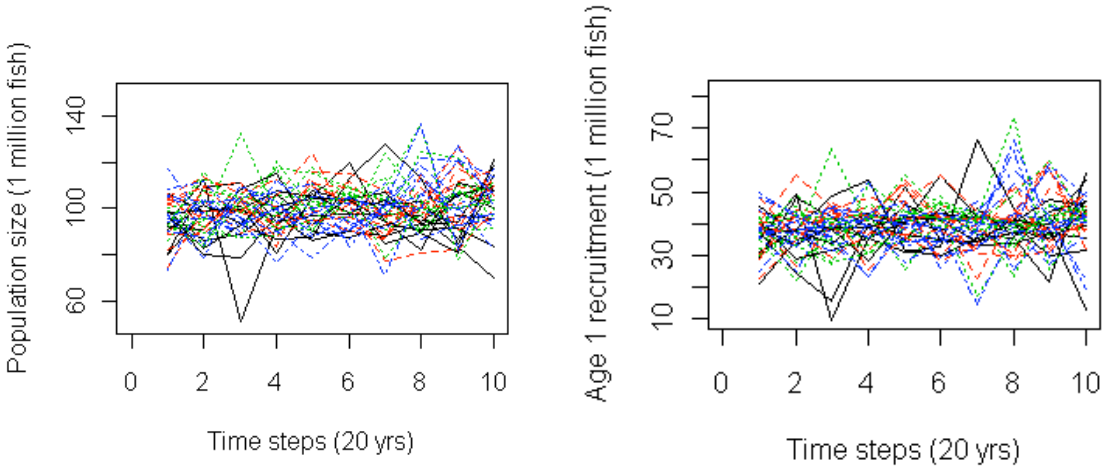
Figure 4.6. Evolution of maturation and growth parameters for males (left) and females (right) in simulations with inherited maturation and growth parameters and including density dependent effects: a) mean (from 10 separate simulations) maturation reaction norms (MRNs) for 40 year intervals, and b) mean (from 10 separate simulations) initial growth rate (K) and maximum attainable length (L_{max}) for 40 year intervals.

Figure 4.7. Population level phenotypic expression for 40 simulations with density independent growth (black, no inheritance; red, inherited maturation parameters; green, inherited growth parameters; blue, inherited growth and maturation parameters): a) total population size, b) number of age 1 individuals, c) mean total length of age 2 super-individuals and d) mean total length of age 10 super individuals.

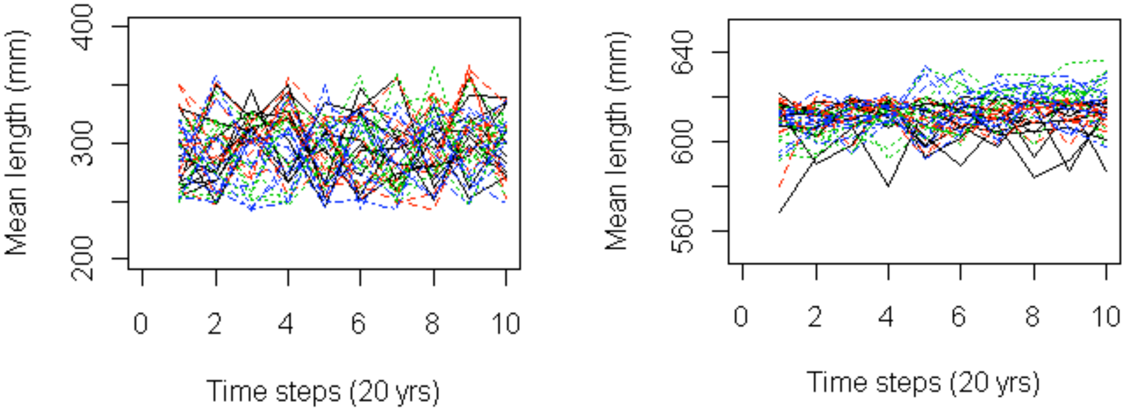
Figure 4.8. Evolution of maturation parameters for males (left) and females (right) in simulations with inherited maturation and fixed growth parameters and including density independent growth: a) mean (from 10 separate simulations) maturation reaction norms (MRNs) for 40 year intervals, b) mean MRNs in year 200 of 30 simulations with different fixed growth parameters (X_i), and c) mean MRNs in year 200 of 30 simulations with different mortality rates (Z).

Figure 4.9. Evolution of growth parameters for males (left) and females (right) in simulations with inherited growth and fixed maturation parameters including density independent growth: a) mean (from 10 separate simulations) initial growth rate (K) and maximum attainable length (Linf) for 40 year intervals, b) mean K and L_{max} in year 200 of 30 simulations with different fixed maturation parameters (M_i), and c) mean K and L_{max} in year 200 of 30 simulations with different mortality rates (Z).

Figure 4.1


Population size

Age 1 recruitment


Age 2 female length

Age 10 female length

Figure 4.2

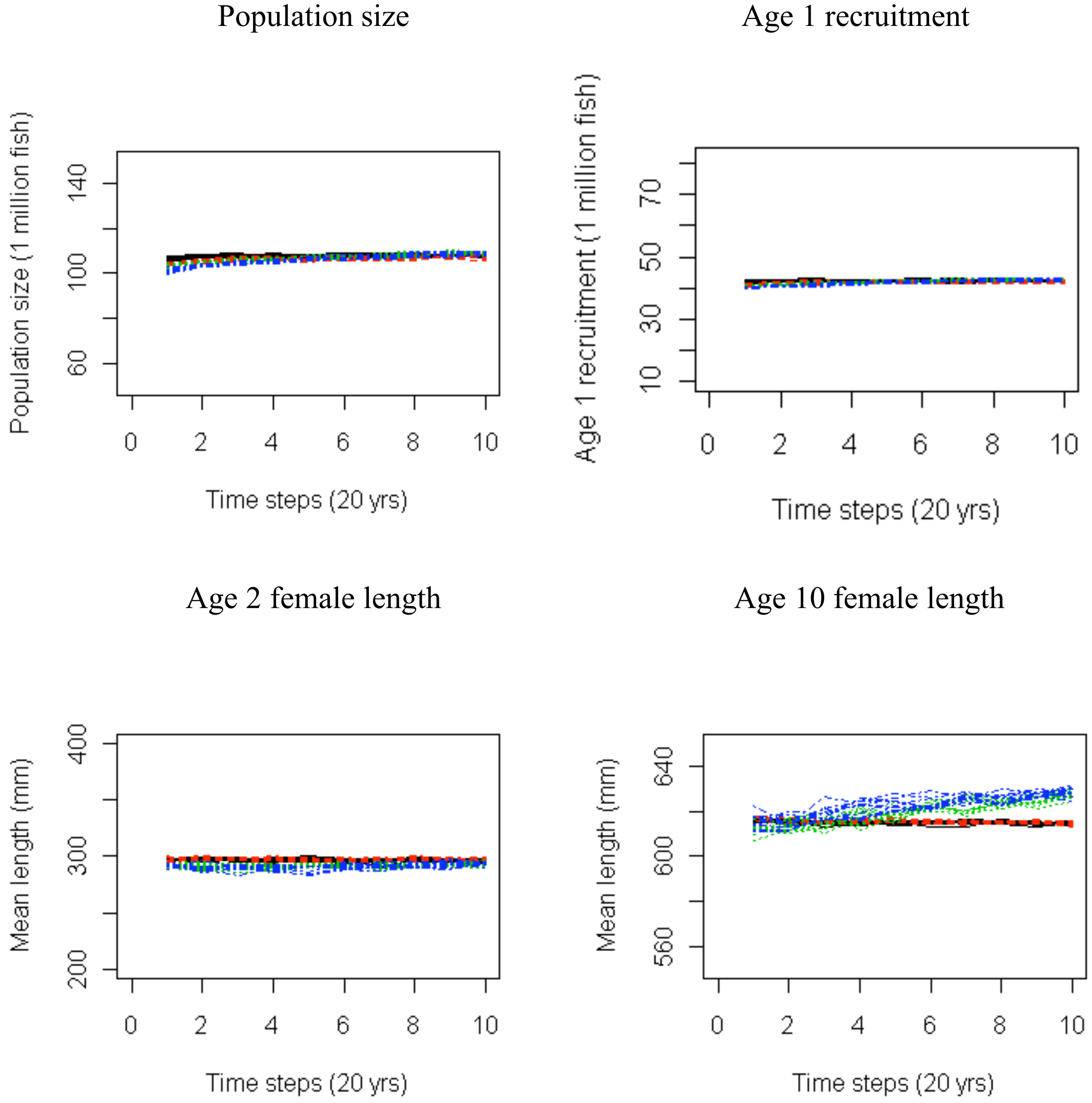
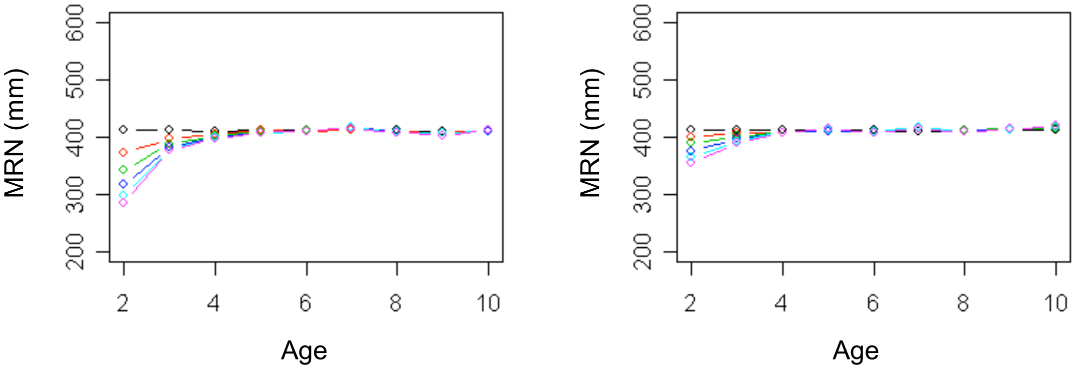

Population size
Population size (1 million fish)
60
100
140
0
2
4
6
8
10
Time steps (20 yrs)
Age 1 recruitment
Age 1 recruitment (1 million fish)
10
30
50
70
0
2
4
6
8
10
Time steps (20 yrs)
Age 2 female length
Mean length (mm)
200
300
400
0
2
4
6
8
10
Time steps (20 yrs)
Age 10 female length
Mean length (mm)
560
600
640
0
2
4
6
8
10
Time steps (20 yrs)

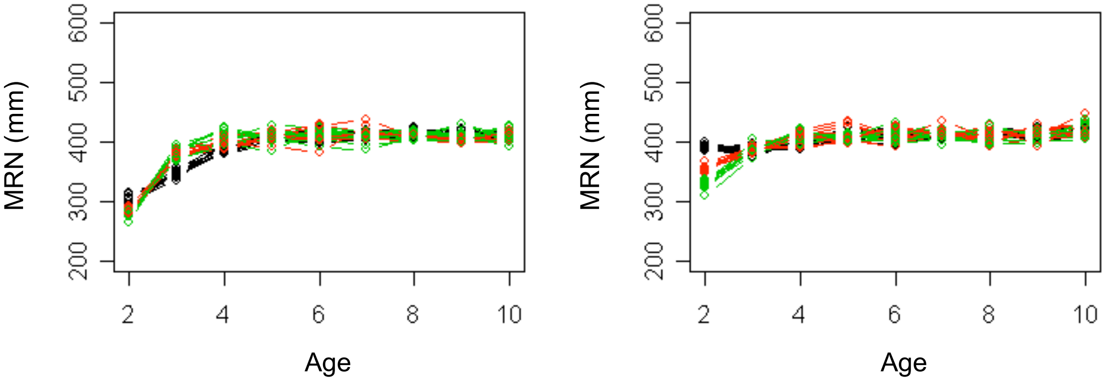
Figure 4.3

Males Females

a) year0, year40, year80, year120, year160, year200



b) X_{1-12} = 0.3, 0.5, 0.7



c) Z = 0.3, 0.5, 0.7

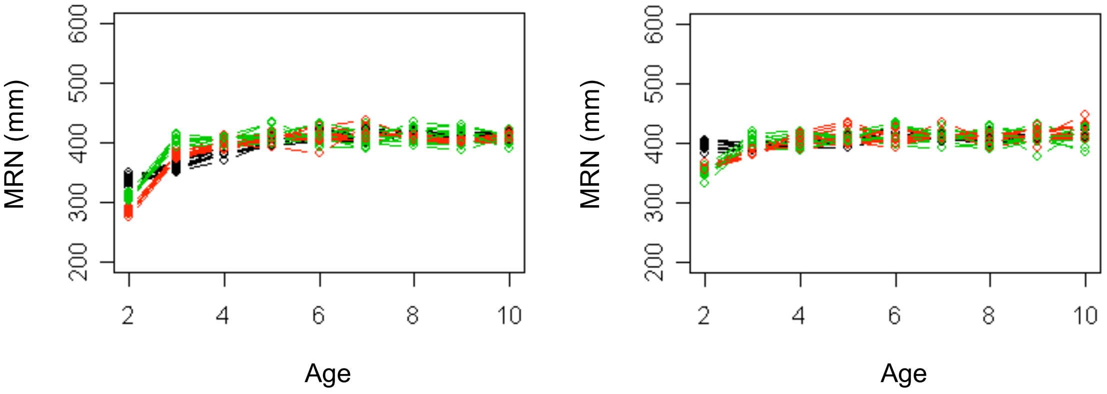
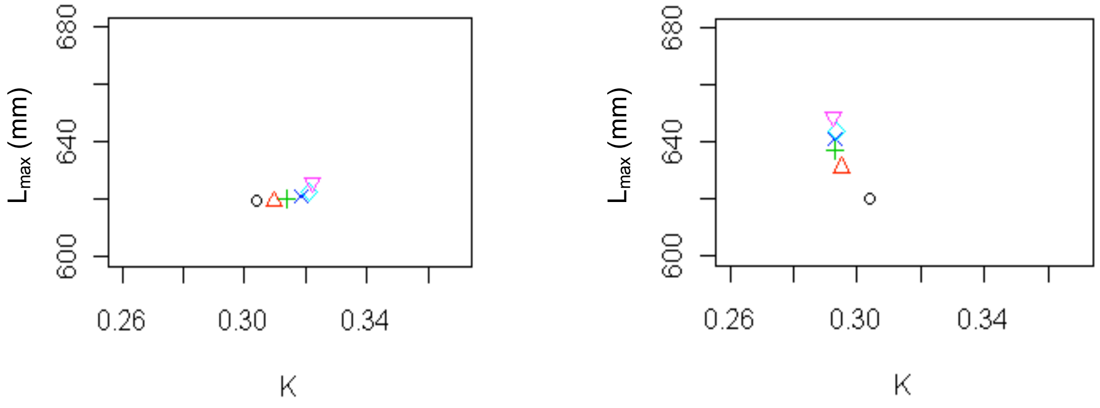


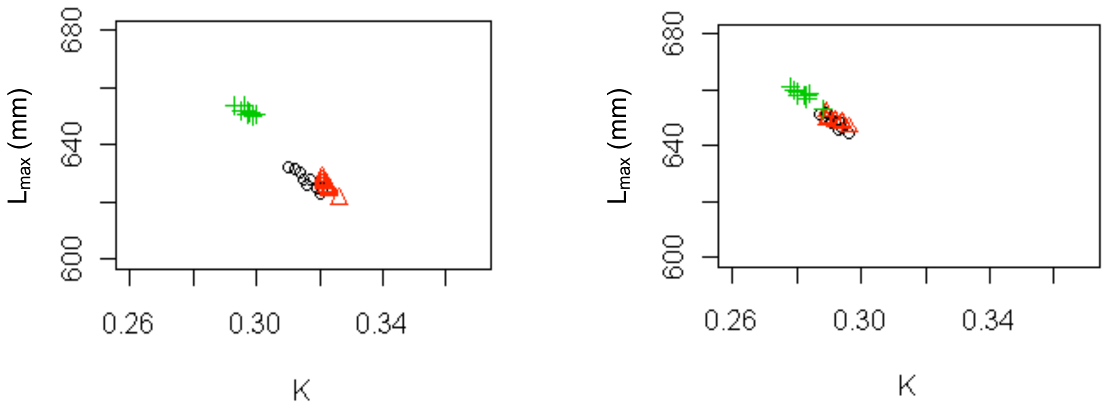
Figure 4.4

Males Females

a) year0, year40, year80, year120, year160, year200



b) $M_{1\text{-}18}$ = 300, 400, 500 mm



c) Z = 0.3, 0.5, 0.7

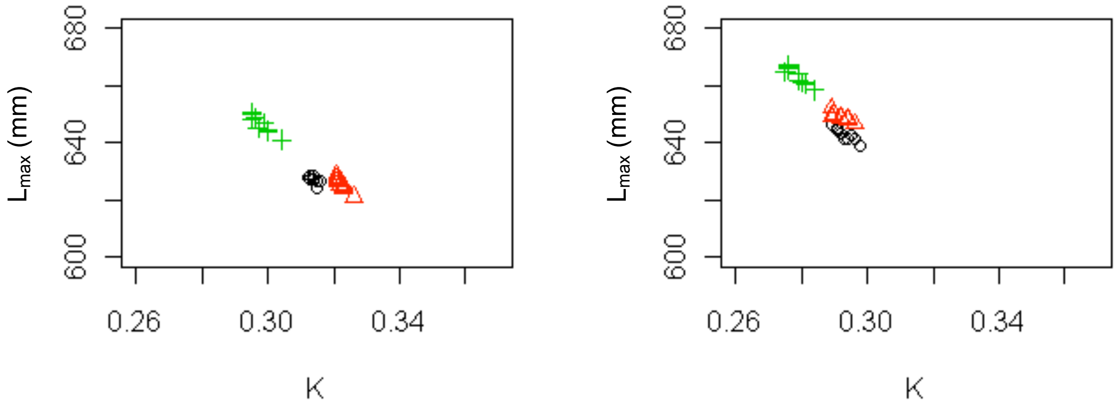
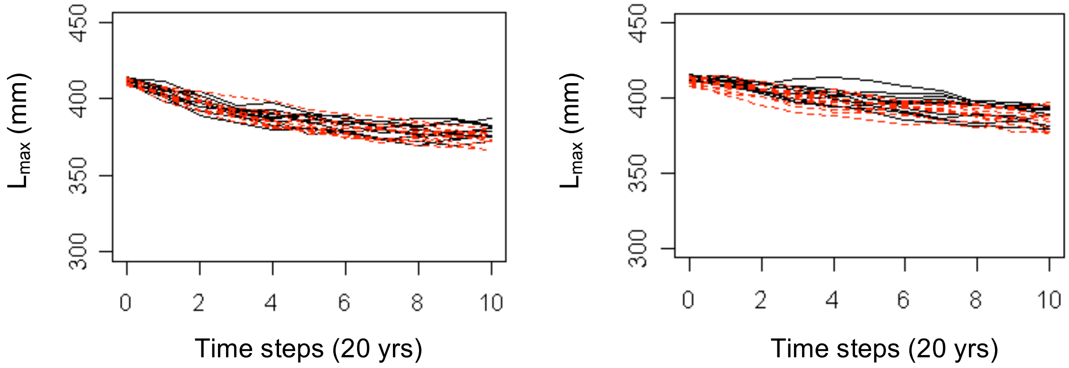


Figure 4.5

Males Females

a) $X_{1-12}=0.5$; X_{1-12} heritable



b) $M_{1-18}=400$ mm; M_{1-18} heritable

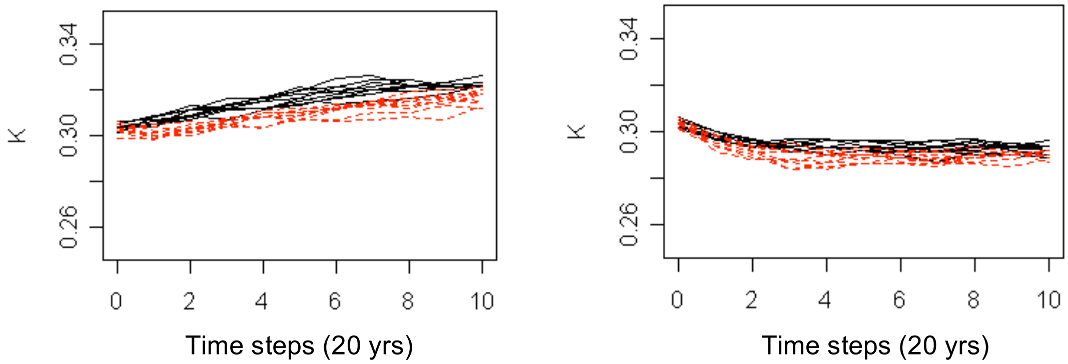
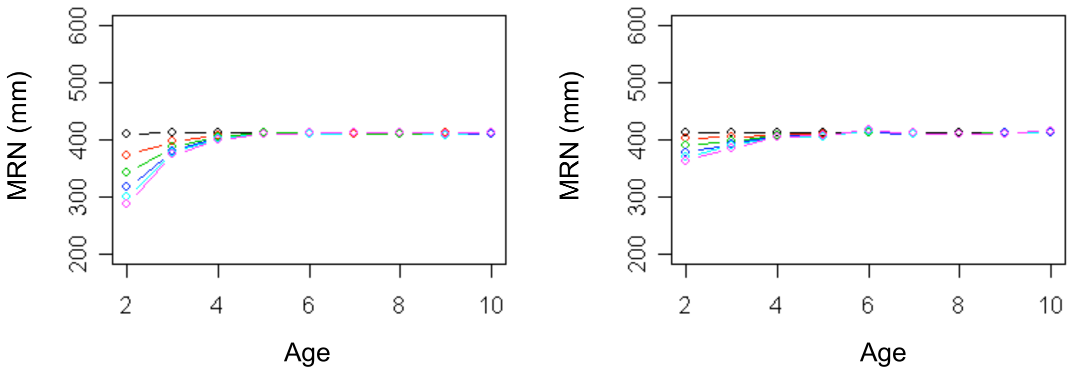


Figure 4.6

Males Females

a) year0, year40, year80, year120, year160, year200



b) year0, year40, year80, year120, year160, year200

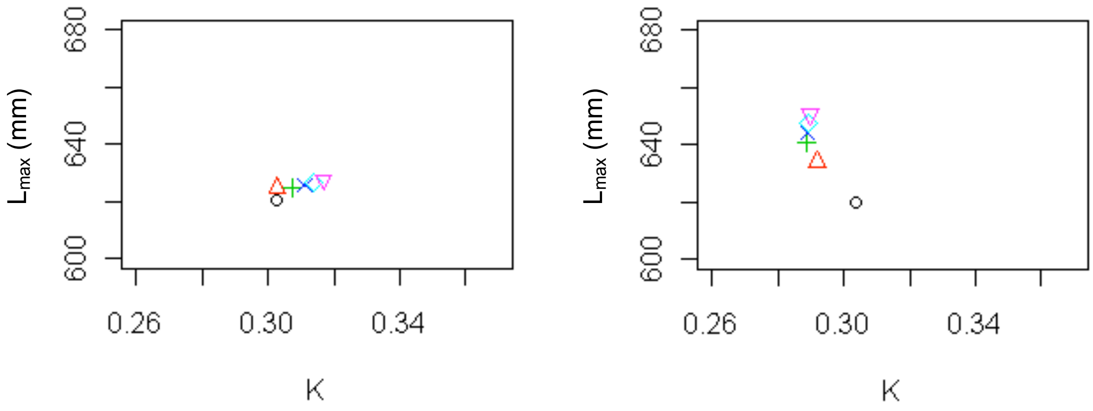
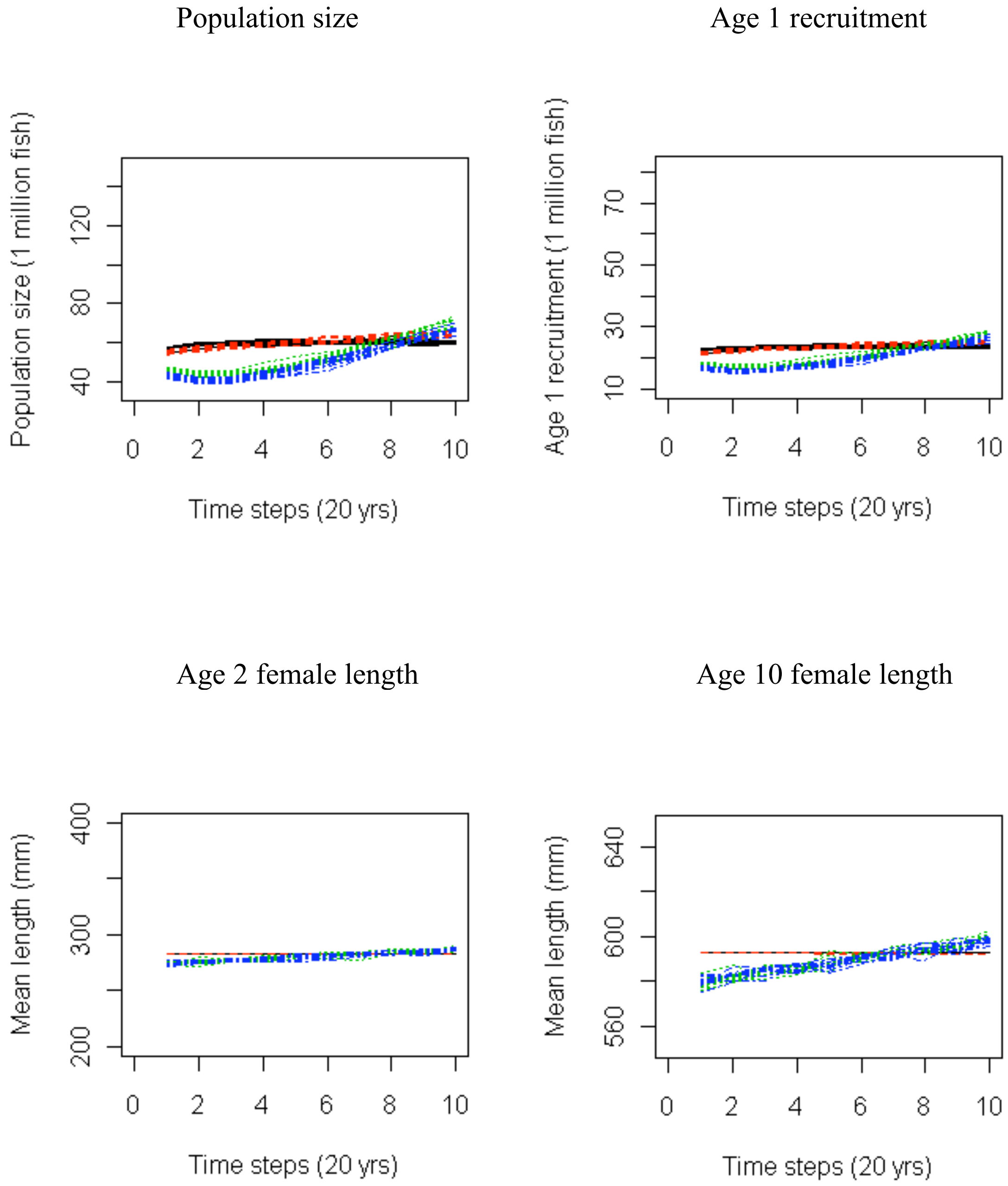


Figure 4.7


Population size

Age 1 recruitment

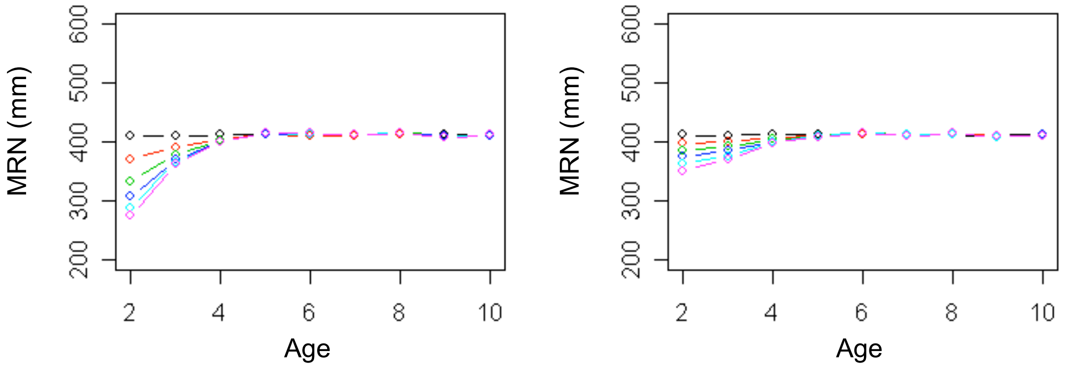
Age 2 female length

Age 10 female length

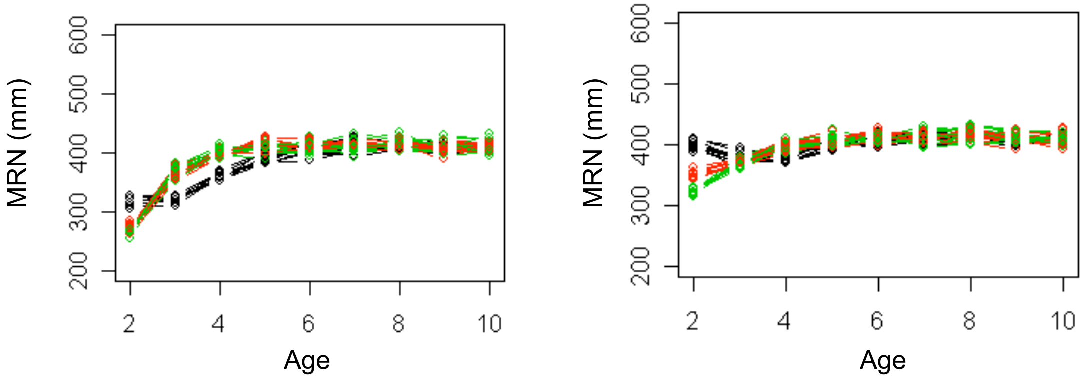
Figure 4.8

Males Females

a) year0, year40, year80, year120, year160, year200



b) $X_{1\text{-}12}$ = 0.3, 0.5, 0.7



c) Z = 0.3, 0.5, 0.7

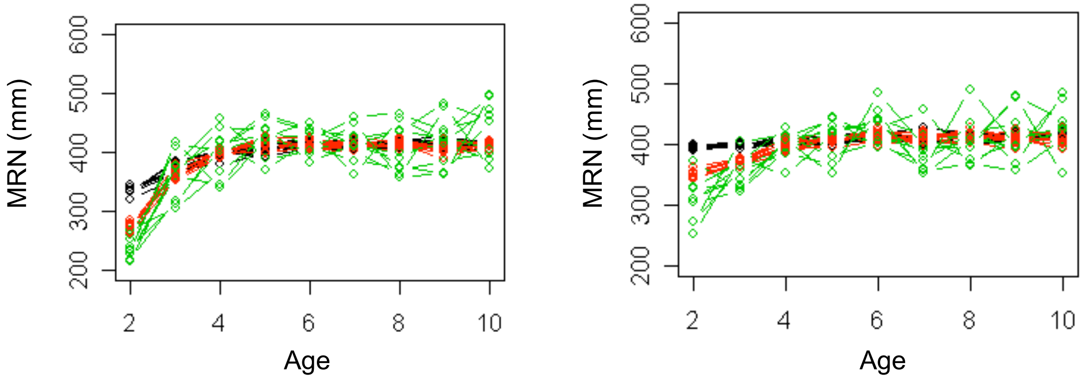
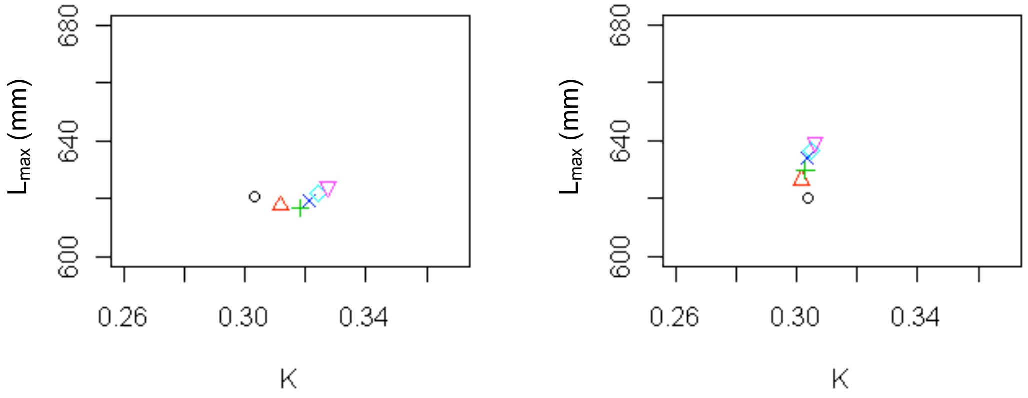


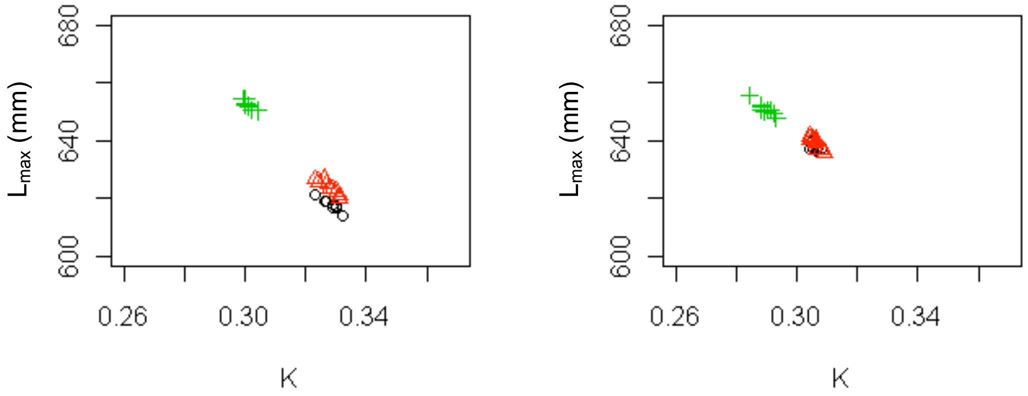
Figure 4.9

Males Females

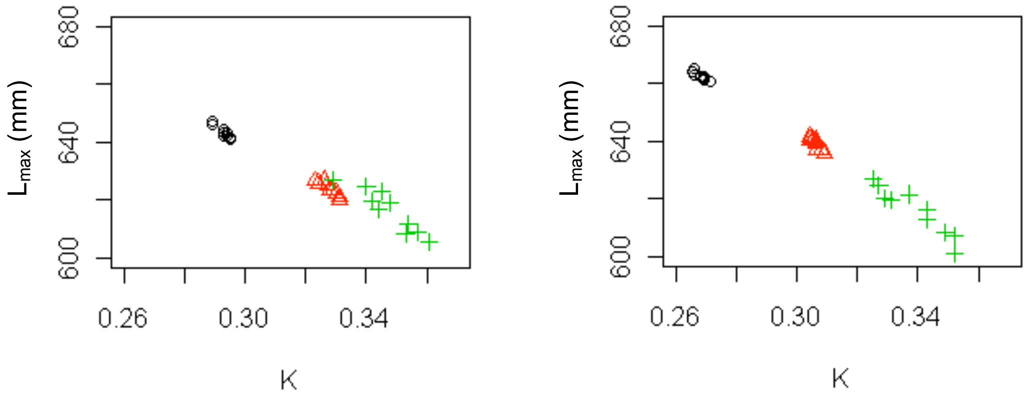
a) year0, year40, year80, year120, year160, year200



b) M_{1-18} = 300, 400, 500 mm



c) Z = 0.3, 0.5, 0.7



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Chapter V

Eco-genetic model to explore fishing-induced ecological and evolutionary effects on life history, recruitment, and fisheries sustainability

Abstract

It is well established that 1) fisheries harvest can reduce population size, 2) selective harvesting can affect individual composition resulting in shifts in age and size structures, and 3) ecological impacts of fishing can plastically alter individual fish phenotypic expression. In addition, there is increasing evidence that fishing may induce potential genetic changes in life history traits that can profoundly influence a population's growth rate and its ability to adapt to a changing environment. Because genetic and plastic effects of fishing may act on different time and space scales and may complement or counteract life history trait expression, it can be difficult to discriminate between these two types of processes and to elucidate their relative impacts on fish population dynamics. We used a generalized eco-genetic individual based modeling approach to explore these potentially complex effects of fishing. The model consists of a virtual fish population and tracks both ecological and genetic dynamics of the population. We conducted experimental simulations to mimic fisheries harvest with two size-limits (targeting large or small fish), an array of fishing mortality rates, and assuming a deterministic or stochastic environment. Our results suggest that while fishing with either size-limit may induce considerable changes in life history trait expression (maturation schedules and growth rates), recruitment, and population size and structure, targeting

large fish would cause more adverse genetic effects and may lead to a less resilient population to environmental stochasticity.

Introduction

Long-term consequences of fishing on a targeted fish population may depend on location, gear, fishing intensity, environmental effects, ecological interactions, and both phenotypically- and genetically-determined life history traits of the targeted species (Law 2000). To effectively achieve long-term fisheries sustainability, it is essential to understand and account for the complexity of fishing-induced effects. Previous research suggests that fishing may cause changes to a suite of fish population-level attributes (e.g., survival and recruitment) as well as various interrelated phenotypic expressions at the individual level (e.g., growth, and size and age at maturation). However, the mechanisms of these changes are often unclear. To illustrate these complex effects of fishing, consider that intensively harvested populations are often comprised of a high proportion of small and/or young fish (Berkeley et al. 2004), and that size-selective fishing harvest will lead to changes in mean size and age of both mature and immature fish by simply truncating the population. Moreover, fishing reduces population size, thereby relaxing intra-population competition of the harvested population. As a result, individuals may grow more rapidly and mature at younger ages or larger sizes (Trippel 1995). Simultaneously, selective harvest of larger, older individuals may over time select for genetically-determined slower growth rates and maturation at younger ages and smaller sizes (Edeline et al. 2007; Jørgensen et al. 2007). Regardless of the mechanisms of action (genetic selection or ecological processes), changes in growth rates or maturation expression will undoubtedly feedback to affect each other, due to trade-offs between growth and reproduction (Hutchings 2005).

Clearly, fishing has a variety of effects on population- and individual-level expression, however, the relative influences of underlying mechanisms, e.g., ecological (plastic) versus evolutionary (genetic) pathways, are less clear. Many studies support the notion that fishing may cause evolutionary changes in harvested populations (summarized in Law 2000; Jørgensen et al. 2007; Hard et al. 2008). Conover and Munch (2002) and Walsh et al. (2006) showed that experimentally harvesting large Atlantic silverside *Menidia menidia* in a laboratory setting could lead to potential genetic and phenotypic changes in several fitness-related traits (growth rates, egg size, feeding rates, etc.). However, these studies were criticized as overestimating the evolutionary effects of harvesting, as the authors applied unrealistically high harvest rates in these laboratory settings (Hilborn 2006, 2007; Brown et al. 2008). Using the parameters from Conover and Munch (2002) with more realistic fishing intensity, Brown et al. (2008) demonstrated that harvest-induced evolution suggested by Conover and Munch (2002) could occur in wild fisheries but at a much slower rate. In addition, fishing-induced evolutionary effects are likely impacted by simultaneous ecological effects induced by fishing and other environmental factors (Rijnsdorp 1993; Kuparinen and Merilä 2007), and may also be affected by seemingly stochastic environmental processes (Blanchard et al. 2005). Understanding the mechanisms through which fishing affects population dynamics should aid in designing harvest practices with an eye towards long-term sustainability.

In this study, we focus on size-dependent fishing-induced genetic and plastic effects on growth and maturation traits, recruitment, and harvest sustainability. We hypothesized that harvest via different size-limits and fishing intensities would induce differential plastic and genetic effects on growth and maturation traits. Further, we hypothesized that environmental stochasticity might dilute both plastic and genetic effects of fishing. To test these hypotheses, we designed a series of simulations using a generalized eco-genetic individual-based model (IBM; Höök and Wang in review). Our objectives were to 1) evaluate evolving and observed life histories, recruitment traits and population size with respect to size-selective fishing mortality (i.e., targeting large or small fish and under different fishing mortality rates [F]), and 2) compare fishing-induced effects under deterministic versus stochastic environments.

Methods

Model

We explored size-selective fishing-induced ecological and evolutionary effects using a generalized eco-genetic individual-based model; IBM (for details see Höök and Wang in review). This model is comprised of a virtual fish population with individuals characterized by a number of state variables (sex, age, maturity state, length, somatic weight, gonadal weight, and heritable parameters that control growth and maturation reaction norms [RNs]; Höök and Wang in review). The model progresses with annual time steps and both individual and population-level variables are summarized every 20 years.

Ecological and genetic components govern maturation and growth processes of model individuals. Onset of maturation occurs when an individual's growth trajectory intersects with genetically-determined maturation RNs (Stearns 1992). Further, growth is depicted via a combination of genetic and ecological processes, and is an integration of von Bertalanffy and biphasic growth models (Quince et al. 2008a, 2008b). Ecological processes include density-dependent controls on growth rate and recruitment: an individual's growth is inversely related to population size, and recruitment is governed by a Ricker type stock-recruitment function. In addition, the model includes two key trade-off functions: a sexually-differentiated somatic and gonadal growth trade-off (i.e., females contribute more reproductive investment than males), and a maternal age-egg quality relationship, (i.e., older females produce larger eggs with better survival rates).

The genetic component of maturation and growth is based on Mendelian inheritance. Each individual carries a set of 36 sex- and age-specific maturation RN parameters: the first 18 parameters represent nine pairs of alleles with each pair co-dominantly coding for the minimum length of maturation for males at ages 2 to ≥10, respectively. The other nine pairs of parameters code for minimum lengths at maturation for females of the same ages. When individuals reproduce, the maturation RN parameters of their offspring are assembled by combining 18 parameters (randomly selecting one parameter from each pair of maturation RN parameters) from each parent's parameters. In addition, each individual carries twelve pairs of growth RN parameters (six pairs of parameters coded for each sex). These growth RN parameters co-dominantly influence magnitudes of growth coefficients, K and L_{max} (we assumed von Bertalanffy coefficient $t_0 = 0$), as well as a negative dependence between K and L_{max} (i.e., K and L_{max} cannot be simultaneously maximized).

Design of simulations

Höök and Wang (in review) used the model to explore the effects of various background mortality rates, the effects of density-dependence, and the effects of singularly and simultaneously heritable growth and maturation parameters on phenotypic expression and genetic parameters. Herein, we extend these analyses to consider the joint ecological and evolutionary effects of fishing. In so doing, we assumed that growth and recruitment are density-dependent and that individuals' growth and maturation parameters are simultaneously heritable. Furthermore, to evaluate effects of environmental stochasticity on population responses to fishing, we included two stochastic processes: 1) stochastic carrying capacity (which influences individuals' growth rates) and 2) stochastic recruitment dynamics. We compared fishing-induced responses between deterministic and stochastic conditions.

Total mortality rate (Z) is sum of natural (M) and fishing (F) mortality rates. We assumed a uniform $M = 0.2\ yr^{-1}$ for all individuals in order to emphasize responses to variable F. Preliminary simulations suggested that comparisons of population responses between size-limits or across different levels of F were not sensitive to level of M or differential M with age (also see Dunlop et al. 2007).

To evaluate size-dependent fishing-induced effects, we first conducted a deterministic baseline simulation (Table 1). The initial age- and sex-specific maturation and growth RN parameters of all individuals were sampled at random from a normal distribution, resulting in the mean values for age-specific maturation RN for both sexes = 400 mm, K = 0.3, and L_{max} = 622 mm (Table 1). The population initially consisted of 5,000 super-individuals (each super-individual represents an aggregation of 50,000 identical fish; Höök and Wang in review). The baseline simulations were run for 1,000 years with 10 replicates, and the mean values of evolved growth and maturation RN were estimated at 20-year intervals. The mean values of final growth and maturation RN estimates from the ten baseline simulation replicates were then used as initial mean trait values for the population undergoing fishing (Figure 1; Figure 2).

We considered two types of size-selective mortality: 1) targeting small fish, we allowed fish <250 mm or >650 mm to fully escape, fish between 250 mm and 400 mm to fully recruit, and fish between 400 mm and 650 mm to partially recruit (i.e., F decreased linearly with length within this size range); 2) targeting large fish, we let fish <250 mm escape harvest, fish of between 250 mm and 400 mm partially recruit (i.e., F increased linearly with length within this size range), and fish ≥400 mm fully recruit to the fishing gear. Again, our preliminary analyses showed that simulation results were not sensitive to the exact shapes of size-dependent mortality functions (but were sensitive to the differences in length ranges harvested).

We first evaluated effects of fishing under deterministic conditions, applying two size-limits (targeting large and small fish, respectively), each for 200 years at F = 0, 0.2, 0.4, 0.6, 0.8, and 1.0, with 10 replicates (with the same number of initial super-individuals). Then, we repeated the baseline and fishing simulations under stochasticity (randomly varying carrying capacity and recruitment). For all simulations, we kept track of population mean values of sex-age-specific maturation RN, sex- specific K and L_{max}, female length-at-age and maturation schedules, age 1 recruitment, and population size at 20-year intervals.

Results

Baseline maturation RN, K, and L_{max} (deterministic)

Through the deterministic baseline simulation, maturation RN parameters, K, and L_{max} evolved differentially between sexes over time. Male maturation RN values generally decreased at younger ages, while female RN parameters evolved less (Figure 1). Further, by the end of the simulation mean K decreased and L_{max} increased more pronouncedly for females than males (Figure 2). Resulting sex- and age-specific mean maturation RN (± 200 mm) and growth RN (± 0.25) parameters were then use as starting conditions for fishing simulations.

Effects of size-selective fishing on evolving maturation RN, K, and L_{max} (deterministic)

Maturation RNs of both sexes responded to differential fishing size-limits and mortality rates. When targeting large fish with increasing F from 0 to 0.6, male maturation RN differed little from the baseline (F = 0), while female maturation RN at young ages decreased more considerably (Figure 3). At F = 0.8 to 1.0, evolving maturation RN of both sexes fluctuated, potentially due to small population size (Figure 3). When targeting small fish with increasing F, maturation RN for males varied little from the baseline, but that of females increased at young ages (Figure 3).

Genetically-determined K and L_{max} appeared to respond to size-limits and fishing mortality rates pronouncedly. Increased fishing mortality rates under both size-limits led to decreases in K and increases in L_{max} (Figure 4, Figure 5). Compared to targeting on small fish, targeting on large fish led to lower K and higher L_{max} values at a given F. Further, when targeting on small fish evolution of K and L_{max} were subtle but, when targeting large fish these individual-parameters responded dramatically at moderate to high F (e.g., $F \geq 0.6$) and fluctuated at a high F (e.g., $F \geq 0.8$). Also notably, when targeting small fish, magnitudes of evolving K and L_{max} for females did not follow fishing mortality rates; e.g., at highest F, K and L_{max} did not evolve the most but achieved intermediate values (Figure 4, Figure 5).

Observed growth rates, maturation schedules, recruitment, and population size under size-selective fishing (deterministic)

Regardless of size-limits, length-at-age patterns (based on female fish data) increased with fishing mortality rates, suggesting that fishing relaxed density-dependent growth constraints (Figure 6). However, the fish population displayed greater length-at-age patterns when harvesting large fish at a given F (Figure 6). Further, when targeting large fish, length-at-age of fish appeared to reach a maximum at a relatively high F ($F \geq 0.6$), and age structure of the population appeared to be truncated at $F \geq 0.8$.

Similarly, maturation schedules (based on mean age of mature females) also varied based on size-limit and fishing mortality rate, but were relatively constant within the 200-year simulations. Under both size-limits, the population displayed decreased maturation schedules with increased F, and the effects of increased F was most pronounced between F = 0 and 0.2 (Figure 6). When targeting large fish, maturation schedules continued decreasing with subsequent increases of F. However, when targeting small fish this metric remained relatively constant at $F \geq 0.4$ (Figure 6). Thus, at a given F, mean age of mature fish tended to be lower when targeting large fish (Figure 6).

Population-level recruitment (based on number of age 1 fish) and abundance also corresponded to size-limits and fishing mortality. When harvesting small fish, recruitment increased and stabilized with $F > 0$ (Figure 7). On the other hand, when targeting large fish, highest recruitment was achieved at low to intermediate F, and relatively high F led to declines and eventually failure of recruitment (e.g., $F \geq 0.8$; Figure 7). As expected, with both size-limits population size declined with increased F (Figure 7). The greatest drop in population size occurred between $F = 0.2$ and 0.4, and the rate of decline of population size decreased with subsequent increases of F (Figure 7). When targeting large fish at relatively high F (e.g., $F \geq 0.8$), the population collapsed, while the population could sustain at high F when targeting small fish (Figure 7).

Influences of stochasticity on fishing-induced effects

To evaluate whether model predictions might be sensitive to stochasticity, we repeated the baseline and fishing simulations by imposing stochasticity in carrying capacity and recruitment. We found that while mean values of evolving traits and observed length-at-age generally were not sensitive to stochasticity, standard deviations of these traits and both mean and standard deviation of recruitment and population size were sensitive to stochasticity. For example, the evolving maturation RN, K, and L_{max} under the stochastic, baseline simulations also resulted in differential patterns between sexes, and mean values of these traits varied only slightly from those generated under deterministic conditions. Similarly, under either size-limit for a given F (e.g., $F = 0.2$ or 0.6), we found that mean values of maturation RN, K, L_{max}, and length-at-age (based on length of females at ages 2 and 7) were generally consistent between deterministic and stochastic conditions, and standard deviations of these traits tended to be similar or slightly greater for the latter (Tables 2, Figure 8).

On the other hand, both mean and standard deviation of recruitment and population size were sensitive to stochasticity. For example, when targeting large fish at a given F, both mean recruitment and population size tended to be higher under deterministic conditions (Table 2). Further, while both metrics reduced when targeting large fish at F = 0.6 under both deterministic and stochastic conditions, the mean values for these two metrics at a given F varied considerably between conditions (Table 2). And, not surprisingly, standard deviations of both metrics at a given F were higher under stochastic conditions (Table 2).

Discussion

We used a generalized eco-genetic IBM approach to conduct simulations with variable size-limits (baseline, and targeting large or small fish), fishing mortality rates (F ranged in [0, 1] with 0.2 increments), and under deterministic and stochastic conditions. While our model is simple, several predictions from our model are supported by empirical studies and were consistent with predictions based on life history theory. By comparing the results, we demonstrated potential simultaneous size-selective fishing-induced evolutionary and ecological effects and the influence of environmental stochasticity on fishing-induced effects.

Discrimination of fishing-induced evolutionary and ecological effects

We identified several aspects of fishing-induced evolution. First, our model predicted that size-selective fishing could impose genetic selection for both maturation reaction norms and growth traits. Targeting large fish at intermediate to high fishing mortality could lead to small decreases in maturation reaction norms at young ages, and considerably alter mean individual growth parameters; together these traits allow for potential early maturation and slow growth rate. In contrast, targeting small fish selected for delayed maturity and less pronounced changes in genetically-determined growth. The results of targeting large fish were consistent with previous studies that suggested declines in length-at-age and age at maturity of commercial fish stocks attributed to potential fishing-induced genetic selection (Olsen et al. 2004, 2005; Swain et al. 2007). While targeting on small fish is unusual, the results were intuitive; fish that grew fast might be able to escape fisheries, and delayed maturity helped maximize somatic growth.

Second, our model predicted that fishing-induced genetic selection might be more pronounced for growth traits than maturation reaction norms. This pattern was not due to unequal evolving potential between maturation reaction norms and growth traits, as we ensured that the initial population possessed sufficiently wide ranges of both maturation and growth reaction norm parameters. While in our design the maturation reaction norm and growth traits evolved independently, we observed that evolution of one trait tended to impede that of the other; i.e.,, a greater change in maturation reaction norm parameters in response to fishing would occur if genetic growth parameters were static (Höök and Wang, in review). Genetic correlation between maturation and growth traits has been suggested (Dieckmann and Heino 2007; Hutchings and Fraser 2008), but we know of no studies that suggest competing effects between evolving traits. Nonetheless, this prediction could be reasonable as in the model fishing effects directly operated on length, not maturation schedules. Furthermore, Dunlop et al. (2005) showed that stability of maturation reaction norms had been maintained for two smallmouth bass *Micropterus dolomieu* populations (both were originally introduced from a single source) even though they experienced different mortality regimes for 100 years.

Third, under baseline and fishing simulations the model predicted that genetic responses varied between sexes. For example, female maturation reaction norms responded more pronouncedly to fishing, and K achieved a lower value while L_{max} achieved a higher value for females than males. Such differential genetic responses were likely due to sexually-different reproductive tradeoffs (females allocated a higher proportion of energy to reproduction and displayed a trade-off between egg quality and egg number). While in our design fish of both sexes experience equal fishing mortality, in reality, many fish display sexually-dimorphic size patterns (females tend to be larger than males) and thus sexually-differential responses to fishing-induced effects likely will occur.

In addition to fishing-induced evolution, our model demonstrated drastic plastic changes of mean growth rates, maturation schedules, and population dynamics. Fishing-induced plastic effects might occur by 1) affecting density-dependent growth and recruitment, 2) altering age and size structures, and 3) changing population maturation schedules via effects 1) and 2) (Law 2000, 2007; Berkeley et al. 2004). It is notable that fishing-induced plastic effects on growth were in an opposing direction to evolutionary effects; i.e., while fishing-induced selection favored slow growth rates (lower K and higher L_{max}), plastic effects increased growth rates. Since the observed female length-at-age patterns increased with F, the plastic effects out-weighed evolutionary effects. On the other hand, both plastic effects on growth and decreased maturation reaction norms by fishing would promote early maturation schedules. Given that length-at-age responded to fishing mortality with a greater magnitude of change than maturation reaction norms, fishing-induced early maturity patterns might be primarily driven by plastic effects.

Our model predictions of fishing-induced evolutionary and plastic effects were comparable to recent eco-genetic modeling studies (Ernande et al. 2004; de Roos et al. 2006; Dunlop et al. 2007). Dunlop et al. (2007) constructed an eco-genetic model based on empirical data on smallmouth bass (whereas our model was based on a generalized approach), and explored fishing-induced plastic and evolutionary effects by simulating harvesting of individuals above a size-limit (18 cm) and age 0, respectively. While Dunlop et al.'s (2007) model predicted no effects on probabilistic maturation reaction norms (PMRN) when targeting age 0 fish (whereas Ernande et al. 2004 and this study showed detectable effects when targeting small fish), they found significant changes in PMRN when targeting large fish and considerable plastic changes in growth and biomass under both size-limits, supporting our findings. Further, both our generalized model (Höök and Wang in review) and Dunlop et al.'s (2007) model showed that plasticity in growth rates might influence the result of fishing-induced evolution.

Integrating fishing-induced effects and environmental stochasticity

Examination of fishing-induced effects under stochastic conditions provided an evaluation of both practical and theoretical importance. Our model results showed that at a given F, mean responses of recruitment and population size were sensitive to stochasticity. However, evolving traits and length-at-age were less sensitive to stochasticity. Further, variability (measured by standard deviation) for almost all traits tended to be higher under stochastic conditions. While these results might be intuitive, they implied that adequate evaluation of fishing-induced effects required taking into account environmental uncertainty (Beddington and May 1977; May et al. 1978).

Since stochasticity is modeled as random deviations from mean carrying capacity and per capita recruitment, it may have little effect on mean responses but may increase variability of evolving traits and length-at-age patterns. Dunlop et al. (2007) evaluated sensitivity of PMRN to stochasticity and indicated consistent findings with ours.

Our study also highlighted the role of fishing on trait variability of a population. We showed that targeting large fish might elevate variability in phenotypic traits (length-at-age, recruitment, and population size). Recent research suggests that size-selective harvesting of large fish may result in populations with truncated age and size structures (Berkeley et al. 2004), and such populations tend to display unstable dynamics (Hsieh et al. 2006; Anderson et al. 2008). Further, although variability of genetic traits was not inflated from F = 0.2 to 0.6 under large size-limit, both evolving maturation reaction norms and growth traits became more variable at F ≥ 0.8. While such increasing stochastic genetic dynamics might simply reflect a relatively small population size at high F in our model, this observation might warrant further exploration on the linkage between genetic and phenotypic variability.

In conclusion, the potential effects of size-selective fishing on life history, growth rates, and population dynamics have been suggested for many commercial and recreational fishes (Beard and Essington 2000; Kuparinen and Merilä 2007). Here, we explored the genetic and ecological pathways of these effects in the context of complex fisheries: via varying size-limits, fishing mortality rates, and under stochastic versus deterministic conditions. We showed that through fisheries harvest life history traits were altered via ecological and evolutionary effects which could then cascade to influence growth patterns and population dynamics in the direction of unsustainable fisheries.

Acknowledgements

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Table 5.1. Parameters used for baseline simulations. Maturation reaction norms (MRN) comprise a set of 36 sex- and age-specific parameters. Von Bertalanffy coefficients K and L_{max} are determined by a set of 24 sex-specific growth RN parameters. Z is total mortality, representing background mortality from all sources excluding fishing.

Parameters	Mean value (range)
MRN	400 (100, 700)
K	0.3 (0.02, 0.65)
L_{max}	622 (400, 800)
Z	0.2
Recruitment coefficient (Ricker type)	a=0.0008 b=0.0000000000055
Stochastic recruitment multiplier	0.5 (0, 4.05)*
Carrying capacity (deterministic)	2E+11
Carrying capacity (stochastic)	2E+11 (5E+10, 3.5E+11)

*: sampled from a right-skewed, log-normal distribution with higher frequency in lower values

Table 5.2. Mean and standard deviation (SD) of evolving growth traits (K and L_{max}), realized individual growth (lengths at ages 2 and 7), and population-level recruitment and abundance under two size-selective fishing options (A: targeting large fish; B: targeting small fish). For each fishing size-limit, we compared individual and population traits under deterministic vs. stochastic conditions, and under relatively low vs. high fishing mortality rates (F = 0.2 vs. F =0.6).

A. Targeting large fish

	Deterministic				Stochastic			
	F=0.2		F=0.6		F=0.2		F=0.6	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
K (male)	0.28	0.02	0.27	0.02	0.27	0.02	0.26	0.02
K (female)	0.25	0.02	0.25	0.02	0.25	0.02	0.24	0.02
L_{max} (male; mm)	682	18	690	16	689	18	695	16
L_{max} (female; mm)	700	16	707	14	705	16	711	14
Age 2 length (mm)	263	8	347	22	266	24	343	22
Age 7 length (mm)	519	19	693	41	521	37	697	43
Age 1 recruitment	53,378,673	80,432	21,771,844	1,359,747	40,386,820	50,321,524	5,285,010	7,786,375
Population size	191,000,000	908,040	42,632,391	3,186,675	168,000,000	78,456,624	9,719,486	10,919,210

B. Targeting small fish

	Deterministic				Stochastic			
	F=0.2		F=0.6		F=0.2		F=0.6	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
K (male)	0.29	0.01	0.29	0.01	0.28	0.01	0.28	0.00
K (female)	0.27	0.00	0.27	0.01	0.26	0.00	0.26	0.00
L_{max} (male; mm)	674	7	676	7	678	6	680	6
L_{max} (female; mm)	691	6	692	6	694	5	695	5
Age 2 length (mm)	256	10	279	3	259	20	284	33
Age 7 length (mm)	515	20	603	10	515	33	602	32
Age 1 recruitment	50,895,010	209,873	52,883,700	164,681	53,543,100	63,807,408	49,530,670	58,658,060

Figure list

Figure 5.1. Average evolving maturation reaction norm (RN; with ± 200 mm confidence envelops) after ten 1,000-year simulations under a baseline, deterministic condition. A: males, B: females.

Figure 5.2. Ten, 1,000 year replicates of evolving K and L_{max} under a baseline, deterministic condition.

Figure 5.3. Ten replicates of final (after 200 years) evolving maturation reaction norms (RN) under deterministic conditions, with two size-limits (targeting large fish vs. small fish) and various fishing mortality rates (F = 0, 0.2, 0.4, 0.6, 0.8, and 1.0; represented as black, red, green, navy blue, cyan, and magenta, respectively).

Figure 5.4. Ten, 200 year replicates of K under deterministic conditions, with two size-limits (targeting large fish vs. small fish) and various fishing mortality rates (F = 0, 0.2, 0.4, 0.6, 0.8, and 1.0; represented as black, red, green, navy blue, cyan, and magenta, respectively).

Figure 5.5. Ten, 200 year replicates of evolving L_{max} under deterministic conditions, with two size-limits (targeting large fish vs. small fish) and various fishing mortality rates (F = 0, 0.2, 0.4, 0.6, 0.8, and 1.0; represented as black, red, green, navy blue, cyan, and magenta, respectively).

Figure 5.6. Ten replicates of final (after 200 years) female length-at-age (upper row) and maturation schedules (average age of mature fish; bottom row) under deterministic conditions, with two size-limits (targeting large fish vs. small fish) and various fishing mortality rates (F = 0, 0.2, 0.4, 0.6, 0.8, and 1.0; represented as black, red, green, navy blue, cyan, and magenta, respectively).

Figure 5.7. Ten, 200 year replicates of age 1 recruitment (left column) and population size (right column) under deterministic conditions, with. two size-limits (targeting large fish vs. small fish) and various fishing mortality rates (F = 0, 0.2, 0.4, 0.6, 0.8, and 1.0; represented as black, red, green, navy blue, cyan, and magenta, respectively).

Figure 5.8. Comparisons of mean (left column) and standard deviation (SD; right column) of maturation reaction norms (MRN) parameters under deterministic vs. stochastic conditions. Each point represents the mean or SD of MRN parameter for a given age and sex (i.e., 18 points). The diagonal line is the 1-to-1 line. A: targeting large fish; B: targeting small fish. In both A and B, the upper rows are at F = 0.2, and the lower rows are at F = 0.6.

Figure 5.1.

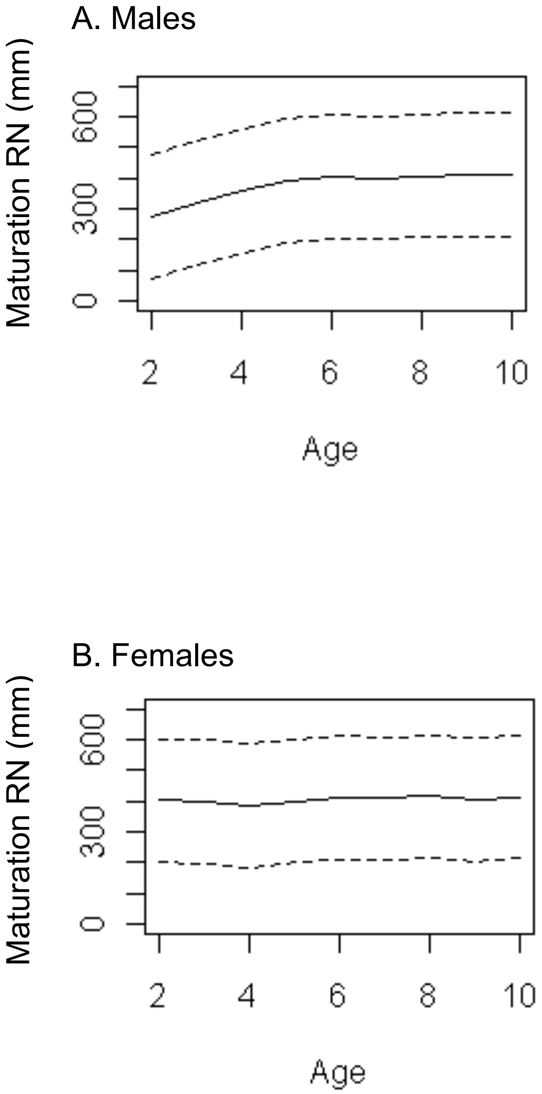
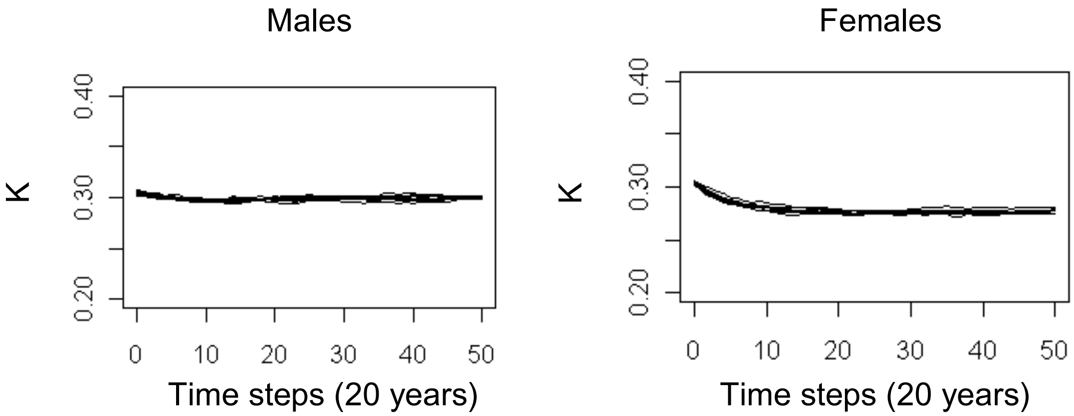

A. Males
Maturation RN (mm)
0
300
600
2
4
6
8
10
Age
B. Females
Maturation RN (mm)
0
300
600
2
4
6
8
10
Age

Figure 5.2.

Evolved K



Evolved L_{max}

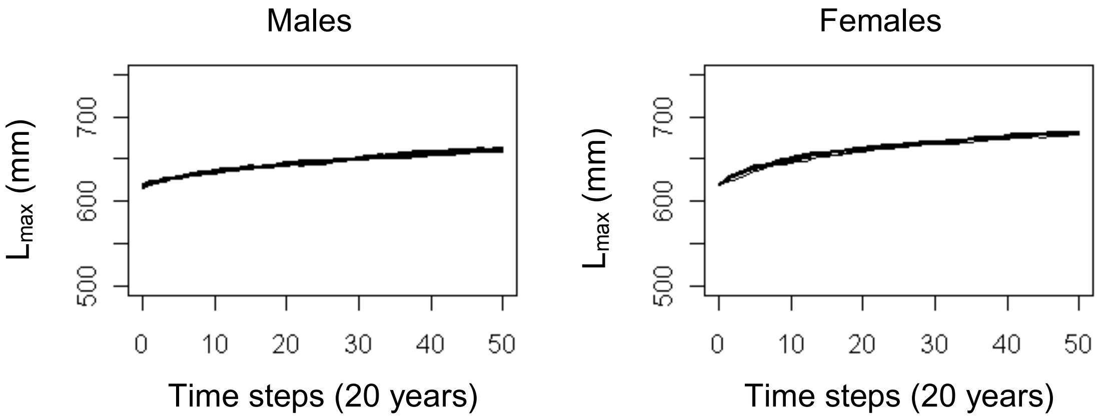
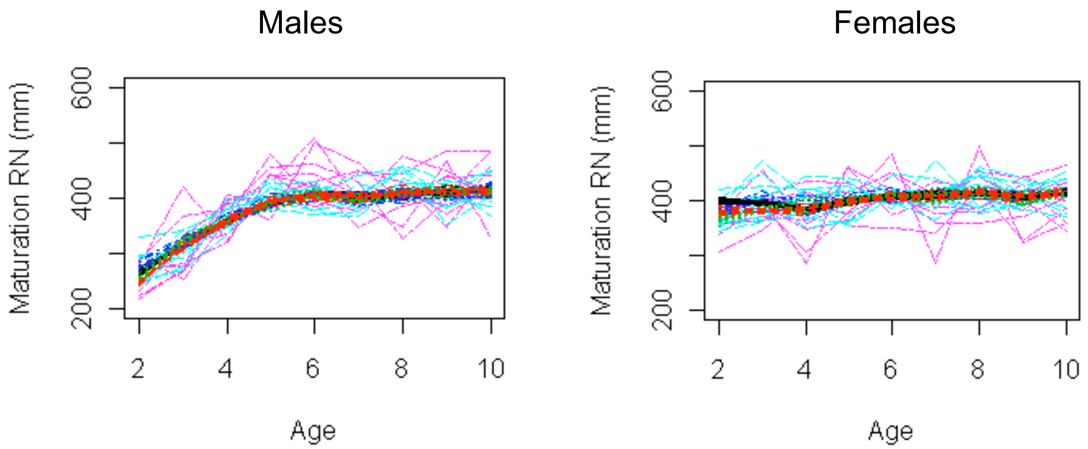


Figure 5.3.

Targeting large fish



Targeting small fish

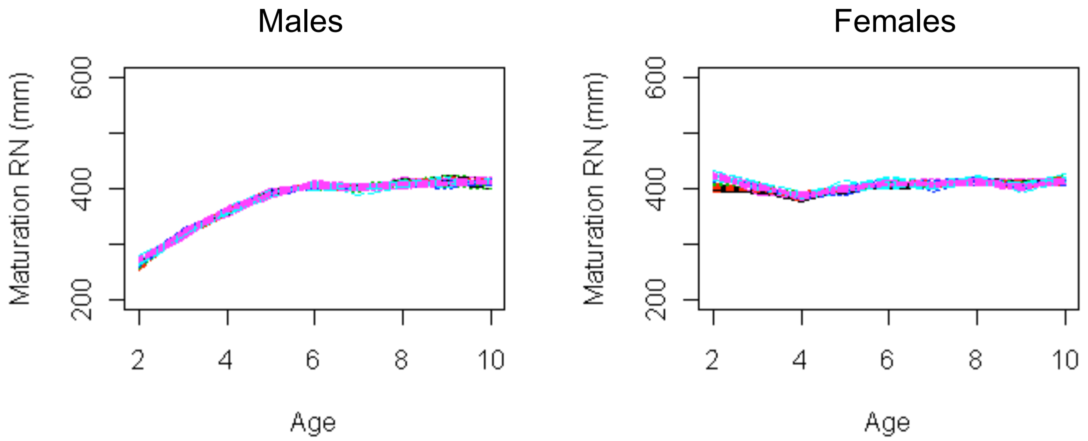
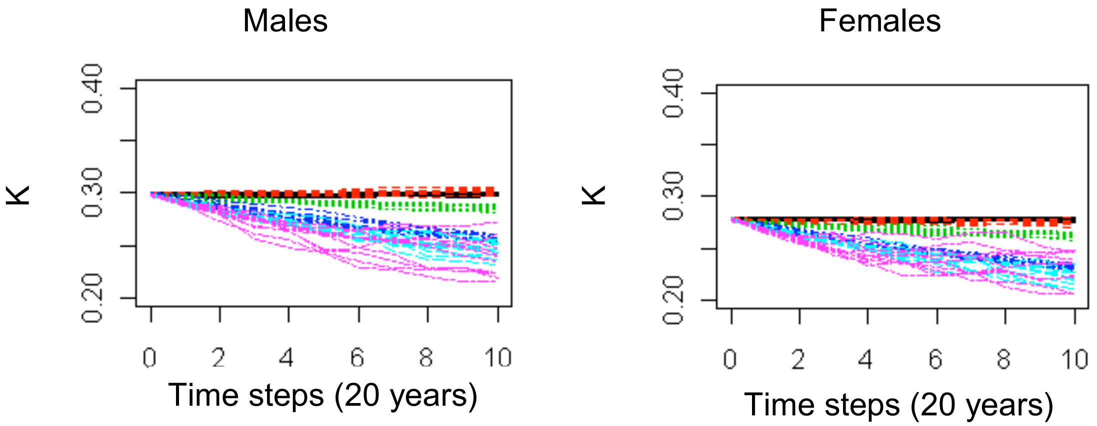


Figure 5.4.

Targeting large fish



Targeting small fish

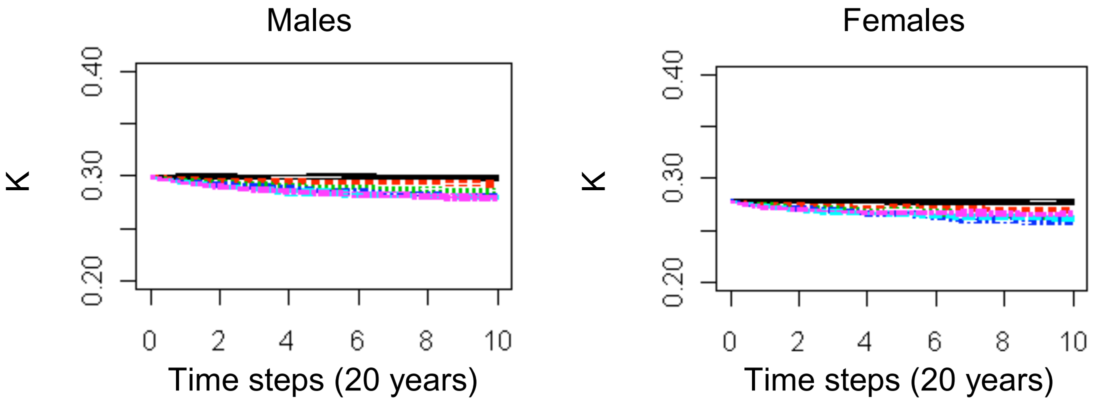
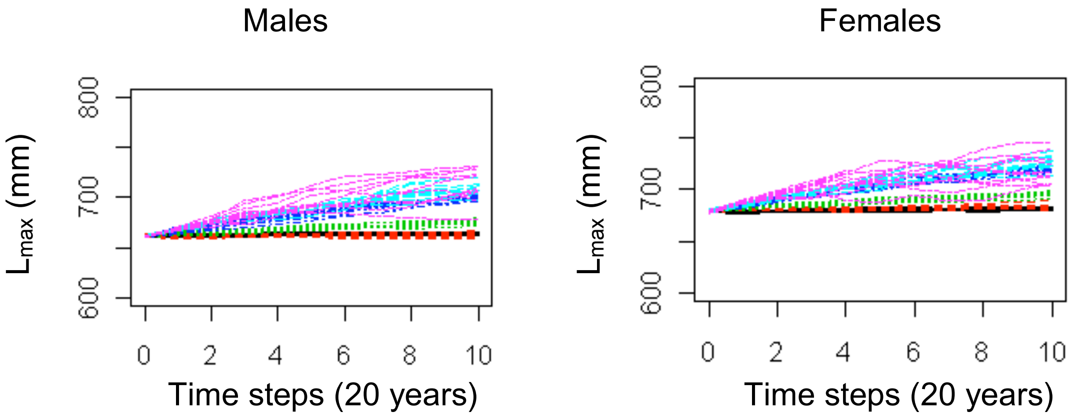


Figure 5.5.

Targeting large fish



Targeting small fish

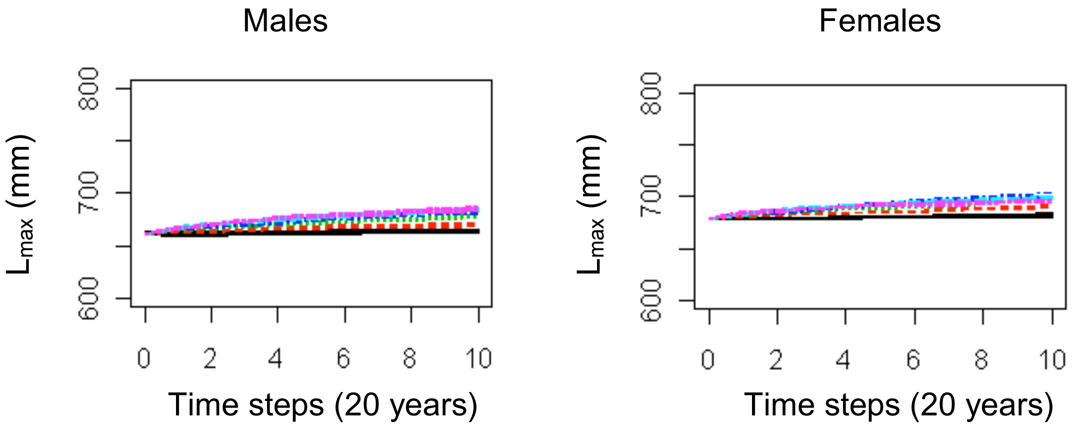


Figure 5.6.

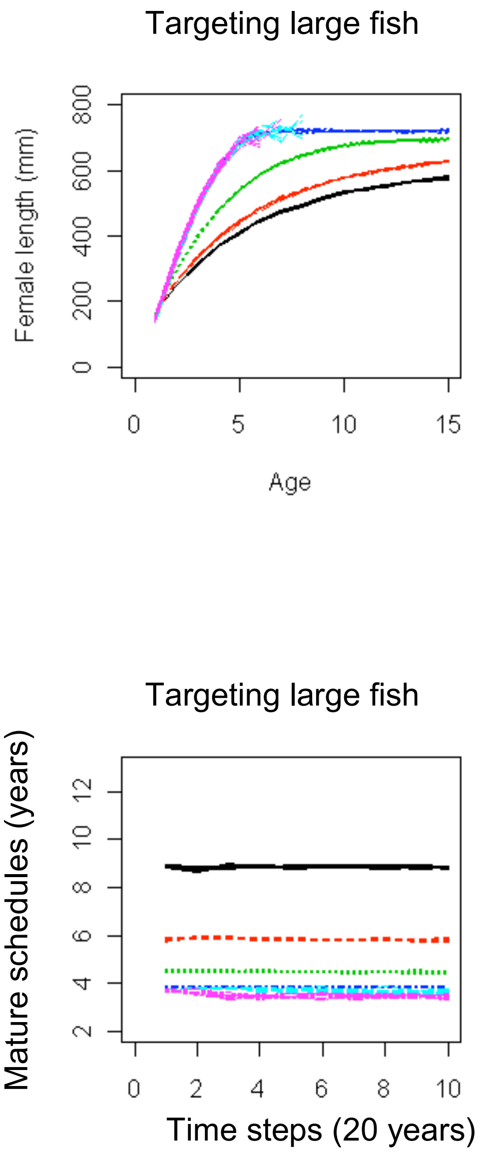
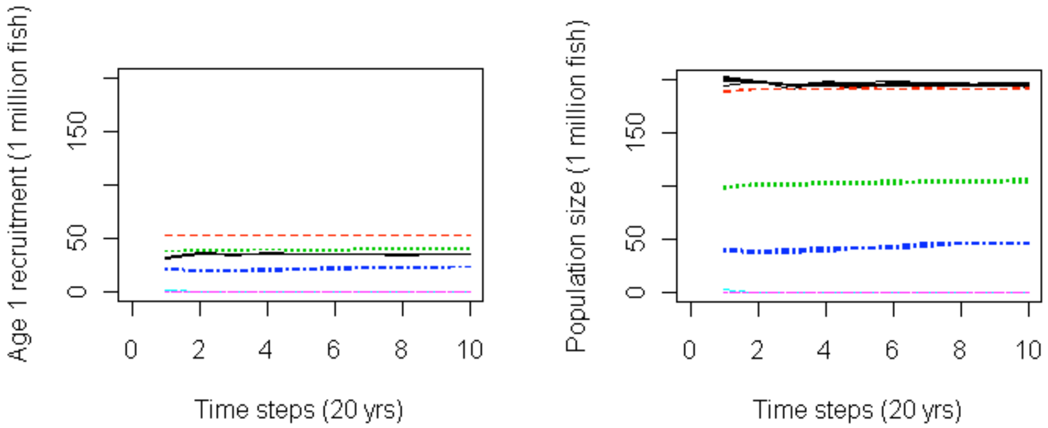

Targeting large fish
Targeting small fish
Female length (mm)
0
200
400
600
800
0
5
10
15
Age
Targeting large fish
Targeting small fish
Mature schedules (years)
2
4
6
8
10
12
0
2
4
6
8
10
Time steps (20 years)

Figure 5.7.

Targeting large fish



Targeting small fish

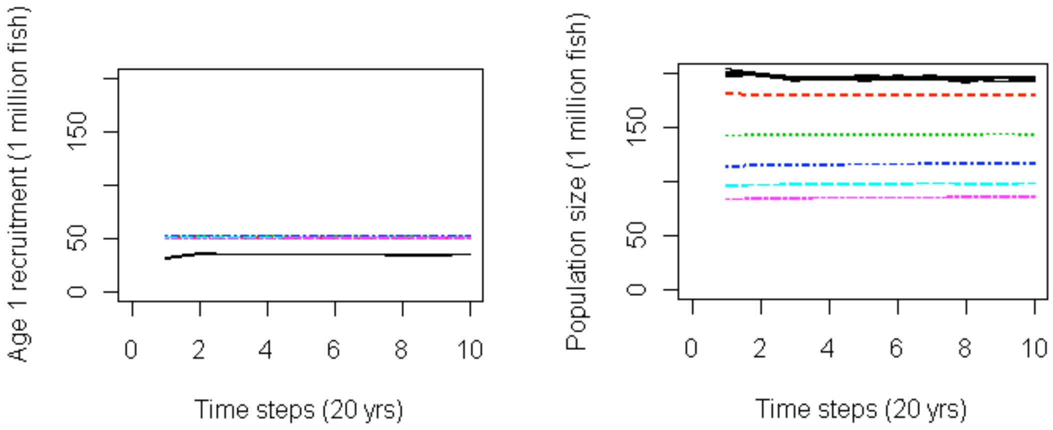
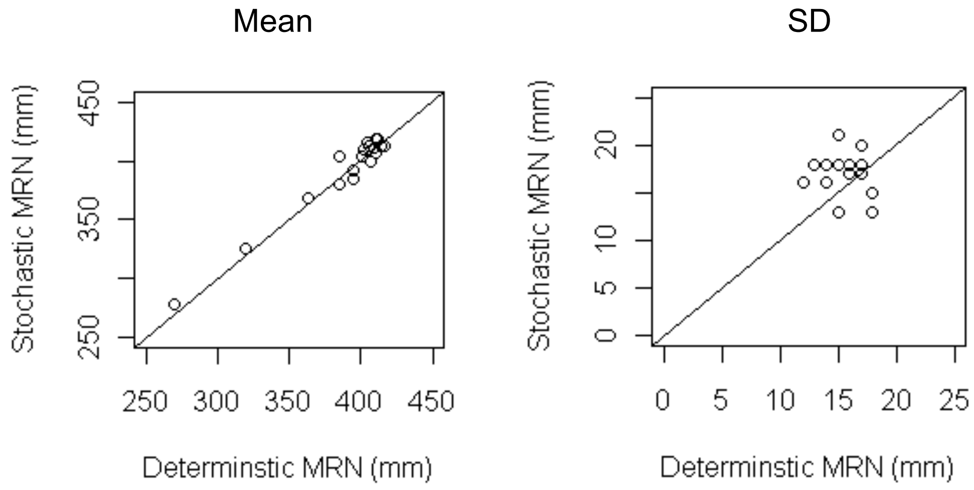


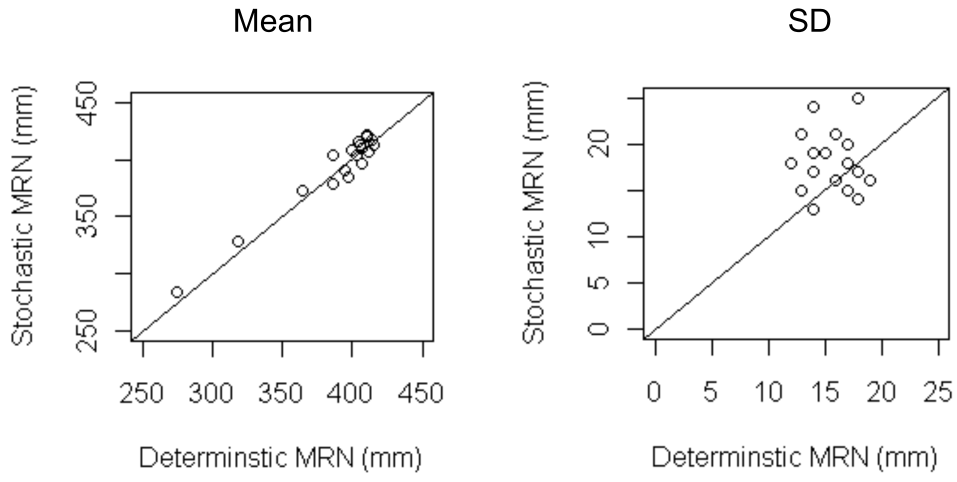
Figure 5.8.

A. Targeting large fish

F = 0.2

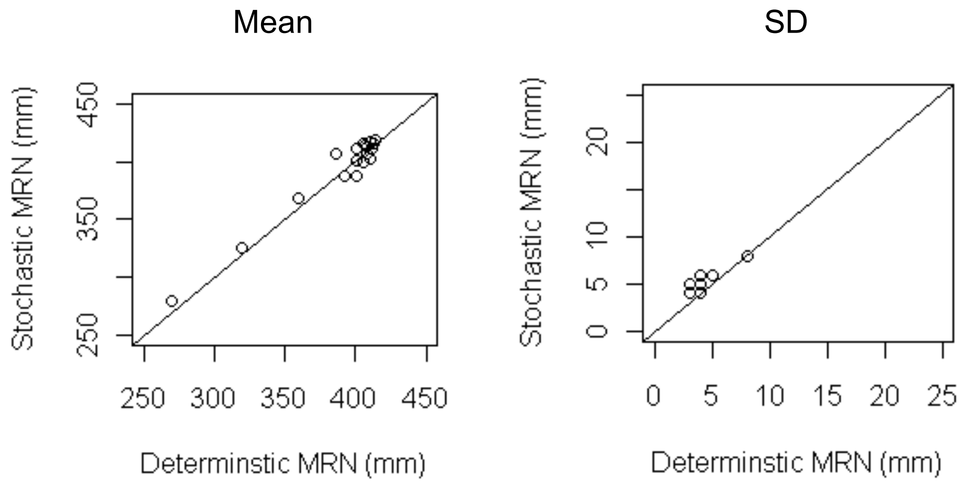


F = 0.6

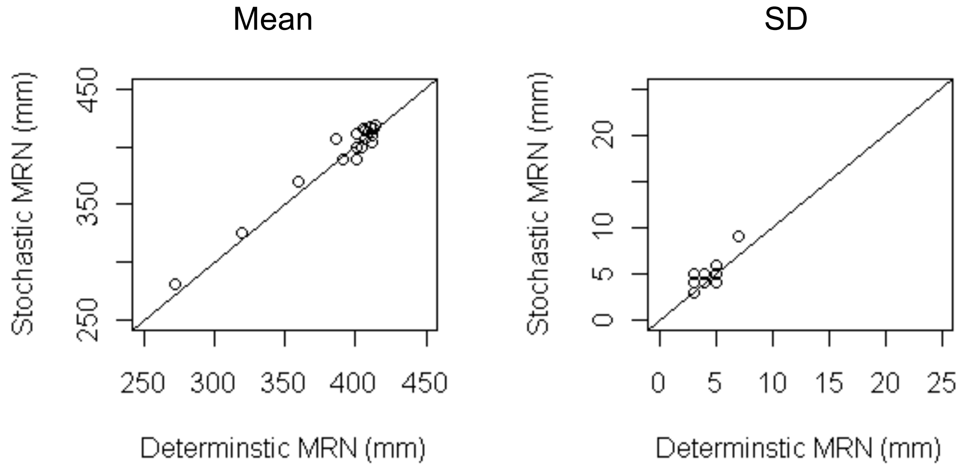


B. Targeting small fish

F = 0.2



F = 0.6



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Chapter VI

Inter-population variation in egg size of walleye *Sander vitreus* from the Great Lakes region

Abstract

Egg size varies intra-specifically among populations and individuals, and such variation may reflect various maternal influences and environmental adaptations. Variation in egg size has important implications for recruitment success, and as common stocking practices may influence selection on egg size, it is informative to consider potential adaptive variation in egg size prior to implementing stocking. We quantified variation in egg size of walleye by stock, year, maternal age, and length using five populations in the Great Lakes region. When accounting for maternal age and length, walleye eggs varied significantly among stocks: egg size was relatively small for fish spawning in Maumee and Sandusky Rivers (western Lake Erie), intermediate in Oneida Lake and Tittabawassee River (Saginaw Bay, Lake Huron), and relatively large in Van Buren Bay (eastern Lake Erie) and Little Bay de Noc (northern Green Bay, Lake Michigan). Stock accounted for a relatively high proportion in overall egg size variation. Moreover, a negative association between mean egg size and system-specific primary production is indicative of potential adaptive variation of egg size. We did not directly evaluate effects of stocking on egg size for walleye. However, given potential adaptive variation of egg size, we suggest that stocking programs should consider egg size variation to limit adverse anthropogenic selection.

Introduction

Recruitment success is related larval growth and survival rates (Meekan and Fortier 1996; Bergenius et al. 2002) which tend to be correlated with egg size (Berkeley et al. 2004). Thus, system-specific recruitment success is likely sensitive to egg size variation and the trade-off between numbers and size of eggs spawned by individual females. While studies of various fish species suggest that maternal characteristics (e.g., age, length, or condition) can play an important role in determining offspring size and/or quality (e.g., Marteinsdottir and Steinarsson 1998; Berkeley et al. 2004), these relationships do not consistently hold for other fish species or stocks (e.g., maternal effects on egg size or quality vary among walleye *Sander vitreus* stocks; Wiegand et al. 2004, 2007). Previous research suggests that relationships between maternal characteristics and egg size (or quality) may be related to spawning environments, e.g., pelagic spawning fish tend to display weaker maternal effects on egg size than demersal spawning fish (e.g., Einum and Fleming 2002). Fish larvae emerging from demersal habitats tend to experience relatively high density-dependent competition or predation, thus selection may favor relatively pronounced maternal effects that could enhance offspring survival or growth rates. This implies that egg size may be influenced via adaptive (changes in egg size due to selection) and/or plastic (changes in egg size caused by factors that influence female growth history) processes (Stearns 1992).

Evidently, egg size, or offspring size in general, may be adaptive to habitat conditions. Studies on a variety of species (including fish) suggest that while offspring size may correspond to physiological processes (e.g., embryonic development time), variation in environmental conditions, e.g., temperatures, can also contribute to offspring size variation (Gillooly and Dodson 2000; Gillooly et al. 2002). Further, Einum and Fleming (1999) demonstrated that selection for brown trout (*Salmo trutta*) egg size varied by quality of habitats. On average, offspring fitness (e.g., survival and growth rates) increases with egg size, but the difference in fitness between small and large eggs decreases with elevated environmental quality (Einum and Fleming 1999). Because female fitness increases with quantity of offspring, with everything else being equal selection should favor production of small eggs in favorable habitats relative to large eggs in unfavorable habitats.

We aimed to investigate relative strengths of maternal influences and habitat-specific selection on variation of egg size of walleye, a semi-pelagic spawning fish that utilizes various spawning habitats throughout North America. Previous studies have explored maternal effects on egg size and quality for a number of walleye populations (Johnston and Leggett 2002; Wiegand et al. 2004, 2007; Moles et al. 2008). Johnston and Leggett (2002) found that effects of maternal age and length on egg size were generally positive for walleye, but the relationships were significant for only a fraction (38%) of the stocks studied. Further, after accounting for maternal effects, the authors documented inter-stock egg size variation and suggested that such variation might be related to habitat conditions (e.g., temperatures and primary productivity). Based on Johnston and Leggett's (2002) results, it appears that effects of habitats would have stronger influence on walleye egg size than maternal effects. However, the authors concluded that the magnitude of within-stock egg size variability was similar to that among different stocks.

Herein, we revisited Johnston and Leggett's (2002) study based on different walleye stocks and analytic methods. We studied five walleye stocks in the Great Lakes region. These stocks support important walleye fisheries, and there is a plethora of available information on their life histories and habitats. Furthermore, these stocks may experience differential selection for egg size as they utilize different spawning habitats and express variable life history patterns. The five stocks include Tittabawassee River, Maumee and Sandusky Rivers, Van Buren Bay, Little Bay de Noc, and Oneida Lake (Figure 1). Two stocks spawn in rivers and inhabit relatively productive habitats: Tittabawassee River (a tributary that flows into Saginaw Bay, Lake Huron) and Maumee and Sandusky Rivers (hereafter referred to as Maumee stock; samples from these rivers were combined due to their close locations and as egg size did not differ between the rivers. Both rivers flow into the western basin of Lake Erie; Figure 1). Nutrient loadings in these rivers and their downstream environments are relatively high (Makarewicz and Bertram 1991; Johengen et al. 1995). Further, compared to the other stocks the two river-spawning stocks display relatively high growth rates and mobility (based on tag recapture records; Wang et al. 2007). Two stocks inhabit less productive regions of the Great Lakes: Little Bay de Noc in the northern Green Bay (a mixture of reef- and river-spawning fish sampled from Little Bay de Noc at the mouth of Whitefish River; hereafter referred to as LBDN stock) and Van Buren Bay of Lake Erie (primarily reef-spawning; hereafter referred to as VB stock) where nutrient loading is relatively low and spawning habitats are deeper and more open. Compared to river-spawning stocks, these two stocks display relatively slow to moderate growth rates and limited mobility (Einhouse and Haas 1995; Schneeberger 2000). Finally, the Oneida Lake stock inhabits an inland lake where growth and mortality rates for walleye are substantially lower (He et al. 2005). Samples of this stock came primarily from river-spawning fish sampled from Scuba Creek. Presently, the two Lake Erie stocks are entirely naturally reproducing while stocking supplements the other three stocks. Supplemental stocking involves planting young hatchery raised fish from wild-caught fish from within the same system.

We tested the hypothesis that inter-stock variation should account for more variation in walleye egg size than maternal effects, and that differences in mean egg size across stocks might reflect variable habitat-specific selection. Specifically, we quantified inter- and intra-stock egg size variation (e.g., explored variation in egg size with respect to different stock, year, and maternal age and length) using analytic tools that facilitated detecting nonlinear patterns.

Materials and methods

Field sampling

Female walleye of five populations in the Great Lakes region were sampled during April 2007 and 2008 in conjunction with state tagging and stocking programs (Michigan [MDNR] and Ohio Department of Natural Resources [ODNR], New York State Department of Environmental Conservation [NYSDEC], and New York State Oneida Fish Cultural Station [hereafter referred as Oneida Lake]; Figure 1; Table 1). Sampling gears varied among sites and generally included electrofishing, trawl, or trapnet (Table 1). For most stocks, we collected data from all “flowing” females (e.g., females who were releasing eggs) encountered, but for the LBDN stock we used stratified random sampling based on length intervals. Total length (mm) of each female was measured, and a small amount (10-30 ml) of egg samples along with the first three dorsal spines, scales, or otoliths were collected. In 2008, we collected chronometric structures for subsequent ageing for all individuals. Similarly, in 2007 we collected chronometric structures from all individuals from 4 of 5 stocks, but from only a fraction of fish from VB (34%). Egg samples were preserved in 10% formalin immediately after collection.

Laboratory analyses

Ages of fish were determined by adding one to number of annuli (estimated from bony structure; see below) because sampling occurred during spawning time. Ages of fish collected in 2007 were estimated by multiple people using a combination of dorsal spines (VB, Oneida, and LBDN stocks), scales (Tittabawassee stock), and otoliths (Maumee stock). In 2008, ages for all five stocks were determined by one person (the first author) using dorsal spines. To evaluate precision among different ageing methods, we collected additional scales from Oneida in 2007 and otoliths from Maumee in 2008. There was good agreement among different chronometric structures: resulting in about 80% agreement, and > 90% of discrepancies within 1 year (A. VanDeValk compared scale and spine ages based on Oneida Lake stock 2007 data, and T. Hartman, ODNR, compared spine and otolith ages based on Maumee stock 2008 data). Also, evaluation of 2007 spine ages among three readers showed high precision: > 90% of the discrepancies within 1 year.

Egg sizes of individual walleye were measured as both dry weight and diameter. To account for within-individual variability in egg dry weight, we measured egg dry weight per female with two replicates: we prepared two aluminum dishes each containing a small number (around 20-30) of eggs, and left the dishes in an oven at 70°C for > 2 days (prior to this study, we examined changes in egg weight in relation to number of days in the oven. We found that egg weight decreased over time for the first two days and stayed constant after day 2). Mean egg dry weight was estimated as net weight of eggs divided by number of eggs per dish. We detected fewer than four samples per population that showed relatively large (e.g., > 0.1 mg) between-dish differences in egg dry weight. After excluding these samples, the correlation (r) between paired egg weight estimates was generally > 0.95.

For measuring egg diameter, we randomly selected 10 wet eggs per sample and measured diameters of each egg under a microscope at 20x. Measurement of egg diameters were facilitated by using a camera and *Image-Pro Plus software* that projected the images under the microscope on a computer screen. We measured the vertical and horizontal diameters (as walleye eggs were not perfectly round) and calculated the average diameter for each egg. Average egg diameter was estimated by averaging across the ten estimated egg diameters for a given female.

Statistical analyses

Correlation between egg dry weight and diameter was relatively high (r = 0.75 and 0.79 for 2007 and 2008 data, respectively). This suggested that either measurement is representative of egg size. Thus, we used egg dry weight as a measure for egg size for the following statistical analysis.

We analyzed data to explore 1) across-population variation in egg size and 2) within-population maternal effects on egg size variation. To evaluate both issues, we used a combination of multiple linear regression and classification and regression tree (CART; Breiman et al. 1984) approaches. Previous studies of walleye egg size variation have primarily relied on multiple linear regression approaches (e.g., Johnston and Leggett 2002; Moles et al. 2008). Although linear regression models are useful to identify the functions that describe associations between explanatory and response variables, it can be difficult to specify a proper (e.g., linear or quadratic) function between a predictor and responses. Also, choosing a priori regression functions may limit exploration of complex or nonlinear associations (De'ath and Fabricius 2000). On the other hand, the CART approach involves partitioning response variance based on cut-off values of predictors without requiring specification of a particular model (see below). Several authors suggest that the CART approach is useful to handle nonlinear relationships between response and predictor variables, and has been increasingly applied for ecological data analysis due to its graphic output that facilitates interpretation (Amrhein et al. 1999; Lamon and Stow 1999).

We conducted multiple regression analyses based on a hypothesis testing criterion ($\alpha = 0.05$). By pooling two years of data, we first examined egg size variation with respect to all factors: stock, year, and maternal age and length (Model I; Table 2). We also built several multiple regression models using different combinations of these predictors. We inspected model fit and assumptions by examining residuals.

For CART analysis, we followed the procedures described in De'ath and Fabricius (2000) and Faraway (2006). First, the data were split into two groups, by which the sum of variation (described as residual sum of squares [RSS]) of the response variable (egg size) is minimized through partitioning. RSS (partitioning) is defined as:

RSS (partitioning) = RSS (group 1) + RSS (group 2)

The partitioning of egg size variation was done by choosing a cutoff level of a predictor from all candidate predictors. Partitioning forms a node with two branches whose lengths describe the amount of egg size variation reduced (RSS (total)-RSS (partitioning)). Then, at each subsequent branch, the subset of data is further partitioned to minimize variation in egg size. Results from CART become a dichotomous structure (i.e., a tree with branches) with a number of terminal nodes describing the mean value of egg size for a given group. We determined optimal number of terminal nodes of a tree by first allowing a relatively large tree (e.g., by setting a large number of terminal nodes) and then performing tree pruning using 50 10-part cross-validations (Lamon and Stow 1999; Faraway 2006). Optimal number of terminal nodes was the mode size of the 50 trees with minimum prediction error (estimated by cross-validations). Further, we restricted number of terminal nodes to be at least three (i.e., a tree with two partitionings) which is comparable to a regression with ≥ 1 predictor.

To explore inter-stock variation, we fit a tree to the data using stock, year, and maternal age and length as predictors. Further, to explore intra-stock variation we fit an individual tree for each stock using maternal age and length as predictors.

Results

Across-stock egg size variation

Our two-year samples showed broad variation of egg size, maternal age and length among and within stocks (Appendix i). Regression analyses showed that egg size varied among stocks and with maternal age and length, but the effect of annual variation on egg size was not significant (Model I; Table 2). Inspection of regression coefficients revealed that egg size was relatively large for LBDN and VB stocks, followed by Tittabawassee, Oneida Lake, and Maumee stocks. With both length and age as predictive variables, egg size was positively associated with maternal length and negatively associated with maternal ages (Table 2). After removing year factor we fit two separate regression models for data of each year (Models II and III; Table 2). The regression fit of each year consistently showed significant variation in egg size among stocks and with maternal age and length. However, the ranking of mean egg size among stocks varied between years. While in 2007 rank of egg size was LBDN, VB, and Oneida > Tittabawassee > Maumee, in 2008 the rank was LBDN > VB > Tittabawassee > Oneida > Maumee (Table 2).

We also explored the effects of interactions between stock and maternal length for data of each year. Although the interaction terms were significant (not shown), we chose not to include interaction terms as they did not substantially improve model fit (adjusted R^2 increased about 0.03). Lastly, in all regression models we found that residuals displayed slight nonconstant variance (not shown). The R^2 for these models were about 0.27-0.36 (Table 2).

Parallel to regression analyses, we also applied CART to partition egg size variation. With all predictors (stock, year, age, and length) included, CART procedures resulted in a tree structure with seven terminal nodes from six divisions of data (Figure

2). The first split, which resulted in greatest reduction of overall egg size variance, was based on stock, where Maumee and Oneida stocks were separated from the other three stocks. The egg size variation was further partitioned based on stock, year, length, and age. For Oneida stock, egg size varied significantly between 2007 and 2008. Further, for the three stocks with relatively large eggs, large egg size was associated with long lengths but intermediate ages (Figure 2). Finally, based on CART the rank for mean egg size was LBDN > VB and Tittabawassee > Oneida > Maumee (Figure 2).

Applying CART procedures on data of either year showed similar, but slightly different, tree structures (Figure 3). While in 2007 egg size was relatively large in LBDN, VB, and Oneida, intermediate in Tittabawassee, and relatively small in Maumee, in 2008 egg size was distinctly largest in LBDN, followed by a group of intermediate egg size (VB and Tittabawassee), and a group of small eggs (Oneida and Maumee; Figure 3). In both years, egg size appeared to be positively associated with length and younger, large females tended to produce larger eggs than older, large females. Length appeared to explain more variation in egg size than age (as multiple splits were based on length cutoffs) for the 2007 data. However, this might be partially due to missing age information for VB stock.

Based on the same predictors, the R^2 values resulting from CART procedures (range from 0.32-0.38) were slightly greater than those of regression models, and residuals appeared to be normal and have constant variance.

Within-stock maternal effects on egg size

Based on regression model approaches, within stock maternal effects on egg size appeared to be quite variable across stocks and between years (Table 3). For example, while in 2007 the effects of maternal age and length on egg size were generally positive (except for LBDN) and significant, patterns of maternal effects were weaker in 2008. Further, within-stock maternal effects on egg size tended to be weak for all stocks (regression models with both age and length as predictors resulted in $R^2 \sim 0.1$ or less for all stocks in both years except for VB data in 2007). We found that for a given stock the effect signs and/or levels of significance of regression coefficients might vary between years (Table 3). Because our sample size was relatively large, such between-year variation of regression coefficients should not be due to low power and would suggest maternal length and age were poor indices for egg size.

Similar to the regression-based inter-stock analysis, we checked the residuals for these within-stock regression models. The assumption of linear relationships between egg size and maternal effects generally was appropriate, but for Maumee in both years and Tittabawassee in 2008 residuals displayed dome-shaped patterns when plotting against maternal length or age. However, subsequent transformation of response or predictors had minimum improvement on fit, and thus model fits based on untransformed data were reported (Table 3).

Notably, we also detected significant annual variation in egg size for four of the five stocks after accounting for maternal effects (Table 4). For Tittabawassee, LBDN, and Maumee stocks, mean egg size increased in 2008, but for Oneida stock mean egg size decreased in 2008. Egg size of VB stock did not change between years.

The CART-based trees for five walleye stocks also indicated variable maternal effects on egg size across stocks and years. In 2007, we found that the trees for Tittabawassee, VB, and Oneida stocks were constructed based on female lengths, while those for LBDN and Maumee stocks were based on ages (Figure 4a). Further, within the group of either length- or age-based trees in 2007, patterns of maternal effects on egg size were similar across stocks even though the cut-off values of predictors varied among stocks (Figure 4a). Mean egg size generally increased with female length (for Tittabawassee, VB, and Oneida stocks), but females of intermediate ages (for LBDN and Maumee) produced relatively large eggs (Figure 4a). On the other hand, in 2008 we found little consistent pattern in maternal effects on egg size among stocks (Figure 4b). The R^2 values of CART-based trees were also higher in 2007 (range in [0.12-0.29]) than in 2008 (range in [0.08-0.20]).

Discussion

Intra-specific variation in egg size may be induced by plastic and adaptive processes. While several studies suggest that maternal effects could influence egg size or quality via plastic processes (e.g., Marteinsdottir and Steinarsson 1998), through size-selective mortality and/or growth potential spawning and nursery habitats also may induce selection for egg size (Einum and Fleming 1999). In this study, we quantified the effects of stock, female age, and length on egg size for walleye using two analytic methods. We demonstrated greater inter-stock than within-stock maternally-induced egg size variation. While inter-stock variation in egg size fluctuated between years, the general spatial patterns appeared to correspond to habitat quality for early life growth.

Furthermore, effects of maternal age and length on egg size were relatively weak and variable among stocks.

By simultaneously accounting for maternal and stock effects, we found that greater amount of egg size variation was attributable to stock than maternal age and length. Also, while the ranks of egg size across stocks varied between years, the general patterns of inter-stock variation held: mean egg size given female age and length was relatively large in Little Bay de Noc, intermediate in Van Buren Bay of Lake Erie, Oneida Lake, and Tittabawassee River, and relatively small in Maumee and Sandusky River. The spatial pattern in egg size appeared to correspond to a gradient of primary productivity among the spawning sites. In our study system, primary productivity was relatively high in the rivers, intermediate in the inland lake, and relatively low in the Bay habitats (Makarewicz and Bertram 1991; Johengen et al. 1995; Idrisi et al. 2001). A negative association between egg size upon primary productivity is consistent with prediction based on life history theory: to overcome low food abundance in an environment, selection would favor females to produce fewer large eggs; in contrast, females should produce many small eggs in an environment with relatively high food abundance.

While within-stock among-individual variation in egg size was considerable, we found that maternal age and length could only account for a small proportion of such variation. Several authors suggest that in addition to age and length, behaviors and other features of females (e.g., weight, condition, lipid content, etc.) could also contribute to the variability in egg size for walleye (Johnston et al. 2007; Moles et al. 2008). However, these additional maternal factors tend to correlate with age and length and may not further improve statistical fitting. Additionally, although post-hatching growth and survival of larvae may be more closely related to the lipid content of eggs than egg size (Johnston et al. 2007), amount of total lipid is generally correlated with egg size (Wiegand et al. 2004). Hence, we suggest that our findings of weak and/or insignificant maternal effects on egg size for walleye was likely not due to insufficient measures of maternal effects or egg quality, but might be a feature of walleye life histories. Here, we provide some plausible reasons for the potential weak maternal effect-egg size relationship based on walleye' spawning life history, selection, and analytic issues.

In contrast to previous research that suggests that maternal effects on egg size can be influential for black rockfish *Sebastes melanops* (Berkeley et al. 2004), our results indicated maternal effects accounted for little variability in egg size for walleye. We believe that the different findings may result from various spawning life histories of the studied species. While black rockfish express internal fertilization and the females offer relatively high degree of parental care by retaining eggs inside their bodies until hatching, walleye broadcast eggs and display minimum degree of parental care. Previous studies (based on theoretical modeling) suggest that females with high degrees of parental care and/or those utilize demersal habitats for spawning (as opposed to pelagic spawning) may express relatively pronounced maternal influences on offspring size and quality (Sargent et al. 1987; Einum and Fleming 2002). In habitats where density-dependent effects are significant, large females may increase offspring success by producing large eggs; while small females may also increase offspring fitness by producing large eggs, the relatively high cost (due to the trade-off between egg size and egg number) may offset the benefit for producing large eggs. On the other hand, for pelagic spawning fish it may not be beneficial for large females to produce large eggs as larval survival may be primarily influenced by stochastic events; thereby a weak relationship between maternal effects and egg size is expected.

Strong habitat- and anthropogenic-induced selection also may confound maternal effects on egg size. Previous research suggests that egg size variation may adapt to the predictability of habitat quality for offspring; more variable egg size is expected when environments are unpredictable (Koops et al. 2003). When habitat quality for offspring growth is uncertain, increased egg size variability may be a means to overcome size-dependent demographic stochasticity (Koops et al. 2003; Dziminski and Alford 2005). Further, it is possible that strength of selection fluctuates in a changing environment, and that could raise randomness of egg size independent of maternal effects. Moreover, anthropogenic activities could induce selection on egg size (Heath et al. 2003). Stocking programs for walleye are operated in Little Bay de Noc, Tittabawassee River, Oneida Lake (previously Tittabawassee River was stocked using eggs from Muskegon River stock, while the other stocks used eggs mainly from its own source), and many inland lakes in Michigan (Schneider et al. 2007). Stocking practices (generally artificial stripping, fertilizing, and incubating eggs) may uniformly increase egg fertilization and survival rates, thereby altering direction and strength of selection that may otherwise differentiate fitness by egg sizes. If everything else is equal, reduced egg size is expected as selection would favor increased fecundity. We investigated the evolutionary effect of stocking on egg size using data for Oneida Lake collected during 2007 and 2008 (this study) and unpublished data collected in 1966 and 1996 (J. Forney, unpublished data).

Nonetheless, our results suggested that egg size of Oneida Lake walleye did not change over time.

Additionally, weak patterns of maternal effects on walleye egg size may partially be related to analytic issues. Several previous studies (and part of our analyses in present study) used multiple linear regression models to investigate maternal effects and reached ambiguous conclusion (e.g. Johnston 1997; Johnston et al. 2007; Moles et al. 2008). While regression models could effectively reveal linear relationships between response and predictor variables, it can be challenging to fit a regression on data that display nonlinear patterns. By simultaneously applying both regression and CART analyses, we found that egg size variation was more effectively quantified with CART. Also, CART-based results showed interesting patterns of maternal effects in 2007: within a stock, egg size generally increased with female size, and females of intermediate ages produce large eggs. However, the 2008 data did not replicate such patterns (but see LBDN plot in Figure 4b), and showed even weaker maternal effects. It is possible that significant year-to-year fluctuations in egg size may result in such temporal changes in variability in egg size induced by maternal effects. Nonetheless, it is unclear what caused the temporal changes in egg size.

Finally, for some of the study stocks we suggest that variation in year-classes could further complicate quantification of maternal effects. The Tittabawassee, Maummee, and Sandusky River stocks are relatively productive in the Great Lakes region and display strong year-classes. As a result, when pooling egg size with female age or length data, sample sizes per age or length interval tend to be unequal, and that may affect the fit by regression models. As an example, data of Tittabawassee River in

2008 showed that variability of egg size was not constant regarding female length, due to that there were more individuals of 500-600 mm and 680-700mm. Such unequal variability in egg size versus female length or age would result in nonconstant distribution of residuals. However, for LBDN where a different sampling approach (e.g., stratified random sampling by length intervals) was employed, the estimated maternal effects on egg size were still weak.

In conclusion, we demonstrated that egg size variation of walleye could be attributable to adaptive responses to habitat-induced selection and phenotypic plasticity by maternal effects. As egg size is correlated with fitness of larval walleye (Johnston 1997; Johnston et al. 2007), it is important to understand the factors that influence egg size and thereby recruitment variability of walleye. Furthermore, it is important to identify potential evolutionary effects caused by management options (Hutchings and Fraser 2008). In particular, as stocking could alter strength of selection on egg and larval size, we suggest that managers should consider potential habitat-induced selection to improve effectiveness of such management practices.

Acknowledgements

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Table 6.1. Description of spawning habitats, sampling gear, and sample size for the five study walleye populations.

Stock	Spawning habitats	Gear	N (2007)	N (2008)
Tittabawassee	River	Electro-fishing	66	174
LBDN	Bay (near river mouth)	Trapnet	92	80
VB	Bay	Trapnet	81	38
Oneida	Inland lake	Trapnet	215	200
Maumee	River	Electro-fishing	112	57

Table 6.2. Summary of multiple linear regression analyses. We first combined two years of data to fit a regression with all predictors (Model I). We then fit year-specific regressions (Models II and III for data of 2007 and 2008, respectively). The signs and level of significance of regression coefficients, ranks of egg size, and R^2 based on each model are listed.

Model	Predictors: length, Age, stock, year	Ranks of egg size (1= largest)	R^2
I	+*, -*, *, +	LBDN[1], VB[1], Tittabawassee[2], Oneida[3], Maumee[4]	0.27
II	+*, -*, *, na	LBDN[1], VB[1], Oneida[1], Tittabawassee[2], Maumee[3]	0.29
III	+*, -*, *, na	LBDN[1], VB[2], Tittabawassee[3], Oneida[4], Maumee[5]	0.36

*: $P \leq 0.05$

Table 6.3. Exploration of stock-specific maternal effects in 2007 (a) and 2008 (b) based on multiple linear regression analyses. For data of a given year and stock, we fit three regression models using 1) length, 2) age, and 3) length and age as predictors, respectively. The signs and level of significance of the regression coefficients as well as R^2 of the model with both predictors are listed.

a. 2007 data

Stock	Predictors			R^2 of full model
	Length	Age	Length, Age	
Tittabawassee	+*	+	+,-	0.14
LBDN	-*	-*	-,-	0.08
VB	+*	+*	-,+*	0.41
Oneida	+*	+*	+*,+	0.10
Maumee	+*	+	+*,-*	0.09

b. 2008 data

Stock	Predictors			R^2 of full model
	Length	Age	Length, Age	
Tittabawassee	+	+	+,-	0.02
LBDN	-	-*	+,-*	0.13
VB	-	-	+,-	0.05
Oneida	+	-	+*,-*	0.03
Maumee	-	-	+,-	0.02

*: $P \leq 0.05$

Table 6.4. Within-stock temporal variation in egg size. Effect of year was estimated by fitting a multiple linear regression with year, female age, and length as predictors on the two-year data for each stock. Difference in mean egg size between years and level of significance for the temporal variation were estimated by inspecting the regression coefficients.

Stock	Year effect (2008 mean - 2007 mean)
Tittabawassee	* (0.108)
LBDN	* (0.043)
VB	n.s.
Oneida	* (-0.048)
Maumee	* (0.051)

*: $P \leq 0.05$; n.s.: $P > 0.05$

Figure list

Figure 6.1. Sampling locations of 2007 and 2008. Female walleye were collected from five populations: Tittabawassee River, Maumee and Sandusky Rivers (samples from the two rivers were combined for analysis), Little Bay de Noc, Van Buren Bay of Lake Erie, and Oneida Lake.

Figure 6.2. A dichotomous structure resulted from classification and regression tree (CART) analysis. The structure comprises seven terminal nodes formed from six partitions of egg size variation. The length of branches corresponds to relative amount of egg size variance reduced by a given partitioning. The values of terminal nodes represent mean egg size (in mg) of each group formed by the partitioning. For divisions based on a quantitative predictor, the group that proceeds to the left represents the fish that fits the logic statement; the groups formed based on a qualitative predictor are labeled with ovals. As the structure shows, among the predictors stock appears to explain relatively large variance of egg size. The inter-stock variation in egg size is LBDN > VB and Tittabawassee > Oneida > Maumee.

Figure 6.3. Structures from classification and regression tree (CART) analysis based on data in 2007 (a) and 2008 (b), respectively. Both structures showed that compared to the other predictors, stock explained a relatively large amount of variance of egg size. The grouping for inter-stock variation varied slightly between years. In 2007 egg size variation was: LBDN, VB, and Oneida > Tittabawassee > Maumee, while in 2008 egg size variation was: LBDN > VB and Tittabawassee > Oneida and Maumee.

Figure 6.4. Exploration of stock-specific maternal effects using data in 2007 (a) and 2008 (b) based on classification and regression tree (CART). For 2007 data, trees were constructed based on length cut-offs for Tittabawassee, Oneida, and VB, and were based on age cut-offs for LBDN and Maumee. In 2008, no generalizable patterns were found in the trees among stocks. The R^2 values were generally low for all stocks in both years, and for a given stock the R^2 values were slightly higher for data in 2007.

Figure 6.1

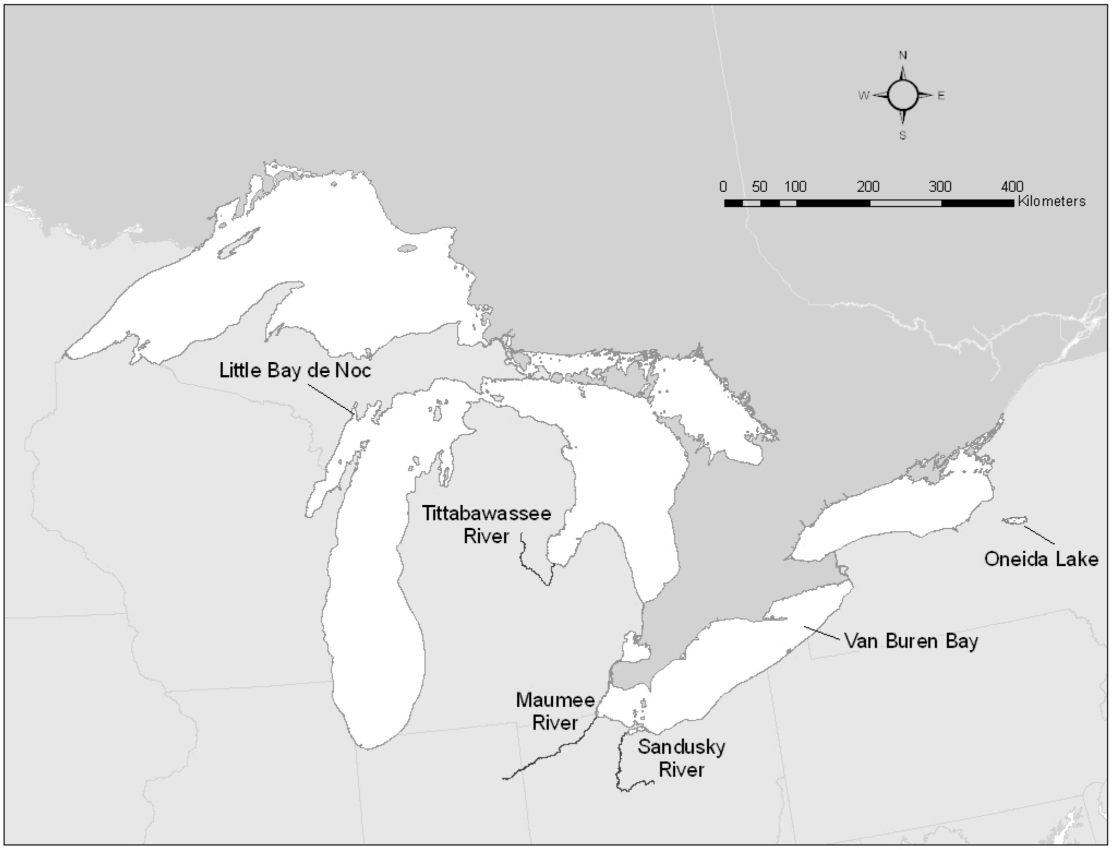

N
W
E
S
0
50
100
200
300
400
Kilometers
Little Bay de Noc
Tittabawassee River
Oneida Lake
Van Buren Bay
Maumee River
Sandusky River

Figure 6.2

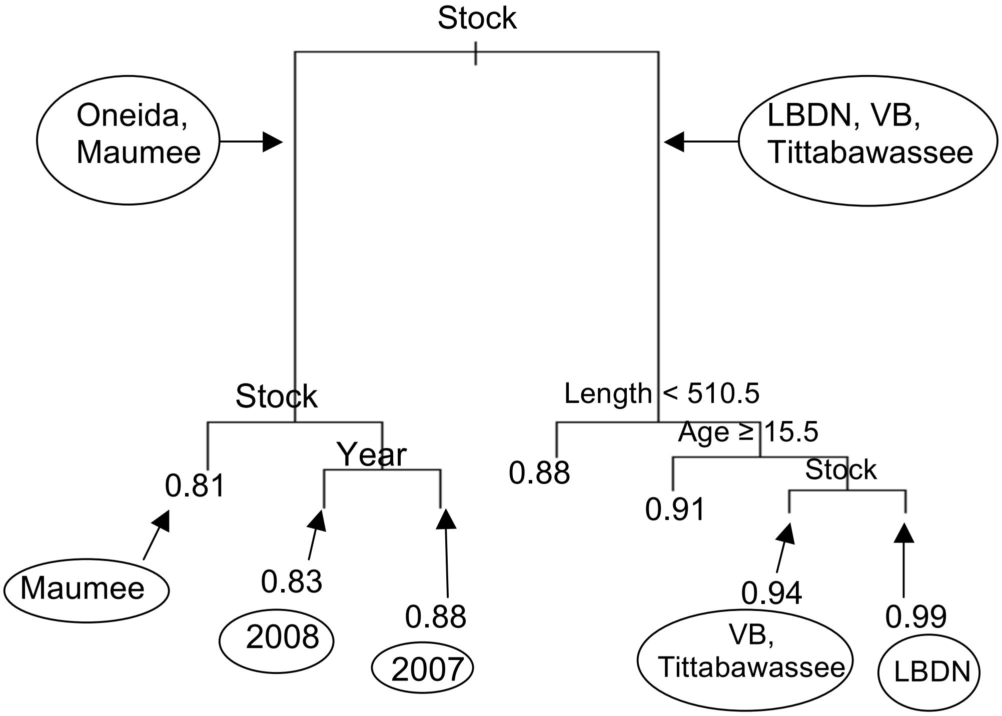
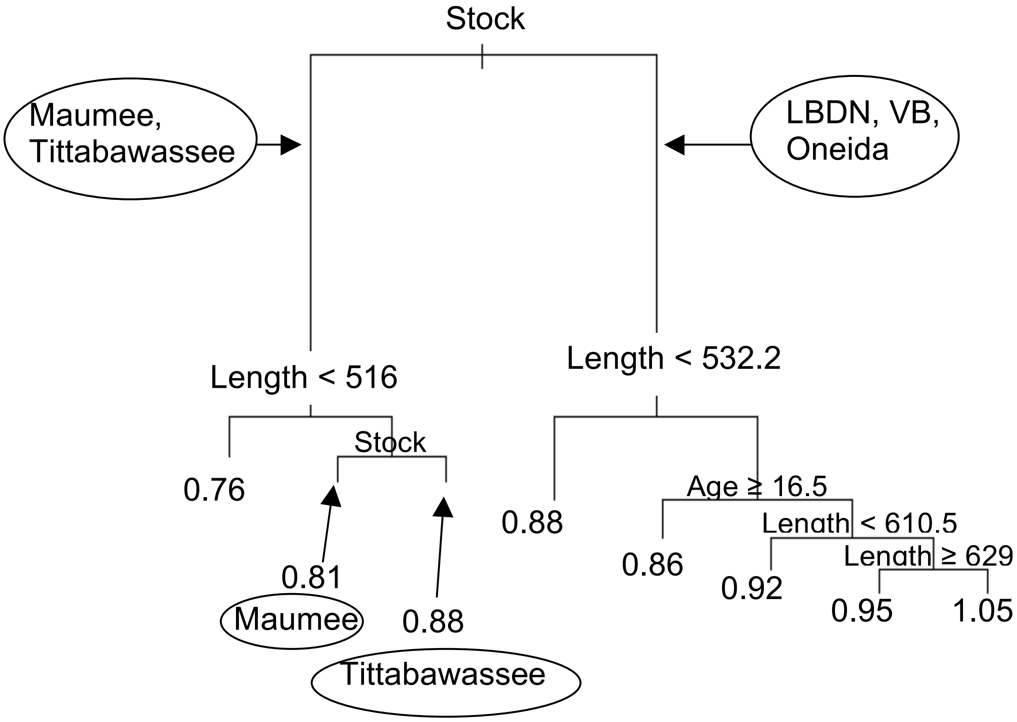

Stock
Oneida, Maumee
LBDN, VB, Tittabawassee
Stock
Length < 510.5
Age ≥ 15.5
Year
0.81
0.88
Stock
0.91
Maumee
0.83
0.94
0.88
0.99
2008
VB, Tittabawassee
2007
LBDN

Figure 6.3

a. 2007 data



b. 2008 data

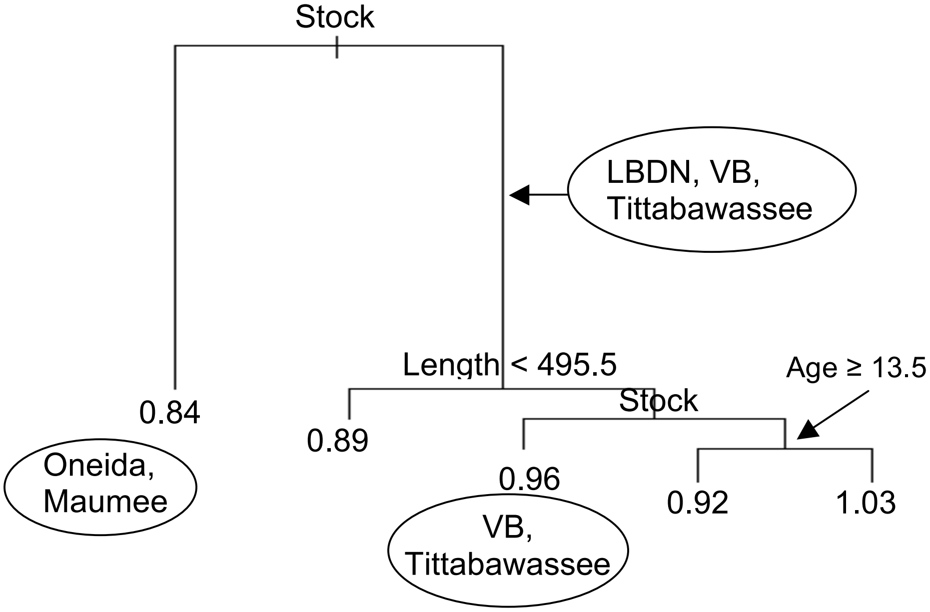
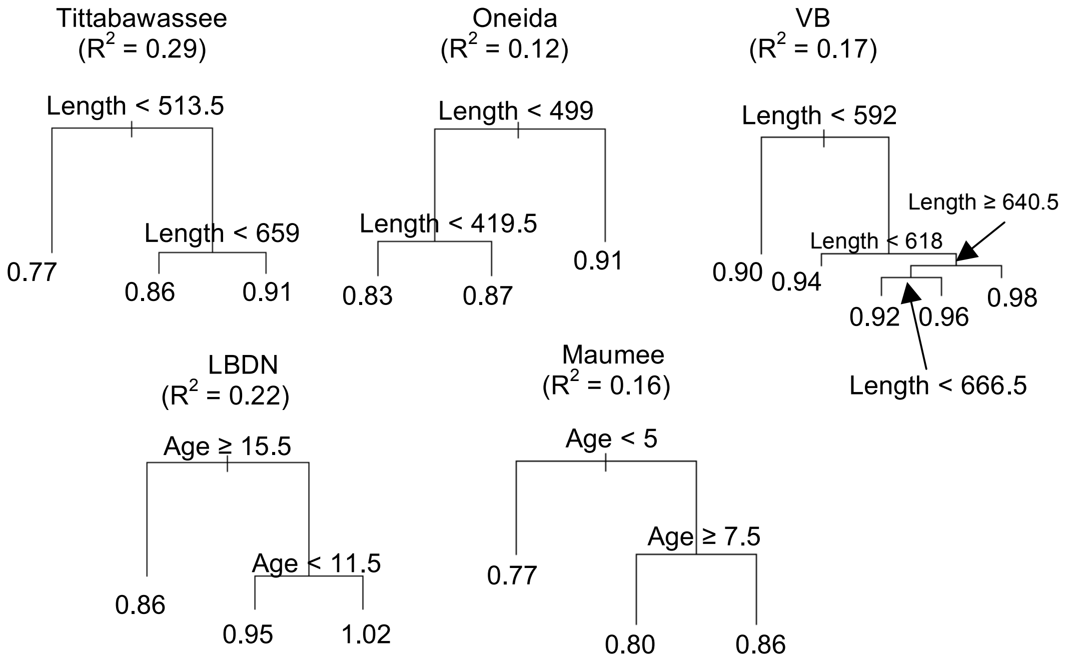
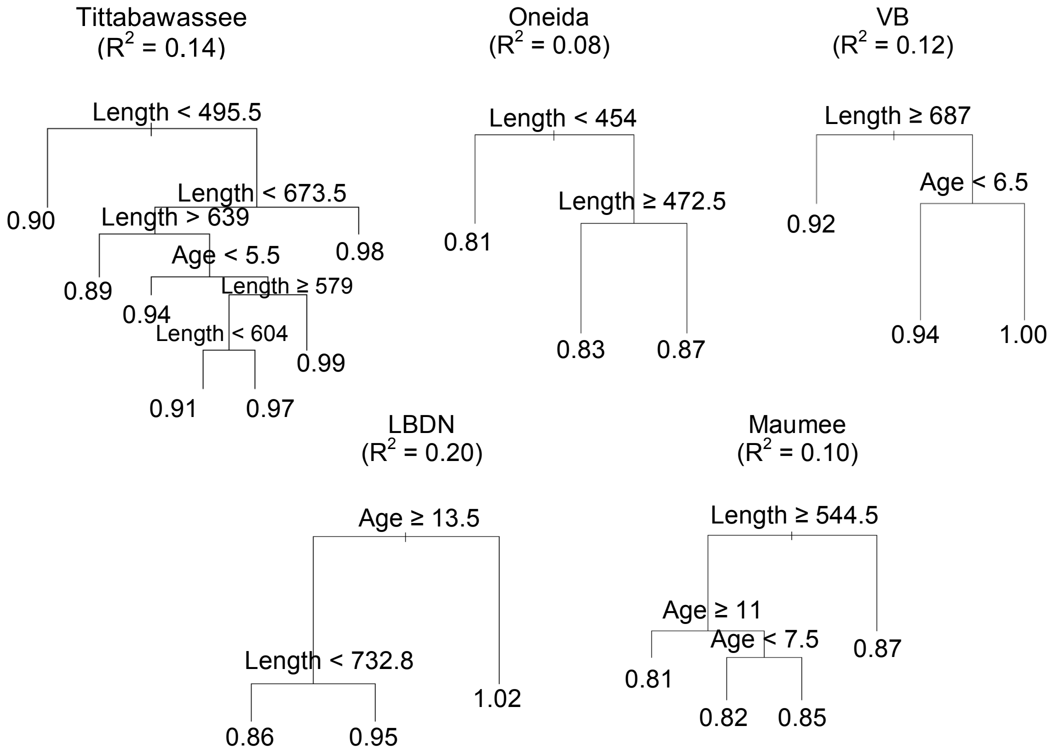

Stock
LBDN, VB, Tittabawassee
Length < 495.5
Age ≥ 13.5
Stock
0.84
Oneida, Maumee
0.89
0.96
VB, Tittabawassee
0.92
1.03

Figure 6.4

a. 2007 data

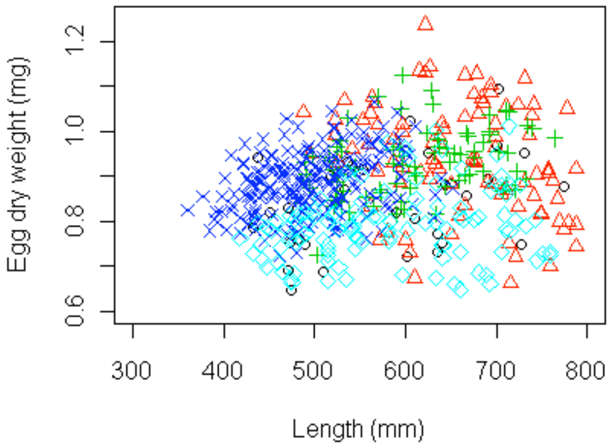


b. 2008 data

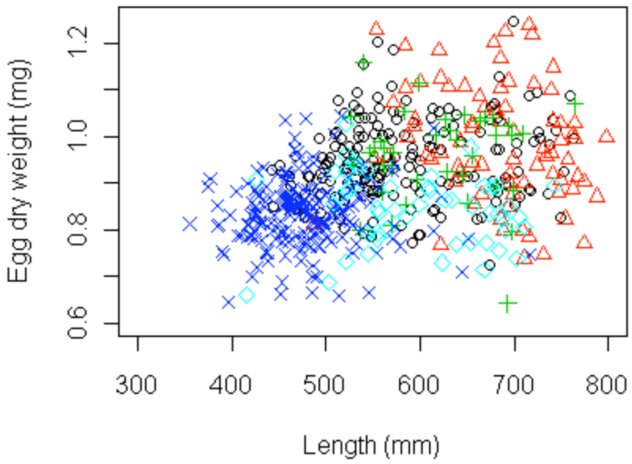

Tittabawassee
(R^2 = 0.14)
Length < 495.5
0.90
Length < 673.5
Length > 639
0.98
0.89
Age < 5.5
0.94
Length ≥ 579
Length < 604
0.99
0.91
0.97
Oneida
(R^2 = 0.08)
Length < 454
0.81
Length ≥ 472.5
0.83
0.87
VB
(R^2 = 0.12)
Length ≥ 687
0.92
Age < 6.5
0.94
1.00
LBDN
(R^2 = 0.20)
Age ≥ 13.5
Length < 732.8
1.02
0.86
0.95
Maumee
(R^2 = 0.10)
Length ≥ 544.5
Age ≥ 11
Age < 7.5
0.87
0.81
0.82
0.85

Appendix i. Egg size versus female length data in 2007 (A) and 2008 (B). Black circles: Titabawassee, red triangles: Little Bay de Noc (LBDN), green plus: Van Buren Bay (VB), navy blue crosses: Oneida, and cyan: Maumee.

A



B



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Chapter VII

Conclusion

Although life history traits generally have low heritability, there is increasing evidence that con-specific populations display potential adaptive variation in life history traits (e.g., maturation schedules and growth) over space and time. Further, as adaptive variation in life history traits may influence long-term population sustainability, it follows that it is important to consider such processes for natural resource management. For example, several authors suggest that size-selective fisheries harvest may induce genetic changes for an array of life history traits, potentially leading to adverse effects on fisheries. However, such evolutionary consequences of life history variation have not historically been taken into consideration for fisheries management.

I investigated plastic and potential adaptive variation in maturation schedules and egg size for lake whitefish and walleye in the Great Lakes. Using a combination of analytic and experimental approaches, I demonstrated that both lake whitefish and walleye displayed distinct maturation patterns among populations. And, these patterns may correspond to both potential plastic and adaptive processes and may be responsive to factors such as ecosystem changes and fishing intensity. I also evaluated robustness among different maturity indices to sampling-induced biases. Compared to common maturity indices (e.g., age and length at 50% maturity), probabilistic maturation reaction norms (PMRNs) were relatively unbiased regarding to sampling month and gear (but were sensitive to accuracy of maturity identification). Together, these results suggest the utility of PMRNs for monitoring maturation patterns.

In addition, I showed that egg size of walleye varied distinctly among different stocks, and suggested that a negative association between egg size and system primary productivity was related to potential adaptive influences. Because egg size may be critical to recruitment success, it is important to consider potential management-induced selection on egg size. For example, to achieve fisheries sustainability, management practices should avoid supplemental stocking if it will select for smaller eggs which are unsuitable in a nutrient poor habitat.

Lastly, I applied a generalized, eco-genetic individual based model to evaluate complex effects (both plastic and genetic) of fishing on life history variation. Given both plastic and adaptive influences on life history traits (based on results from analyses of maturation schedules of lake whitefish and walleye), the eco-genetic model delineates growth and maturation traits as a product of genetic variability and phenotypic plasticity. With designed fishing intensities and size-limits, model predictions were consistent with previous empirical and modeling studies. For example, at moderate to high fishing mortality rates, fisheries that target large fish could induce both plastic and genetic changes in individual maturation and growth rates and considerable changes in recruitment and population abundance. Moreover, effects of fishing likely will interact with environmental stochasticity to elevate variability in population responses (may be plastic or genetic). Once again, these results highlight the necessity to identify and consider adaptive life history variation for sustainable fisheries management.