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

Hui-Yu Wang, Tomas O. Höök, Mark P. Ebener, Lloyd C. Mohr, and Philip J. Schneeberger

Abstract: Fish maturation schedules 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 probabilistic maturation reaction norms (PMRNs; a metric that accounts for effects of growth and mortality). Collectively, these estimates indicated variation in maturation schedules between sexes (i.e., males tend to mature at younger ages and shorter lengths than females) and among systems (midpoint 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 (e.g., declines of the native amphipod, *Diporeia* spp.). 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.

Résumé : Les calendriers de maturation des poissons varient considérablement dans le temps et d'un système à un autre, ce qui reflète à la fois leurs réactions plastiques et adaptatives à la structure de l'écosystème, aux habitats physiques et à la mortalité (naturelle et due à la pêche). Nous examinons les calendriers de maturation des grands corégones (*Coregonus clupeaformis*) exploités commercialement dans les Grands Lacs laurentiens (lacs Michigan, Huron et Supérieur) en estimant les âges et les longueurs à 50 % de maturité, les ogives de maturité spécifiques à l'âge (probabilité d'être mature en fonction de l'âge) et les normes de réaction probalistes de maturation (PMRNs, une métrique qui tient compte de la croissance et de la mortalité). Dans leur ensemble, ces estimations indiquent qu'il y a une variation des calendriers de maturation entre les sexes (c'est-à-dire que les mâles tendent à arriver à maturité à un âge et une longueur inférieurs à ceux des femelles) et selon les systèmes (les estimations médianes des PMRNs sont plus basses au lac Michigan, intermédiaires chez les poissons du bassin principal du lac Huron et maximales chez les poissons de la baie Georgienne du lac Huron et ceux du lac Supérieur). À l'échelle temporelle, les accroissements récents de l'âge auquel 50 % des poissons sont matures dans les lacs Huron et Michigan peuvent représenter principalement des réactions plastiques à la diminution des taux de croissance associée aux changements dans les écosystèmes (par ex., le déclin des amphipodes indigènes *Diporeia* spp.). Puisque les changements plastiques et adaptatifs dans les calendriers de maturation peuvent survenir en même temps et nécessiter des attentions de gestion différentes, nous recommandons de faire une analyse concomitante de plusieurs indicateurs de maturation.

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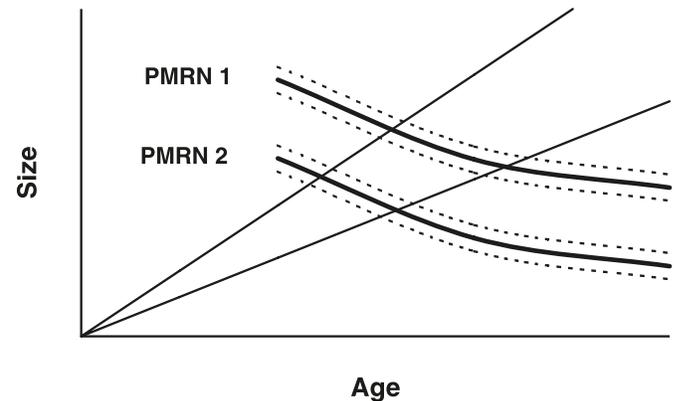Can. J. Fish. Aquat. Sci. Vol. 65, 2008

Introduction

Maturation schedules constitute key demographic attributes for fisheries management. Intraspecific 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 genetic and phenotypic 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 intraspecific temporal and spatial variation in maturation schedules of fish stocks is adaptively determined, as (*i*) maturation schedules influence yield and recruitment potential (Jensen 1981), (*ii*) selection-induced variation in life history traits may be difficult to reverse (Conover and Munch 2002), and (*iii*) as suggested by Olsen et al. (2004) for Atlantic 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). Intraspecific variation of maturation schedules of whitefish has been measured using traditional methods (i.e., age and length at 50% maturity; e.g., Beauchamp et al. 2004). However, such estimates can not 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 (PMRNs) 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. 2004*a*; Dieckmann and Heino 2007). PMRNs (usually expressed as a midpoint (at which probability of maturing = 0.5) with 95% confidence interval (CI)) represent individual variability within a population and characterize an intrinsic population-level expression of probability of maturation under different growth rates (Fig. 1; Dieckmann and Heino 2007; Kraak 2007). Conceptually, changes in growth rates (through either plastic or adaptive effects; Dieckmann and

Fig. 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 broken curves represent probability of maturing = 0.5 and 95% confidence interval (CI), 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).

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).

It should be noted that while conceptually maturation reaction norms allow for discrimination between genetic and environmental determinants of maturation, evidence demonstrating that PMRNs are solely genetically determined is lacking. In fact, studies have reached differential conclusions regarding the relative merit of using PMRNs to explore spatial and temporal variation in genetically determined maturation schedules (e.g., Kraak 2007; Morita and Fukuwaka 2007). Herein, we apply the PMRN concept to assess potential adaptive (and not genetic) responses in maturation schedules (Olsen et al. 2004; Dunlop et al. 2005). Given that we do not know the extent to which PMRNs reflect genetic variation, similar to other authors (e.g., Ernande et al. 2004) we use the term adaptive to describe changes in traits that arise from a combination of plastic and evolutionary processes.

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: (*i*) age and length at 50% maturity, (*ii*) midpoints of age-specific maturity ogives, and (*iii*) age-specific PMRN midpoints. The upper Great Lakes represent interesting systems to evaluate subtle, intraspecific variation in maturation schedules because they are large, interconnected water bodies where whitefish stocks may intermix and environmental and anthropogenic factors may influence maturation schedules of whitefish in relatively similar ways (i.e., there would likely be greater differences in environ-

Table 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.

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

Note: OMNR Lake Huron survey data are separated by main basin (MB) and Georgian Bay (GB).

mental 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 (Ebener et al. 2005; Nalepa 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 with fish in the other lakes, Lake Superior whitefish mature relatively late because of 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 data sets (from three sources; Table 1) that contain information on total length, sex, and maturation status of whitefish: (*i*) fishery-independent biological survey data from the Michigan Department of Natural Resources (MDNR) and Ontario Ministry of Natural Resources (OMNR) and (*ii*) 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 (Fig. 2) in Lake Michigan during April to October 1989–1993 using commercial trap nets (114.3 mm stretched mesh; Schneeberger et al. 2005) and in Lake Superior during May to October 1971–1996 using mostly large-mesh gill nets (114.3 mm stretched mesh) and, less frequently, graded-mesh gill nets (38.1–114.3 mm mesh in 12.7 mm increments). OMNR surveys (1979–2005) were primarily conducted in August (Georgian Bay) and June and September (southeast region (OH3 and OH4/5) of the main basin of Lake Huron; Fig. 2) using multipanel index gill nets (38.1–127.0 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; Fig. 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 (September–October)). 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 years), 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 gill nets (≥114 mm stretched mesh) or trap nets in the 1836-ceded waters of Lakes Michigan, Huron, and Superior (Fig. 2; Ebener et al. 2005). These data were primarily collected from May to November 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). Because of small sample sizes of immature fish in the commercial catches, a small percentage (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 gill nets of 50.8–152.4 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, unpublished data). While pooling data collected by different sampling gears

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Fig. 2. Sampling areas of (*i*) Chippewa Ottawa Resource Authority's Inter-Tribal Fisheries and Assessment Program (CORA–ITFAP; data from commercial catches and assessment programs) in 1836-ceded waters (outlined with black thick lines), (*ii*) Ontario Ministry of Natural Resources (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 (*iii*) Michigan Department of Natural Resources (MDNR) biological surveys in lake whitefish (*Coregonus clupeaformis*) 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.
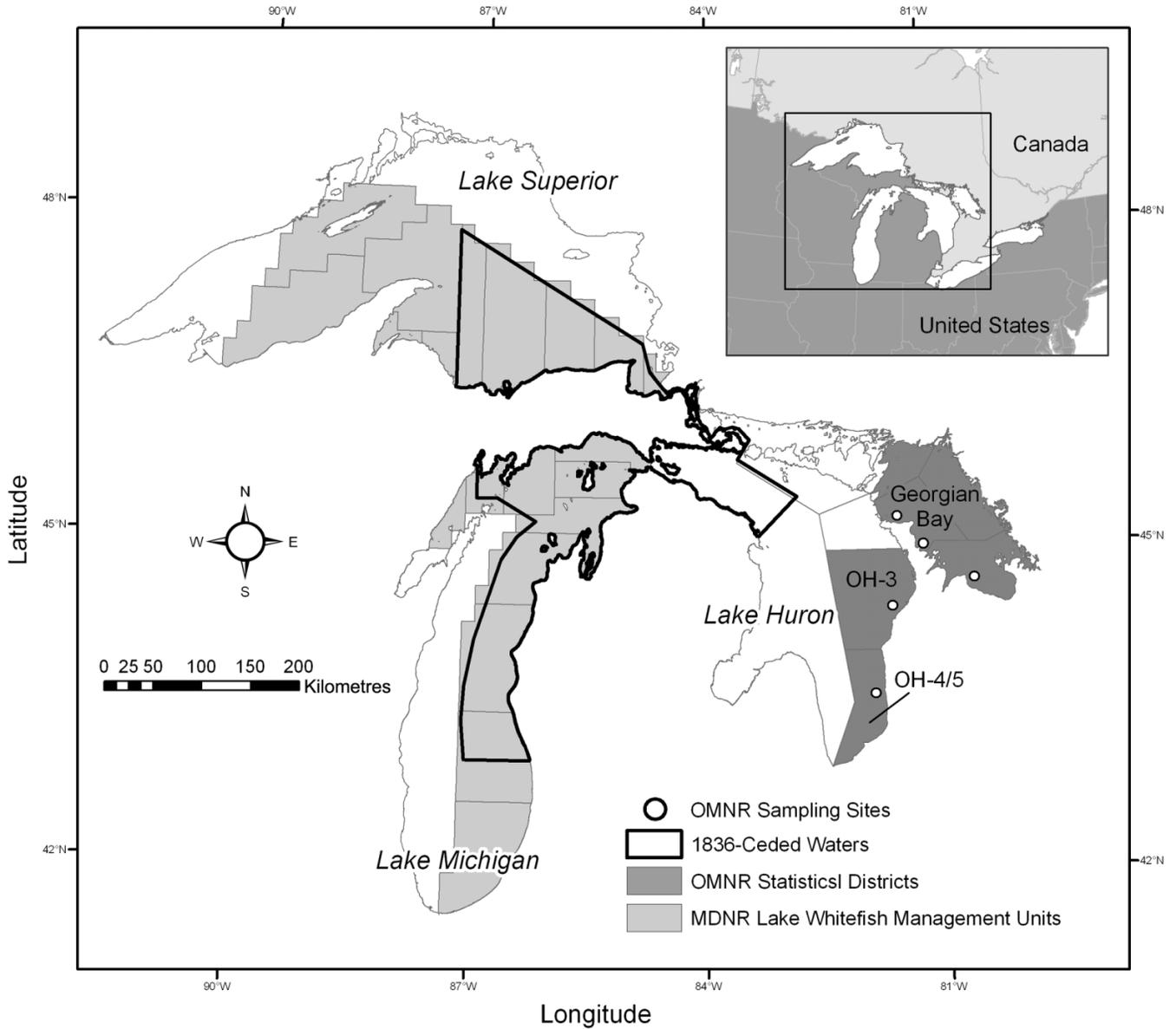
may bias length and age distributions, the effect of gear bias was minimized when estimating PMRN midpoints (described below), because this analytic procedure facilitates analyses of biased length and age distributions (Heino et al. 2002; Barot et al. 2004*a*, 2004*b*). All of the ITFAP samples from both commercial catches and assessment programs were aged using scales. While sex of mature fish was determined via external examination during the spawning season (October and November), sex of immature fish and sex and maturity status of fish sampled during nonspawning 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 October) 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; Fig. 2). The inclusion of data collected over a 6-month period could lead to potential biases related to (*i*) seasonal variation in size at age and (*ii*) 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 6-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 data set allowed us to conduct analyses based on subsets of fish collected during August to October. We found that estimates of age-specific maturity ogive and PMRN midpoints based on data from August to October were either not significantly different or slightly smaller than estimates based on data from May to October. 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, Fig. S1[3]).

To compare temporal changes in maturation schedules within each lake, we aggregated cohort-specific data into two groups: fish born during or before 1990 (before 1990 cohorts) and fish born after 1990 (after 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: (*i*) age and length at 50% maturity, (*ii*) midpoints of age-specific maturity ogives, and (*iii*) 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 data set, 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% CI of the A_{50} and L_{50} estimates were estimated using bootstrap techniques (Manly 1997). We randomly selected fish samples with replacement to generate 1000 sets of data, each of equivalent sample size as the original data set, and we fitted logistic regression on each of 1000 bootstrapped data sets to generate 1000 A_{50} and L_{50} estimates. The 95% CI of A_{50} or L_{50} was calculated as the sorted 25th (lower bound) and 975th (upper bound) values of the 1000 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% CI.

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:

$$(1) \qquad \text{logit}(o_a) = \ln\left(\frac{o_a}{1 - o_a}\right) = \beta_0 + \beta_1 \times L_a$$

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). The 95% CIs 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. (2004*a*, 2004*b*) to estimate midpoints of PMRNs. After estimating age-specific maturity ogives (from eq. 1), we then estimated the age-specific probability of maturing (*m*):

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

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*) describes 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 eq. 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. 2004*a*, 2004*b*). 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*, 2004*b*) 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 (2004*a*) 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 (eqs. 3 and 4):

$$(3) \qquad \text{logit}\,(m(L_a)) = \beta_0 + \beta_1 \times L_a$$

$$(4) \qquad \text{Lp}_{50,a} = -\frac{\beta_0}{\beta_1}$$

The 95% CIs of Lp$_{50,a}$ were estimated using bootstrap techniques. We generated 1000 bootstrapped data sets of

[3] Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3823. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

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Table 2. Age (A_{50}, years) and length (L_{50}, mm) at 50% maturity with (95% confidence interval (CI) in parentheses) of male and female lake whitefish (*Coregonus clupeaformis*) among the three upper Great Lakes based on (*i*) Ontario Ministry of Natural Resources (OMNR) and Michigan Department of Natural Resources (MDNR) surveys and (*ii*) Chippewa Ottawa Resource Authority's Inter-Tribal Fisheries and Assessment Program (ITFAP) data.

Lake	Male			Female		
	N	A_{50}	L_{50}	N	A_{50}	L_{50}
(*i*) Surveys						
Michigan	1546	2.8 (2.7, 2.9)	412 (407, 415)	1408	3.5 (3.4, 3.5)	456 (452, 461)
Huron (MB)	6952	4.2 (4.1, 4.3)	445 (442, 447)	6342	4.9 (4.8, 5.0)	484 (481, 487)
Huron (GB)	5999	4.0 (3.9, 4.1)	493 (489, 497)	5034	4.5 (4.5, 4.6)	538 (533, 543)
Superior	1044	5.3 (5.1, 5.4)	470 (463, 477)	982	5.9 (5.7, 6.1)	505 (497, 512)
(*ii*) ITFAP						
Michigan	7187	2.9 (2.7, 3.0)	410 (407, 412)	6728	3.4 (3.3, 3.5)	412 (409, 415)
Huron	9009	4.2 (4.1, 4.3)	415 (413, 417)	6421	5.1 (5.1, 5.2)	429 (427, 431)
Superior	5790	3.9 (3.8, 4.0)	414 (407, 419)	5119	4.5 (4.4, 4.6)	437 (432, 441)

Note: Estimates for Lake Huron based on OMNR survey data are separated by main basin (MB) and Georgian Bay (GB).

Table 3. Temporal variation (before vs. after 1990 cohorts) in age (A_{50}, years) and length (L_{50}, mm) at 50% maturity (with 95% CI in parentheses) of male and female lake whitefish (*Coregonus clupeaformis*) based on (*i*) Ontario Ministry of Natural Resources (OMNR) Lake Huron survey data in the main basin (MB) and Georgian Bay (GB) and (*ii*) Chippewa Ottawa Resource Authority's Inter-Tribal Fisheries and Assessment Program (ITFAP) data in the three upper Great Lakes.

Gender	Lake	Before 1990 cohorts			After 1990 cohorts		
		N	A_{50}	L_{50}	N	A_{50}	L_{50}
(*i*) OMNR							
Male	MB	4902	3.6 (3.5, 3.7)	443 (440, 445)	2050	5.5 (5.4, 5.7)	450 (445, 456)
	GB	3385	3.7 (3.6, 3.7)	483 (479, 488)	2614	4.7 (4.6, 4.8)	519 (510, 530)
Female	MB	4428	4.4 (4.3, 4.5)	489 (486, 492)	1914	5.8 (5.6, 5.9)	466 (461, 472)
	GB	2728	4.3 (4.2, 4.4)	532 (527, 538)	2306	5.1 (4.9, 5.3)	558 (544, 574)
(*ii*) ITFAP							
Male	Michigan	4388	2.7 (2.4, 2.9)	415 (411, 420)	2799	4.1 (3.9, 4.3)	406 (403, 409)
	Huron	3697	2.5 (2.2, 2.9)	412 (406, 417)	5312	5.3 (5.2, 5.3)	416 (414, 418)
	Superior	2946	3.9 (3.7, 4.1)	413 (402, 421)	2844	4.0 (3.8, 4.1)	418 (411, 424)
Female	Michigan	4003	3.1 (2.8, 3.2)	429 (425, 433)	2725	4.3 (4.1, 4.4)	403 (399, 406)
	Huron	2455	4.2 (4.0, 4.4)	444 (440, 449)	3966	5.7 (5.7, 5.8)	425 (422, 428)
	Superior	2639	4.6 (4.4, 4.7)	426 (415, 434)	2480	4.6 (4.5, 4.7)	446 (441, 451)

age a and age $a - 1$ (each of equal sample size as the original data set) and then generated 1000 estimates of $\text{Lp}_{50,a}$ (using eqs. 1–4). The 95% CI of $\text{Lp}_{50,a}$ was given as the sorted 25th (lower bound) and 975th (upper bound) value of $\text{Lp}_{50,a}$ 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

A_{50} and L_{50} 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 2). 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 2). 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 in 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 2).

Within-lake temporal changes were evident for both A_{50} and L_{50} values (Table 3). Most noteworthy, based on both survey and ITFAP data, A_{50} values in Lakes Huron and Michigan increased significantly from before 1990 to after 1990 cohorts. On the other hand, there

Fig. 3. Midpoints of age-specific maturity ogives ($L_{50,a}$; male (*a*) and female (*b*)) and probabilistic maturation reaction norms (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 Michigan Department of Natural Resources (in 1971–1996) and Ontario Ministry of Natural Resources (in 1979–2005) survey data sets. Error bars represent 95% confidence intervals (CIs). The labels of numbers represent significant interlake variation of age-specific estimates based on 95% CIs (i.e., if the 95% CIs 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.
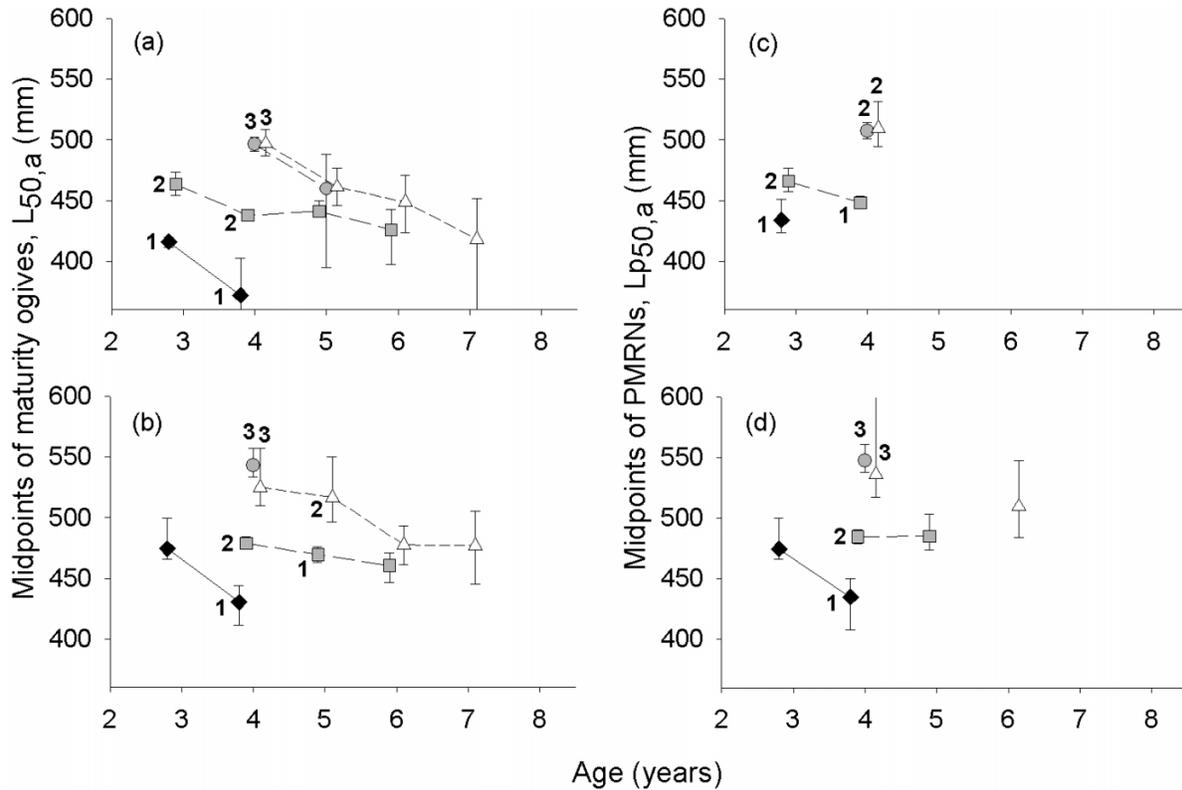
were no significant changes in A_{50} values for Lake Superior, and temporal trends of L_{50} values were inconsistent (Table 3).

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 interlake differences tended to be insignificant based on comparison of 95% CIs (CIs of estimates for older ages are relatively large because of fewer immature fish at older ages; Figs. 3*a*, 3*b*, 4*a*, 4*b*). Interlake comparisons were possible when age-specific $L_{50,a}$ and 95% CI were estimable for more than one lake. Based on survey data, $L_{50,a}$ estimates for Lake Michigan fish (for both sexes) were significantly lower than estimates for Lakes Huron and Superior (Fig. 3*a*, 3*b*). 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 ages 5–6 males and ages 4–6 females were significantly lower in Lake Michigan than in the other lakes (Figs. 4*a*, 4*b*). While differences between Lakes Huron and Superior were less pronounced, age 4 female $L_{50,a}$ was significantly greater for Lake Superior than for Lake Huron (Fig. 4*b*).

Temporal changes in $L_{50,a}$ estimates were minimal. However, based on OMNR survey data, $L_{50,a}$ estimates for ages 4–5 males in Lake Huron's main basin and age 4 males in Georgian Bay increased significantly from before 1990 to after 1990 cohorts (see supplemental material Fig. S2[3]). Also, based on ITFAP data, $L_{50,a}$ estimates for age-5 females in Lake Michigan decreased significantly from before 1990 to after 1990 cohorts while no significant temporal changes were observed in the other lakes (see supplemental material Fig. S3[3]).

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 ages 3–4 males and age 4 females), based on both survey (Figs. 3*c*, 3*d*) and ITFAP data (Figs. 4*c*, 4*d*). For both sexes, survey-based $Lp_{50,a}$ estimates showed that compared with fish in Lakes Huron and Superior, Lake Michigan fish matured at smaller lengths for a given age (Figs. 3*c*, 3*d*). Further, $Lp_{50,a}$ estimates for both males and females in the main basin of Lake Huron were smaller than

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Fig. 4. Midpoints of age-specific maturity ogives ($L_{50,a}$; male (*a*) and female (*b*)) and probabilistic maturation reaction norms (PMRNs, $Lp_{50,a}$; male (*c*) and female (*d*)) for lake whitefish (*Coregonus clupeaformis*) in Lakes Michigan, Huron, and Superior based on Inter-Tribal Fisheries and Assessment Program (in 1980–2003) data sets. Error bars represent 95% CIs. The labels of numbers represent significant interlake variation of age-specific estimates based on 95% CIs (e.g., CI of a lake labeled with "1,2" overlaps with CI of lake 1 and CI of lake 2, while CIs 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.
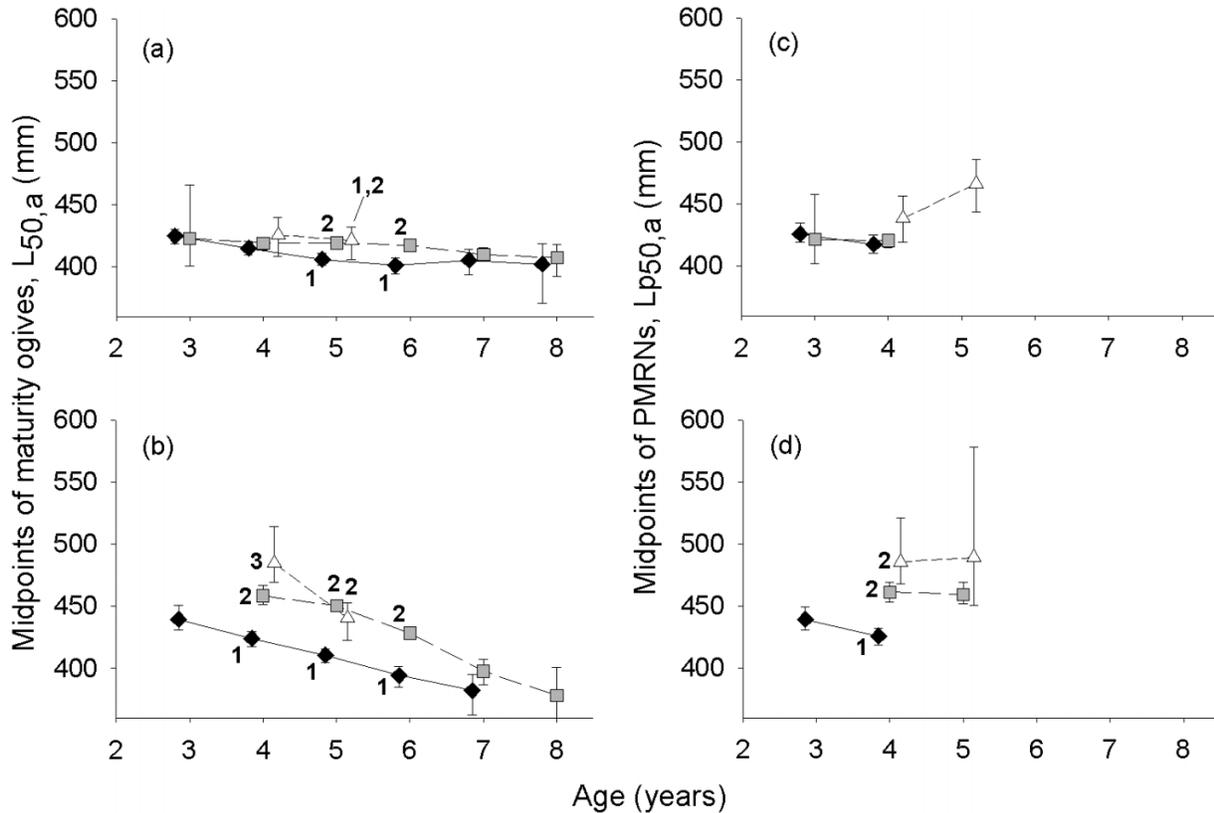
estimates for Georgian Bay, and there were no significant differences in $Lp_{50,a}$ estimates between fish in Georgian Bay and Lake Superior (Figs. 3*c*, 3*d*). While patterns were qualitatively similar based on ITFAP data, only $Lp_{50,a}$ for age 4 females differed significantly among lakes (Figs. 4*c*, 4*d*).

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 before to after 1990 cohorts (Figs. 5*a*, 5*c*). However, estimates for females in the main basin did not change significantly (Fig. 5*b*). 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 (Fig. 6).

Discussion

We demonstrate that maturation schedules of upper Great Lakes 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}), midpoints of age-specific maturity ogives ($L_{50,a}$), and PMRNs ($Lp_{50,a}$)) suggest that (*i*) intrinsic variation in maturation schedules exists between sexes (i.e., females tend to mature at older ages and larger sizes than males); (*ii*) 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 (*iii*) A_{50} increased significantly from before 1990 to after 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 trade-off 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 trade-off between reproduction and somatic growth), and therefore, one might expect that male whitefish should mature at relatively small sizes and early ages.

Fig. 5. Temporal (before and after 1990 cohorts) patterns (based on Ontario Ministry of Natural Resources survey data, 1979–2005) of midpoints of probabilistic maturation reaction norms (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% confidence intervals (CIs). The labels of numbers represent significant temporal variation of age-specific estimates based on 95% CIs. To facilitate visual inspection, estimates for before 1990 cohorts are slightly offset along *x* axis. Solid diamonds, before 1990 cohorts; open diamonds, after 1990 cohorts. The norms of $Lp_{50,a}$ for before and after 1990 cohorts are shown by connecting age-specific estimates with lines in different patterns.
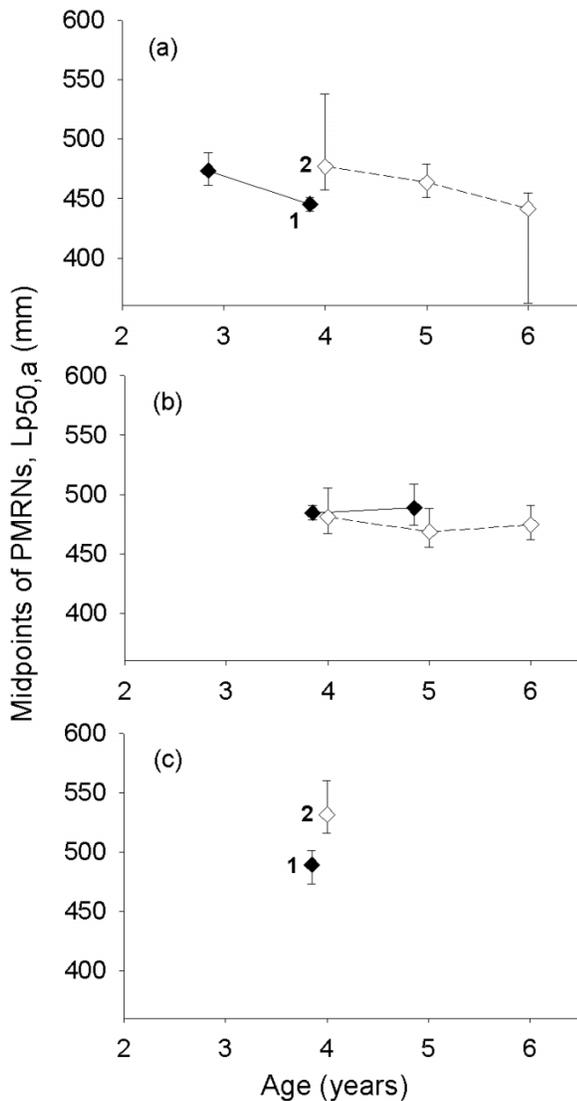
Spatial variation

Across-lake variation in $L_{50,a}$ values 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) owing 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 (*i*) the large geographic extent and heterogeneous habitats of the Great Lakes, (*ii*) spatially variable selection pressures within these lakes (Taylor et al. 1992), and (*iii*) potential reproductive isolation among substocks.

Temporal variation

Large increases in A_{50} of whitefish from before 1990 to after 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 interspecific 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 intraspecific, 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 (Schorfhaar 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 signifi-

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Fig. 6. Temporal (before and after 1990 cohorts) patterns (based on Inter-Tribal Fisheries and Assessment Program data, 1980–2003) of midpoints of probabilistic maturation reaction norms (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% confidence intervals (CIs). To facilitate visual inspection, estimates for before 1990 cohorts are slightly offset along *x* axis. Solid diamonds, before 1990 cohorts; open diamonds, after 1990 cohorts. The norms of $Lp_{50,a}$ for before and after 1990 cohorts are shown by connecting age-specific estimates with lines in different patterns.
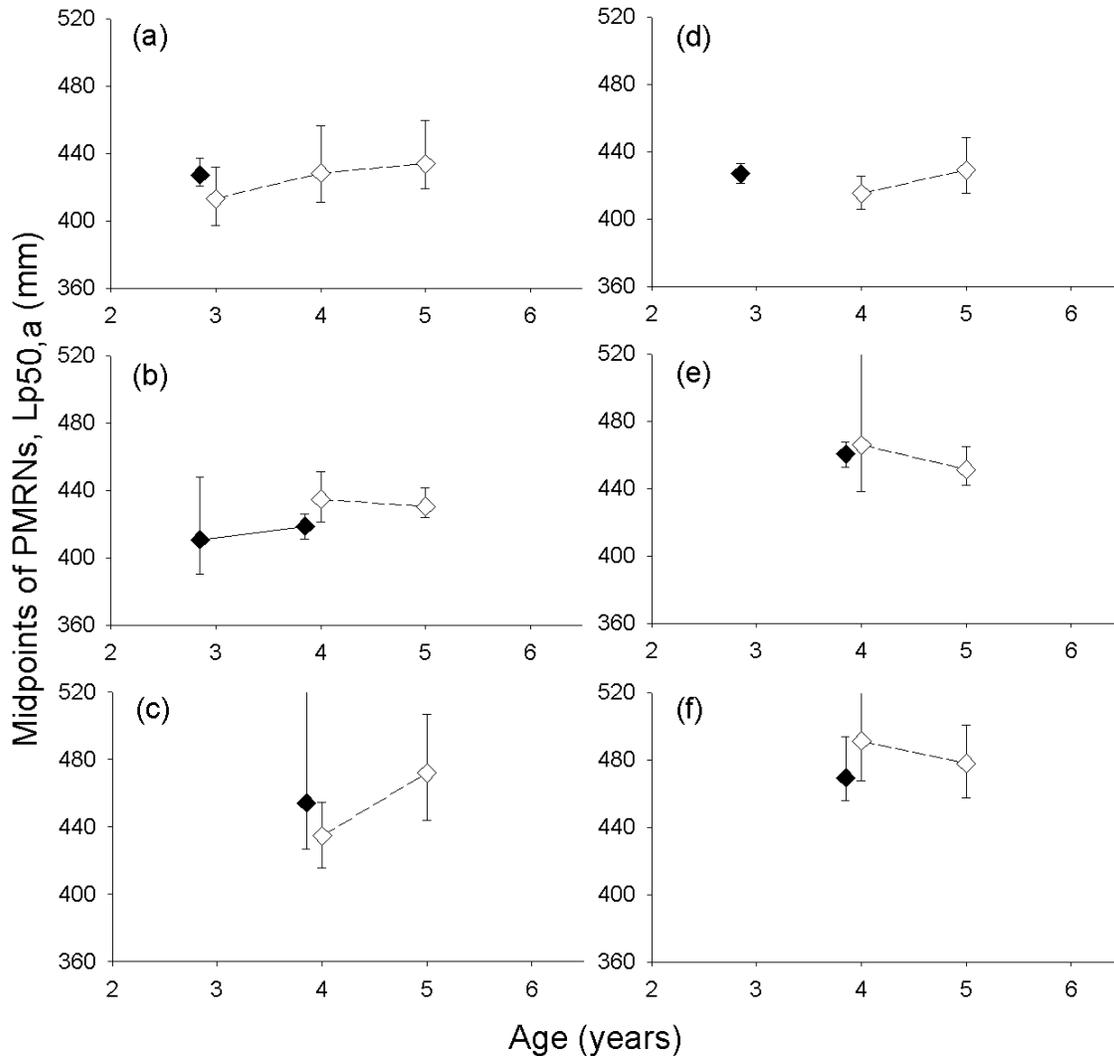
cant temporal variation in A_{50} estimates for Lake Superior whitefish.

Temporal changes in $L_{50,a}$ and $Lp_{50,a}$ 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 $Lp_{50,a}$ values for Lake Huron male fish did change from before 1990 to after 1990 cohorts. Relative to temporal trends in fisheries pressure, Lake Huron's ecosystem struc-

ture changed dramatically from before 1990 to after 1990 (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 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 age-specific measures ($L_{50,a}$ and $Lp_{50,a}$; 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 A_{50} and L_{50} 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, $L_{50,a}$ and $Lp_{50,a}$ 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 nongenetically determined, plastic variation of maturation schedules. We recommend that fisheries agencies should assess maturation schedules of fish stocks via these different maturation metrics to identify plastic and adaptive changes in maturation schedules that may occur simultaneously and require different management considerations.

In evaluating $Lp_{50,a}$ indices, 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 intraspecific, 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 $Lp_{50,a}$ values 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 because of 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 Figs. S4, S5[3]).

In addition, other partially genetically determined processes may influence the expression of maturation schedules. For example, recent studies suggest that growth rates may vary genetically within and between populations (Conover and Munch 2002; Walsh et al. 2006). As a result, variation in maturation schedules could be 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 intraspecific genetic variation in growth has minimal biasing effects on PMRN estimates.

While previous research has suggested that PMRNs may be used as a sign of potential evolved changes in maturation schedules (Olsen et al. 2004), this estimate alone does not unequivocally indicate local adaptation. Further, as suggested above, evidence demonstrating that PMRNs are solely genetically determined is lacking, and studies have reached differential conclusions regarding the relative merit of using PMRNs to explore spatial and temporal variation in genetically determined maturation schedules (e.g., Kraak 2007; Morita and Fukuwaka 2007). We suggest that PMRN analysis should be considered with growth, condition, and genetic evidence to explore adaptive changes in maturation schedules (Marshall and McAdam 2007). Also, explicit investigation of the ability of PMRN to reveal genetic variation would greatly benefit future PMRN analyses.

Data considerations and conclusions

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 percentage (58%) of fish collected in fall in Lake Michigan than in Lakes Huron (30%) and Superior (25%)). These seasonal distributions would suggest that $L_{50,a}$ and $Lp_{50,a}$ estimates for Lake Michigan could be positively biased (owing to additional growth during summer and fall). However, we observed the opposite (i.e., sex- and 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-, and 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. Because estimation of $L_{50,a}$ and $Lp_{50,a}$ is relatively robust to different sampling procedures (Heino et al. 2002) and invalid assumptions (e.g., adults and juveniles for given ages have the same growth increments; Barot et al. 2004a, 2004b), such differences in maturation indices between the two types of data could reflect agency biases, including the possibility that different agencies sample different whitefish substocks within a lake. However, our analyses based on different types of data led to the same qualitative conclusions regarding temporal and across-lake patterns of white-

fish maturation schedules, suggesting that maturation schedules may differ among Great Lakes whitefish stocks and that recent within-lake shifts in maturation schedules are primarily attributable to plastic processes.

Acknowledgements

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