

Reproductive life-history strategies in lake whitefish (*Coregonus clupeaformis*) from the Laurentian Great Lakes

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Abstract: Recent food-web changes in the Laurentian Great Lakes are affecting energy and nutrient allocation to lake whitefish (*Coregonus clupeaformis*) with potential downstream effects on egg condition and recruitment. We tested whether egg condition was conserved or varied with maternal condition in eight stocks from Lakes Erie, Michigan, and Superior. Egg condition was conserved across stocks based on (i) a lack of correlation between females and eggs for total lipid, DHA, and other essential fatty acids; (ii) higher levels of energy and long-chain polyunsaturated fatty acids (LC-PUFA) in eggs compared with females; and (iii) no among-stock differences for those same variables in eggs. Females from northern Lake Michigan generally made the greatest trade-offs between egg size and fecundity. Highly fecund females provisioned less lipid, but more n-3 LC-PUFA to their eggs. A lack of stock-level patterns in energy and nutrient allocation suggests that trade-offs occur at the level of individual females and that females in poor condition make greater trade-offs among egg size and fecundity, total lipids, and n-3 LC-PUFA than females in good condition.

Résumé : Des modifications récentes des réseaux trophiques dans les Grands Lacs laurentiens ont une incidence sur l'allocation d'énergie et de nutriments chez les grands corégones (*Coregonus clupeaformis*), incluant des effets en aval potentiels sur l'état des œufs et le recrutement. Nous avons tenté d'établir si l'état des œufs était conservé ou variait selon l'état d'embonpoint maternel au sein de huit stocks des lacs Érié, Michigan et Supérieur. L'état des œufs était conservé dans tous les stocks à la lumière (i) de l'absence de corrélation entre les femelles et les œufs sur le plan des lipides totaux, de l'ADH et d'autres acides gras essentiels, (ii) de niveaux plus élevés d'énergie et d'acides gras polyinsaturés à longue chaîne (AGPLC) dans les œufs que chez les femelles et (iii) de l'absence de variation au sein des stocks en ce qui concerne ces mêmes variables dans les œufs. Les femelles de la partie nord du lac Michigan sont celles qui présentaient les compromis les plus importants entre la taille des œufs et la fécondité. Les femelles très fécondes transféraient moins de lipides, mais plus d'AGPLC n-3 à leurs œufs. L'absence de tendance en matière d'allocation d'énergie et de nutriments à l'échelle des stocks donne à penser que les compromis s'exercent à l'échelle individuelle chez les femelles et que les femelles en mauvais état d'embonpoint font de plus grands compromis entre la taille des œufs et la fécondité, les lipides totaux et les AGPLC n-3 que les femelles en bon état. [Traduit par la Rédaction]

Introduction

Lake whitefish (*Coregonus clupeaformis*) support important commercial, recreational, and aboriginal subsistence fisheries throughout the Laurentian Great Lakes. From 1995 to 2005, lake whitefish growth and body condition declined precipitously in northern Lake Michigan (Pothoven et al. 2001; Madenjian et al. 2002), Lake Huron (Modeling Subcommittee – Technical Fisheries Committee 2005), and Lake Ontario (Lumb et al. 2007). In contrast, growth and condition of lake whitefish in Lakes Erie and Superior remained stable during that same period (Cook et al. 2005; Kratzer 2006). Biologists initially hypothesized that declines in lake whitefish growth and condition in Lakes Huron and Michigan were caused by recent food-web restructuring, including loss of the native lipid-rich amphipod *Diporeia* (Nalepa et al. 2005), and subsequent diet shifts to inferior quality prey, such as non-native dreissenid

mussels (Pothoven 2005; McNickle et al. 2006; Rennie et al. 2009). By 2005, *Diporeia* were nearly extirpated from northern Lake Michigan (Nalepa et al. 2009), but their abundance remained stable in Lake Superior (Fig. 1). *Diporeia* abundance has historically been insufficient to support lake whitefish predation in Lake Erie. These contrasting environments experienced by lake whitefish in the Laurentian Great Lakes provide an opportunity to explore the consequences of variable maternal conditions on relative reproductive investment, which is the focus of this paper.

Lake whitefish are intermediate between *r*- and *k*-selected species, characterized by delayed sexual maturation, iteroparity, high fecundity, large adult body size, and a long life-span (Winemiller and Rose 1992). Stochastic environmentally induced variation in early survival may play an important role in the observed interannual recruitment variation in addition to variation

Received 9 May 2013. Accepted 5 April 2014.

Paper handled by Associate Editor Jordan Rosenfeld.

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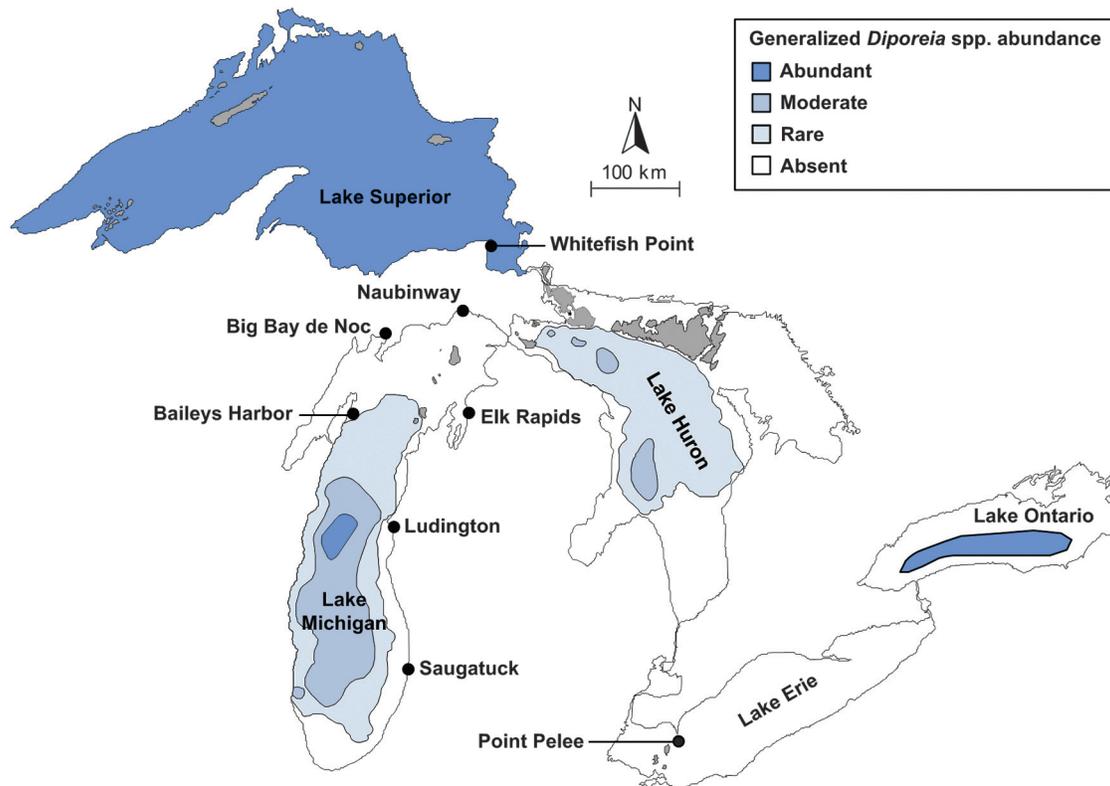
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Fig. 1. Sampling sites for gravid female lake whitefish and their eggs in Lakes Michigan, Superior, and Erie. Generalized *Diporeia* spp. abundance data for Lake Michigan were adapted from Nalepa et al. (2009) and for the other lakes from United States Environmental Protection Agency (2009); no data for Georgian Bay.



in total reproductive output (Lawler 1965; Freeberg et al. 1990; Brown et al. 1993). Eggs with a small amount of low-density yolk are produced in large numbers to compensate for low larval survival (Hjort 1914). A common reproductive trade-off in fishes is between egg size and number (i.e., fecundity) (Hutchings 1991; Winemiller and Rose 1993; Kamler 2005). Egg size is positively linked to survival in many fishes, with larger larvae often hatching from larger eggs and having higher survival than those hatching from smaller eggs (Hutchings 1991; Winemiller and Rose 1993). Large larvae and age-0 juveniles have greater resistance to starvation (Miller et al. 1988; Trippel et al. 1997; Keckeis et al. 2000), better ability to ingest larger prey (Teska and Behner 1981; Miller et al. 1988; Freeberg et al. 1990), increased growth rates (Gutreuter and Anderson 1985; Hurst and Conover 1998), reduced predation rates (Cushing 1982; Miller et al. 1988), and increased winter survival (Rice et al. 1987a, 1987b; Pangle et al. 2004) compared with smaller larvae. Larval size-at-hatch is directly linked to egg condition (Kamler 1992, 2005); therefore, it is an important determinant of survival during these critical early mortality periods and thus a key driver of recruitment.

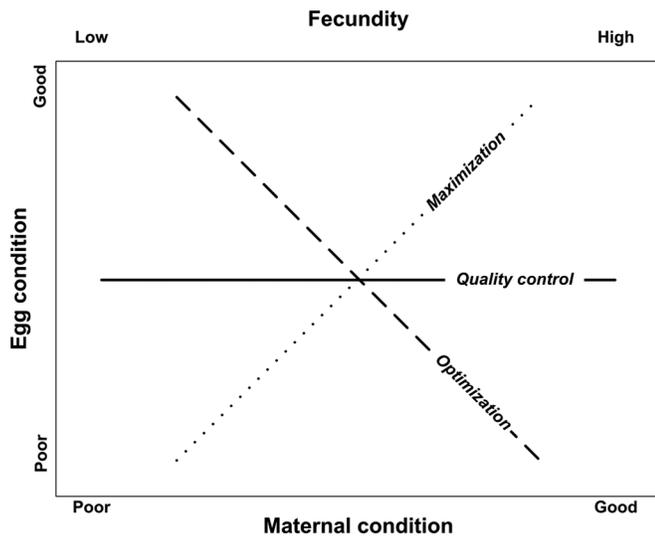
Trade-offs among the various energetic and nutritional constituents provisioned to eggs versus those retained to support female somatic growth also affect recruitment for many temperate freshwater fishes (Kamler 2005), including lake whitefish (Brown and Taylor 1992). For example, different fatty acids (FAs) have been linked to metabolism and membrane transport (Olsen 1999), neuronal development (Bell and Sargent 1996), anabolic processes, growth, and reproduction (Bell and Sargent 1996; Sargent et al. 1999), immune responses (Arts and Kohler 2009), and survival (Kelly and Kohler 1999; Pangle et al. 2004; Glencross 2009). Therefore, changes in diet, such as the loss of a lipid-rich prey (i.e., *Diporeia* spp.) that affect maternal condition may have fitness consequences that ultimately affect recruitment. The realized conse-

quences, however, will depend on how these changes influence natural mortality and how female lake whitefish adjust reproductive investment in eggs, especially when resources are limited. Our study focused on reproductive strategies relating to the provisioning of eggs with energy and nutrients, rather than total reproductive investment because of the strong influence of egg condition (i.e., size, energy, and nutrients) on survival and recruitment in intermediate *r*- and *k*-selected species.

Le Cren (1951) suggested that the seasonal patterns of energy and nutrient allocation between growth and reproduction in mature females are a function of their nutritional condition and body size. Consistent with Kamler's (2005) parental-effects model, this "Reproductive Maximization Hypothesis" proposes that females maximize their reproductive investment to the extent possible given their available resources. That is, the condition and number of eggs produced by a female reflects her biological condition. For example, females in poor condition (e.g., high muscle moisture content and low lipid or essential FA content, or both) will have minimal energy and nutrients available for reproduction and will, therefore, produce few, low-condition eggs (e.g., small size, high moisture content, low lipid or essential FA content, or both). This hypothesis predicts that egg number and condition should reflect maternal condition and, in particular, egg number, and condition variables will be positively correlated with maternal condition variables within and among stocks (Fig. 2). Under this hypothesis, if female condition falls below a level that could support reproduction, natural mortality would increase substantively and recruitment failure could occur. In addition, a corollary of this hypothesis is that the magnitude of variation in condition metrics for females and their unfertilized eggs should be similar (i.e., positively correlated).

Alternatively, the "Reproductive Quality Control Hypothesis" postulates that egg condition (i.e., quality) is conserved across

Fig. 2. Relationships among egg and maternal condition (i.e., proximate and lipid composition) and fecundity (i.e., egg number) predicted by the Maximization, Quality Control, and Optimization reproductive hypotheses.



variable environments through thresholds for key energetic and nutritional constituents provisioned to the egg during gametogenesis, below which egg viability is compromised. This hypothesis predicts that individual females will maintain high egg condition through trade-offs among fecundity, egg size, and the various energetic and nutritional constituents provisioned to the developing eggs versus energy and nutrients retained to support female somatic growth (Fig. 2). In this sense, trade-offs represent a compromise in energy and nutrient allocation between individual female growth and survival and the maintenance of egg condition above some threshold level required for successful reproduction (Tocher 2010). Because trade-offs occur at the level of the individual female, this hypothesis predicts both minimal population-level variation in egg condition compared with variation in female condition and inconsistent relationships between egg condition and maternal body condition within and among stocks. Resource-limited females may be able to meet the demands for essential long-chain polyunsaturated fatty acids (LC-PUFA) by developing fewer eggs (i.e., reduced fecundity). Docosahexaenoic acid (22:6n-3; DHA), one type of LC-PUFA, is critical for embryonic neuronal development and cell membrane fluidity (Arts and Kohler 2009), which influences cold tolerance (Kelly and Kohler 1999). Eggs of some fishes require a threshold level of DHA and other essential FAs to be viable (Adams 1999), but the levels required vary by species and are not yet well defined for freshwater fishes (Tocher 2010).

The Reproductive Quality Control Hypothesis, if true, also predicts that changes in fish condition may not strongly influence recruitment dynamics because of compensatory regulation of egg condition, particularly if the hypothesis that total reproductive investment (i.e., egg quality, egg size, and fecundity) is not strongly linked to female condition is also true. That is, if the Reproductive Quality Control Hypothesis is true, minimum egg condition will be maintained at the expense of individual female condition and fecundity, or some combination of these outcomes, and the potential effects of reduced fecundity on recruitment will be compensated for by a higher probability of survival for adequately provisioned eggs compared with greater numbers of poorly provisioned eggs. Total reproductive investment could become decoupled from female body condition when current reproduction is prioritized and environmental conditions are favorable (i.e., lots of food).

A third potential reproductive strategy, the “Reproductive Optimization Hypothesis”, is that individual females will optimize reproductive investments on the basis of current environmental conditions. For example, when environmental conditions are favorable, females will be in good condition and, therefore, may invest relatively less energy into current reproduction because the likelihood of offspring survival and future adult reproduction is high. By contrast, when environmental conditions are unfavorable, females will be in poor condition and, therefore, may invest relatively more into current reproduction because the chance of surviving to reproduce again is low and to better provision offspring in a harsh environment. Thus, a directed, population-level response to environmental gradients is predicted and, therefore, a negative correlation between egg condition and maternal condition within and among stocks (Fig. 2). This pattern of resource allocation is exactly opposite that predicted by the Reproductive Maximization Hypothesis.

The objectives of this study were to (1) determine whether lake whitefish are primarily using a “Maximization”, “Quality Control”, or “Optimization” reproductive strategy and (2) compare spatial patterns of variation in gravid female condition and the condition of their unfertilized eggs among lake whitefish stocks in Lakes Michigan, Superior, and Erie that have experienced contrasting changes in prey abundance. Identifying which reproductive strategy lake whitefish use and whether strategies differ among individuals and stocks might facilitate a better understanding of reproductive consequences associated with ongoing food-web restructuring and shifts in lake whitefish dynamics in the Laurentian Great Lakes. This knowledge may assist managers to appropriately respond to changes in lake whitefish condition when developing harvest strategies and management plans and to provide general insights into how environmental influences on maternal condition affect trade-offs related to investment in egg condition.

Methods

Fish collections

Gravid female lake whitefish were collected during fall 2004 and 2005 from six sites in Lake Michigan, one site in Lake Superior, and one site in Lake Erie using a combination of commercial trap nets and gill nets (Fig. 1). Sampling was undertaken on or adjacent to known spawning locations. For that reason, each sampling location was assumed to be a stock (VanDeHey et al. 2009; Ebener et al. 2010), defined as a subset of the population that spawns together.

Upon capture, lake whitefish were examined to determine their sex and reproductive state. Thirty pre-ovulatory females (i.e., not freely expelling eggs when pressure was applied to the abdomen) were placed live in a 100 L holding tank and transported to shore where total length (± 1 mm) and wet mass (± 1 g) were recorded for each individual. Muscle tissue represents the greatest mass of fish tissue, is used to supply critical phospholipids when triacylglyceride reserves are depleted, is a good source of omega-3 (n-3) FAs (Arts and Kohler 2009), and is the main energy source for coregonid gonad formation (Dabrowski 1982, 1983). Therefore, muscle tissue is a practical tissue for use as a conservative, long-term indicator of fish health and condition. Two skinless, dorsal muscle plugs were collected approximately 5 mm anterior to the dorsal fin of each fish and used for proximate composition and lipid analyses. Both gonads were removed from each female and wet mass was recorded (± 1 g). Three 5 g subsamples from the anterior, mid, and posterior of the left ovary were preserved in Gilson’s fluid prior to fecundity, egg size, and egg mass measurements. Two other ovary subsamples, as well as the dorsal muscle plugs, were flash-frozen on dry ice (-50 °C) and transferred to a -80 °C cryo-freezer until proximate composition and FA analyses.

Table 1. Definitions of condition variables measured from gravid female lake whitefish and their unfertilized eggs from Lakes Michigan, Erie, and Superior.

Variable	Symbol	Unit	Description
Total length	L_t	mm	Distance from the tip of the premaxilla to the tip of the caudal fin when the tail is compressed
Wet mass	M_w	g (females); mg (eggs)	Measured using an electronic digital scale
Dry mass	M_D	g (females); mg (eggs)	Measured using an electronic digital scale after oven drying at 40 °C for 24 h
Gonad mass	M_G	g	Mass of both ovaries measured using an electronic digital scale
Soma mass	M_s	g	$M_w - M_G$
Relative mass	M_r	—	Calculated for females according to Rennie and Verdon (2008)
Fecundity	F	—	Total number of eggs per female
Relative fecundity	F_R	Eggs·g ⁻¹	F/M_w
Gonadosomatic index	GSI	—	M_G/M_s
Total protein	N	%	% N × 6.25
Moisture content		% Muscle	[(wet mass – dry mass)/wet mass] × 100
Energy density		J·g dry mass ⁻¹	Measured by calorimetry on 0.5 g dried muscle tissue homogenates
Total lipid		% Dry mass in muscle or eggs	Mean for two replicates
Total fatty acids	FA	µg FAME·mg dry mass ⁻¹ (of tissue extracted)	Mass fraction of all 37 fatty acid methyl esters (FAME) measured
Unsaturation index	UI	—	$\sum_{i=1}^n (\text{proportion of fatty acid}_i \times \text{number of double bonds of fatty acid}_i)$; Wagner et al. (2010)
Σ n-3		µg·mg dry mass ⁻¹	Total mass fraction of n-3 fatty acids (i.e., α-linolenic acid (ALA), eicosatrienoic acid, eicosapentaenoic acid (EPA), docosapentaenoic acid (DPA), and docosahexaenoic acid (DHA))
Σ n-6		µg·mg dry mass ⁻¹	Total mass fraction of n-6 fatty acids (i.e., linolelaidic acid, linoleic acid (LNA), γ-linolenic acid, homo γ-linolenic acid, and arachidonic acid (ARA))
Σ PUFA		µg·mg dry mass ⁻¹	Total mass fraction of polyunsaturated fatty acids (i.e., carbon chain that has more than one double or triple bond per molecule)
Σ MUFA		µg·mg dry mass ⁻¹	Total mass fraction of monounsaturated fatty acids (i.e., carbon chain that has one double or triple bond per molecule)
Σ SAFA		µg·mg dry mass ⁻¹	Total mass fraction of saturated fatty acids (i.e., carbon chain has no double bonds between carbon atoms)
DHA/ARA		—	Ratio of the DHA to ARA mass fraction
EPA/ARA		—	Ratio of the EPA to ARA mass fraction
Egg diameter	D	mm	Mean diameter of 90 eggs sampled from anterior, mid, and posterior gonad

Indices of maternal and egg condition

We quantified four reproductive variables and 21 variables that have previously been linked to fish condition (Wootton 1979; Rennie and Verdon 2008; Wagner et al. 2010) from gravid female lake whitefish (Tables 1 and 2). We also quantified 20 variables to describe egg condition (i.e., size and quality; Kamler 2005; Tocher 2010; Tables 1 and 3) for egg samples collected from the gravid females. These variables, described below, included general indices of fish health as well as direct measures of proximate and lipid composition (see Table 1 for list of variables and their definitions).

Maternal body condition

Body condition of gravid females was quantified using a relative mass relationship: $M_r = (M_w \cdot M_s^{-1}) \times 100$, where M_w was the measured wet mass, and M_s was the length-specific mean mass of a mature female calculated from 385 North American lake whitefish populations (Rennie and Verdon 2008).

Fecundity and egg size

The total number of eggs per female (i.e., fecundity) and their size (i.e., egg diameter and wet and dry mass) were estimated for each female using anterior, mid, and posterior ovary subsamples. After the Gilson’s fluid had broken down the connective tissue, samples were decanted, rinsed, and strained. Egg diameter was measured on digital images for 30 eggs from each subsample using Northern Eclipse digital imaging software (Empix Imaging, Inc., Mississauga, Ontario), and mean egg diameter was calculated for each female. From each subsample, 200 eggs were removed, measured for wet mass (±1 g), and dried in a drying oven for 24 h at 40 °C to obtain egg dry mass.

Proximate composition, lipids, and FAs of females and their eggs

Moisture content, energy density, and protein content of gravid female muscle tissue and eggs were estimated using standard Association of Official Analytical Chemists procedures (Helrich 1990) and according to the methods described by Muir et al. (2010). Briefly, moisture content was determined after oven drying for 24 h at 40 °C and reweighing samples to the nearest 0.0001 g until a constant mass was achieved. Energy density of 0.5 g dried tissue homogenates was measured by bomb calorimetry, and the enthalpy of hydrocarbon fuel combustion (±0.0001 °C) was measured (J·g dry mass⁻¹). Nitrogen was measured by combustion and converted to protein equivalents (Helrich 1990; Kamler 1992). Total lipid (dry mass basis) and a standard suite of 37 fatty acid methyl esters (µg FAME·mg dry mass⁻¹) of females and their eggs were analyzed in three steps: gravimetric extraction, derivitization, and quantification on a gas chromatograph. The specific methods used for total lipid and FA analyses are given by Zellmer et al. (2004) and Arts et al. (2012), respectively.

Of the 37 FAME measured, we focused on those known to have physiologically substantial functions in fishes (Adams 1999; Arts and Kohler 2009; Parrish 2009). Fatty acids studied included DHA, EPA (eicosapentaenoic acid; 20:5n-3), LNA (linoleic acid; 18:2n-6), and ALA (α-linolenic acid; 18:3n-3). The n-6 FAs, especially ARA (arachidonic acid; 20:4n-6), have been associated with nearshore food webs, including benthic prey (Kuusipalo and Käkälä 2000) and exotic mussels (*Dreissena* spp.; Newton et al. 2013). By contrast, LC-PUFA (such as DHA and EPA; ≥20 carbons (C) and ≥3 double bonds; also referred to as HUFA) are abundant in prey, such as *Mysis diluviana* and *Diporeia*, typically occurring in the offshore

Table 2. Mean \pm standard error for condition variables measured on gravid female lake whitefish collected from Lakes Michigan, Erie, and Superior.

Variable	Michigan						Erie	Superior
	Naubinway	Big Bay de Noc	Elk Rapids	Bailey's Harbor	Ludington	Saugatuck	Point Pelee	Whitefish Point
<i>n</i>	60	60	60	47	30	40	34	53
<i>L_t</i>	483.33 \pm 3.67	518.43 \pm 4.09	500.22 \pm 5.14	552.21 \pm 5.07	542.8 \pm 5.27	527.4 \pm 4.31	538.06 \pm 9.3	593.09 \pm 9.25
<i>M_w</i>	988.87 \pm 28.47	1271.37 \pm 36.85	1179.63 \pm 46.15	1587.46 \pm 49.19	1642.56 \pm 50.49	1479.7 \pm 37.76	1777 \pm 108.35	2266.15 \pm 134.91
<i>M_G</i>	143.77 \pm 6.44	202.27 \pm 8.93	171.66 \pm 10.44	263.53 \pm 12.49	238.15 \pm 15.86	248.45 \pm 11.88	384.99 \pm 34.92	356.21 \pm 29.51
<i>M_S</i>	845.09 \pm 23.34	1069.1 \pm 29.41	1007.96 \pm 36.7	1341.7 \pm 38.47	1404.41 \pm 40.04	1237.45 \pm 31.72	1392.01 \pm 77.23	1909.94 \pm 106.72
<i>M_r</i>	78.58 \pm 0.7	81 \pm 1.07	83.41 \pm 0.88	82.78 \pm 1.06	90.96 \pm 1.04	90.2 \pm 1.37	98.31 \pm 1.58	90.61 \pm 1.27
<i>F</i>	23 265.36 \pm 1 138.36	30 912.12 \pm 1 353.37	30 241.84 \pm 2 222.15	44 370.79 \pm 2 251.93	52 231.13 \pm 1 796.36	34 208.21 \pm 1 693.66	66 523.76 \pm 4 498.34	50 195.69 \pm 3 839.73
<i>F_R</i>	23.19 \pm 0.77	24.07 \pm 0.57	24.67 \pm 1.04	27.4 \pm 1.07	31.9 \pm 0.67	23.17 \pm 1.06	37.49 \pm 1.41	21.52 \pm 0.57
GSI	0.17 \pm 0	0.19 \pm 0	0.17 \pm 0.01	0.19 \pm 0.01	0.17 \pm 0.01	0.2 \pm 0.01	0.27 \pm 0.01	0.18 \pm 0.01
Total lipid	8.52 \pm 0.53	15.09 \pm 1.32	8.09 \pm 0.55	9.9 \pm 0.72	10.57 \pm 0.76	8.64 \pm 0.74	40.69 \pm 3.2	13.58 \pm 1.45
ARA	1.52 \pm 0.05	1.53 \pm 0.08	1.44 \pm 0.04	1.26 \pm 0.05	1.26 \pm 0.06	1.33 \pm 0.06	1.2 \pm 0.04	1.06 \pm 0.05
EPA	3.19 \pm 0.14	4.26 \pm 0.16	3.31 \pm 0.12	3.97 \pm 0.11	3.68 \pm 0.13	3.46 \pm 0.15	4.3 \pm 0.14	3.36 \pm 0.14
ALA	0.45 \pm 0.02	0.83 \pm 0.05	0.47 \pm 0.02	0.57 \pm 0.03	0.57 \pm 0.03	0.48 \pm 0.04	0.89 \pm 0.08	0.49 \pm 0.04
DHA	9.86 \pm 0.34	10.97 \pm 0.33	12.11 \pm 0.27	10.89 \pm 0.28	11.35 \pm 0.33	10.27 \pm 0.33	7.27 \pm 0.39	11.82 \pm 0.3
LNA	0.45 \pm 0.02	0.69 \pm 0.05	0.42 \pm 0.02	0.47 \pm 0.03	0.51 \pm 0.02	0.41 \pm 0.03	1.16 \pm 0.09	0.6 \pm 0.05
DHA/ARA	6.63 \pm 0.23	7.85 \pm 0.36	8.82 \pm 0.29	8.96 \pm 0.25	9.78 \pm 0.65	8.16 \pm 0.37	6.15 \pm 0.31	11.99 \pm 0.45
EPA/ARA	2.14 \pm 0.1	2.88 \pm 0.11	2.36 \pm 0.08	3.25 \pm 0.09	3.03 \pm 0.11	2.67 \pm 0.1	3.71 \pm 0.16	3.33 \pm 0.14
Σ n-3	14.72 \pm 0.49	17.64 \pm 0.51	17.09 \pm 0.38	16.81 \pm 0.42	16.83 \pm 0.38	15.58 \pm 0.5	14.04 \pm 0.51	16.87 \pm 0.44
Σ n-6	2.06 \pm 0.06	2.38 \pm 0.12	1.93 \pm 0.06	1.83 \pm 0.08	1.87 \pm 0.08	1.83 \pm 0.08	2.52 \pm 0.12	1.78 \pm 0.1
Σ SAFA	8.81 \pm 0.21	10.06 \pm 0.3	8.64 \pm 0.19	8.61 \pm 0.23	8.84 \pm 0.21	7.99 \pm 0.27	13.56 \pm 0.57	9.36 \pm 0.28
Σ MUFA	3.56 \pm 0.22	6.1 \pm 0.52	3.42 \pm 0.25	4.34 \pm 0.33	4.37 \pm 0.24	3.48 \pm 0.29	19.18 \pm 1.45	6.03 \pm 0.64
Σ PUFA	16.86 \pm 0.53	20.13 \pm 0.58	19.08 \pm 0.42	18.75 \pm 0.49	18.81 \pm 0.4	17.51 \pm 0.55	16.73 \pm 0.54	18.74 \pm 0.52
UI	306.19 \pm 5.6	301.61 \pm 4.82	331.49 \pm 2.09	322.36 \pm 2.85	329.13 \pm 4.04	336.52 \pm 11.52	254.86 \pm 12.6	350.08 \pm 10.87
<i>N</i>	90.28 \pm 0.65	88.68 \pm 0.74	86.09 \pm 0.79	86.38 \pm 0.79	85.33 \pm 0.94	86.42 \pm 0.98	71.4 \pm 1.95	79.99 \pm 1.12
Energy density	22.98 \pm 0.22	22.95 \pm 0.29	22.58 \pm 0.17	23.51 \pm 0.35	23.06 \pm 0.22	23.58 \pm 0.29	26.05 \pm 0.34	24.01 \pm 0.25
Moisture	76.74 \pm 0.19	76.17 \pm 0.28	76.02 \pm 0.28	77.28 \pm 0.2	76.95 \pm 0.29	77.87 \pm 0.31	69.92 \pm 1.27	73.11 \pm 0.37

Note: See Table 1 and text for definitions of variables.

Table 3. Mean \pm standard error for condition variables measured on unfertilized eggs collected from gravid female lake whitefish from Lakes Michigan, Erie, and Superior.

Variable	Michigan						Erie		Superior
	Naubinway	Big Bay de Noc	Elk Rapids	Bailey's Harbor	Ludington	Saugatuck	Point Pelee	Whitefish Point	
Total lipid	34.7 \pm 0.45	35.43 \pm 0.4	35.35 \pm 0.37	34.24 \pm 0.5	35.99 \pm 0.73	33.44 \pm 0.36	35.68 \pm 0.53	38.6 \pm 0.49	
ARA	7.05 \pm 0.17	6.8 \pm 0.19	7.75 \pm 0.27	5.69 \pm 0.33	4.39 \pm 0.13	5.23 \pm 0.21	4.32 \pm 0.14	4.98 \pm 0.18	
EPA	14.12 \pm 0.39	17.6 \pm 0.26	15.16 \pm 0.41	17.16 \pm 0.37	14.74 \pm 0.27	15.38 \pm 0.33	16.48 \pm 0.39	14.89 \pm 0.32	
ALA	1.2 \pm 0.05	1.76 \pm 0.05	1.34 \pm 0.07	1.5 \pm 0.08	1.3 \pm 0.08	1.15 \pm 0.06	0.93 \pm 0.05	1.02 \pm 0.04	
DHA	26.49 \pm 0.58	24.12 \pm 0.38	27.13 \pm 0.65	24.25 \pm 0.46	25.74 \pm 0.46	27.47 \pm 0.78	25.36 \pm 0.6	31.36 \pm 0.88	
LNA	1.57 \pm 0.05	2.03 \pm 0.05	1.72 \pm 0.06	1.76 \pm 0.07	1.61 \pm 0.08	1.47 \pm 0.06	1.35 \pm 0.06	1.67 \pm 0.05	
DHA/ARA	3.85 \pm 0.11	3.77 \pm 0.15	3.74 \pm 0.14	4.85 \pm 0.26	6.01 \pm 0.2	5.59 \pm 0.29	6.12 \pm 0.27	6.54 \pm 0.19	
EPA/ARA	2.06 \pm 0.07	2.72 \pm 0.09	2.08 \pm 0.09	3.34 \pm 0.14	3.43 \pm 0.11	3.09 \pm 0.12	4.03 \pm 0.22	3.18 \pm 0.13	
Σ n-3	47.18 \pm 0.64	48.97 \pm 0.43	48.68 \pm 0.79	48.1 \pm 0.73	46.54 \pm 0.61	49.68 \pm 1.01	47.92 \pm 0.95	51.73 \pm 1.13	
Σ n-6	9.27 \pm 0.21	9.47 \pm 0.24	9.99 \pm 0.32	7.99 \pm 0.41	6.64 \pm 0.21	7.29 \pm 0.24	6.16 \pm 0.19	7.23 \pm 0.22	
Σ SAFA	28.86 \pm 0.25	30.26 \pm 0.21	29.2 \pm 0.26	28.52 \pm 0.3	27.39 \pm 0.33	26.15 \pm 0.38	30.62 \pm 0.31	29.53 \pm 0.34	
Σ MUFA	18.58 \pm 0.33	19.32 \pm 0.28	18.78 \pm 0.29	20.49 \pm 0.48	20.75 \pm 0.34	19.71 \pm 0.3	27.69 \pm 0.53	22.42 \pm 0.35	
Σ PUFA	56.83 \pm 0.76	58.86 \pm 0.5	59.03 \pm 1.02	56.44 \pm 0.98	53.65 \pm 0.7	57.49 \pm 1.12	54.37 \pm 0.9	59.36 \pm 1.27	
UI	299.04 \pm 1.51	293.36 \pm 1.03	300.92 \pm 1.55	293.98 \pm 1.47	294.24 \pm 1.32	308.39 \pm 1.73	277.16 \pm 2.22	300.48 \pm 2.01	
Total protein	61.73 \pm 0.65	62.6 \pm 0.74	63.39 \pm 0.79	63.39 \pm 0.79	61.33 \pm 0.94	63.15 \pm 0.98	63.8 \pm 1.95	60.94 \pm 1.12	
Energy density	27.41 \pm 0.26	25.72 \pm 0.16	26.86 \pm 0.18	27.08 \pm 0.23	27.08 \pm 0.26	26.52 \pm 0.19	24.46 \pm 0.33	27.52 \pm 0.14	
Moisture	63.92 \pm 0.22	62.74 \pm 0.15	62.99 \pm 0.65	65.89 \pm 0.49	63.19 \pm 0.22	66.49 \pm 0.26	63.69 \pm 0.92	61.28 \pm 0.16	
M_w	0.00311 \pm 0.00006	0.00305 \pm 0.00005	0.00284 \pm 0.00005	0.00306 \pm 0.00005	0.00255 \pm 0.00013	0.00322 \pm 0.00007	0.00245 \pm 0.00005	0.00317 \pm 0.00004	
D	2 \pm 0.01	2.12 \pm 0.01	2.11 \pm 0.03	2.02 \pm 0.02	1.88 \pm 0.03	2.22 \pm 0.03	2.02 \pm 0.02	2.14 \pm 0.01	

Note: See Table 1 and text for definitions of variables and Table 2 for female data.

food web (Mida Hinderer et al. 2012; Pothoven et al. 2012). Although freshwater fishes have some ability to elongate and desaturate ALA to EPA and DHA (Tocher et al. 1989; Tocher and Sargent 1990), both n-3 LC-PUFA are considered essential and are primarily obtained from the diet. EPA plays a key role in maintaining membrane competency (i.e., fluidity) as well as functioning as a precursor for anti-inflammatory eicosanoids, critical for a healthy immune system (Arts and Kohler 2009). DHA is important for central nervous system development and function (Masuda et al. 1999), vision (Sargent et al. 1999), and sperm development (Labbé et al. 1993, 1995) in fishes. In addition, eight FA indices were also calculated for females and their eggs (Table 1).

Treatment of data

Statistical procedures (significance level $\alpha = 0.05$) were conducted using R (2.15.2; <http://www.r-project.org>) and SigmaPlot 11 (Systat Software Inc., San Jose, California) according to the methods of Zar (1999) and Zuur et al. (2009). All data were $\ln(y + 1)$ -transformed to standardize units of measure and normalize the error distributions. The data for females are a subset of those presented by Muir et al. (2010); females with a gonadosomatic index <0.05 ($n = 45$ fish) were outliers and, therefore, excluded from the current analyses as unlikely spawners or partially spent females. In addition, the lipid data for the Big Bay de Noc and Naubinway stocks were presented by Wagner et al. (2010), and total lipid and DHA data for lake Michigan fish were presented by Fagan et al. (2012).

Reproductive strategy

To determine whether lake whitefish are using a Maximization, Quality Control, or Optimization reproductive strategy (Objective 1), we examined the nature of correlations between 16 condition variables measured in gravid females and their unfertilized eggs and compared the total variation for these variables between females and their eggs. The direction and magnitude of the Pearson correlation coefficient (r) was tallied for each of the 16 variables to determine which of the three reproductive strategies were most likely used by lake whitefish — i.e., expected signs (+ or -) and significance levels (P) in support of the three hypotheses were as follows: Reproductive Maximization Hypothesis = $P < 0.05$ and sign positive (+); Reproductive Optimization Hypothesis = $P < 0.05$ and sign negative (-); and Reproductive Quality Control Hypothesis = $P > 0.05$ (i.e., nonsignificant relationship; Fig. 2).

This analysis used the following 16 variables as indicators of maternal and egg condition (see Table 1 for definitions): (1) total lipid, (2) ARA, (3) EPA, (4) ALA, (5) DHA, (6) LNA, (7) unsaturation index, (8) Σ n-3 PUFA, (9) Σ n-6 PUFA, (10) Σ PUFA, (11) Σ MUFA, (12) Σ SAFA, (13) DHA/ARA, (14) EPA/ARA, (15) energy density, and (16) moisture content. To determine if reproductive strategy differed as a function of female condition, female muscle total lipid content was used to split the dataset into a poor condition group (the lower 50% of individuals with lowest muscle total lipid content) and a good condition group (the upper 50% of individuals with highest muscle total lipid content) for all lakes combined, which were analyzed separately as described above. This split is justified because maternal lipid content is a good proxy for recruitment potential in fishes, lipid reserves in fish co-vary with potential prey abundance (Marshall et al. 1999), and because lipids are an important energy source for developing embryos (Lane and Kohler 2007; Wilson 2009).

Means and coefficients of variation (CV) for the 16 variables measured from females and their eggs were plotted to visualize and assess the magnitude of differences between mean condition variables in the soma versus those allocated to developing eggs, as well as the variation associated with those allocations. Differences in mean condition variables between females and their eggs were interpreted as greater or lesser allocations by females to reproduction. For instance, higher means for variables in eggs than in

female muscle tissue indicated a greater mass-specific allocation of energy to reproduction than growth. Low variation in an egg condition variable suggested conservation to maintain a threshold for successful reproduction. By contrast, high variation in female relative to eggs condition was interpreted as evidence of somatic trade-offs to maintain egg condition, whereby poor condition females were depleted of energetic and nutrient reserves relative to good condition females within a stock.

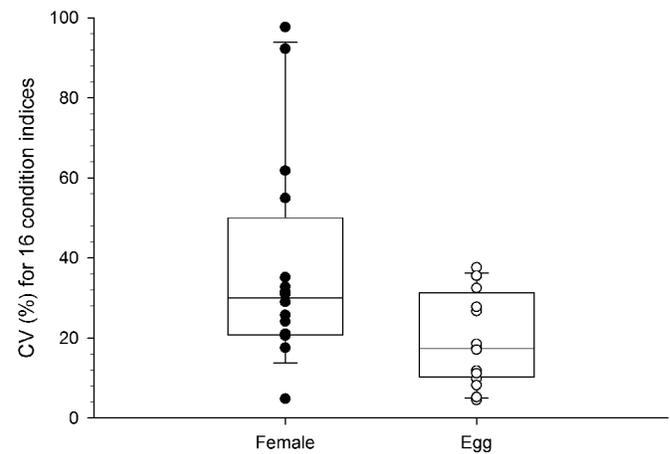
Trade-offs between fecundity and egg condition (e.g., size and FA composition) are common in fishes (Kamler 2005). From a reproductive strategy standpoint, the respective benefits of investing in egg number versus egg condition may vary with environmental conditions selecting for variation in reproductive strategies among individuals. From an energy budget standpoint, as fecundity increases, egg size, total lipid, and total PUFA provisioned to the egg might be expected to decrease at some point because the energy and nutrients available for gamete production exist in finite supply. This finite supply depends in part on the condition of the female and on her body size. Larger females at least have the potential to invest greater supplies of energy and nutrients into egg production. To control for the effect of body size on fecundity, residuals from a linear regression of $\ln(\text{fecundity} + 1)$ versus $\ln(\text{soma mass} + 1)$ were retained as a standardized fecundity measure (Kooops et al. 2004). Separate linear models for each stock were fit using standardized fecundity as the independent variable and egg diameter as the dependent variable, where a negative slope indicated a trade-off between fecundity and egg size. To test for trade-offs between fecundity and PUFA content of eggs, a linear model was fit using standardized fecundity as the independent variable and Σ PUFA in eggs as the dependent variable with female condition (good versus poor) as a factor. The interaction between body condition and fecundity was included to test for differences in slopes. A negative slope indicated a trade-off between fecundity and PUFA provisioned to eggs.

A linear model ($(F \times E_i) \sim K_n + S$) tested the effect of female body condition (K_n) on total reproductive output (i.e., fecundity (F) \times egg total lipid (E_i)) while accounting for fish size (i.e., soma mass (S)). A significant model was interpreted as an effect of female condition on total reproductive output, and variables were examined for their contribution to the explained variation. The resulting model was then used to examine how differences in body condition between high and low condition groups translated into a difference in total reproductive output among females.

Spatial patterns in lake whitefish condition and egg condition

Diporeia spp. is an important source of n-3 PUFA, especially DHA (M. Arts, Environment Canada, unpublished data). Given the markedly contrasting availability of *Diporeia* among our study sites (Fig. 1) and the spatial variation in other food resources (Nalepa et al. 2009; Barbiero et al. 2012; Mida Hinderer et al. 2012), we expected relationships between female and egg condition variables to vary spatially. To compare spatial variation in mature female lake whitefish condition and the condition of their unfertilized eggs, variation in selected egg condition variables was partitioned as a function of a random stock effect and selected fixed effects of maternal condition (Objective 2). Egg total lipid, egg DHA/ARA and EPA/ARA ratios, and egg wet mass were independently modeled as a function of stock, standardized fecundity, female muscle total lipids, female DHA/ARA, and female EPA/ARA. These variables were selected because they are known physiological indices of condition and reproductive investment (Bell and Sargent 1996; Adams 1999; Tocher 2003, 2010), and the FA indices selected reflect underlying differences in trophic resource use (Kuusipalo and Käkälä 2000). All data were centered (mean = 0) prior to analysis. The following mixed model was used to partition the variation in egg condition:

Fig. 3. Total variation (i.e., coefficient of variation, CV%) for 16 variables measuring female lake whitefish condition and the condition of their unfertilized eggs. The lower boundary of each box indicates the 25th percentile, the line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles, respectively, and the dots represent the data for the 16 variables. See Table 1 for definitions of variables.



$$Y_{ij} = \alpha + \beta_1 X_1 + \beta_2 X_2 \dots \beta_n X_n + a_j + \varepsilon_{ij}$$

where Y is a measure of egg condition for fish i ($i = 1, \dots, 384$) belonging to stock j ($j = 1, \dots, 8$), the random effect of stock (representing stock–stock variation) is given by a_j , and the residual term ε is $N(0, d^2)$. Each of the four egg condition variables was modeled separately. Models were fit and selected using the protocol of Zuur et al. (2009), where terms were sequentially dropped from the full mixed model on the basis of their significance. Model selection was conducted using a maximum-likelihood ratio test and verified by Akaike information criterion (AIC). The final model that included all significant terms was refit, and variance components were estimated using restricted maximum likelihood. In this way, the number of variables in the fixed term varied on the basis of their ability to explain variation in egg condition. The variance estimates in the random effects term were used to calculate the correlation between observations from the same stock (i.e., intrastock correlation) according to the following formula given by Zuur et al. (2009): $\text{SD intercept}^2 / (\text{SD intercept}^2 + \text{SD residual}^2)$. High (>0.5) intrastock correlations were interpreted as a strong stock effect.

Results

Reproductive strategy

Consistent with a Reproductive Quality Control strategy, (Objective 1), egg condition varied little in comparison with female condition (Fig. 3), and variable means were typically much higher in eggs than in females (Fig. 4). Lack of a relationship between eggs and maternal condition was true for about half of the variables assessed, including the physiologically important n-3 PUFA and DHA, further supporting the Reproductive Quality Control Hypothesis. A complete lack of negative correlations between variables measured in females and their unfertilized eggs ruled out the Reproductive Optimization Hypothesis as a likely reproductive strategy for the lake whitefish populations examined in this study.

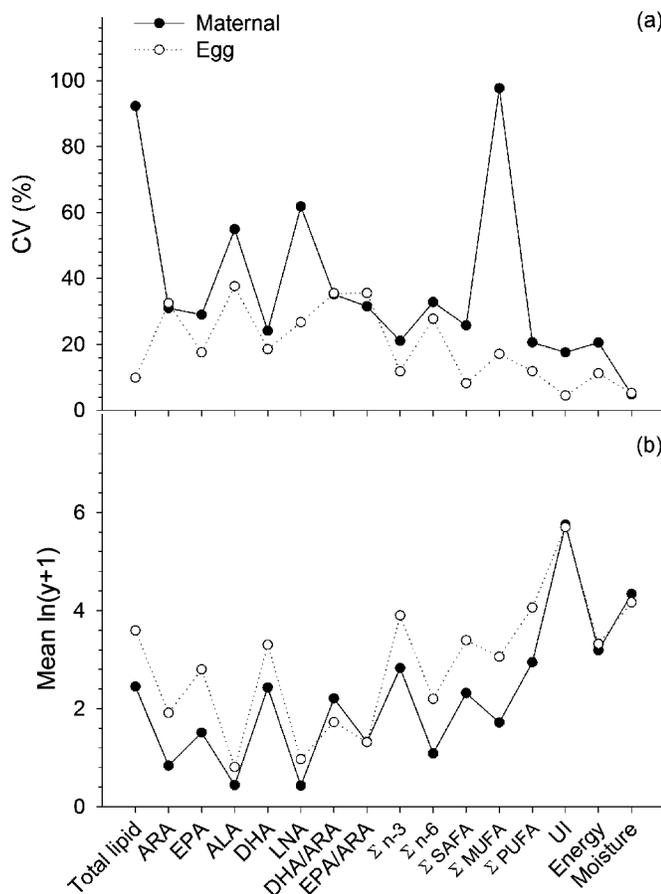
A greater number of nonsignificant correlations between poor condition females and their unfertilized eggs suggest that they make greater energetic and nutritional (i.e., somatic) trade-offs to maintain egg condition than good condition females (Table 4).

Table 4. Pearson correlation coefficients (*r*) for the association between condition variables measured from gravid female lake whitefish and their unfertilized eggs from Lakes Michigan, Erie, and Superior.

Condition variable	Poor condition females			Good condition females		
	P < 0.05 (+)	Quality		P < 0.05 (+)	Quality	
		P > 0.05	Control		Optimization	P > 0.05
Total lipid		0.11			0.02	
ARA	0.20			0.43		
EPA	0.31			0.39		
ALA	0.36			0.37		
DHA		0.11			0.02	
LNA		0.04			0.09	
DHA/ARA	0.36			0.33		
EPA/ARA	0.70			0.70		
Σ n-3		0.01			0.01	
Σ n-6		0.05		0.26		
Σ SAFA		0.01		0.32		
Σ MUFA	0.40			0.57		
Σ PUFA		0.06			0.05	
UI		0.05		0.29		
Energy density		0.06			0.12	
Moisture content	0.18			0.32		
Frequency	7	9	0	10	6	0

Note: See Table 1 and text for definitions of variables.

Fig. 4. Variation (CV, %; panel a) and mean (ln(y + 1)-adjusted; panel b) for 16 variables measuring female lake whitefish condition and condition of their unfertilized eggs from Lakes Michigan, Superior, and Erie. See Table 1 for definitions of variables.



With the exception of EPA and ARA, other physiologically important FAs (Glencross 2009), especially those LC-PUFA linked to egg condition, were among the variables and indices not correlated between females and their eggs. In poor condition females, these variables included muscle total lipids ($r = 0.11$; $P = 0.1$), DHA ($r = 0.11$; $P = 0.1$), LNA ($r = 0.04$; $P = 0.6$), Σ n-3 ($r < 0.01$; $P = 0.9$), Σ n-6 ($r = 0.05$; $P = 0.5$), Σ SAFA ($r = 0.01$; $P = 0.9$), Σ PUFA ($r = 0.06$; $P = 0.4$), unsaturation index (UI) ($r < 0.05$; $P = 0.5$), and energy density ($r < 0.06$; $P = 0.4$). Similarly, muscle total lipids ($r = 0.02$; $P = 0.8$), DHA ($r = 0.02$; $P = 0.8$), and Σ n-3 ($r < 0.01$; $P = 1.0$) were disassociated between good condition females and their eggs.

More positive correlations between good condition females and their eggs across lakes suggest that when energy was abundant, egg condition better reflected female condition (i.e., Reproductive Maximization strategy; Table 4). Among the FA indices, EPA/ARA and Σ MUFA were most strongly correlated to egg condition in poor condition ($r = 0.70$ and 0.40 , respectively) and good condition ($r = 0.70$ and 0.57 , respectively; Table 4) females. As such, eggs were provisioned with similar amounts of these FAs, regardless of female condition. However, ARA ($r = 0.20$), EPA ($r = 0.31$), ALA ($r = 0.36$), DHA/ARA ($r = 0.36$), and moisture content ($r = 0.18$) were also weakly correlated between poor condition females and their eggs (all $P < 0.05$). In addition to ARA ($r = 0.43$), EPA ($r = 0.39$), ALA ($r = 0.37$), DHA/ARA ($r = 0.33$), moisture content ($r = 0.32$), Σ n-6 ($r = 0.26$), Σ SAFA ($r = 0.32$), and UI ($r = 0.29$) were also correlated between good condition females and their eggs (all $P < 0.05$; Table 4).

The lack of correlation for muscle total lipids, DHA, and essential n-3 FAs between poor and good condition females and their eggs across lakes, coupled with a lack of significant differences among stocks for those same variables in eggs (see results below and data in Tables 2 and 3), strongly suggests that eggs were adequately provisioned with sufficient energy and essential FAs critical for development, regardless of female condition. However, significant correlations for ALA, but not LNA, suggests that 18C n-3 FAs are more important than 18C n-6 FAs or that these fish do not have problems getting access to abundant sources of 18C n-6 FAs in their environment, or both. Fish cannot synthesize the 18C n-3 FAs and are therefore entirely dependent on dietary access to these

essential compounds. It is therefore noteworthy that the content of ALA is positively associated with egg condition.

The Reproductive Quality Control Hypothesis also predicts that egg condition will be less variable than female condition within and among stocks. Overall, variation in maternal condition was about twice as high as in their eggs (Fig. 3). Variation in females exceeded that of their eggs for 12 of 16 condition variables (Fig. 4a). Muscle total lipid content, LNA, ALA, Σ SAFA, Σ MUFA, and UI showed considerably more variation in females than their eggs. As a result, some females likely were depleted in some of the less physiologically important FAs, whereas other females did not show depletion.

On average, energy density was only 12% higher in eggs than in female muscle tissue (Fig. 4b) and did not vary among sites ($F_{[7,351]} = 1.1$; $P = 0.363$; Table 3). Thus, females allocated similar amounts of energy to their eggs, regardless of their own body condition. By contrast, total lipid was 133% higher in eggs than in female muscle tissue on average (Fig. 4b), and with the exception of the Whitefish Point stock, egg total lipid varied little among stocks (Table 3). Again, the high requirement of eggs for lipids was met by females, regardless of their condition.

Female lake whitefish from northern Lake Michigan (i.e., Naubinway ($r^2 = 0.35$), Elk Rapids ($r^2 = 0.56$), and Bailey's Harbor ($r^2 = 0.27$); all $P < 0.01$) were the only populations where the trade-offs between egg size and fecundity were significant (Fig. 5). Egg size was not related to fecundity at Big Bay de Noc ($r^2 = 0.001$); females had mean relative fecundity F_R (24.07 eggs·g⁻¹) relative to the other stocks, but moderately large eggs (mean $W_w = 3.05$ mg; mean $D = 2.12$ mm). By contrast, females from Whitefish Point had the lowest relative fecundity (mean $F_R = 21.52$ eggs·g⁻¹) among the stocks sampled, but the largest eggs on average (mean $W_w = 3.17$ mg; mean $D = 2.14$ mm; Table 3). In addition, egg size was less variable at Big Bay de Noc and Whitefish Point compared with the other sites.

A linear model described the relationship between egg Σ PUFA and standardized fecundity ($F_{[3,371]} = 20.3$; $P < 0.001$), but little variation in egg Σ PUFA could be explained by differences in fecundity between good and poor condition females ($r^2 = 0.13$; Fig. 6). The lack of an interaction ($t = -1.24$; $P = 0.22$) indicated that the relationship between egg PUFA content and fecundity did not differ by fish condition. However, a negative slope between the Σ PUFA and standardized fecundity suggests that when females are in poor condition, they may make slightly greater trade-offs in egg number (i.e., sacrifice more somatic potential) to maintain egg PUFA concentrations than good condition females.

The Reproductive Quality Control Hypothesis also predicts that changes in fish condition will not strongly influence recruitment dynamics if total reproductive investment (i.e., fecundity \times egg quality = egg total lipid) is not strongly linked to female condition. A linear model showed that total reproductive investment was related to female condition and soma mass ($F_{[2,309]} = 291.3$; $P < 0.001$; adjusted $r^2 = 0.65$). Female condition ($t = 2.95$; $P = 0.003$) and soma mass ($t = 21.08$; $P < 0.001$) variables were significant; however, when K_n was removed from the model, soma mass alone explained nearly the same variation as the overall model ($F_{[1,310]} = 560.1$; $P < 0.001$; adjusted $r^2 = 0.64$), suggesting that the relationship is almost completely driven by body size, with female condition being weakly related to this measure of total reproductive investment. On average, a difference in body condition between the high and low condition groups translated into a 2.1% difference in total reproductive output for a fixed body size (mean soma mass of all females = 1247.16 g).

Spatial patterns in lake whitefish condition and egg condition

Maternal condition affected egg condition (likelihood ratio; all $P < 0.001$), but those effects differed among stocks (Table 5). Stock (random effect) was significant in all models, but within-stock observations were only weakly correlated for egg mass (intrastock corre-

lation = 0.34), egg DHA/ARA (intrastock correlation = 0.35), EPA/ARA (intrastock correlation = 0.24), and egg lipid (intrastock correlation = 0.10). Weak intrastock correlations were insufficient to account for the maternal effects observed, but suggest the potential for differences in energy availability among stocks.

Despite the lack of a strong stock effect, some general spatial differences occurred in the FA indices. The Σ n-6 FA was high and the DHA/ARA index was low in female muscle tissue from northern Lake Michigan and Lake Erie compared with the other stocks. In addition, total lipid was three to five times higher in Lake Erie female muscle tissue than in all other stocks, but that was mostly due to elevated Σ MUFA and Σ SAFA as opposed to the more physiologically important Σ PUFA. These spatial differences in FAs suggest that fish from northern Lake Michigan and Lake Erie were probably consuming a greater proportion of nearshore or benthic prey, such as dreissenid mussels, compared with fish at other locations, which are obtaining more n-3 FAs from offshore sources. However, these spatial differences in female muscle lipid composition did not translate into clear differences in FA signatures in their unfertilized eggs.

In general, the trade-offs explored with mixed modeling showed that highly fecund females tended to provision less total lipid but more n-3 (e.g., DHA and EPA) to their eggs. Lipid-rich females, especially those with a high proportion of n-3 essential FAs, tended to allocate more total lipid to their eggs, and a higher proportion of those lipids were DHA and EPA. The trade-offs among the various FA provisioned to eggs were a function of individual maternal condition.

Discussion

Reproductive strategy

The analyses presented support the hypothesis that lake whitefish primarily use a Reproductive Quality Control strategy, where females maintain egg condition through compensatory trade-offs among their own somatic condition, fecundity, egg size, and the lipid FA constituents provisioned to eggs during gametogenesis. Females in poor condition made more and greater trade-offs between somatic condition and fecundity, egg size, total lipids, and especially PUFA to maintain egg condition than females in good condition. Low variation in physiologically important egg constituents, including total lipid, Σ n-3, DHA, and energy density, suggests the requirement for conserving threshold levels is important for lake whitefish reproduction. Other attributes (e.g., n-6 FAs, Σ SAFA, and Σ MUFA) were not conserved and positively correlated with female condition, consistent with a Reproductive Maximization Strategy. However, these variables were among the less physiologically important of the variables measured. In addition, the expected pattern of similar variation (CV; Fig. 3) between females and their eggs and the patterns of allocation between somatic and reproductive investment predicted by the Reproductive Maximization Hypothesis were not observed. The Reproductive Optimization Hypothesis can be eliminated as a potential explanation for lake whitefish reproductive strategy because it is entirely unsupported by our analysis.

The reproductive strategy used by a fish species will determine the extent to which maternal condition affects condition of eggs and offspring (Wootton 1979; Winemiller and Rose 1992; Kamler 2005). On average, 25% of dietary energy consumed by freshwater fishes is available for growth and reproduction (Wootton 1998). Changes in the prey base, such as the loss of lipid-rich *Diporeia* throughout much of Lake Michigan (Nalepa et al. 2009), could reduce the availability of n-3 LC-PUFA to lake whitefish, causing a shift in energy and nutrient allocation between somatic and reproductive growth. Trade-offs among egg size, fecundity, energy, and nutrient content, and among the various other constituents provisioned to the egg during vitellogenesis (e.g., vitamins, trace metals, amino acids, sterols, etc.), can ultimately affect recruitment

Fig. 5. Linear regression of egg diameter ($\ln(\text{egg diameter} + 1)$) versus standardized fecundity for lake whitefish collected from Naubinway, Big Bay de Noc, Elk Rapids, Bailey's Harbor, Ludington, and Saugatuck in Lake Michigan, Point Pelee in Lake Erie, and Whitefish Point in Lake Superior. The linear model and coefficient of determination (r^2) are given.

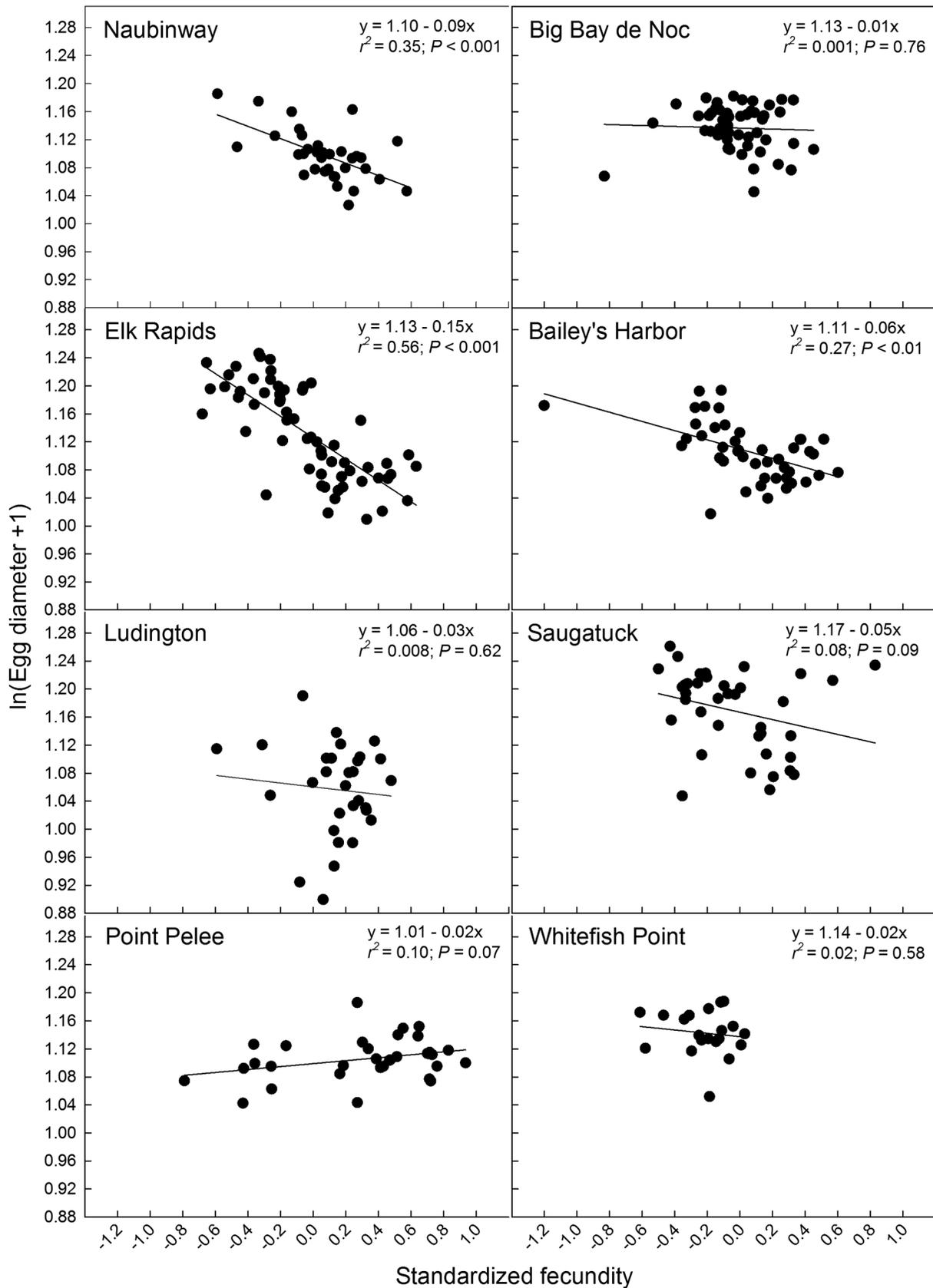


Fig. 6. Scatter plot of $\ln(\Sigma \text{ PUFA } \mu\text{g}\cdot\text{mg dry mass}^{-1}) + 1$ in eggs versus standardized fecundity for good and poor condition lake whitefish collected from Naubinway, Big Bay de Noc, Elk Rapids, Bailey's Harbor, Ludington, and Saugatuck in Lake Michigan, Point Pelee in Lake Erie, and Whitefish Point in Lake Superior. A linear model describing this relationship was significant ($F_{[3,371]} = 20.3$; $P < 0.001$), but little variation in egg total PUFA content could be explained by differences in fecundity between good and poor condition females ($r^2 = 0.13$).

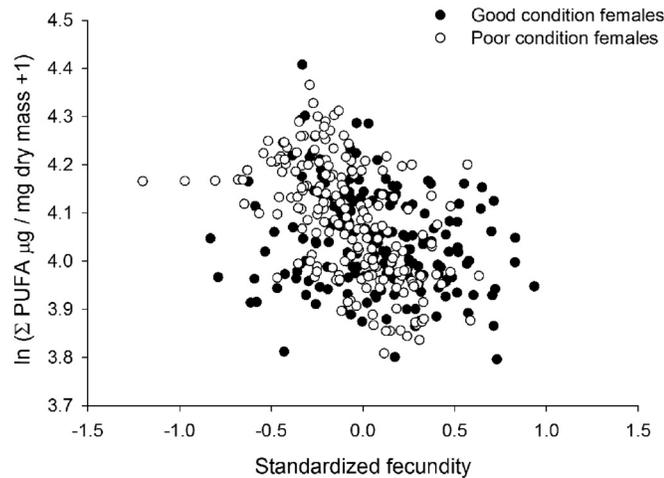


Table 5. Mixed effects modeling results for egg total lipid, DHA/ARA, EPA/ARA, and wet mass as a function of female fecundity, total lipid, DHA/ARA, and EPA/ARA (fixed effects) and stock (random effect).

Parameter	Estimate	SE	t	P
Egg total lipid				
Intercept	-0.0002	0.01		
Fecundity	-0.041	0.02	-2.66	<0.01
Total lipid	0.021	0.01	2.04	<0.04
DHA/ARA	0.047	0.02	2.64	<0.01
Egg DHA/ARA				
Intercept	0.029	0.06		
Fecundity	0.146	0.04	3.79	<0.001
Total lipid	0.101	0.03	3.80	<0.001
DHA/ARA	0.243	0.04	5.29	<0.001
Egg EPA/ARA				
Intercept	0.017	0.03		
Fecundity	0.134	0.03	5.02	<0.001
DHA/ARA	-0.076	0.04	-2.12	0.03
EPA/ARA	0.656	0.05	14.32	<0.001
Egg wet mass				
Intercept	-0.00004	1.06e-04		
Total lipid	-0.0002	8.48e-05	-2.35	0.02

Note: Stock effects were significant for all models (likelihood ratio; all $P < 0.001$).

(Stearns 1992). For example, Brown and Taylor (1992) reported that larval length-at-hatch was positively related to egg caloric content and also that larval endogenous growth was positively related to percent lipid content and egg total lipid content. Many of the variables controlling larval survival and growth are size-dependent (Miller et al. 1988; Kamler 2005); therefore, reproductive trade-offs to maximize size-at-hatch and larval growth of lake whitefish could affect recruitment.

Consistent with the Reproductive Quality Control Hypothesis, overall lake whitefish egg condition varied little among stocks relative to among-stock variation in female condition. Total lipid was 2.5 times higher in eggs than in females, but variance was nearly 10 times greater in females compared with eggs. Other

studies reported that lake whitefish egg lipid content and energy density was less variable than female body condition (Brown and Taylor 1992; Kratzer et al. 2007). Egg quality (i.e., energy in the form of lipids) was comparable to or exceeded that observed for other fishes. Egg energy density in the current study ranged from 24.5 J·mg dry mass⁻¹ at Point Pelee (Lake Erie) to 27.5 J·mg dry mass⁻¹ at Whitefish Point (Lake Superior; mean for all sites combined = 27 J·mg⁻¹). In comparison, mean egg energy density for lake whitefish exceeded the mean energy density of eggs from 50 marine and freshwater species (24 J·mg⁻¹; reviewed by Wootton (1979)). Lake whitefish eggs from Naubinway (northern Lake Michigan) had higher energy density (mean = 28 J·mg⁻¹) during the mid-2000s (current study) than those from Bayport (Lake Huron; mean = 27 J·mg⁻¹; $P = 0.042$) during the 1980s, prior to the invasion of dreissenid mussels to the Great Lakes (Brown and Taylor 1992). Taken together, the data presented above show that during the early 2000s, when growth and condition was severely depressed in northern Lake Michigan, lake whitefish continued to produce high-quality eggs (from the perspective of total lipid).

Female lake whitefish appeared to maintain egg condition primarily through trade-offs in egg size, number, and lipids, with poorer condition females in northern Lake Michigan (i.e., Naubinway and Elk Rapids) making the most significant trade-offs compared with good condition females in Lakes Erie and Superior. For example, females with high fecundity tended to provision less total lipid to their eggs, but a greater proportion of that lipid consisted of n-3 LC-PUFA as opposed to nonessential n-6 FAs. Female lake whitefish from Point Pelee (Lake Erie) have never had access to abundant *Diporeia* (Dermott and Kerec 1997), but showed growth comparable to that in Lake Superior and had the highest levels of muscle tissue total lipids among the stocks sampled. However, a greater proportion of those lipids were MUFA and SAFA, rather than PUFA and LC-PUFA, such as DHA. Despite these attributes, females produced eggs that were not depleted in DHA, n-3, or total PUFA relative to other stocks. A similar trend was true of the Naubinway stock, which was slow-growing, reached a small asymptotic adult size, and had experienced dramatic declines in *Diporeia* availability (Fig. 1; Nalepa et al. 2009). Despite these attributes, females from this stock produced eggs with the fourth highest DHA content among the stocks sampled, and egg UI was comparable to that in Lake Superior. Given the critical role of LC-PUFA during ontogeny, it is perhaps not surprising that LC-PUFA were preferentially provisioned to eggs, that is traded off against fecundity, total lipids, and nonessential FAs (Tocher 2010).

Fish lacking in EPA, DHA, and ARA develop pathologies and show suboptimal growth (Glencross 2009; Tocher 2010). Many fishes, including salmonines, have a weak ability to desaturate and elongate dietary ALA to EPA and DHA (Tocher 2003); therefore, EPA and DHA are considered essential and must be obtained, at least in part, from the diet. Dietary requirements of DHA for salmonines are unknown (Tocher 2010), but eggs of some species have an absolute requirement for a threshold quantity of DHA for egg viability (Lavens et al. 1999; Lane and Kohler 2007; Wilson 2009). Once a fish makes a "decision" to reproduce, it must invest sufficient FAs into eggs to guarantee a threshold condition level and hence egg viability, irrespective of muscle tissue levels. This generates a strong inference that during gametogenesis, DHA is likely diverted from the diet and tissues or organ reserves to egg production, leaving female somatic tissue depleted and in poor condition.

Poor and good condition females and their eggs had highly correlated EPA/ARA signatures ($r^2 = 0.70$), but DHA/ARA signatures were moderately correlated ($r^2 = 0.35$). This pattern of DHA allocation to eggs indicated precedence for DHA (rather than EPA or ARA) investment into eggs over retention in female muscle tissues. DHA-deficient juvenile Atlantic herring (*Clupea harengus*) were unable to feed effectively at low light intensities (Bell et al. 1995), likely rendering them more vulnerable to predation

(Blaxter and Jones 1967). These data are consistent with evidence showing the essential requirement for DHA in larval ontogeny (Wirth et al. 1997; Tocher 2010).

Spatial patterns in lake whitefish condition and egg condition

Consistent with the Reproductive Quality Control Hypothesis, spatial differences in female muscle lipid composition did not translate into clear differences in FA signatures in their unfertilized eggs. However, we sampled spawning stocks that may not feed together nor feed in the same geographic location during other times of the year. For example, on the basis of genetic (VanDeHey et al. 2009; Stott et al. 2010) and tagging data (Ebener et al. 2010), some lake whitefish stocks in Lake Michigan were described as being spatially discrete, while others, such as the Big Bay de Noc stock, moved from northern Lake Michigan west into Wisconsin waters during summer to feed, and therefore, comingled with other lake whitefish stocks. These data were not available when our study was designed and samples collected. The movement of stocks within Lake Michigan potentially confounds the interpretation of spatial patterns in resource use and the link between fish condition and “stock” as a proxy for the availability of those resources. Despite this caveat, female condition, and therefore egg condition, should be a function of the amount and quality of available prey within the spatial distribution of the stock, especially for sedentary stocks, such as Naubinway and Elk Rapids (Ebener et al. 2010).

The lack of a clear spatial pattern in reproductive investment is consistent with previous studies showing weak among-stock parental effects (Muir et al. 2010), lack of a spatial pattern in health indices (Wagner et al. 2010), and no demonstrable spatial effect of trophic resource use on condition (Fagan et al. 2012) for the same lake whitefish stocks studied herein. For instance, stock explained only 23% of the variation in age-0 juvenile physiological condition, and about 60% of the variation in juvenile physiological condition could not be explained by parental condition (Muir et al. 2010). In addition, Wagner et al. (2010) showed that a large proportion of the total variation in lake whitefish health indicators for some of the same stocks we sampled could not be attributed to spatial or temporal sources; rather the majority of the variation occurred among individual fish. Finally, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures showed that despite modest differences in trophic resource use among stocks, trophic niche and resource use could not explain spatial variation in lake whitefish condition (Fagan et al. 2012). Fagan et al. (2012) concluded that their data did not support the hypothesis of a relationship between lake whitefish condition and prey use. On the basis of these three lines of evidence, we propose that energetic and nutritional trade-offs between somatic and reproductive growth could account for the large residual variation in lake whitefish health and condition that could not be accounted for by Muir et al. (2010), Wagner et al. (2010), and Fagan et al. (2012).

If the Reproductive Quality Control Hypothesis explains the primary strategy used by lake whitefish to provision eggs, and total reproductive output is not strongly linked to female condition, then changes in female growth and condition should not be a primary driver of recruitment in this species, at least over the range of conditions and metrics examined herein. Gamete quality control could explain why lake whitefish recruitment was remarkably stable during the 2000s when growth and condition in the southern main basin of Lake Huron and in areas of northern Lake Michigan were dramatically depressed (Modeling Subcommittee – Technical Fisheries Committee 2007). In addition, fish from Naubinway, in northern Lake Michigan, had access to the poorest quality prey (Nalepa et al. 2009), were the slowest growing among the stocks studied, differed in their FA signatures, yet catch per unit effort of juvenile lake whitefish in the aboriginal trap fishery was stable between 1991 and 2012 (M. Ebener, Chippewa Ottawa Resource

Authority, unpublished data). High and stable recruitment from lake whitefish stocks that were in poor condition is consistent with the Reproductive Quality Control Hypothesis.

Dynamic and adaptive energy allocation processes in conjunction with muted conditional effects on total reproductive investment may buffer effects of changes in energy availability on recruitment potential. A Quality Control reproductive strategy may have evolved in lake whitefish as an adaptive response to selective pressures associated with variable and unpredictable north-temperate environments (Winemiller and Rose 1992). Further, a Quality Control reproductive strategy may enable lake whitefish populations to thrive at the southern limit of their physiological tolerance in the Laurentian Great Lakes. Although reproductive trade-offs dampen effects of short-term food-web perturbations, continued changes in food-web structure and habitat may force more substantial trade-offs, and recruitment could become compromised over the long term. Future research could use controlled rearing experiments to tease apart maternal and environmental components of variation and to make quantitative measures of hatching success and larval growth and survival in relation to parental diet, growth, and condition.

A Quality Control reproductive strategy has several implications for lake whitefish fishery management in the Laurentian Great Lakes. For example, this type of strategy may buffer recruitment variation, making whitefish populations somewhat resilient to effects of fishing mortality set against a backdrop of large-scale changes in community composition and energy and nutrient dynamics (such as those that have occurred during the past century in the Great Lakes). In other words, if environmental conditions are favourable, large year classes can be produced from very small spawning stocks (Christie 1963). A dynamic and responsive strategy for energy and nutrient allocation between somatic and reproductive growth that maintains egg quality also provides some resistance against the often systematic effects on food-web dynamics caused by non-native species introductions in the Laurentian Great Lakes.

In summary, the data presented here supported the Reproductive Quality Control Hypothesis, which predicts that female lake whitefish trade off their own body condition (e.g., muscle total lipid content, DHA, n-3 LC-PUFA) and fecundity to adequately provision eggs for survival (i.e., large size, high total lipid content, and high DHA and other n-3 PUFA content). Trade-offs were more common and of greater magnitude in poor condition individuals than in good condition individuals. Importantly, trade-offs occur at the level of the individual female, which could explain why the underlying mechanisms for population-level changes in lake whitefish growth and condition have been difficult to resolve (e.g., DeBruyne et al. 2008; Muir et al. 2010; Wagner et al. 2010; Fagan et al. 2012).

Acknowledgements

We thank E. Volkman, A. Bedford, C. Benoit, A. Charlton, R. Cripe, G. Fodor, J. Hoffmeister, V. Lee, A. McAlexander, R. Mollenhauer, S. Shaw, D. Rajchel, M. Rudy (formerly Drebenedt), J. Willis, B. Williston, and W. Zak for their assistance in the field and laboratory. Thanks to D. Tagerson for assistance with the Lake Superior samples, to C. Krause on Lake Erie, and to L. Barbeau, D. Frazier, D. Hickey, K. King, T. King, R. Kinnunen, P. Jensen, P. Peeters, B. Peterson, and J. Peterson for lake whitefish collections in Lake Michigan. We also thank H. Ahman, J. Chao, M. Rudy, and S. Wolfaardt (Environment Canada) for their help with the lipid analyses. We appreciated thorough reviews and constructive feedback from two reviewers and the Associate Editor. Support for this research was provided by the Great Lakes Fishery Trust, project No. 2004.570, the Department of Forestry and Natural Resources at Purdue University, Environment Canada (MTA), and Fisheries and Oceans Canada (MAK).

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