Maternal effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*)

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Abstract: Changes that occurred in the distribution of adult Lake Michigan yellow perch (*Perca flavescens*) phenotypic traits suggest that maternal effects on larval traits may be substantially influencing the recruitment of this heavily exploited species. We investigated maternal effects on yellow perch larvae at hatching in 10 maternal lines to test the null hypothesis of no effect of maternal phenotype on offspring phenotype and condition. Analyses lead to a rejection of the null hypothesis and indicated that the observed maternal effects likely resulted from differences among females in size, age, gonadosomatic index, and egg production. The observed maternal effects were expressed in the offspring by differences in larval total length, yolk volume, dry weight, and DNA quantity. Older, larger females were found to have high fecundity, yet low gonadosomatic index. Furthermore, older, larger females produced offspring that were, on average, short with large yolk sacs and high quantities of body reserves, as measured by dry weight and total DNA content. We conclude that the distribution of Lake Michigan yellow perch larval traits at hatching is linked to maternal influences and that this linkage may provide a mechanism through which managers can help rebuild the population.

Résumé : Les changements survenus dans la distribution des caractéristiques phénotypiques des Perchaudes (*Perca flavescens*) adultes du lac Michigan laissent croire que les effets maternels sur les caractéristiques larvaires influencent de façon substantielle le recrutement chez cette espèce fortement exploitée. Nous avons étudié les effets maternels sur des larves néonates de Perchaudes de 10 lignées maternelles dans le but de tester l'hypothèse nulle de l'absence d'effets du phénotype maternel sur le phénotype et la condition de la descendance. Nos analyses nous amènent à rejeter l'hypothèse nulle et indiquent que les effets maternels observés résultent probablement de différences dans la taille, l'âge, l'indice ganadosomatique et la production d'oeufs des femelles. Les effets maternels se manifestent dans la progéniture par des différences dans la longueur totale, le volume du vitellus, la masse sèche et la quantité d'ADN des larves. Les femelles plus âgées et plus grosses ont une forte fécondité, malgré un indice ganadosomatique faible. De plus, ces femelles produisent des petits qui sont, en moyenne, courts avec de gros sacs vitellins et d'importantes réserves corporelles, en masse sèche et en contenu d'ADN total. En conclusion, la distribution des caractère larvaires des Perchaudes du lac Michigan est reliée aux influences maternelles; ces liens peuvent fournir aux gestionnaires un outil qui les aidera à restaurer les populations.

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Introduction

Recruitment variability is likely attributable to processes in early life history (Houde 1987; Pepin 1989; Leggett and Deblois 1994). The extreme variability in vital rates that characterizes early life stages produces larvae with a wide range of characteristics on which phenotypic selection may act (Rice et al. 1993). Recognition of the potential importance of interindividual variability has led to suggestions that recruitment research may be more successful if it were to focus on individuals rather than on populations (Crowder et al. 1989). For example, many recruitment mechanisms have been found to be size dependent (Miller et al. 1988). Because of this size dependence, small initial size differences within a population can result in very large survival and recruitment differences (Adams and DeAngelis 1987; Crowder et al. 1989; Rice et al. 1993).

Previous research has linked observed variation in the early life history traits among individuals of many finfish species to maternal influences (Chambers and Leggett 1992, 1996). Maternal effects can be defined as comprising "a class of phenotypic effects that parents have on phenotypes of their

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offspring that are unrelated to the offspring's own genotype" (Bernardo 1996). Maternal influences result from differential reproductive investment by males and females. The female's energetic investment provides the nutritional requirements essential for proper development and survival until first feeding. These investments by the female can be measured by the morphological and biochemical condition of the offspring. In contrast, paternal investment and its impact on subsequent survival are believed to be small. Recent research on parental influences in Atlantic cod (*Gadus morhua*) did not show any consistent effects of male size on fertilization success (Rakitin et al. 1999). Furthermore, Rakitin et al. (1999) found that differences in hatching success and survival in Atlantic cod could not be explained by differences in male size or sperm density.

Much of the previous research on maternal effects has focused on detecting maternal effects in the phenotypic traits of eggs. Significant female effects on egg size have been observed in many freshwater, marine, and anadromous species (e.g., Hislop 1988; Chambers and Leggett 1996; Chambers and Waiwood 1996). In contrast, research on maternal effects on the size, condition, and growth rates of larvae has been limited (Benoît and Pepin 1999). Significant maternal effects in larval traits have been observed in a few species. The traits for which these effects have been documented are size at hatch (chum salmon (*Oncorhynchus keta*), Beacham and Murray 1985; Atlantic silverside (*Menidia menidia*), Bengston et al. 1987), yolk volume at hatch (chum salmon, Beacham and Murray 1985; capelin (*Mallotus villosus*), Chambers et al. 1989), and size at metamorphosis (winter flounder (*Plueronectes americanus*), Chambers and Leggett 1992). Chambers and Leggett (1996) concluded that "body size during larval life was likely to be significantly influenced by maternal effects." For most other species where significant maternal effects have been reported in larval traits, such correlations have been extrapolated from significant maternal effects in phenotypic egg traits, which may be inappropriate (Pepin and Miller 1993; Benoît and Pepin 1999).

Maternal effects have the potential to substantially impact the recruitment dynamics of heavily exploited populations. Changes in the distributions of size, age, and condition of the spawning population that result from exploitation can potentially cause changes in egg production, fertilization success, and hatching success (Rijnsdorp 1989). Furthermore, changes in the size and condition distribution of newly hatched offspring of a population can potentially lead to changes in their susceptibilities to starvation and predation. In theory, such shifts can result in increased mortality, decreased recruitment, and ultimately recruitment failure.

An ideal model for research on the influence of maternal effects on recruitment is yellow perch (*Perca flavescens*). Historically, yellow perch has supported one of the most important commercial and recreational fisheries in Lake Michigan (Francis et al. 1996). However, the population has experienced nearly constant recruitment failure since 1990. In 1998, the yellow perch population level was reported to be 20% of 1990 levels (Pradeep Hirethota, Wisconsin Department of Natural Resources Fish Unit (WDNRFU), 600 E. Greenfield Ave., Milwaukee, WI 53204, U.S.A., unpublished data). In addition to declines in abundance, the age structure of the population changed over this period as well (Francis et al. 1996). In the mid- and late 1980s, the population was dominated by yellow perch 2–4 years of age, with a relatively small portion of the total population exceeding 4 years of age. By 1994, the population had shifted to one composed of almost exclusively greater than 4-year-old yellow perch. Furthermore, there are very few yellow perch remaining in the population that are greater than 7 years of age (Pradeep Hirethota, WDNRFU, Milwaukee, WI 53204, U.S.A., unpublished data). In response to the population decline, the average growth rates of female yellow perch have increased substantially since 1983 (Shroyer and McComish 1999). In the early and mid-1980s, female yellow perch reached a size of about 250 mm at an age of 12 years, while in the mid-1990s, females were reaching that same size at an age of only 4 years.

The changes in the population structure that have occurred over the past decade reflect the impact of an extremely size-selective fishery, which targeted the larger female yellow perch. It is likely that the high fishing mortality rate, the highly size-selective nature of the fishery, and a lack of recruitment caused the overall population decline and shifts in the population sex ratio, which have further weakened reproduction and recruitment. The changes in the female portion of the Lake Michigan yellow perch population structure suggest that the distribution of female phenotypes has been significantly altered. Large females that are predominantly greater than 4 years of age, but that are historically young for their size, dominate the female portion of the population (Shroyer and McComish 1999). The lack of recruitment further fuels this phenotypic bottleneck. These changes suggest that maternal effects may now play a dominant role in the recruitment dynamics of yellow perch in Lake Michigan.

Here, we investigate the role of maternal effects within the Lake Michigan yellow perch population. The objectives of this study were threefold: to determine whether maternal effects on larvae of Lake Michigan yellow perch were present, to determine which larval traits accounted for any detected maternal effects, and to determine which female traits correlate with the larval traits that account for any observed maternal effects.

Materials and methods

We investigated our objectives within a single experiment, which involved quantifying the relationship between 10 different females and their offspring at hatching. Additional objectives were investigated within a continuation of this experiment out to 32 days posthatch; however, those results will be examined elsewhere. All females for this experiment were collected in Lake Michigan. Subsequent experimental work was conducted at the University of Wisconsin's WATER Institute, Milwaukee, Wis. The experiment was conducted as a randomized complete block design consisting of three blocks of 20 tanks with two replicate tanks per female per block.

Collection of parental brood stock and gametes

Yellow perch were collected in June 1998 off Green Can Reef (42°50′00″ N, 87°50′00″ W), a historic yellow perch spawning ground offshore of Milwaukee. Fish were collected in bottom-set, graded-mesh gill nets (mesh from 5.7 to 6.4 cm bar) fished overnight. Female yellow perch were determined to be green (not ready to spawn, eggs not fully hydrated), ripe (eggs fully hydrated and

Table 1. Maternal and larval traits measured in each of the yellow perch females and sampled offspring of the 10 maternal lines.

Maternal trait	Larval trait
Linear measures	
Total length (mm)	Total length (mm)
Weight (g)	Eye diameter (mm)
Body depth at the anterior base of the first dorsal fin (FBD_1) (mm)	Minor yolk axis (mm)
Body depth at the posterior base of the second dorsal fin (FBD_2) (mm)	Major yolk axis (mm)
Age (years)	Body depth at insertion point of the pectoral fin (BDIP) (mm)
Egg production (no.)	Body depth at insertion point of the first dorsal fin (BDID) (mm)
	Body depth at insertion point of the anus (BDIA) (mm)
Biochemical measures	
	RNA content (RNA) (μg)
	DNA content (DNA) (μg)
Derived measures	
Fulton's condition factor k ($g \cdot mm^{-3}$)	Yolk volume (mm^3)
GSI	Dry weight (mg)
	RNA:DNA

easily expressed), or spent. Eggs of ripe female yellow perch were immediately expressed, weighed, and then fertilized with the milt from no fewer than three and no more than eight ripe males. Fertilized egg skeins were kept separate and transported back to the laboratory in Ziploc bags. The adult females and males used to produce each fertilized egg skein were killed and kept in separate bags on ice for transportation back to the laboratory. Egg skeins from five female yellow perch were obtained on 2 June 1998; five additional egg skeins were obtained on 4 June 1998.

Determination of maternal characteristics

We quantified eight maternal traits (Table 1). The total length and weight of each female were measured in the laboratory. Fulton's condition factor (k) was calculated for each female as k = (weight/length^3) × 100 000. Additionally, the body depths at the anterior base of the first dorsal fin and the posterior base of the second dorsal fin were measured. The sagital otoliths of each female were removed for age analysis. Each female's gonadosomatic index (GSI) was determined as

$$(1)\quad GSI = \frac{\text{wet wt. eggs} + \text{wet wt. stripped ovary}}{\text{wet wt. stripped female} + \text{wet wt. eggs} + \text{wet wt. stripped ovary}}$$

When the ovary from each female was removed, there were some green eggs remaining in each ovary. These eggs were determined to be eggs that would not have been released during spawning and would most likely have been reabsorbed by the female; therefore, our estimates of total egg production for each female are based solely on the ripe eggs expressed. Since the green eggs remaining in the ovary were assumed to be eggs that would have been reabsorbed, their weight was included in the weight of the stripped ovary.

Egg sampling

The total volume of each female's egg skein was measured in the laboratory. Independent 1-mL subsamples (n = 3) of each egg skein were taken and the eggs in each subsample were enumerated. The total egg production per female was defined as the product of the skein volume and the average egg concentration per unit volume. An additional subsample of each female's eggs was videotaped for subsequent analysis of morphometry (n = 15). For unknown reasons, the gelatinous matrix of Female 2 did not hold together. While we were able to get egg production estimates for Female 2, we did not videotape her eggs to avoid risking loss of too many eggs.

Husbandry of eggs

Once egg skeins from 10 females were available, the eggs were randomly assigned to, and incubated in, flow-through, temperature-controlled 10-gal (US) aquaria. Based upon the previously determined number of eggs per millilitre (checked again on 4 June 1998 to adjust for swelling associated with water hardening), a volume of skein equivalent to 2000 eggs was placed into each tank assigned to that female. The egg skein for Female 5 was crushed in transport and some eggs were damaged; the total number of usable eggs for Female 5 was only 1400 per tank.

Hatching began on 14 June 1998 in all tanks. Hatching was encouraged by gently mixing the water and the broken egg skeins to allow those larvae trapped within the gelatinous matrices to be freed. The broken egg skeins and any dead eggs and larvae were removed.

Larval sampling

We sampled 15 larvae at hatch from each tank, resulting in a total of 90 larvae per female. The larvae were anesthetized with tricaine methansulfonate (MS 222) and videotaped for analysis of morphometry. We sampled 12 larval traits, of which nine were morphometric measures and three were biochemical measures of condition (Table 1). The individual larvae were then placed into cryovials and flash-frozen in liquid nitrogen and then stored at –80°C for subsequent extraction of nucleic acids. There was a loss of a portion of videotape record for each female due to a problem with the video recording device that was not evident until analysis of the videotape began. Therefore, means of individual larval traits are based upon variable sample sizes ranging from 67 to 81 larvae per female.

Postsampling processing of eggs and larvae

Analysis of morphometric landmarks of the eggs and larvae from videotaped images was conducted with an image analysis system at the Chesapeake Biological Laboratory in Solomons, Md. The two-dimensional surface area and three sides of a triangle inscribed within the outline of each female's individual eggs and egg yolks were measured. Total egg volume and egg yolk volume were then determined based upon the following equations adapted from Miller et al. (1995):

Table 2. Phenotypic characteristics of the 10 female yellow perch caught off Green Can Reef (42°50′00″N, 87°50′00″W), Lake Michigan.

Female	Total length (mm)	Weight (g)	Fulton's condition factor *k*	Age (years)	FBD_1 (mm)	FBD_2 (mm)	GSI	Egg production (no.)
1	250	145.3	0.9299	4	53	47	0.3589	22 600
2	227	124.7	1.066	4	46	44	0.6284	11 000
3	280	255.6	1.164	4	72	57	0.5676	36 100
4	249	151.3	0.9802	2	54	43	0.6170	23 600
5	256	169.9	1.013	3	55	46	0.3824	11 600
6	285	261.4	1.292	5	65	61	0.2869	36 700
7	287	255.7	1.082	6	65	62	0.2168	29 400
8	216	113.1	1.122	3	47	40	0.4064	30 600
9	222	115.7	1.058	3	45	41	0.2875	22 000
10	242	115.4	0.8145	4	49	46	0.3989	32 800

Note: Females 1–5 were collected on 2 June 1998 and Females 6–10 were collected on 4 June 1998. Trait abbreviations are as defined in Table 1.

$$\text{Volume}(\text{mm}^3) = \frac{4}{3}\pi R^3 \quad (2)$$

$$R = \frac{abc}{4K} \quad (3)$$

$$K = \sqrt{s(s-a)(s-b)(s-c)}$$

$$s = \frac{a+b+c}{2}$$

where R is the estimated radius of the sphere and a, b, and c represent the three triangle sides inscribed within each egg and egg yolk.

Total length, eye diameter, body depth at the insertion point of the pectoral fin, body depth at the insertion point of the first dorsal fin (inclusive of the yolk sac), and body depth at the insertion point of the anus were measured for each individual larva sampled. The two-dimensional surface area of each larva's yolk sac was measured along with the major and minor yolk axes. Total yolk sac volume was then estimated as

$$\text{Volume } (\text{mm}^3) = \frac{4}{3}(\text{length of the minor yolk axis} \times \text{yolk surface area}) \quad (4)$$

The two-dimensional body area of each larva was also measured, and a calibration from other newly hatched yellow perch larvae between two-dimensional body area (square millimetres) and dry weight (milligrams) allowed estimation of individual larval dry weight (dry weight = $[(2 \times 10^{-6}) \times (\text{body area})^2 + (6 \times 10^{-5}) \times (\text{body area}) + (3 \times 10^{-5})] \times 1000$, $n = 171$, $r^2 = 0.9836$, $p = 0.0001$).

Nucleic acids were extracted from each individual larva by a modification of the sarcosyl extraction technique described by Caldarone and Buckley (1991). Whole frozen larvae were placed in individual microcentrifuge tubes containing 150 µL of 1% sarcosyl solution (*N*-lauroylsarcosine: Sigma L-5125). After vortexing for 1 h, 1.35 mL of Tris buffer (5 mM Tris–HCl (Trizma base: Sigma T-8524, HCl: Sigma H-1758), 0.5 mM EDTA (Sigma E-5134), pH 7.5) was added to reduce the sarcosyl concentration to 0.1%, and the tubes were centrifuged at 14 000 × *g* for 15 min to sediment any remaining tissue structures. Nucleic acids were quantified with a fluorometric technique described by Wagner et al. (1998). Seventy-five-microlitre aliquots of the supernatant from each microtube were combined with 75 µL of ethidium bromide (ISC Bioexpress C-5515-10) in 96-well microplates. A dilution series of 18s, 28s calf liver rRNA (Sigma R-0889) and calf thymus DNA (Sigma D-4764) standards, blanks of 0.1% sarcosyl, and an extracted 9 days posthatch yellow perch homogenate control were also combined with ethidium bromide (75 µL : 75 µL) on each plate. After shaking for 15 min, the microplate was scanned on a fluorescence plate reader (Ex = 545 nm, Em = 575 nm, bandwidth = 9 nm) (IDEXX FCA-VIP, IDEXX Corp., Portland, Me.) to determine total nucleic acid fluorescence in each sample. A volume of 7.5 µL of RNase A (Sigma R-6513) was then added to each well of the microplate. The plate was shaken for 20 min to digest the RNA in each sample and scanned a second time to determine the quantity of DNA in each sample. The fluorescence remaining after the addition of RNase was attributed to DNA only after verification that the addition of DNase yielded background fluorescence values similar to the 0.1% sarcosyl blanks. The fluorescence due to RNA was calculated from the difference in fluorescence between total nucleic acid values and DNA values for each sample. The concentrations of RNA and DNA in each sample were determined from the standard calibration curves run with each plate, and the ratio of total RNA to total DNA (RNA:DNA) in each sample was calculated. To reduce error associated with any one day's reading, only a few of the larvae from an individual tank were read on a given day.

Statistics

Separate statistical analyses were conducted to address our three objectives. All statistical analyses were conducted using SAS software version 6.12 (SAS Institute Inc. 1996). We used 12 larval and eight maternal traits in our analyses (Table 1). The presence of significant maternal effects at hatching in the offspring of the 10 females was determined by multivariate analysis of variance (MANOVA, SAS, Proc GLM) on all larval traits at hatching. The MANOVA was based upon the mean value of each larval trait within each tank for each female nested within her date of fertilization (2 June or 4 June 1998). Significance of MANOVA was determined based upon a Wilks λ statistic with 96 and 259.507 degrees of freedom.

The larval traits that accounted for the observed maternal effects at hatch were determined by univariate analysis of variance (ANOVA, SAS, Proc Mixed) on biologically important larval traits within each tank for each female nested within her date of fertilization. Significance of each ANOVA was determined based upon an *F* statistic with 8 and 48 degrees of freedom.

To determine which female traits correlated with the larval traits that accounted for the observed maternal effects at hatch, we performed a canonical correlation analysis on the female and larval data (SAS, Proc Cancorr). Significance of the overall canonical

Table 3. Mean initial number of eggs (±SD) in each female's replicate tank (n = 6), mean number of offspring at hatching (±SD), and percent hatching success in the 10 yellow perch maternal lines.

Female	Mean initial number of eggs (n = 3)	Mean initial number of offspring (hatching success) (n = 6)	Hatching success (%)
1	2002±14	1615±289	80.7
2	1968±11	89±20	4.5
3	2000±18	896±181	44.8
4	2024±15	1538±133	76.0
5	1392±12	1148±198	82.5
6	2040±12	1269±228	62.2
7	2020±11	1610±290	79.7
8	2002±6	1061±381	53.0
9	2032±14	1379±164	67.9
10	1965±17	1287±188	65.5

correlation analysis was based upon a Wilks λ statistic with 80 and 274.95 degrees of freedom. We report the trait loadings on significant canonical correlation axes only.

Results

The females had a wide distribution of phenotypic traits. Female total length ranged from 216 to 287 mm and female weight ranged from 113 to 261 g. Females ranged in age from 2 to 6 years. GSI ranged from 0.22 to 0.63, while egg production ranged from 11 400 to 36 720 eggs (Table 2). Correlation analysis indicated that female total length, weight, Fulton's condition factor k, body depth, age, and egg production were all positively correlated with one another and negatively correlated with GSI.

Mean hatching success of the eggs was highly variable among the 10 maternal lines. The lowest mean number of offspring observed was for Female 2, representing 4.5% hatching success. Excluding Female 2, given the poor quality of her egg skein, the range of hatching success varied from 44.8% hatching success for Female 3 to 82.5% for Female 5 (Table 3).

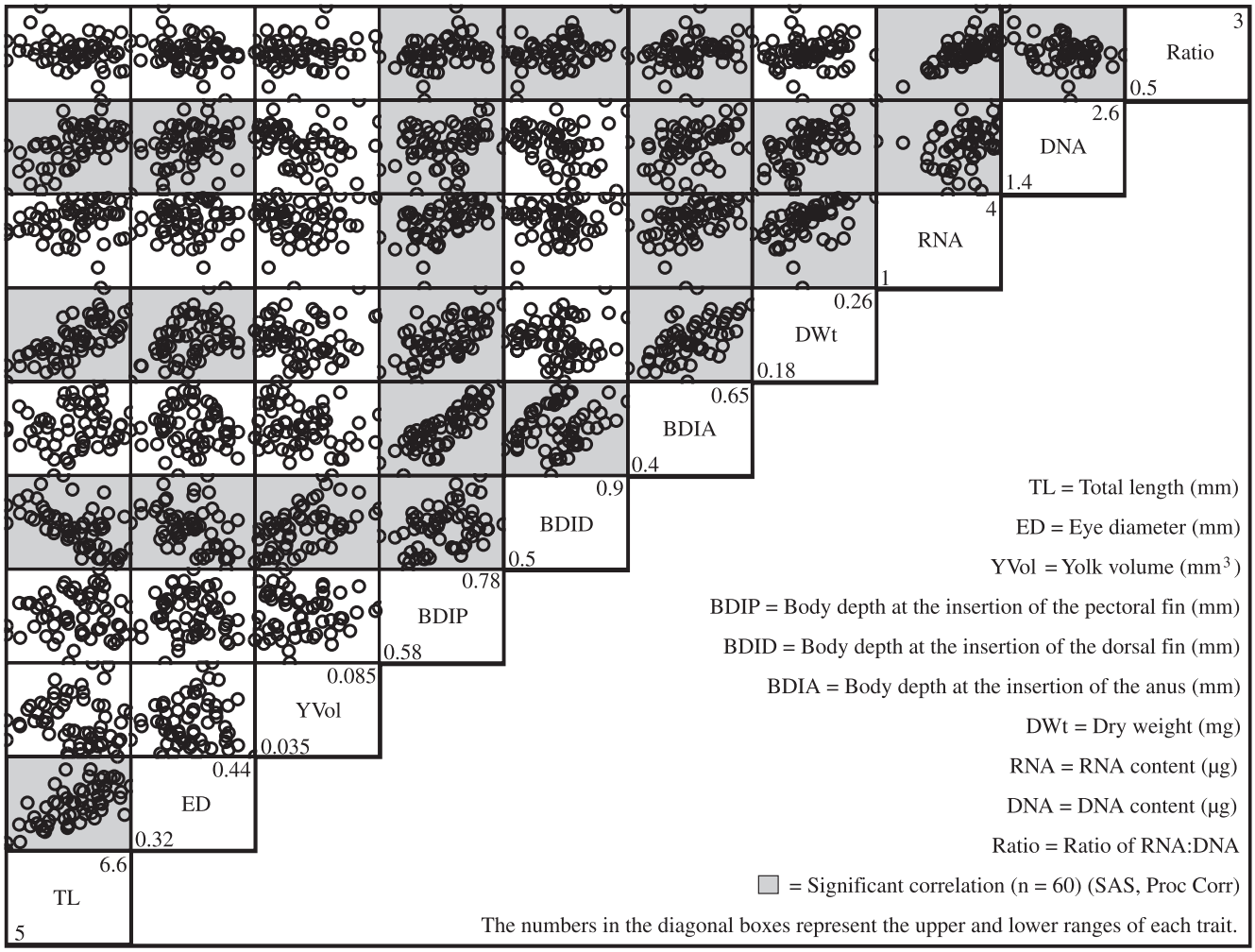
Means (±SD) for each trait are provided (Table 4). Mean larval total length ranged from 5.5 ± 0.43 mm (Female 9) to 6.2 ± 0.39 mm (Female 2). Mean eye diameter varied the least among all females. Female 3 had the lowest mean yolk volume, 0.04 ± 0.012 mm^3, while Female 7 exhibited the highest, 0.07 ± 0.017 mm^3. Mean body depth at the insertion point of the pectoral fin ranged from 0.65 ± 0.081 mm (Female 9) to 0.73 ± 0.088 mm (Female 4), mean body depth at the insertion point of the first dorsal fin ranged between 0.63 ± 0.087 mm (Female 1) and 0.8 ± 0.11 mm (Female 7), and mean body depth at the insertion point of the anus ranged from 0.51 ± 0.078 mm (Female 8) to 0.59 ± 0.079 mm (Female 4). Mean dry weight ranged from 0.19 ± 0.016 mg (Female 9) to 0.24 ± 0.024 mg (Female 7). Mean RNA ranged from 2.7 ± 0.63 μg (Female 9) to 3.8 ± 0.55 μg (Female 7), while DNA ranged from 1.7 ± 0.21 μg (Female 9) to 2.3 ± 0.30 μg (Female 7) between the hatchlings. Despite relatively large differences in the mean quantity of RNA and DNA in the larvae, the mean RNA:DNA only varied between 1.5 ± 0.32 (Female 5) and

Table 4. Mean phenotypic characteristics (±SD) of the yellow perch offspring of the 10 maternal lines sampled at hatching on 14 June 1998.

Female	n	Mean total length (mm)	Mean eye diameter (mm)	Mean yolk sac volume (mm^3)	Mean BDIP (mm)	Mean BDID (mm)	Mean BDIA (mm)	Mean dry weight (mg)	Mean RNA (μg)	Mean DNA (μg)	Mean RNA:DNA
1	80	6.1±0.47	0.38±0.044	0.05±0.015	0.7±0.091	0.63±0.087	0.56±0.083	0.22±0.023	3.4±0.98	2.1±0.34	1.7±0.69
2	70	6.2±0.39	0.39±0.042	0.04±0.014	0.68±0.093	0.64±0.094	0.54±0.021	0.22±0.019	3.2±0.93	2.2±0.30	1.5±0.45
3	78	6.1±0.47	0.39±0.05	0.04±0.012	0.68±0.086	0.66±0.091	0.55±0.087	0.22±0.022	3.4±0.5	2.1±0.37	1.7±0.47
4	81	6.2±0.46	0.38±0.044	0.05±0.015	0.73±0.088	0.67±0.083	0.59±0.079	0.23±0.022	3.4±0.66	2.2±0.29	1.6±0.43
5	76	6.1±0.44	0.39±0.043	0.05±0.015	0.69±0.086	0.64±0.087	0.56±0.081	0.22±0.017	3.2±0.6	2.1±0.25	1.5±0.32
6	77	5.5±0.48	0.42±0.047	0.06±0.012	0.67±0.087	0.75±0.085	0.53±0.069	0.20±0.018	3±0.61	1.9±0.31	1.6±0.71
7	67	6.1±0.41	0.39±0.045	0.07±0.017	0.72±0.077	0.8±0.11	0.57±0.088	0.24±0.024	3.8±0.55	2.3±0.30	1.6±0.29
8	75	5.6±0.4	0.38±0.048	0.06±0.015	0.69±0.091	0.8±0.14	0.51±0.078	0.2±0.019	2.9±0.68	1.8±0.38	1.7±0.67
9	70	5.5±0.43	0.35±0.04	0.05±0.011	0.65±0.081	0.73±0.096	0.51±0.075	0.19±0.016	2.7±0.63	1.7±0.21	1.6±0.41
10	78	5.7±0.42	0.42±0.036	0.07±0.014	0.69±0.096	0.76±0.112	0.51±0.081	0.21±0.018	3.3±0.53	1.9±0.42	1.8±0.78

Note: Trait abbreviations are as defined in Table 1.

Fig. 1. Bivariate correlations among 10 larval traits of yellow perch. Data plotted are mean values of each trait based on analysis of between 67 and 81 larvae in each of 60 tanks that comprised the experiment.



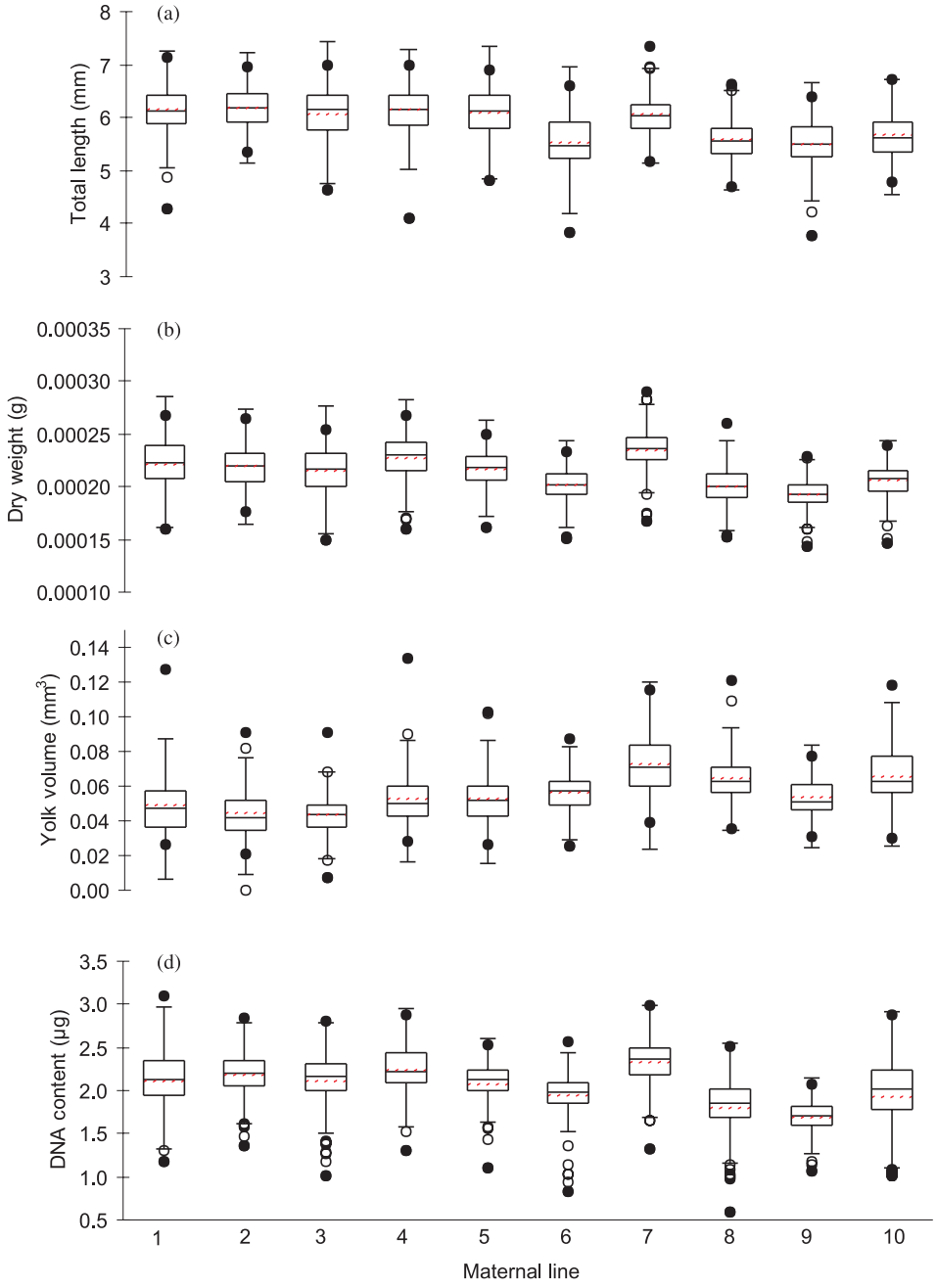
1.8 ± 0.78 (Female 10) among the offspring of the 10 maternal lines.

Correlation analysis of tank mean values for 10 larval traits showed a highly variable covariance structure (Fig. 1). Some trait pairs were highly correlated (e.g., larval body depth at the insertion of the pectoral fin and larval body depth at the insertion of the anus (r = 0.8297, n = 60, p = 0.0001), larval total length and larval dry weight (r = 0.7093, n = 60, p = 0.0001), and RNA and RNA:DNA (r = 0.7406, n = 60, p = 0.0001)). Both negative and positive correlations were present in the morphometric data (Fig. 1). However, other trait pairs exhibited no significant correlation (e.g., larval total length and larval yolk volume (r = –0.1309, n = 60, p = 0.3188) and larval yolk volume and larval dry weight (r = 0.0527, n = 60, p = 0.6893)). Nucleic acid based traits showed strong correlations internally. However, with the exception of a correlation between DNA and larval dry weight, there were only weak correlations between nucleic acid based traits and morphometric traits.

We were able to reject the null hypothesis of no overall maternal effect among the offspring of the 10 maternal lines for larval traits based upon MANOVA results ($F_{96,\ 259.507}$ = 2.21, p = 0.0001). Univariate ANOVAs indicated an overall significant difference between the offspring of the 10 maternal lines for larval total length, larval yolk volume, larval dry weight, and DNA (Table 5; Fig. 2).

There was a significant canonical correlation between the maternal and larval traits ($F_{80,\ 274.95}$ = 4.51, p = 0.0001). The canonical correlation analysis indicated that canonical correlation axes I, II, and III were the only significant correlations, with canonical correlation axis I explaining 54% of the variance, canonical correlation axis II explaining 33.6%, and canonical correlation axis III explaining 5.5% of the variance. Because canonical correlation axis III explained only 5.5% of the variance, we did not consider it further. The female traits age, GSI, and egg production were strongly associated with the Female I canonical correlation. Female age and egg production were weighted negatively on canonical correlation Female I, while GSI was weighted positively (Table 6). The canonical correlation Female II was a strong positive descriptor of female size and age (Table 6). The larval traits larval total length, larval yolk volume, and larval body depth at the insertion of the first dorsal fin were strongly associated with the Larval I canonical correlation. Larval total length was weighted positively on canonical correlation Larval I, while larval yolk volume and larval body depth at the insertion of the first dorsal fin were weighted negatively on the axis (Table 7). The canonical correlation

Fig. 2. Box and whiskers plot of (*a*) total length, (*b*) dry weight, (*c*) yolk sac volume, and (*d*) DNA content of yellow perch offspring from 10 maternal lines at hatching. The upper and lower limits of the box represent the third (Q_3) and first (Q_1) quartiles, respectively. The solid horizontal line within the box represents the median value of the data. The dashed horizontal line within the box represents the mean value of the data. The upper and lower extremes of the whiskers represent ($Q_3 + 1.5(Q_3 - Q_1)$) and ($Q_1 - 1.5(Q_3 - Q_1)$), respectively. Data outside the whiskers are considered outliers and are represented by open circles. Solid circles represent the minimum and maximum values of the data.



Larval II was a strong positive descriptor of larval size and nucleic acid content (Table 7).

Furthermore, 54% of the variation that we observed among the larvae of the 10 maternal lines was explained most by differences in larval total length, larval yolk volume, and larval body depth at the insertion of the first dorsal fin and was associated most with differences in female GSI, egg production, and age (Table 8). An additional 33.6% of the variation among the larvae of the 10 maternal lines was expressed most in larval size (particularly larval dry weight) and nucleic acid content and was most associated with differences in female size and age (Table 8).

Discussion

We detected significant maternal effects at hatch among the offspring of the 10 yellow perch females. Analyses indicate that these effects likely result from differences among

Table 5. Univariate ANOVA results for tests of significant yellow perch maternal effects, for individual larval traits, among the offspring of the 10 maternal lines (n = 752).

Larval trait	AIC	F	Pr > F
Mean total length	7.41	5.86	0.0001
Mean eye diameter	75.80	0.55	0.81
Mean yolk volume	199.12	3.45	0.0032
Mean BDIP	104.28	1.69	0.12
Mean BDID	98.11	2.04	0.062
Mean BDIA	103.48	1.62	0.14
Mean dry weight	178.72	10.78	0.0001
Mean RNA	–49.65	1.68	0.13
Mean DNA	18.14	7.31	0.0001
Mean RNA:DNA	–17.74	0.00	1.0

Note: Trait abbreviations are as defined in Table 1. Univariate tests were performed with 8 and 48 degrees of freedom. AIC, Akaike's information criterion.

Table 6. Canonical correlation analysis: female loading results for the eight female phenotypic traits of the 10 female yellow perch.

	Canonical correlation	
Female trait	Female I	Female II
Total length	0.0140	0.5477
Weight	–0.0476	0.4185
Fulton's condition factor k	–0.0474	–0.1657
Age	–0.4114	0.4898
GSI	0.6980	–0.0551
Egg production	–0.5160	0.0808
FBD_1	0.0800	0.4096
FBD_2	–0.1976	0.4985

Note: Trait abbreviations are as defined in Table 1.

females in size, age, GSI, and egg production. Furthermore, larvae expressed the maternal effects by differences in larval total length, larval yolk volume, larval dry weight, and DNA quantity. However, we found no significant differences in egg volume or egg yolk volume among the eggs from the different females.

Previous research on maternal effects has focused largely on correlations between the phenotypic traits of the female and the phenotypic traits of her eggs. There has been substantially less focus on the relationship between female phenotypic traits and the phenotypic traits of her offspring, both immediately following hatching and throughout the larval stage. This focus is perhaps driven by the need of fisheries scientists to predict recruitment as early as possible in the fish's ontogeny and by the underlying hypotheses that egg size is predictive of larval size and subsequent performance (see reviews by Chambers and Leggett 1996; Chambers and Waiwood 1996). Also, propagule size is an obvious expression of maternal effects that should correlate with the female's phenotype (Bernardo 1996; Solemdal 1997). In light of this, our failure to detect maternal effects in egg volume or egg yolk volume of yellow perch is surprising. The most likely explanation for the absence of a relationship between either egg volume or egg yolk volume and maternal phenotype or larval phenotype is the reproductive style of yellow perch. Yellow perch females release an egg skein in

Table 7. Canonical correlation analysis: larval loading results for the 10 larval phenotypic traits from the 10 yellow perch maternal lines.

	Canonical correlation	
Larval trait	Larval I	Larval II
Total length	0.6226	0.4855
Eye diameter	0.4139	0.2733
Yolk volume	–0.6858	0.4244
BDIP	0.2217	0.4417
BDID	–0.7681	0.2451
BDIA	0.3847	0.3566
Dry weight	0.3887	0.7954
RNA	0.1192	0.5172
DNA	0.4416	0.7385
RNA:DNA	–0.1574	0.0429

Note: Trait abbreviations are as defined in Table 1.

Table 8. Canonical correlation analysis: correlation results between the female canonical correlations and the individual larval traits for the 10 yellow perch maternal lines.

	Canonical correlation	
Larval trait	Female I, driven by female GSI (+) and female egg production (–)	Female II, driven by female size and age (+)
Proportion of variance (%)	54	33.6
Total length	0.5852	0.4410
Eye diameter	0.3891	0.2483
Yolk volume	–0.6446	0.3856
BDIP	0.2804	0.4013
BDID	–0.7220	0.2226
BDIA	0.3616	0.3240
Dry weight	0.3653	0.7226
RNA	0.1120	0.4698
DNA	0.4151	0.6710
RNA:DNA	–0.1480	0.0390

which their eggs are suspended in a matrix of gelatinous material. While it is not clear how reproductive energetic investment is partitioned between the individual eggs and the skein material, it is obvious that as fecundity increases, the quantity of egg skein produced must also increase to accommodate additional eggs. Therefore, the assumption that egg volume is related to GSI cannot be made, and it is likely that differences in yellow perch GSI and egg production do not translate to differences in egg size. We also believe that our lack of data on egg traits partially accounts for the results observed. Had we been able to collect more data on a larger sample size, or on a wider array of the females' egg traits (e.g., dry weight, protein content, nucleic acids content, and lipid content), maternal effects in the egg stage of yellow perch may have been expressed.

Our inability to detect maternal effects in the egg volume or egg yolk volume of yellow perch was not a precursor to a lack of detectable maternal effects in the newly hatched off-

spring. Differences in the phenotypic traits of the hatchlings from the 10 maternal lines were significantly explained by differences in the phenotypic traits of the females. Previous research on other species has shown that maternal effects were expressed in hatching length, size, yolk sac volume, and oil globule volume (Chambers et al. 1989; Buckley et al. 1991; Chambers and Leggett 1996). Our findings suggest that in yellow perch, maternal effects are expressed most in larval length, yolk sac volume, dry weight, and DNA content. We can ignore the expression of maternal effects in larval body depth at the insertion of the first dorsal fin because this measure is inclusive of the yolk sac and is likely to be driven by yolk sac volume. Also, since the quantity of DNA in a cell is relatively constant within a given species, we expect a higher number of cells in larger larvae than in smaller larvae, and thus a higher quantity of DNA. Therefore, there should be a correlation between larval size and DNA content. Thus, if maternal effects were expressed in one trait, they would be expressed in the other. Near allometric relationships have been shown between larval length and total DNA for capelin, cunner (*Tautogolabrus adspersus*), and radiated shanny (*Ulvaria subbifurcata*) (Pepin et al. 1999); our results provide further evidence for this pattern.

A lack of significant maternal effects in the RNA content and RNA:DNA of the hatchlings from the 10 maternal lines indicates that condition of larvae was not significantly different at hatching. This suggests that differences in protein synthesis may not be exhibited until larvae begin feeding on exogenous food sources, or perhaps until they have utilized much of their endogenous food source. Changes in condition are likely to occur at different rates once the larvae begin depleting their yolk sacs and body reserves and begin first feeding. Such variability in RNA:DNA of first-feeding larvae has been shown for Atlantic herring (*Clupea harengus*) (Clemmensen 1994), Iberian sardine (*Sardina pilchardus*) (Chicharo 1998), and red drum (*Sciaenops ocellatus*) (Rooker et al. 1997).

Female GSI, age, size, and egg production are the key female phenotypic traits that explained differences in the size, yolk sac volume, and DNA content of offspring. Correlation analyses and canonical correlation analyses indicate a potential trade-off between the GSI of the female and her age, size, and egg production. It appears that old, large females with high egg production exhibit low GSI values, whereas younger, smaller females have high GSI values while producing fewer eggs. Ideally, such conclusions would be drawn from a larger sample size of females; however, the depressed Lake Michigan spawning stock was a severe limiting factor in conducting this research. However, despite a small sample size of females, the distribution of female traits used in our experiments was representative of the 1998 adult spawning population in Lake Michigan (Pradeep Hirethota, WDNRFU, Milwaukee, WI 53204, U.S.A., personal communication).

The strong association between larval total length and larval yolk sac volume and female GSI, egg production, and age suggests that it is these female traits that potentially determine the length and amount of yolk a larva may have at hatching. Additionally, the association between female size and age and larval size, as measured mostly by dry weight, and nucleic acid content suggests that it is these female traits that potentially determine the size and amount of nucleic acids of a larva at hatching. On average, older, larger females with high fecundity and low GSI were found to produce offspring that were short with large yolk sacs and high quantities of body reserves, as measured by dry weight and total DNA content. These results suggest that the traits of larvae produced by inexperienced spawners (i.e., spawners of a young age) may be very different from the traits of larvae produced by experienced spawners. While previous studies of maternal effects have not shown trade-offs between larval characteristics that are driven by female characteristics, some correlations have been found. Larval size has been positively correlated with female size (Bernardo 1996), and female size and age have been positively correlated with fecundity (Hislop 1988; Buckley et al. 1991; Chambers and Waiwood 1996).

The correlation between canonical correlation Female I and the larval traits from the canonical correlation analysis clearly identifies a trade-off between hatchling total length and larval yolk sac volume. Further, evidence for this trade-off is observed in the box plots for hatchling total length and yolk volume. Across all maternal lines, except Maternal Line 7, those hatchlings with a mean total length greater than the grand mean exhibited mean yolk volumes less than the grand mean, and vice versa. The nonsignificant correlation between larval total length and yolk volume is likely due to the offspring of Maternal Line 7, which exhibited mean total lengths and mean yolk volumes that were greater than the grand means. It is not clear why the offspring of Maternal Line 7 did not exhibit the same pattern as offspring from the other maternal lines. Despite these correlation results, there is a trend in the data suggesting that a negative relationship between larval total length and yolk volume does exist. The trade-off between larval size and yolk volume, when coupled with the strong positive association between larval yolk volume and larval dry weight and DNA content, has potentially substantial implications on the larvae's vulnerability to starvation and predation.

Larger larvae may have an advantage over smaller larvae in that they have been shown to swim faster and thus avoid predators more easily, search greater distances for food, capture larger sizes and quantities of prey, and survive periods of food shortages longer (Miller et al. 1988; Chambers et al. 1989; Chambers and Leggett 1996). However, this does not take into consideration the dangers of initial starvation or the consequences of potential spatial and temporal overlap with prey. Should a larva be faced with a lack of food within a few days of hatching, it will be solely dependent upon its remaining yolk sac and body reserves for survival. Our results indicate that a trade-off exists between larval size and yolk volume that is driven by key characteristics of the female spawning stock. Under circumstances of persistent food limitation after hatching, we would expect smaller larvae with larger yolk sacs and high quantities of body reserves, like those produced by older, larger females, to have a survival advantage over larger larvae with smaller yolks and less body reserves, in terms of starvation. However, assuming that the food limitation is not indefinite, then we would begin to expect the larger larvae to again have a survival advantage over the smaller larvae as feeding and predator avoidance begin to become important. This suggests that po-

tentially, bigger, as measured by total length, may not necessarily be better in all cases.

Heavily exploited fisheries, especially those that target faster growing, larger females, will be much more susceptible to phenotypic bottlenecking of the female population and subsequently may be at higher risk to recruitment failure when environmental conditions shift. Solemdal (1997) argued that overfishing of the female portion of the spawning stock will cause a population to shift from its fitness peak, since maternal effects are phenotypic. We believe that overfishing of the female portion of the Lake Michigan yellow perch population imposed a phenotypic bottleneck on the population, which was a strong component of the causes of the recruitment failure. The Lake Michigan ecosystem has dramatically changed over the past decade and a half with the introduction of many new exotic species, particularly the zebra mussel (*Dreissena polymorpha*), and it is likely that changes in the environment and high fishing pressure have resulted in stresses on the yellow perch population that contributed to the declines in abundance.

We conclude that the distribution of Lake Michigan yellow perch larval traits at hatching is linked to maternal influences. However, the larval traits that confer a survival advantage likely vary from year to year according to the biotic and abiotic conditions in the lake. The distribution of larval traits artificially selected for through high fishing pressure may not be sufficient for adequate survival and successful recruitment in some years. Therefore, it would be best to manage for a diverse female age and size structure to protect against the inherent environmental uncertainty that exists in nature and to ensure an adequate level of recruitment each year. Managing for diversity of phenotypic traits in commercially valuable species that have declined in abundance is not a new concept. For example, it has been suggested that contributions to sustained annual recruitment of Chesapeake Bay striped bass (*Morone saxatilis*) can result from the maintenance of a diverse female age structure (Secor 2000). No single recruitment mechanism is likely to be responsible for recruitment variation and failure. Rather, a combination of many mechanisms is likely responsible (Leggett and Deblois 1994). However, Solemdal (1997) has argued that because of the complex nature of recruitment mechanisms, maternal effects may be the only recruitment mechanism that can be effectively managed in a fishery through regulation.

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