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Parental effects on early life history traits of haddock *Melanogrammus aeglefinus*

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Gametes from five male and three female haddock (*Melanogrammus aeglefinus*) were crossed to produce 15 half-sibling families that were used to evaluate potential parental contributions to early life history variability. Larval morphology at 0 and 5 days post-hatch (dph) and time to starvation in the absence of food were examined. Maternal influences on larval standard length and yolk area were significant at 0 and 5 dph. Paternal effects on larval standard length were significant at 0 and 5 dph, whereas paternal effects on yolk area were only significant at 5 dph. Larval eye diameter was influenced by maternity at day 0 post-hatch and by both maternity and paternity at 5 dph. Myotome height of larvae was subject to maternal and paternal influences at 0 and 5 dph. Growth rate was significantly influenced by both paternity and maternity. Yolk utilization efficiency was significantly influenced by parental interaction, while the time taken for larvae to die in the absence of food was affected only by maternity. Results of this study not only confirm the importance of female contributions to larval development but also indicate a paternal influence on the development and the early life history success of marine fish.

Keywords: growth rate, haddock, hatch rate, larval morphology, parental effects, yolk utilization efficiency.

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Introduction

Recruitment success of marine fish may be determined during the larval stage, when mortality rates are highest (Hjort, 1914; Gulland, 1965; McGurk, 1986; Leggett and Deblois, 1994). Larval survival is strongly influenced by morphological traits such as body size and yolk supply, as well as metabolic traits such as growth rate and yolk utilization efficiency. Large larvae have swimming capabilities superior to those of small larvae and, consequently, may be more successful in the search for prey and avoidance of predation (Blaxter, 1986; Houde, 1987; Pepin and Myers, 1991; but also see Litvak and Leggett, 1992), and their larger yolk supply may improve their ability to withstand starvation during periods of low prey abundance (Theilacker, 1981; Rana, 1985). Fast growth results in a shorter time to metamorphosis (i.e. less time spent in the highly susceptible larval stage) and may increase the probability of survival. Understanding the factors that influence larval morphology and metabolism could improve our understanding of recruitment variability.

Phenotypic variation is a product of both environmental and parental influences. The latter can be separated into two key attributes: the genetic endowment of the offspring by its parents and the "direct affection of the offspring's phenotype through the phenotype of its parents" (Bernado, 1996). Many aspects of the parental phenotype may impact the offspring including nutrition, condition, size, and behaviour (Bernado, 1996). In marine fish, parental effects have been demonstrated on egg size (Ferguson *et al.*, 1995; Chambers and Leggett, 1996; Marteinsdottir and Steinarsson, 1998; Vallin and Nissling, 2000; Vøllestad and Lillehammer, 2000; Heyer *et al.*, 2001; Pakkasmaa *et al.*, 2001), egg survival (Nagler *et al.*, 2000), larval standard

length at hatch (Panagiotaki and Geffen, 1992), yolk size (Rideout *et al.*, 2004a), age of metamorphosis, age at first-feeding, age of maturation (Bradford and Peterman, 1987; Marteinsdottir and Steinarsson, 1998), and even migratory behaviour (Kallio-Nyberg *et al.*, 2000).

Haddock (*Melanogrammus aeglefinus*) support important North Atlantic fisheries and the species is a candidate for mariculture in temperate waters (Hamlin *et al.*, 2000). Knowing the impact of parental effects may increase our ability to estimate the reproductive potential of wild stocks (Trippel, 2003a), as well as enhance breeding programme design for aquaculture (Trippel, 2003b). For haddock, significant differences in egg size and weight exist among females (Hislop, 1988), and larger eggs hatch into larger larvae (Rideout *et al.*, 2005). In addition, significant paternal effects have been demonstrated for larval standard length, myotome height, jaw length, and yolk size (Rideout *et al.*, 2004a).

Since the maternal contribution to the fertilized egg is much greater than the paternal contribution (i.e. sperm contain virtually no extra-nuclear material), it is commonly assumed that the impact of maternal effects largely overwhelms paternal effects (Thorpe and Morgan, 1978; Chambers and Leggett, 1996). However, only a few authors have assessed the relative importance of paternal and maternal effects during early life (e.g. Saillant *et al.*, 2001; Trippel *et al.*, in press). In this study, crossing of sperm and eggs from multiple males and females in a factorial design allowed the simultaneous evaluation and comparison of potential maternal and paternal influences on the variability of haddock early life history traits: hatching success, larval morphometrics, growth rate, yolk utilization efficiency, and starvation resistance.

Material and methods

Ripe female and male haddock were collected by bottom trawl from Georges Bank (41.402°N 66.109°W) using the RV *Alfred Needler* on 21 February 2003. Fork length and body weight of the parents were recorded (Table 1). Within three hours of collection, eggs from each of three randomly chosen females were subdivided into five portions of equal size in 250-ml beakers and fertilized with sperm of five random males to produce 15 half-sibling families. Eggs were fertilized with a few drops of semen to achieve a concentrated sperm/egg ratio that yielded maximum fertilization success. Each beaker was filled with 200 ml of filtered seawater. Eggs and sperm in the beakers were gently stirred for one minute using a glass rod. After fertilization, eggs were transferred to 450-ml glass jars. Excess sperm and dead eggs were removed with a large pipette.

Eggs were held at 6°C with daily water changes. Dead eggs were removed and stored, starting at 3 days post-fertilization (dpf). At 7 dpf, the research vessel returned to port, and all surviving eggs of each of the 15 families were subdivided into five replicates in 250-ml beakers containing an average of 260 larvae (standard deviation = 82.6). The 75 replicates were randomly arranged in a temperature-controlled room (6°C) with 24-h low-level fluorescent light (approximately 30 lux). Water within the beakers was exchanged every second day. Dead eggs and hatched larvae were enumerated and removed daily.

Egg diameters were measured at 8 dpf (40× magnification). About 5–20 larvae from each replicate were sampled on 0 and 5 dph. Larvae were stored in 2.0% formaldehyde for approximately four weeks. A total of 835 larvae was sampled on 0 dph and 755 larvae on 5 dph. All larvae were individually photographed (100× magnification) after 27 or 28 days of preservation with a digital camera attached to a stereomicroscope. Image analysis software (OPTIMAS™ 6.2) was used to determine (i) larval standard length (SL), the distance from tip of snout to tail end of notochord, (ii) yolk area (YA), (iii) eye diameter, and (iv) myotome height.

Growth rate (daily length increment) for each half-sibling family was calculated as the difference in mean standard lengths between 0 and 5 dph, divided by 5, the time period between sampling.

Yolk utilization efficiency (YUE) (Hardy and Litvak, 2004) was calculated using the following equation:

$$\mathrm{YUE} = \frac{\left(\mathrm{SA}_{\mathrm{day}\ 5} - \mathrm{SA}_{\mathrm{day}\ 0}\right)}{\left(\mathrm{YA}_{\mathrm{day}\ 0} - \mathrm{YA}_{\mathrm{day}\ 5}\right)},$$

where SA is somatic body area and YA is yolk area.

To estimate time to starvation, 5–25 larvae from each family replicate were placed in 50-ml beakers and arranged in a random pattern. Larvae were kept under 24-h fluorescent light (approximately 30 lux) at 6°C. Three-quarters of the water within each beaker was changed every third day. With a disposable pipette, dead larvae were counted and removed daily. Mean time to starvation of each family replicate was calculated as the arithmetic mean of days until death of individual larva within each beaker.

Table 1. Sex, fork length, and body weight of eight adult haddock used in factorial crossing of gametes.

			Egg diameter	
Fish #	Length (cm)	Weight (g)	Mean	*n*
Female 1	54	1 704	1.579	58
Female 2	55	1 724	1.539	66
Female 3	57	2 230	1.505	68
Male 1	56	2 062	–	–
Male 2	53	1 516	–	–
Male 3	55	1 666	–	–
Male 4	56	1 898	–	–
Male 5	60	2 048	–	–

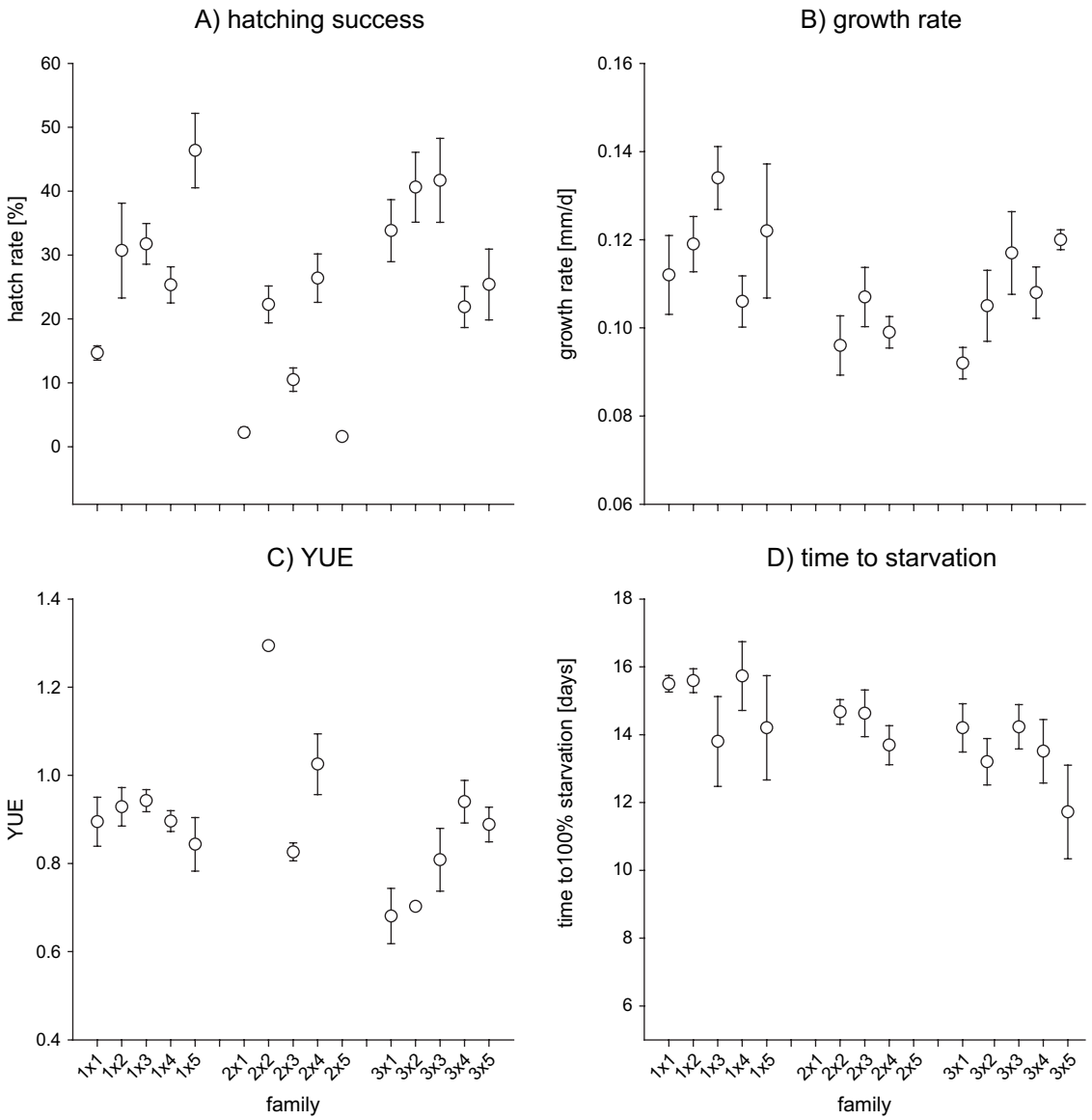

Figure 1. Half-sibling family means of larval morphometrics at 0 dph and 5 dph. Families are labelled with the first label number designating females 1−3 and second label number designating males 1−5. Error bars represent standard error. $n = 5$ for all half-sibling family means except for families 1×3 ($n = 4$), 2×1 ($n = 1$), 2×3 ($n = 3$), 2×5 ($n = 2$), and 3×5 ($n = 4$) at 0 dph and families 1×3, 2×3, 3×3, and 3×5 at 5 dph ($n = 4$).

Statistical analysis

Mean egg diameters of the three females were compared using one-way analysis of variance (ANOVA). Maternal and paternal contributions to hatching success, larval morphology growth rate, and time to starvation were analysed with a model II two-way ANOVA. Significance levels were set at $p = 0.05$ for main effects and $p = 0.20$ for sire−dam interactions in order to minimize the potential for a type II error (Winer, 1971). In cases of significant sire−dam interaction terms, one-way ANOVAs for each male and female pair were performed to resolve the maternal and paternal contributions to variability in progeny performance. Sample sizes of $n < 3$ (families 2×1 and 2×5) were excluded from the analyses. Variation in larval traits was broken down into male, female, male × female interaction, and error components (Sokal and Rohlf, 1995).

Results

Adult fork length ranged from 53 to 60 cm and body weight from 1516 to 2062 g (Table 1). Egg diameter ranged from

Table 2. Summary of model II two-way ANOVAs performed for larval morphometrics, growth rate, YUE, and mean time to starvation. Female and male represent independent variables (factors), where female represents maternal origin and the male represents paternal origin of half-sibling family larvae. SS = sum squares, d.f. = degrees of freedom, MS = mean squares, F = critical values, p = probability of significance, and % = relative variance components. Italic p-values are below significance threshold of $\alpha = 0.05$. SL = standard length, YA = yolk area, ED = eye diameter, MH = myotome height, YUE = yolk utilization efficiency, GR = growth rate, 0 dph = first day of hatch, and 5 dph = five days post-hatch.

Variable	Source of variation	SS	d.f.	MS	F	p	%
Hatch rate	Female	1.197	2	0.598	47.3	*<0.001*	35.1
	Male	0.363	4	0.091	7.17	*<0.001*	3.3
	Female × male	0.943	8	0.118	9.32	*<0.001*	38.5
	Error	0.759	60	0.0127			23.1
SL (0 dph)	Female	0.280	2	0.140	49.0	*<0.001*	54.8
	Male	0.158	4	0.039	13.8	*<0.001*	22.6
	Female × male	0.022	8	2.4×10^{-3}	0.90	0.522	0.0
	Error	0.154	49	3.2×10^{-3}			22.6
SL (5 dph)	Female	0.327	2	0.163	51.8	*<0.001*	64.4
	Male	0.053	4	0.013	4.23	*0.002*	6.7
	Female × male	0.018	6	3.1×10^{-3}	0.82	0.561	0.9
	Error	0.172	46	4.2×10^{-3}			27.9
YA (0 dph)	Female	0.147	2	0.073	4.05	*0.017*	29.0
	Male	0.075	4	0.019	1.01	0.403	5.6
	Female × male	0.111	6	0.018	3.74	*0.004*	20.7
	Error	0.243	49	5.4×10^{-3}			44.6
YA (5 dph)	Female	0.024	2	0.012	7.67	*<0.001*	22.2
	Male	0.020	4	5.1×10^{-3}	3.24	*0.012*	15.3
	Female × male	0.010	6	2.2×10^{-3}	1.60	0.167	6.7
	Error	0.047	46	1.1×10^{-3}			55.8
ED (0 dph)	Female	8.7×10^{-4}	2	4.4×10^{-4}	5.00	*0.007*	22.0
	Male	3.0×10^{-4}	4	7.5×10^{-5}	0.87	0.483	3.0
	Female × male	7.1×10^{-4}	8	8.8×10^{-5}	1.24	0.295	4.0
	Error	3.5×10^{-3}	49	7.1×10^{-5}			71.0
ED (5 dph)	Female	5.2×10^{-2}	2	5.2×10^{-2}	239.2	*<0.001*	83.2
	Male	3.4×10^{-3}	4	1.7×10^{-3}	7.66	*0.001*	2.2
	Female × male	3.1×10^{-3}	6	5.2×10^{-4}	2.39	*0.042*	2.7
	Error	1.1×10^{-2}	46	2.2×10^{-4}			11.7
MH (0 dph)	Female	2.6×10^{-2}	2	1.3×10^{-2}	22.1	*<0.001*	13.9
	Male	1.1×10^{-2}	4	2.7×10^{-3}	4.66	*0.003*	71.6
	Female × male	6.3×10^{-3}	8	7.9×10^{-4}	1.37	0.234	1.1
	Error	2.8×10^{-2}	49	5.8×10^{-4}		13.40	13.4
MH (5 dph)	Female	6.3×10^{-3}	2	3.3×10^{-3}	31.5	*<0.001*	1.1
	Male	1.4×10^{-3}	4	4.2×10^{-4}	3.07	*0.015*	6.0
	Female × male	1.1×10^{-3}	6	2.1×10^{-4}	1.22	0.314	4.3
	Error	4.3×10^{-3}	45	4.3×10^{-4}			88.5
YUE	Female	0.096	2	0.096	6.31	*0.016*	13.8
	Male	0.056	4	0.028	1.85	0.171	9.5
	Female × male	0.284	6	0.047	3.10	*0.014*	28.0
	Error	0.594	39	0.015			48.6
GR	Female	3.2×10^{-3}	2	1.4×10^{-3}	4.45	*0.017*	15.3
	Male	3.1×10^{-3}	4	1.0×10^{-3}	2.70	*0.043*	13.1
	Female × male	1.4×10^{-3}	6	3.4×10^{-4}	0.63	0.709	5.6
	Error	0.014	46	2.7×10^{-4}			66.0
Time to starvation	Female	30.2	2	15.1	4.87	*0.027*	10.9
	Male	18.9	4	4.73	1.53	0.318	2.4
	Female × male	18.6	6	3.10	0.79	0.580	3.6
	Error	191.4	49	3.91			83.1

Table 3. Summary of one-way ANOVA results for hatching success. To investigate for maternal and paternal effects, half-sibling family means were grouped by males and females, respectively, comparing offspring of three females within each male and offspring of five males within each female. SS = sum squares, d.f. = degrees of freedom, MS = mean squares, and F and p are critical values and probability of significance tests, respectively. Italic p-values are below significance threshold of $\alpha = 0.05$.

Grouping by	Source of variation	SS	d.f.	MS	F	p
Female 1	Between males	0.330	4	0.083	5.71	*0.003*
	Within males	0.289	20	0.014		
	Total	0.619	24			
Female 2	Between males	0.780	4	0.195	29.7	*<0.001*
	Within males	0.131	20	0.007		
	Total	0.912	24			
Female 3	Between males	0.195	4	0.049	2.88	*0.049*
	Within males	0.338	20	0.017		
	Total	0.533	24			
Male 1	Between females	0.56	2	0.28	42.4	*<0.001*
	Within females	0.079	12	0.007		
	Total	0.639	14			
Male 2	Between females	0.102	2	0.051	2.42	0.131
	Within females	0.254	12	0.021		
	Total	0.356	14			
Male 3	Between females	0.377	2	0.189	16.5	*<0.001*
	Within females	0.137	12	0.011		
	Total	0.514	14			
Male 4	Between females	0.008	2	0.004	0.50	0.619
	Within females	0.098	12	0.008		
	Total	0.106	14			
Male 5	Between females	1.090	2	0.546	34.3	*<0.001*
	Within females	0.191	12	0.016		
	Total	1.280	14			

1.51 to 1.58 mm (Table 1) and differed significantly among females (one-way ANOVA, $F_{2,163} = 264.0$, $p < 0.001$).

Peak hatch occurred at 20 dpf. Hatching success was highly variable, ranging from 1.6% for family 2×5 to 46.4% for family 1×5 (Figure 1). A significant sire−dam interaction was observed for hatching success (Table 2). Consequently, one-way ANOVAs were run to test for differences in hatching success between half-sibling progenies. For all three females, hatching success was influenced significantly by paternity, while maternal effects were revealed only in three of five males (Table 3).

Mean larval standard length of each half-sibling family ranged from 3.99 to 4.29 mm at hatch and from 4.56 to 4.81 mm at 5 dph (Figure 2). Significant maternal and paternal effects were evident for both sampling days, while no significant parental interaction term was detected (Table 2).

Yolk area ranged from 0.462 to 0.807 mm^2 at 0 dph and from 0.083 to 0.182 mm^2 at 5 dph (Figure 2). Owing to a significant male−female interaction between male and female origins, separate one-way ANOVAs were used to analyse the observed variation in yolk area at 0 dph. Sire effects were not significant, while significant dam effects were observed in two of five males (Table 4). At 5 dph, yolk area was influenced by maternity and paternity (Table 2).

Mean eye diameter per half-sibling family ranged from 0.312 to 0.329 mm at 0 dph and from 0.366 to 0.393 mm at 5 dph (Figure 2). Because male−female interactions were significant (Table 2), separate one-way ANOVAs were run for each male and female. At 0 dph, maternal effects were significant only for the crosses with male 4, while sire influence on eye diameter was not significant in any of the crosses (Table 5). At 5 dph, significant maternal effects were found in the crosses with all five males, while the paternal effect was only significant for offspring produced in crosses with female 1.

Mean larval myotome height of each half-sibling family ranged from 0.288 to 0.316 mm at 0 dph and from 0.289 to 3.58 mm at 5 dph (Figure 2). Paternal effects were significant at 0 and 5 dph.

Relative maternal and paternal variance components were highest for larval standard length, eye diameter at 5 dph, and myotome height at 0 dph (Table 2). Variance component analysis further indicated a higher maternal contribution to larval variance in all traits but myotome height.

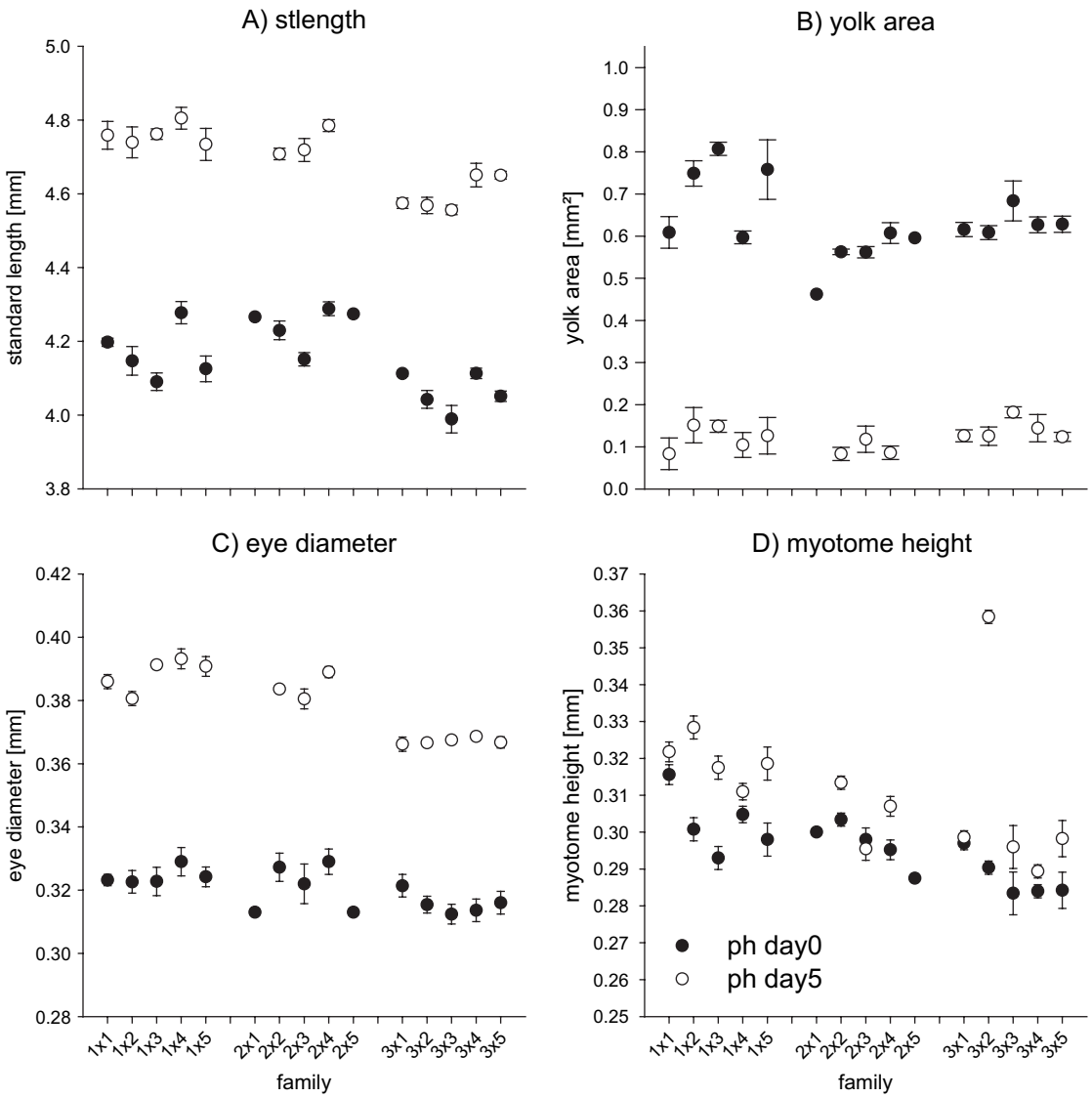

Figure 2. Half-sibling family means of egg and larval performance traits. Families are labelled with the first label number designating females 1−3 and second label number designating males 1−5. Error bars represent one standard error. For hatching success and growth rate $n = 5$ for all half-sibling family means except for families 1×3, 2×3, 3×3, and 3×5 ($n = 4$). For YUE $n = 5$ except for families 1×3, 2×2, 2×3, 3×2, 3×3, and 3×5 ($n = 4$). For time to 100% starvation $n = 5$ except for family 3×5 ($n = 4$).

Growth rate (up to 5 dph) ranged from 0.092 to 0.120 mm d^{-1} for the 15 half-sib families (Figure 1). The interaction between sire and dam was not significant, while both maternal and paternal contributions to larval growth rate were significant (Table 2).

Yolk utilization efficiency ranged from 0.680 to 1.29 (Figure 1) and displayed a significant sire−dam interaction in the two-way ANOVA (Table 2). When analysing the sire−dam interaction with separate one-way ANOVAs, significant sire effects were found within the crosses of females 2 and 3 and significant dam effects were evident within the crosses of male 1 (Table 6). Progeny of male 2 did not provide sufficient data owing to high mortality before hatch.

All larvae in the starvation experiment were dead by 20 dph. Mean time to starvation for the half-sibling groups ranged from 11.7 to 15.7 days (Figure 1) and was significantly influenced by maternity but not paternity (Table 2). The interaction between sire and dam was not significant.

Discussion

The results of this study demonstrate the importance of maternal and paternal effects as well as their interaction

Table 4. Summary of one-way ANOVA results for yolk area. To investigate for maternal and paternal effects, half-sib family means were grouped within males and females, respectively, comparing offspring of three females within each male and offspring of five males within each female. SS = sum squares, d.f. = degrees of freedom, MS = mean squares, F and p are critical values and probability of significance tests, respectively, 0 dph = first day of hatch, and 5 dph = five days post-hatch. Italic p-values are below significance threshold of $\alpha = 0.05$.

		0 dph				
Grouping by	Source of variation	SS	d.f.	MS	F	p
Female 1	Between males	0.100	4	0.025	2.12	0.117
	Within males	0.223	19	0.012		
	Total	0.322	23			
Female 2	Between males	0.006	2	0.003	2.13	0.170
	Within males	0.015	10	0.001		
	Total	0.021	12			
Female 3	Between males	0.018	4	0.004	1.21	0.340
	Within males	0.069	19	0.004		
	Total	0.087	23			
Male 1	Between females	0.000	1	0.000	0.03	0.873
	Within females	0.034	8	0.004		
	Total	0.034	9			
Male 2	Between females	0.094	2	0.047	23.4	*<0.001*
	Within females	0.024	12	0.002		
	Total	0.118	14			
Male 3	Between females	0.104	2	0.052	9.28	*0.006*
	Within females	0.050	9	0.006		
	Total	0.154	11			
Male 4	Between females	0.002	2	0.001	0.57	0.581
	Within females	0.023	12	0.002		
	Total	0.026	14			
Male 5	Between females	0.037	1	0.037	2.49	0.159
	Within females	0.105	7	0.015		
	Total	0.143	8			

on early life history traits of haddock. Previous studies have demonstrated maternal and paternal effects separately for this species (Hislop, 1988; Rideout *et al.*, 2004a). However, few studies have attempted to investigate the effects of maternity and paternity within a single experiment (Saillant *et al.*, 2001; Trippel *et al.*, in press) and to assess their interaction and relative importance to offspring variability.

All nine early life history traits analysed in this study were subject to maternal influence, and eight of these traits were also influenced by paternity. In general, a higher proportion of variance in larval traits was attributable to maternity. Because maternal contributions to progeny can be genetic and phenotype-based (i.e. yolk), it is difficult to attribute maternally derived differences in larval traits to either. In haddock, egg size is influenced by maternal age and nutrition (Hislop, 1988; Trippel and Neil, 2004), and influences various larval morphological traits, including standard length, yolk size, eye diameter, myotome height, and finfold area (Rideout *et al.*, 2005). In contrast, sperm contain virtually no extra-nuclear material and, therefore, any paternally induced differences in larval morphology are genetic in origin. Because of this difference in parental contributions to progeny, Rideout *et al.* (2004a) suggested that paternal effects on the early life history of fish may be overwhelmed by large maternal effects and appear unimportant. Here, however, we clearly demonstrate that, while maternity may have a larger influence, paternity also affects early life history traits to significant extents.

Significant parental interaction terms may indicate a form of incompatibility among parents. This interpretation is supported by the results of the one-way ANOVAs, where significance of maternity or paternity depended on the mate combination. This, in turn, is an indirect evidence of the importance of both males and females on the early life history of progeny. If female effects are significant for crosses with one male but not another, then paternity obviously influences early life history.

Table 5. Summary of one-way ANOVA results for eye diameter. To investigate for maternal and paternal effects, half-sib family means were grouped within males and females, respectively, comparing offspring of three females within each male and offspring of five males within each female. SS = sum squares, d.f. = degrees of freedom, MS = mean squares, F and p are critical values and probability of significance tests, respectively, 0 dph = first day of hatch, and 5 dph = five days post-hatch. Italic p-values are below significance threshold of $\alpha = 0.05$.

		0 dph					5 dph				
Grouping by	Source of variation	SS	d.f.	MS	F	p	SS	d.f.	MS	F	p
Female 1	Between males	1.5×10^{-4}	4	3.6×10^{-4}	0.54	0.707	5.1×10^{-4}	4	1.3×10^{-4}	4.05	*0.015*
	Within males	1.3×10^{-3}	19	6.7×10^{-4}			6.0×10^{-4}	19	3.2×10^{-5}		
	Total	1.5×10^{-4}	23				1.1×10^{-3}	23			
Female 2	Between males	4.9×10^{-5}	2	4.4×10^{-3}	0.40	0.682	1.6×10^{-4}	2	8.0×10^{-5}	3.89	0.053
	Within males	1.1×10^{-3}	9	0.000			2.3×10^{-4}	11	2.1×10^{-5}		
	Total	9.4×10^{-4}	11				3.9×10^{-4}	13			
Female 3	Between males	2.4×10^{-4}	4	5.9×10^{-5}	1.07	0.400	1.7×10^{-5}	4	4.0×10^{-6}	0.35	0.842
	Within males	1.1×10^{-3}	19	5.6×10^{-5}			2.3×10^{-4}	18	1.2×10^{-5}		
	Total		23				2.5×10^{-4}	22			
Male 1	Between females	9.0×10^{-5}	1	4.5×10^{-5}	0.16	0.696	1.0×10^{-3}	1	1.0×10^{-3}	43.3	*<0.001*
	Within females	3.6×10^{-4}	8	4.5×10^{-5}			1.8×10^{-4}	8	2.3×10^{-5}		
	Total	4.5×10^{-4}	9				1.2×10^{-4}	9			
Male 2	Between females	3.4×10^{-4}	2	1.7×10^{-4}	2.62	0.114	7.9×10^{-4}	2	3.9×10^{-4}	37.4	*<0.001*
	Within females	7.7×10^{-4}	12	6.4×10^{-5}			1.3×10^{-4}	12	1.1×10^{-5}		
	Total	1.1×10^{-3}	14				9.2×10^{-4}	14			
Male 3	Between females	2.9×10^{-4}	2	1.4×10^{-4}	1.51	0.272	1.1×10^{-3}	2	5.6×10^{-4}	25.1	*<0.001*
	Within females	8.6×10^{-4}	9	9.5×10^{-5}			2.0×10^{-4}	9	2.2×10^{-5}		
	Total	1.2×10^{-3}	11				1.3×10^{-3}	11			
Male 4	Between females	8.1×10^{-4}	2	4.0×10^{-4}	4.71	*0.031*	1.7×10^{-3}	2	8.6×10^{-4}	37.3	*<0.001*
	Within females	1.0×10^{-3}	12	8.6×10^{-5}			2.8×10^{-4}	12	2.3×10^{-5}		
	Total	1.8×10^{-3}	14				2.0×10^{-3}	14			
Male 5	Between females	2.3×10^{-4}	1	1.1×10^{-4}	3.72	0.095	1.3×10^{-3}	1	1.3×10^{-3}	34.2	*0.001*
	Within females	4.7×10^{-4}	7	5.9×10^{-5}			2.7×10^{-4}	7	3.8×10^{-5}		
	Total	7.1×10^{-4}	8				1.5×10^{-3}	8			

Table 6. Summary of one-way ANOVA results for yolk utilization efficiency (YUE). To investigate for maternal and paternal effects, half-sib family means were grouped within males and females, respectively, comparing offspring of three females within each male and offspring of five males within each female. For male 2 data were not sufficient to perform one-way ANOVA. SS = sum squares, d.f. = degrees of freedom, MS = mean squares, F and p are critical values and probability of significance tests, respectively. Italic p-values are below significance threshold of $\alpha = 0.05$.

Grouping by	Source of variation	SS	d.f.	MS	F	p
Female 1	Between males	0.028	4	0.007	0.68	0.615
	Within males	0.195	19	0.010		
	Total	0.222	23			
Female 2	Between males	0.088	1	0.088	6.08	*0.043*
	Within males	0.101	7	0.014		
	Total	0.189	8			
Female 3	Between males	0.187	3	0.062	3.91	*0.032*
	Within males	0.224	14	0.016		
	Total	0.411	17			
Male 1	Between females	0.114	1	0.114	6.51	*0.034*
	Within females	0.140	8	0.018		
	Total	0.254	9			
Male 2	Between females			Insufficient data		
	Within females					
	Total					
Male 3	Between females	0.043	2	0.021	2.11	0.178
	Within females	0.091	9	0.010		
	Total	0.134	11			
Male 4	Between females	0.043	2	0.022	1.69	0.225
	Within females	0.152	12	0.013		
	Total	0.195	14			
Male 5	Between females	0.005	1	0.005	0.33	0.585
	Within females	0.097	7	0.014		
	Total	0.102	8			

The larval traits for which we observed paternal effects differed slightly from previous studies. For example, Saillant *et al.* (2001) found no paternal influence on standard length, Rideout *et al.* (2004a) found no paternal influence on YUE, and Trippel *et al.* (in press) found a significant paternal effect on starvation resistance. These differences are likely the result of variable parental compatibility owing to the fact that gametes were fertilized artificially (i.e. no natural mate selection) (Wedekind *et al.*, 2001). Because paternity is a random effect in such analyses (i.e. results can vary depending on the parent selected), using a small number of parents can cause the magnitude of parental effects to vary. Factorial experiments with large number of parents could potentially alleviate these problems but would require a huge effort.

Parentally derived differences in progeny morphology may diminish through compensatory growth during the late larval and juvenile stages of marine fish (Chambers and Leggett, 1992; Bertram *et al.*, 1993). In our study, the variability in standard length among half-sib families decreased from 0 to 5 dph (Figure 2), indicating compensatory growth during early larval ontogeny, although parental effects were still evident at 5 dph. Rideout *et al.* (2004a) found paternal effects until 10 dph, but with decreasing sire effect on standard length. Under both high and low prey abundance, Rideout *et al.* (2005) reported that initial differences in haddock egg and larval sizes were still evident at 20 dph. At high prey levels, such initial differences in egg and larval sizes do not appear to influence progeny quality in haddock (Rideout *et al.*, 2004b, 2005), but at low prey levels, these differences can translate into differential survivorship (Rideout *et al.*, 2005). Further work is needed to determine the duration of differential parental influences on progeny morphology, and how these differences could affect early life history success and recruitment in haddock and other marine fish (Clemmesen *et al.*, 2003).

In addition to its potential value in understanding variability in recruitment, examining the relationship between parentally induced variability in larval morphology and life history success can be used to evaluate family progeny performance and aid in the development of broodstock

selection programmes for aquaculture. Many larval morphological parameters are correlated with egg size (Rideout *et al.*, 2005), which may be related to female body size (Trippel and Neil, 2004) and spawning experience (Trippel, 1998), suggesting that the use of large repeat spawning females as broodstock could be beneficial. Optimal nutrition can increase sperm and egg quality and result in increased larval growth and survival (Reznick *et al.*, 1996; Lu and Takeuchi, 2004). It is also important to remember that haddock are serial spawners and that batch number influences egg size (Trippel and Neil, 2004; Rideout *et al.*, 2005). Selecting males in good condition before spawning can ensure high fertilization success (Trippel and Neil, 2004). Apart from using adult phenotype to ensure high gamete quality and early life fitness, the results of traditional family-based breeding programmes that monitor progeny performance through to market size will continue to yield the key genetic-based information necessary for the choice of superior pedigree (Gjerde *et al.*, 2004; Kolstad *et al.*, 2006).

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