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Fatty acid content of eggs determines antipredator performance of fish larvae

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ABSTRACT

Recent work has suggested that provisioning of eggs with certain critical nutrients could be a more meaningful measure of maternal investment and correlate of offspring fitness than traditional measures of egg size. The aim of our study was to assess variability in egg quality and larva quality and to identify connections between them and the implications for larval survival. Egg size, proximate composition, and fatty acid composition were measured for 40 batches of eggs from 8 captive pairs of red drum (Osteichthyes: *Sciaenops ocellatus*). We reared larvae from these batches of eggs to a common size (10 mm total length, 2–3 weeks posthatching) and assessed routine activity and escape response performance of 671 individuals. Egg fatty acid composition varied more than egg size or proximate composition. Concentrations of certain long chain, highly unsaturated essential fatty acids (e.g., arachidonic acid and docosahexaenoic acid) were the only egg traits that were significantly related to larva quality (measured as escape performance). Reduced escape performance of larvae from eggs with low fatty acid concentrations was not compensated by 3 weeks of feeding on a diet enriched with fatty acids, suggesting irreversible developmental effects. Since fatty acids in eggs originate from the maternal diet, offspring survival may be determined in part by availability of nutrient-rich prey to pre-spawning adults. Migrations, regime shifts, and exploitation of marine communities could operate through this mechanism to influence recruitment in fish populations. Our findings underscore the importance of non-genetic maternal contributions to egg quality and the linkage between environmental conditions experienced by adult females and offspring fitness.

1. Introduction

Propagule (or egg) size has been traditionally used as a proxy for per-offspring maternal investment for assessments of life-history strategies (Stearns, 1992). Recent reviews of life-history trade-offs (Zera and Harshman, 2001) and maternal resource allocation (Stephens et al., 2009) suggest that provisioning of eggs with certain critical nutrients could be a more meaningful measure of investment than egg size. For example, higher levels of vitamins and carotenoids in gull eggs reduce oxidative stress in the offspring and thus increase survival (Costantini, 2008; Royle et al., 1999). The amounts of essential fatty acids (those that cannot be synthesized de novo) in fish eggs influence hatching success, early survival, and larval growth rate (Berkeley et al., 2004; Tocher, 2003). This focus on composition rather than size, provides a new perspective on the linkage between the environmental conditions experienced by adult females and offspring fitness (Stephens et al., 2009).

Some organisms maximize fecundity by producing propagules approaching the minimum viable size. Many marine fishes exhibit this strategy and produce very small eggs that hatch as altricial larvae and receive no parental care (Winemiller and Rose, 1993). Those fish larvae experience mortalities as high as 20% per day and 99% over the larval period (Houde, 2002) so that even small changes in mortality rate can generate order-of-magnitude differences in annual recruitment (Caley et al., 1996; Houde, 1987). Environmental factors such as advection, temperature, abundances of predators and prey, and larval supply explain only part of the variability in early mortality (Chambers and Trippel, 1997). Current research is turning toward non-genetic maternal effects as important determinants of offspring quality, survival, and recruitment potential (Berkeley et al., 2004; Green, 2008; McCormick, 2006). Egg and larva traits can vary significantly among and within batches of offspring, reflecting environmental conditions experienced by the mothers. For instance, Chambers and Waiwood (1996) found that 26% of the total variation in egg diameter of Atlantic cod (*Gadus morhua*) occurred among batches within females. Similarly, Fuiman et al. (2005) found significant and coordinated differences in antipredator performance among batches of red drum (*Sciaenops ocellatus*) larvae. This latter study suggested that the variability in antipredator performance among batches may be a product of seasonality in egg quality.

The aim of our study was to assess the variability in traits of egg quality and larva quality in red drum larvae and to identify linkages between specific traits at these two stages toward a better understanding of their role in early life survival. Our work emphasized

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the proximate composition and fatty acid composition of eggs and the vital rates, routine activity, and escape response performance of larvae. Maternally derived fatty acids have been linked to hatching success and early larval growth rate (e.g. Lane and Kohler, 2006; Pickova et al., 2007). Moreover, behavioral performance of fish larvae can be improved by providing them a diet rich in certain essential fatty acids (Benítez-Santana et al., 2007; Nakayama et al., 2003). We found that concentrations of certain essential fatty acids in eggs were strongly related to escape response performance of larvae and that other measures of per-offspring investment (including egg size) were not related to these larva performance traits.

2. Methods

Relationships between egg quality traits and larva quality traits were explored by sampling spawns from captive pairs of red drum that were induced to spawn through manipulations of temperature and photoperiod. Red drum are fractional spawners, with the capacity to spawn tens of thousands to hundreds of thousands of eggs at a time and to do this repeatedly over many months. A subsample of eggs from each sampled spawn was frozen for subsequent analysis of egg quality traits, and eggs were incubated and their larvae reared to a common size when larva vital rates, routine activity, and escape response performance were measured. Spawning and experiments were conducted between 21 April and 26 August 2005 and between 23 May and 6 September 2006.

2.1. Broodstock care

Broodstock were maintained by staff of Texas Parks and Wildlife Department at the CCA/CPL Marine Development Center in Corpus Christi, TX. Adult red drum that had been collected from the wild and held in captivity for at least 1 year but no more than 4 years, were distributed in pairs (1 male, 1 female) among five spawning tanks located in three separate rooms (2, 2, and 1 tank per room). After the first year, female broodstock were replaced but the same males were left in the spawning tanks for the second year (Table 1). Spawning tanks were cylindrical (13 m^3) and connected to an external filter box with completely recirculating water. Temperature was maintained between 24 and 26 °C and salinity ranged from 30 to 38 ppt. Each pair of broodstock was fed a maturation diet for 5 months (152 days) consisting of 0.91 kg of shrimp and 0.45 Kg of squid every Monday and Friday and 0.22 kg of shrimp, 0.22 kg of squid, 0.45 kg of beef liver, and 0.45 kg of Atlantic mackerel every Wednesday. After 5 months, the broodstock were switched to a spawning diet consisting of 1.36 kg of shrimp every Monday and Friday and 0.91 kg of shrimp and 0.45 kg of squid every Wednesday for 7 months (214 days). For the 2005 experiments, squid and mackerel used in the diets originated from Maine (purchased through Triton Seafood Products, Corpus Christi, TX). For the 2006 experiments, squid and mackerel used in the diets originated from New Jersey (purchased through Capt. Mark's Seafood, Freeport, TX). Fatty acid composition of the broodstock diets and diet components are shown in Table 2.

2.2. Larva care

Red drum broodstock spawned during the evening and their eggs flowed into a collector which was checked every morning. An attempt was made to sample eggs from every spawn, but limited capacity for rearing larvae greatly reduced the number of spawns that could be reared for lava performance trials. When spawns were sampled, they were collected between 0700 and 0900 h. A subsample of approximately 10 ml (approximately 10,000 eggs) was placed in a tube and immersed in an ice bath. A larger subsample of eggs (c. 20,000 eggs) was placed in a bucket containing (15 l) of sea water. The two subsamples of eggs were transported by automobile (approximately 48 km) to laboratory facilities at the University of Texas Marine

Table 1
Sources of data for egg and larva quality measurements. Number of spawns assayed is the number of spawns from which eggs were sampled for measurements of egg quality and larvae were reared for measurements of larva quality. Broodstock in tank numbers 7 (in 2005) and 10 in 2006 did not spawn.

Year	Broodstock			Number of spawns assayed
	Tank number	Length (mm)	Weight (kg)	
2005	5	♀: 1041	♀: 13.4	1
		♂: 838	♂: 11.1	
	6	♀: 990	♀: 11.3	4
		♂: 863	♂: 8.6	
	7	♀: 1016	♀: 15.9	0
		♂: 914	♂: 13.1	
	8	♀: 939	♀: 15.0	14
		♂: 939	♂: 14.5	
	10	♀: 939	♀: 10.7	5
		♂: 914	♂: 12.2	
2006	5	♀: 1062	♀: 13.2	1
		♂: 838	♂: 11.1	
	6	♀: 1081	♀: 12.3	3
		♂: 863	♂: 8.6	
	7	♀: 1204	♀: 14.1	4
		♂: 914	♂: 13.1	
	8	♀: 997	♀: 9.1	8
		♂: 939	♂: 14.5	
	10	♀: 1036	♀: 10.0	0
		♂: 914	♂: 12.2	

Table 2
Fatty acid profile for broodstock diet components and broodstock diets. Values are expressed as mg fatty acid per g dry weight and are based on diet components purchased through Triton Seafood Products, Corpus Christi, TX in 2008. Values for the diets were calculated from measurements of the diet components and the proportions of each component used in each diet (see Methods).

Fatty acid	Diet component				Diet	
	Shrimp	Squid	Liver	Mackerel	Maturation	Spawning
8:0	0.0	0.0	0.0	0.0	0.0	0.0
10:0	0.0	0.0	0.0	0.0	0.0	0.0
11:0	0.0	0.0	0.0	0.0	0.0	0.0
12:0	0.0	0.0	0.0	0.0	0.0	0.0
13:0	0.0	0.0	0.0	0.0	0.0	0.0
14:0	0.4	2.3	0.9	9.9	2.0	0.6
15:0	0.1	0.4	0.3	1.0	0.3	0.2
15:01	0.0	0.1	0.4	0.2	0.1	0.0
16:0	13.0	14.1	14.2	25.3	14.8	13.2
16:1ω7	1.2	2.0	1.2	9.8	2.4	1.3
16:2ω4	0.1	0.7	0.0	1.7	0.4	0.2
17:0	0.5	0.6	0.9	0.8	0.6	0.5
16:3ω4	0.1	0.4	0.4	1.0	0.3	0.1
18:0	4.4	2.8	25.7	5.1	6.4	4.2
18:1ω9	13.0	7.6	21.5	16.8	12.9	12.4
18:1ω7	2.2	2.9	0.0	5.4	2.5	2.3
18:2ω6	10.6	1.3	10.8	2.8	7.2	9.5
18:3ω6	0.1	0.1	0.1	0.3	0.1	0.1
18:3ω4	0.1	0.1	0.0	0.1	0.1	0.1
18:3ω3	0.6	0.8	0.4	2.0	0.8	0.6
18:4ω3	0.1	0.6	0.2	3.5	0.6	0.1
20:1ω9	0.5	7.6	0.2	29.9	5.7	1.3
20:2ω6	1.1	0.5	0.2	0.5	0.8	1.0
20:3ω6	0.2	0.1	4.0	0.1	0.6	0.2
20:4ω6	1.4	1.1	15.1	1.2	2.8	1.4
20:3ω3	0.1	0.6	0.0	0.4	0.3	0.2
20:4ω3	0.2	0.5	0.0	1.0	0.3	0.2
20:5ω3	4.3	10.0	0.4	9.9	6.1	4.9
22:1ω9	0.0	6.3	0.1	56.3	8.0	0.7
22:2ω6	0.0	0.0	0.0	0.4	0.0	0.0
22:5ω6	0.1	0.4	0.0	0.4	0.2	0.1
22:5ω3	0.4	0.6	1.8	1.9	0.8	0.4
22:6ω3	4.0	27.1	0.8	14.5	11.2	6.5
Total fatty acids	58.9	91.5	99.5	202.1	88.4	62.5