An ovary transcriptome for all maturational stages of the striped bass (*Morone saxatilis*), a highly advanced perciform fish

Benjamin J Reading¹†, Robert W Chapman²†, Jennifer E Schaff³, Elizabeth H Scholl⁴, Charles H Opperman⁴ and Craig V Sullivan¹,⁵*

**Abstract**

**Background:** The striped bass and its relatives (genus *Morone*) are important fisheries and aquaculture species native to estuaries and rivers of the Atlantic coast and Gulf of Mexico in North America. To open avenues of gene expression research on reproduction and breeding of striped bass, we generated a collection of expressed sequence tags (ESTs) from a complementary DNA (cDNA) library representative of their ovarian transcriptome.

**Results:** Sequences of a total of 230,151 ESTs (51,259,448 bp) were acquired by Roche 454 pyrosequencing of cDNA pooled from ovarian tissues obtained at all stages of oocyte growth, at ovulation (eggs), and during preovulatory atresia. Quality filtering of ESTs allowed assembly of 11,208 high-quality contigs ≥ 100 bp, including 2,984 contigs 500 bp or longer (average length 895 bp). Blastx comparisons revealed 5,482 gene orthologues (E-value < 10⁻³), of which 4,120 (36.7% of total contigs) were annotated with Gene Ontology terms (E-value < 10⁻⁶). There were 5,726 remaining unknown unique sequences (51.1% of total contigs). All of the high-quality EST sequences are available in the National Center for Biotechnology Information (NCBI) Short Read Archive (GenBank: SRX007394). Informative contigs were considered to be abundant if they were assembled from groups of ESTs comprising ≥ 0.15% of the total short read sequences (≥ 345 reads/contig). Approximately 52.5% of these abundant contigs were predicted to have predominant ovary expression through digital differential display in silico comparisons to zebrafish (*Danio rerio*) UniGene orthologues. Over 1,300 Gene Ontology terms from Biological Process classes of Reproduction, Reproductive process, and Developmental process were assigned to this collection of annotated contigs.

**Conclusions:** This first large reference sequence database available for the ecologically and economically important temperate basses (genus *Morone*) provides a foundation for gene expression studies in these species. The predicted predominance of ovary gene expression and assignment of directly relevant Gene Ontology classes suggests a powerful utility of this dataset for analysis of ovarian gene expression related to fundamental questions of oogenesis. Additionally, a high definition Agilent 60-mer oligo ovary 'UniClone' microarray with 8 × 15,000 probe format has been designed based on this striped bass transcriptome (eArray Group: Striper Group, Design ID: 029004).

**Background**

The striped bass and its relatives in the genus *Morone* (the temperate basses) are ecologically and economically important aquaculture and fisheries species native to estuaries and rivers of the Atlantic coast and Gulf of Mexico in North America [1,2]. Although the striped bass and its hybrids have been reared as commercial aquaculture products in the United States since the late 1980s, little genetic information is available for these species in public databases at the National Center for Biotechnology Information (NCBI) or elsewhere, consisting only of microsatellite DNA markers [3,4], the mitochondrial genome (GenBank: HM447585), and a medium density genetic linkage map [5]. A major factor

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contributing to restricted growth of hybrid striped bass farming nationwide is reproductive dysfunction of female striped bass, resulting in non-viable eggs, embryos, and larvae [6]. These reproductive failures hamper selective breeding efforts required for species domestication and improvement. The exact cause(s) of poor egg quality and embryonic mortality in farmed fishes, however, still remain to be discovered, making appropriate and timely corrective measures difficult to achieve [review: [7,8]].

Functional genomics has emerged as a major research field and gene expression (transcriptomics) and proteomics studies are promising approaches to gain new insights into reproductive molecular biology [7,9-12]. Marked advancement in striped bass reproductive technology based on such “Omic” analyses is, however, currently restricted due to the lack of an available, comprehensive sequence database for this species or for other members of the genus *Morone* that are important in aquaculture (e.g. hybrid striped bass) or as research models (e.g. white perch, *M. americana*). Transcriptome resources are currently available for other commercially important fishes, including rainbow trout (*Oncorhynchus mykiss*) [13-16], coho salmon (*Oncorhynchus kisutch*) [17], tilapia (*Oreochromis mossambicus*) [18], Atlantic halibut (*Hippoglossus hippoglossus*) [19], Senegalese sole (*Solea senegalensis*) [20], Atlantic salmon (*Salmo salar*) [21], and cod (*Gadus morhua*) [22].

The emergence of pyrosequencing and later generation DNA sequencing technologies has made acquisition of significant genomic resources accessible and affordable for non-model organisms [23-25]. Vast numbers of expressed sequence tags (ESTs) can readily be generated using these methods, providing direct evidence of gene transcription, and collections of such EST sequences are presently the most important resources used for transcriptome exploration [26]. Depending on the number of ESTs sequenced, resulting databases can represent a high proportion of the total number of gene transcripts expressed by a given tissue (i.e. transcriptome), making downstream procedures for transcriptome profiling, such as oligo microarray or real-time quantitative reverse transcription PCR, tractable without the need for an entire genome sequence.

When sequencing depth is limited, organ specific EST collections permit more efficient gene expression analyses using ‘UniClone’ microarrays, which are comprised of probe sequences isolated from a single organ type [27-30]. UniClone arrays represent a larger proportion of a target organ transcriptome and have reduced redundancy when compared to arrays comprised of ESTs derived from several different tissue types. Additionally, to realize the full benefits of proteomic analyses based on mass spectrometry, species-specific ESTs are required, since algorithms used for spectral analyses (e.g. SEQUEST, Proteome Discoverer Software, Thermo Scientific, West Palm Beach, FL) require a homologous reference sequence database. For non-model organisms, sequence information from even closely related species can be insufficient for the accurate identification of peptides, since these algorithms tend to be conservative and heterospecific amino acid substitutions can result in peptide misidentification or an inability to detect orthologues [31].

Therefore, the goal of the present study was to provide an ovary transcriptome database representative of all stages of oogenesis and atresia in striped bass, one that could provide the requisite foundation for functional genomics and proteomics investigations of reproduction and egg quality in this species and that would support similar studies in the other temperate basses.

**Results**

A total of 230,151 EST short read sequences with a combined length of 51,259,448 bp (average length 224 bp) were generated from cDNA pooled from ovarian tissues and eggs encompassing the various stages of ovary growth, maturation and atresia. A total of 11,208 high-quality contigs with a length of at least 100 bp were assembled and these included 2,984 contigs that were 500 bp or longer (average length 895 bp; total length 5,068,343 bp) (Additional File 1). Blastx comparisons revealed 5,482 orthologues, of which 4,120 (36.7%) were annotated with Gene Ontology (GO) terms. The number of unique sequences was 5,726 (51.1%). The breakdown of GO annotation classes within the three categories of GO terms for all annotated sequences is shown in Figure 1: Biological Process (2nd level) and Molecular Function and Cellular Component (3rd level). A complete list, in FASTA format, of the contig assemblies identified by their annotations are included as Additional File 2 and a list of the assemblies and their GO terms are included as Additional File 3.

There were 66 contigs that were each assembled from groups of ESTs that comprised ≥ 0.15% of the total 230,151 reads (i.e. ≥ 345 reads per contig) and these contigs were considered to have abundant ovary expression. These contigs were identified by NCBI UniGene cluster and compared to zebrafish, *Danio rerio*, orthologues evaluated by Digital Differential Display (DDD) (Table 1). Twenty-two striped bass genes from this list (33.3% of the total listed) either had no blastx returns (i.e. were novel), or were identified as being unnamed gene products, or had gene names but no zebrafish UniGene orthologues. These were excluded from further evaluation. Of the remaining informative 44 genes, 23 (52.5%) are predicted to have predominant ovary expression based on DDD of zebrafish orthologues, 11 (25.0%)
Figure 1 Gene ontology graph of A. Cellular Component (3rd level GO terms), B. Molecular Function (3rd level GO terms), and C. Biological Process (2nd level GO terms) of annotated genes in the striped bass ovary transcriptome. The number of GOs in each class is shown and sections that contained 50-150 entities are represented in black, 151-500 by dark gray, 500 and up by light gray, and the predominant class is indicated in white.
| Contig Number | BLAST 2GO Annotation | Genes (zebrafish taxid: 7955 orthologue) | Assembled contig length (bp) | Number of observe sequence reads | % Total sequence reads (230,151) | Fraction of ESTs that mapped to the zebrafish UniGene by DDD | Zebrafish UniGene |
|---------------|---------------------|----------------------------------------|-------------------------------|-------------------------------|---------------------------------|----------------------------------------------------------|-----------------|
| 1 10186       | cyclin b2           | ccnb2                                   | 368316                        | 1284                          | 1146                            | 0.4979340                                               |                 |
| 2 10415       | zona pellucida      | zp2.3                                   | 114439                        | 1329                          | 1076                            | 0.4675192                                               |                 |
| 3 10181       | novel protein with  | si: ch211-14a17.7                      | 368669                        | 646                           | 1001                            | 0.4349318                                               |                 |
| 4 9349        | zona pellucida      | zpcx                                    | 334011                        | 2036                          | 923                             | 0.4010411                                               |                 |
| 5 146         | nad h quinone 1     | nqo1                                    | 322506                        | 916                           | 908                             | 0.3945236                                               |                 |
| 6 8878        | tubulin beta 2c     | zgc: 123194                             | 641421                        | 1510                          | 869                             | 0.3754057                                               |                 |
| 7 9768        | egg envelope        | si: dkeyp-S0F7.2                        | 334036                        | 2890                          | 864                             | 0.3684538                                               |                 |
| 8 10472       | fatty acid binding  | fabp1b.1                                | 554095                        | 419                           | 848                             | 0.3332595                                               |                 |
| 9 9294        | –                    | –                                       | –                             | –                             | –                               |                                                          |                 |
| 10 10137      | choriogenin 1       | zp3b                                    | 64692                         | 1389                          | 817                             | 0.3265421                                               |                 |
| 11 11102      | hypothetical protein| pol2a                                   | 553347                        | 774                           | 767                             | 0.3067551                                               |                 |
| 12 11074      | –                    | –                                       | –                             | –                             | –                               |                                                          |                 |
| 13 10663      | zgc: 175135 protein | zgc: 165551                             | 100003969                     | 636                           | 706                             | 0.2932857                                               |                 |
| 14 9917       | heat shock protein 8| hspa8                                   | 573376                        | 2266                          | 699                             | 0.2772093                                               |                 |
| 15 11091      | novel protein with  | LOC100331707                            | 100331707                     | 1219                          | 675                             | 0.266504                                               |                 |
| 16 3          | –                    | –                                       | –                             | –                             | –                               |                                                          |                 |
| 17 11147      | fatty acid-binding  | fabp11a                                 | 447944                        | 581                           | 638                             | 0.2511395                                               |                 |
| 18 10883      | mgc86501 protein    | wu: f138e01                             | 798996                        | 568                           | 623                             | 0.2433185                                               |                 |
| 19 9329       | histone             | h33c                                    | 336231                        | 945                           | 619                             | 0.2220281                                               |                 |
| 20 10302      | voltage gated       | LOC573838 (h2af11o)                     | 100332229                     | 447                           | 607                             | 0.2220281                                               |                 |
| 21 11112      | egg envelope        | zpc3                                    | 563179                        | 1527                          | 610                             | 0.214604                                               |                 |
| 22 30         | histone h2a         | LOC573838                               | 100332229                     | 447                           | 607                             | 0.207932                                               |                 |
| 23 10079      | –                    | –                                       | –                             | –                             | –                               |                                                          |                 |
| 24 10058      | beta-actin          | bactn2                                  | 57935                         | 1874                          | 578                             | 0.198365                                               |                 |
| 25 10823      | apolipoprotein d    | zgc: 123339                             | 567972                        | 816                           | 560                             | 0.193606                                               |                 |
| 26 10825      | –                    | –                                       | –                             | –                             | –                               |                                                          |                 |
| 27 10773      | hypothetical protein| LOC100349339                            | –                             | –                             | –                               |                                                          |                 |
| 28 6635       | h1 histone member   | h1m                                     | 327403                        | 823                           | 523                             | 0.187868                                               |                 |
| 29 11098      | adp atp translocase | slc25a5                                 | 192321                        | 1243                          | 515                             | 0.176504                                               |                 |
| 30 127        | nucleoside diphosphate kinase b | nme2b | 30083                        | 834                           | 511                             | 0.165296                                               |                 |

Table 1: Transcripts abundantly expressed in the striped bass ovary.
| Contig Number | BLAST 2GO Annotation | Gene | GeneID | Assembled contig length (bp) | Number of observe sequence reads (230,151) | % Total sequence reads | Fraction of ESTs that mapped to the zebrafish UniGene by DDD | Zebrasfish UniGene |
|---------------|----------------------|------|--------|-------------------------------|---------------------------------------------|----------------------|---------------------------------------------------------|------------------|
| 31            | 10309 60 s acidic ribosomal protein p0 | rplp0 | 58101 | 932 | 497 | 0.2159452 | 0.0008 < 0.0033 | Dr.53617 |
| 32            | 11081 loc494706 protein (oogenesis-related gene) | org | 100001110 | 601 | 495 | 0.2150762 | 0.0016 > 0.0001 | Dr.80745 |
| 33            | 10120 elongation factor 1 alpha | efla | 30516 | 1744 | 492 | 0.2137727 | 0.0032 < 0.0108 | Dr.31797 |
| 34            | 10015 heat shock protein 90 | hsp90ab1 | 30753 | 1900 | 485 | 0.2107312 | 0.0006 < 0.0020 | Dr.35688 |
| 35            | 11073 unnamed protein product | * | – | – | – | – | – | – |
| 36            | 10797 complement component (3b 4b) receptor 1 | LOC55541 | 565541 | 1696 | 470 | 0.2042138 | * | * | Dr.91858 |
| 37            | 92 cyclin b1 | ccb1 | 58025 | 738 | 470 | 0.2042138 | 0.0035 > 0.0002 | Dr.121261 |
| 38            | – NA– | – | – | – | – | – | – | – |
| 39            | 126 karyopherin alpha 2 (rag cohort importin alpha 1) | zgc: 55877 | 406343 | 1085 | 469 | 0.2037793 | 0.0010 > 0.0002 | Dr.20877 |
| 40            | – NA– | – | – | – | – | – | – | – |
| 41            | 10900 zpb protein | LOC100334275 | 100334275 | 1561 | 461 | 0.2003033 | * | * | Dr.141250 |
| 42            | 36 claudin 4 | cldh | 81583 | 731 | 456 | 0.1981308 | 0.0004 > 0.0001 | Dr.75663 |
| 43            | 216 stathmin 1 oncprotein 18 variant 8 | stmn1b | 550548 | 964 | 450 | 0.1955238 | 0 < 0.0004 | Dr.105609 |
| 44            | – NA– | – | – | – | – | – | – | – |
| 45            | 9337 Securin [Anoplopoma fimbria] | LOC566690 | 566690 | 435 | 414 | 0.1798819 | 0.0002 > 0 | Dr.118007 |
| 46            | 9321 dna replication inhibitor | gmmn | 368320 | 1121 | 412 | 0.1790129 | n.d. = n.d. | Dr.119358 |
| 47            | 10986 cell division cycle 20 homolog (cerevisiae) | cdc20 | 406353 | 1597 | 410 | 0.1781439 | 0.0005 > 0.0001 | Dr.105018 |
| 48            | 11071 – NA– | – | – | – | 215 | 402 | 0.1746679 | – | – | |
| 49            | 10743 – NA– | – | – | – | 273 | 398 | 0.1729299 | – | – | |
| 50            | 1174 cyclin k | LOC100331304 | 100331304 | 3331 | 397 | 0.1724954 | 0.0009 > 0 | Dr.148591 |
| 51            | 10438 ribonucleotide reductase m2 polypeptide | rm2 | 30733 | 1621 | 396 | 0.1720610 | 0.0018 > 0.0003 | Dr.75098 |
| 52            | 11198 ribosomal protein s20 | rps20 | 406485 | 477 | 393 | 0.1707575 | 0.0014 > 0.0008 | Dr.18943 |
| 53            | 11014 karyopherin alpha 2 (rag cohort importin alpha 1) | kproa2 | 436607 | 534 | 380 | 0.1651090 | 0.0009 > 0.0002 | Dr.75097 |
| 54            | – NA– | – | – | – | 299 | 375 | 0.1629365 | – | – | – |
| 55            | 10265 unnamed protein product | – | – | – | 1075 | 375 | 0.1629365 | – | – | – |
| 56            | 771 cytochrome c oxidase copper chaperone | cox17 | 447914 | 410 | 375 | 0.1629365 | 0.0007 > 0.0001 | Dr.82168 |
| 57            | 10107 tubulin, alpha 1c | MGI171407 | 573122 | 697 | 374 | 0.1625020 | n.d. = n.d. | Dr.120425 |
| 58            | – NA– | – | – | – | 2532 | 371 | 0.1611985 | – | – | – |
| 59            | 231 epididymal secretory protein e1 precursor | npc2 | 282673 | 728 | 360 | 0.1564190 | – | – | – |
would be expected to have no difference in expression between ovary and other tissues of the body based on the DDD results, and 10 (22.7%) would likely have predominant expression in other tissues of the body based on the DDD comparison. Overall, the estimated 66 most abundantly expressed striped bass ovary genes were assembled from ~1/6 of the total number of short read sequences (Table 1).

All of the high-quality ESTs have been deposited in the NCBI Short Read Archive (GenBank: SRX007394) and annotated contigs are posted under “Resources” on the National Animal Genome Research Program Aquaculture Genome Projects website (http://www.animalgenome.org/aquaculture/database/) [32]. These contigs also have been submitted to Agilent Technologies eArray (Santa Clara, CA) for ovary UniClone microarray design (http://www.chem.agilent.com/). We designed a high definition 60-mer SurePrint oligo array with 8 x 15,000 probe format comprised of 11,145 UniGene reads that mapped to the zebrafish UniGene by DDD. ESTs reported herein represent a comparatively valuable transcriptome resource for striped bass.

If the 11,208 contigs are considered to be UniGenes, this represents a substantial proportion of the estimated total protein-coding gene transcripts expressed by the striped bass ovary (i.e. transcriptome) as the average number of mRNA transcripts expressed by a single tissue type is estimated to be between 10,000–15,000 [34], but can be as low as 8,200 [35]. Since over 1,300 GOs from Biological Process classes of Reproduction (121), Reproductive process (55), and Developmental process (1,188) were assigned to the annotated contigs (Figure 1), this sequence collection should prove to be a powerful tool for analysis of ovarian gene expression related to fundamental questions of oogenesis.

### Table 1 Transcripts abundantly expressed in the striped bass ovary. (Continued)

| Contig Number | Gene Annotation | Genes | GeneID | Assembled length (bp) | Number of observed sequence reads | % Total sequence reads (DDD, 15.8730570) | Fraction of ESTs that mapped to the zebrafish UniGene by DDD | Zebrafish UniGene |
|---------------|-----------------|-------|--------|-----------------------|-----------------------------------|----------------------------------------|-------------------------------------------------|-----------------|
| 61 10741      | ppi a protein (peptidylprolyl isomerase A) | ppi a | 336612 | 825 | 356 | 0.1546811 | 0.0005 < 0.0011 Dr.104642 |
| 62 9354       | superoxide dismutase | sod1 | 30553 | 795 | 356 | 0.1546811 | n.d. = n.d. Dr.75822 |
| 63 10048      | ubiquitin b | ubb | 550134 | 169 | 355 | 0.1542466 | n.d. = n.d. Dr.104259 |
| 64 10083      | cyclin a2 | ccna2 | 192295 | 2108 | 351 | 0.1525086 | n.d. = n.d. Dr.121874 |
| 65 10746      | eukaryotic translation elongation factor 1 gamma | eef1g | 195822 | 1533 | 350 | 0.1520741 | 0.0006 < 0.0011 Dr.75657 |
| 66 10761      | egg envelope component zpax | si: dkeyp-5072 | 334036 | 2731 | 347 | 0.1507706 | 0.0017 > 0.0003 Dr.105787 |

Genes are ranked (1-66) by number of observed 454 short read sequences used in each contig assembly. Digital Differential Display (DDD) results of orthologous sequences in zebrafish are also shown. Annotation “–NA–” indicates no blastx return; Dashes (–) indicate unknown or data not available; asterisks (*) indicate the UniGene was not present in the EST libraries used for DDD. Sequences with expression differences evaluated by DDD (FET, P ≤ 0.05) are indicated by “>” (enhanced ovary expression) or “<” (enhanced body expression); “n.d.” indicates no significant difference in expression between ovary and body (=)

**Discussion**

This collection of ESTs represents the first contribution of a large reference sequence database for species of the genus *Morone* and provides a basis for future gene expression studies in these temperate basses. Availability of characterized ovarian transcriptomes from fishes other than zebrafish is limited. Partial transcriptomes have been reported for tilapia (474 EST assemblies) [18] and for cod (1,361 EST assemblies) [22]. Several thousand ovarian ESTs have been reported for salmonid fishes [13,15,33] and references therein, but to our knowledge these have not been assembled into a comprehensive ovarian transcriptome. Numbers of total ESTs currently available in the NCBI EST database for some other commercially important finfishes are as follows: rainbow trout (287,967), coho salmon (4,942), tilapia (Genus *Oreochromis*, 121,346), Atlantic halibut (20,836), Senegalese sole (10,631), Atlantic salmon (498,212), and cod (229,094). Therefore, the 230,151 ESTs reported herein represent a comparatively valuable transcriptome resource for striped bass.
Approximately 52.5% of the informative contigs considered to have abundant ovary expression (i.e. those with ≥ 345 reads per contig) were also predicted to have predominant expression in striped bass ovary through DDD comparisons to zebrafish orthologues (Table 1). These include cyclin B2 (ccnb2, contig10186), several egg envelope and zona pellucida proteins, histone H2A (h2af10, contig00030), oogenesis-related gene (org, contig11081), cyclin B1 (ccnb1 contig00092), karyopherin alpha 2 (kpna2, contig00126 and 11014), claudin 4 (cldn4, contig00036), securin (LOC566690, contig 09337), cell division cycle 20 homolog (cdc20, contig10986), cyclin K (LOC100331304, contig11174), ribonucleotide reductase M2 polypeptide (rrm2, contig10438), ribosomal protein S20 (rps20, contig11198), cytochrome C oxidase copper chaperone (cox17, contig00771), and epididymal secretory protein E1 (npc2, contig00231). Many of these are well-characterized ovary transcripts and several recent and informative papers have been published detailing the functions of these genes and their protein products in fish oocytes and embryos [see: 7,8,13-20,27,28,36-38]; others are briefly detailed below.

The remaining 47.5% of abundant striped bass ovary genes that were compared to zebrafish orthologues in the DDD were predicted to have indifferent or predominant expression levels in other tissues of the body relative to the ovary. These may represent constitutively expressed genes or those expressed at high levels in the ovary albeit comparatively lower than in other tissues of the body, respectively. Examples of potential genes with constitutive expression include NADH quinone 1 (nqo1, contig00146), tubulin (zgc:123194, contig08878 and MGC171407, contig10107), fatty acid binding proteins (fabp1b, contig10472 and fabp1l1a, contig11147), H1 histone member oocyte-specific (h1m, contig06635), nuclease diphosphate kinase B (nm2e2b, contig00127), geminin DNA replication inhibitor (gmin, contig09321), superoxide dismutase (sod1, contig09354), ubiquitin B (ubb, contig10048), and cyclin A2 (ccna2, contig10083). Of these, fatty acid-binding protein heart (fabp1l1a) has been shown to be up-regulated in ovary of rainbow trout females that mature precociously [13] and an orthologue of h1m (H1foo) is generally considered to be an oocyte specific histone in mouse (Mus musculus) [39,40], contrary to the DDD prediction. The UniGene EST Profile of zebrafish h1m (Dr. 75735) indicates that it is predominantly expressed in skin, however the second most abundant site of expression is the reproductive system.

The following genes expressed in striped bass ovary are also expressed in zebrafish ovary, however the DDD indicates that they are predominantly expressed in other tissues of the body (Table 1): histone (h3f3c, contig09329), beta-actin (bactin2, contig10058), ADP/ATP translocase (slc25a5, contig11098), 60S acidic ribosomal protein P0 (rplp0, contig10309), elongation factor 1 alpha (ef1a, contig10120), peptidylprolyl isomerase A (ppia, contig10741), eukaryotic translation elongation factor 1 gamma (eef1g, contig10746), stathmin 1 oncprotein 18 variant 8 (stmn1b, contig00216), and heat-shock proteins 8 (hspa8, contig09917) and 90 (hsp90ab1, contig10015). Ovarian representation of gene transcripts that show predominant expression in other tissues of the body is not surprising given the heterogeneous complexity of the ovary, which is comprised of vasculature, blood and other connective tissues, the somatic follicle, and germ cells. Furthermore, most of these genes, for example ef1a and bactin2, are considered to have constitutively high expression in most tissues, and this is supported by the corresponding zebrafish UniGene EST Profiles (Dr. 31797 and Dr. 75125, respectively). There were, however, three exceptional genes whose expression, although considered to be lower in comparison to other tissues of the body by DDD, have been shown to be highly expressed in ovary. Stathmin (stmn) is expressed in oocytes and pre-implantation embryos of mice [41] and in cod ovary [22], and Stmn proteins have been detected in zebrafish ovary [36]. Contig00216 encodes a full-length, 147 amino acid Stmn and has been putatively identified as stmn1b, however it is highly similar to two zebrafish stmn isoforms (95% and 94% amino acid identity with stmn1b and stmn1a, respectively). Although stmn1b has body predominant expression in zebrafish by DDD (Table 1), zebrafish stmn1a (UniGene Dr. 52664) shows ovary predominant expression and, therefore, contig00216 may actually be orthologous to stmn1a. Given the high similarity of this sequence to both zebrafish stmn1 isoforms, it is not possible to definitively assign identity without comparison to the other striped bass stmn isoform, which is unavailable. Recently, hsp8 and hsp90 (corresponding to striped bass hspa8 and hsp90ab1, respectively) have been characterized as some of the most abundant genes expressed in mouse and fish eggs at both the transcript and protein levels [36,37,42].

This inconsistent result may relate to the inherent weaknesses of DDD, since only highly expressed genes are adequately represented in the EST libraries used to conduct the in silico comparisons and the Fisher’s exact test (FET) is conservative [43]. Although this method does not offer quantitation, ranking of the striped bass contigs by number of short reads used in assembly paired with comparisons to zebrafish orthologues evaluated by DDD proved to be a useful tool for estimating relative ovarian abundance of the striped bass gene transcripts. Reservation must be taken when considering such interspecific DDD comparisons for the purpose of excluding genes that are predicted to have less predominant expression in one tissue compared to another, since they may be highly expressed in both. This is a promising approach
for characterization of novel gene transcripts from EST libraries and has recently been used to identify ovary specific genes in zebrafish [44] and rainbow trout [15], however such results should be further validated using an experimental evaluation of gene expression.

The growing oocyte is considered to be largely transcriptionally inactive, acting as a storehouse of specific maternal RNAs, proteins, and other molecules required for competency for fertilization, initiation of zygotic development, and transition to embryonic gene expression [review: [37,38]]. These maternal factors may be stored in oocytes for extended periods of time until use (e.g. months to years). Therefore, a system of regulatory proteins and RNAs must mediate the oocyte cell cycle during growth, ovarian maturation (OM), and zygotic transcriptionally inactive, acting as a storehouse of specific genes in zebrafish [44] and rainbow trout [15], however such results should be further validated using an experimental evaluation of gene expression.

The growing oocyte is considered to be largely transcriptionally inactive, acting as a storehouse of specific maternal RNAs, proteins, and other molecules required for competency for fertilization, initiation of zygotic development, and transition to embryonic gene expression [review: [37,38]]. These maternal factors may be stored in oocytes for extended periods of time until use (e.g. months to years). Therefore, a system of regulatory proteins and RNAs must mediate the oocyte cell cycle during growth, ovarian maturation (OM), and zygotic development from fertilization until activation of the embryonic genome at the mid-blastula transition [45]. A number of known cell-cycle regulators and proteins critical for these processes have been identified as predominantly expressed in striped bass ovary (Table 1). Examples include cyclins B1 and B2 (ccnb1, ccnb2) [46-49], cyclin K (ccnk) [50], securin [51], cdc20 [27], kpna2 [22,52], gmn [53], h2af1o [54] and org [44]. Transcripts encoding several different cell division and cell cycle regulatory proteins were similarly reported in the ovaries of cod [22] and rainbow trout [13].

Solute carrier protein (SLC) family members are selected to illustrate representation of sequences in the striped bass ovary transcriptome encoding proteins from a large gene series. The SLCs are a diverse group of eukaryotic membrane proteins that control cellular influx and efflux of solutes, including ions, fatty acids, amino acids, sugars, drugs, and vitamins [55,56]. The Human Genome Gene Nomenclature Committee [57] classifies approximately 400 different human SLCs into 47 families. At least one representative protein from 19 (~0.4%) of these families was identified in the striped bass ovary transcriptome (Table 2). Characterization of SLC gene expression in growing oocytes and during OM would be of direct importance to understanding mechanisms of oogenesis and egg quality in light of what is known of oocyte and egg physiology. Due to osmoregulatory requirements imposed by both fresh and marine waters, embryos of egg-laying fishes develop during embryogenesis as a medium and substrate for biochemical reactions and as a diluent for waste products (e.g. ammonia). Furthermore, water contributes to appropriate egg buoyancy, especially in marine fishes that spawn pelagic eggs. Prior to ovulation, a hyperosmotic solute concentration develops within the oocytes of these species, followed by passive influx of water through aquaporin membrane channels [review: [58,59]]. Inorganic ions have primarily been implicated in this phenomenon, however the exact mechanisms of their entry have not been verified. Bobe et al. [14] demonstrated up regulation of slc26 (Pendrin) and aqp4 (aquaporin 4) expression in ovary of rainbow trout during OM. Gene transcripts encoding a slc26a6-like protein, along with several other ion transporters (Table 2) and aquaporin 1 (contig08717) were identified in striped bass ovary. This indicates the potential for discovery of previously unknown mechanisms of teleost oocyte hydration by gene expression analyses of these particular SLCs and water transport genes in the striped bass and related species (genus Morone), which can tolerate a wide range of environmental salinities.

**Conclusions**

In summary, as we continue to advance our understanding of reproduction in temperate basses of the genus *Morone*, this reference sequence database of ovarian transcripts will provide the requisite foundation for gene expression studies and will open avenues of research related to reproduction and egg quality. Several important candidate genes have already been identified for future study. Furthermore, these sequences have been used to design an ovary UniClone oligo microarray for assessing changes in gene expression during oogenesis and in female striped bass spawning good and poor quality eggs. Our recent deployment of this microarray in a study of striped bass egg quality has allowed us to detect differences in ovarian gene expression explaining and predicting most of the eventual variance in early embryo mortality among good and poor quality spawners.

**Methods**

**Sample collection and preparation**

Striped bass were reared in outdoor tanks at the N.C. State University Pamlico Aquaculture Field Laboratory [60]. As the striped bass is a group synchronous, single clutch, iteroparous spawner, ovarian tissues were collected by dissection or through ovarian biopsy [61] from females whose most advanced clutch of oocytes/eggs represented one of several stages (≥3 females/stage) of oocyte growth (early primary growth oocytes, diameter 49-81 μm; late primary growth oocytes showing evidence of lipid droplet accumulation, diameter 162-184 μm; vitellogenic growth oocytes, diameter 558-764 μm [see: [62],[63])], oocyte maturation (post-vitellogenic and maturing oocytes, diameter >900 μm), and atresia [64], and ovulated eggs. All samples were preserved in RNeasy® (Applied Biosystems/Ambion; Austin, TX). Tissues were pooled in equal weight by oocyte/egg stage and total RNA was extracted in TRIzol® Reagent (Invitrogen; Carlsbad, CA). RNA quality was assessed by agarose gel
| Contig | Gene | Gene ID | Contig Length (bp) | Solute carrier family function |
|-------|------|---------|-------------------|-----------------------------|
| 04292 | slc3a2 | 796322 629 | Heavy subunit of the heteromeric amino acid transporters (Na⁺-independent, transport of large neutral amino acids: phenylalanine, tyrosine, leucine, arginine and tryptophan) |
| 10145 | slc3a2-like | 100003805 1740 | Heavy subunit of the heteromeric amino acid transporters (Na⁺-independent, transport of large neutral amino acids: phenylalanine, tyrosine, leucine, arginine and tryptophan) |
| 09132 | slc4a7 | 568872 563 | Electroneutral Na⁺ and HCO₃⁻-dependent cotransporter |
| 11036 | slc7a2 | 100007793 815 | Cationic amino acid transporter/glycoprotein-associated amino-acid transporter (transport of the cationic amino acids including arginine, lysine and ornithine) |
| 00672 | slc7a8 | 100007704 987 | Na⁺-independent, transporter of small and large neutral amino acids such as alanine, serine, threonine, cysteine, phenylalanine, tyrosine, leucine, arginine and tryptophan; when associated with Slc3a2, acts as an amino acid exchanger |
| 05979 | slc7a10 | 567420 240 | Na⁺-independent, high affinity transport of small neutral D- and L-amino acids |
| 04450 | slc9a3r1 | 327272 385 | Na⁺/H⁺ exchanger |
| 02807 | slc10a3 | 406519 692 | Na⁺/bile acid cotransporter |
| 06556 | slc10a4 | 556491 249 | Na⁺/bile acid cotransporter |
| 03289 | slc12a5-like | 572215 251 | Electroneutral cation/C¹⁻ cotransporter (K⁺/Cl⁻ transporter) |
| 04100 | slc19a2-like | 100329244 778 | Thiamine transporter |
| 00585 | slc20a1a | 406458 2129 | Na⁺-dependent PO₄³⁻ transporter |
| 05003 | slc20a1b | 321541 246 | Na⁺-dependent PO₄³⁻ transporter |
| 00176 | slc25a3 | 322362 1448 | Mitochondrial carrier (PO₄³⁻ transporter) |
| 01417 | slc25a5 | 192321 1302 | Mitochondrial carrier (ADT/ATP translocator) |
| 01400 | slc25a12 | 337675 693 | Mitochondrial carrier (aspartate/glutamate transporter) |
| 01037 | slc25a26 | 560478 349 | Mitochondrial carrier (S-adenosylmethionine transporter) |
| 09234 | slc25a29 | 569008 579 | Mitochondrial carrier ( carnitine/acylcarnitine transporter) |
| 06849 | slc25a43 | 796731 254 | Mitochondrial carrier |
| 07197 | slc25a46 | 436831 251 | Mitochondrial carrier |
| 08784 | slc26a6-like | 557779 215 | Multifunctional anion exchanger (Pendrin-like; Cl⁻, oxalate, SO₄²⁻, and HCO₃⁻ transporter) |
| 04105 | slc27a1 | 541410 265 | Fatty acid transporter (FATP-1; long-chain fatty acid translocator) |
| 01329 | slc29a1 | 563580 260 | Facilitative nucleoside transporter (cellular uptake of nucleosides) |
| 05237 | slc30a2 | 563540 293 | Zinc transporter |
| 06016 | slc30a2-like | 560642 608 | Zinc transporter |
| 05293 | slc30a5 | 436594 506 | Zinc transporter |
| 03716 | slc30a7 | 327439 392 | Zinc transporter (zinc efflux transporter) |
| 09883 | slc31a2 | 312132 2142 | Copper transporter (low affinity copper uptake) |
| 02632 | slc35a2 | 368487 186 | Nucleoside-sugar transporter (UDP-galactose transporter) |
| 07709 | slc33e1-like | 100332364 249 | Nucleoside-sugar transporter |
| 04693 | slc38a8-like | 795255 414 | Na⁺-coupled neutral amino acid transporter |
| 05870 | slc38a9 | 562137 243 | Na⁺-coupled neutral amino acid transporter |
| 02706 | slc38a17 | 550337 347 | Na⁺-coupled neutral amino acid transporter |
| 02072 | slc39a3 | 321324 414 | Metal ion transporter (zinc influx transporter) |
| 08253 | slc39a13 | 368686 239 | Metal ion transporter (zinc influx transporter) |
| 05275 | slc44a1 | 100333577 256 | Choline transporter |
| 02670 | slc44a2-like | 321056 269 | Choline transporter |
| 07718 | slc44a4-like | 393385 255 | Choline transporter |
electrophoresis and NanoDrop™ spectrophotometry (Fisher Scientific; Pittsburgh, PA). Dynabeads® (Invitrogen) were used to purify mRNA as described by the manufacturer.

cDNA library construction and sequencing
Ovary mRNA was submitted for cDNA synthesis at the N. C. State University Genomic Sciences Laboratory (Raleigh, NC). First and second strand cDNA was synthesized from 2.5 μg of Dnase treated mRNA using the SuperScript™ Double-Stranded cDNA Synthesis Kit (Invitrogen) and oligo (dT)17 according to the manufacturer. Approximately 2 μg of cDNA was prepared for FLX sequencing using standard Roche protocols [65]. Briefly, cDNA was nebulized to generate fragments averaging ~500 bp in length, fragment ends were repaired, and adapters containing PCR and sequencing primer annealing sites were ligated. Fragments were immobilized on beads, clonally amplified and then sequenced on a 1/2 plate using standard FLX platform (Roche; Indianapolis, IN).

Sequence assembly and annotation
Short reads were assembled into contigs using Roche’s Newbler software (gsAssembler) with default settings except that the minimum overlap was set to 30 bp. Parameters were set to generate files for large contigs (> 500 bp) and for all contigs > 100 bp. High quality contig assemblies were subjected to BLAST (blastx) [66] of the NCBI database and annotated according to the Gene Ontology Consortium [67] using Blast2GO 2048 M version 12.2.0 [10,68,69]. Parameters for blastx were: Expect value 1.0E-3 and HSP Length Cutoff 0. Combined GO graphs for the annotated sequences (4,120 total) were created using percentages of 2nd level GO terms for Biological Process and 3rd level GO terms for Molecular Function and Cellular Component. Represented GO classes were restricted to those with 50 or more entries (sequence cutoff = 50.0); Sequence Filter = 50, Score alpha = 0.6, Node Score Filter = 10. Parameters for the Combined Graphs, Level Pie Configuration were: Ontology Level = Level 2 or 3 as described above.

Estimation of abundant gene transcripts
Contigs that were assembled from a number of ESTs comprising > 0.15% of the total 230,151 short reads (i.e. those having ≥ 345 reads per contig) were considered to be abundant [see: [38]]. These contigs were ranked by relative abundance and compared to zebrafish orthologues shown to be ovary predominant by NCBI UniGene DDD [70], see: [15,44]. Zebrafish EST libraries were used to determine relative representation by DDD of orthologous UniGene clusters in ovary (104, 986 ESTs; Lib.IDs 20503, 15519, 20772, 20502, 19214, 15930, 9874, 9767) and body tissues excluding gonads (714, 604 ESTs; Lib.IDs 1520, 1521, 15438, 1028, 17704, 17768, 19753, 1522, 19745, 19746, 20694, 20725, 15518, 21372, 19747, 19748, 4913, 9766, 21371, 19741, 19749, 20771, 19739, 19740, 10504, 19737, 13027, 1029, 17276, 15077, 19752, 15517, 2387, 17282, 17284, 19738, 9968, 9993, 14182, 14249, 19217, 24670, 20072, 20071, 19253, 19219, 19218, 19215, 17283, 17275, 14410, 14409, 13866, 12106, 9706, 4264, 1727). Libraries with sequences derived from embryos, larvae, or whole bodies including gonads were excluded. The Fisher’s exact test (FET) was used to determine difference between the number of times sequences from the ovary or body libraries were assigned to a specific UniGene cluster (P ≤ 0.05). Numerical DDD scores of genes with significantly different expression profiles were reported as the fraction of sequences within the EST libraries that mapped to the UniGene cluster.

Availability of supporting data
The data sets supporting the results of this article are available in the National Center for Biotechnology Information repository, Short Read Archive: SRX007394 and the National Animal Genome Research Program Aquaculture Genome Projects repository, http://www.animal-genome.org/aquaculture/database/.

Additional material
Additional file 1: Striped bass ovary contig assemblies in FASTA format
Additional file 2: Striped bass ovary contig assemblies identified by their annotations in FASTA format
Additional file 3: List of striped bass ovary contig assemblies and their GO terms

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**Author details**
1. North Carolina State University, Department of Biology, Raleigh, NC, USA.
2. South Carolina Department of Natural Resources, Charleston, SC, USA.
3. North Carolina State University, Genomic Sciences Laboratory, Raleigh, NC, USA.
4. North Carolina State University, Department of Plant Pathology, Raleigh, NC, USA.
5. Department of Biology, North Carolina State University, Room 127 David Clark Laboratories, Raleigh, NC, 27695-7617, USA.

**Authors’ contributions**
B.R. conducted the sample preparation, DDD statistical analyses, and drafted the manuscript. J.E.S performed the FLX pyrosequencing and contig sequence assemblies. R.W.C performed the GO annotations. R.W.C., E.H.S. and C.H.O participated in design of the study and critical review of the manuscript. C.V.S conceived the study, participated in its design and coordination, and helped draft the manuscript. All authors read and approved the final manuscript.

**Competing interests**
The authors declare that they have no competing interests.

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