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Evolution of genome size in fishes: a phylogenetic test of the Hinegardner and Rosen hypothesis

Marcio R. Pie · Rodrigo A. Torres · Diego M. A. Brito

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Abstract Despite remarkable advances in genomic studies over the past few decades, surprisingly little is known about the processes governing genome evolution at macroevolutionary timescales. In a seminal paper, Hinegardner and Rosen (Am Nat 106:621–644, 1972) suggested that taxa characterized by larger genomes should also display disprovportionately stronger fluctuations in genome size. Therefore, according to the Hinegardner and Rosen (HR) hypothesis, there should be a negative correlation between average within-family genome size and its corresponding coefficient of variation (CV), a prediction that was supported by their analysis of the genomes of 275 species of fish. In this study we reevaluate the HR hypothesis using an expanded dataset (2050 genome size records). Moreover, in addition to the use of standard linear regression techniques, we also conducted modern comparative analyses that take into account phylogenetic non-independence. Our analyses failed to confirm the negative relationship detected in the original study, suggesting that the evolution of genome size in fishes might be more complex than envisioned by the HR hypothesis. Interestingly, the frequency distribution of fish genome sizes was strongly skewed, even on a logarithmic scale, suggesting that the dynamics underlying genome size evolution are driven by multiplicative phenomena, which might include chromosomal rearrangements and the expansion of transposable elements.

Keywords DNA loss · Genome duplication · Polyploidy · Genome evolution · Genome size independent contrasts

M. R. Pie (✉)
Laboratório de Parasitologia Evolutiva,
Departamento de Zoologia, Setor de Ciências Biológicas,
Universidade Federal do Paraná, C.P. 19020,
Curitiba PR 81531-980, Brazil
e-mail: pie@ufpr.br

R. A. Torres · D. M. A. Brito
Laboratório de Genômica Evolutiva e Ambiental,
Departamento de Zoologia, Universidade Federal
do Paraná, Curitiba PR 81531-980, Brazil

Introduction

Despite remarkable advances in genomic studies over the past few decades, surprisingly little is known about the processes governing genome evolution at macroevolutionary timescales. For instance, several lines of evidence suggest that both gene and whole genome duplication play a fundamental role both in adaptive evolution (Ohno 1970; Lynch and Conery 2000; Castillo-Davis et al. 2004; Le Comber and Smith 2004) and in the establishment of reproductive isolation (Lynch and Force 2000; Otto and Whitton 2000; Taylor et al. 2001). Yet, it is unclear how such microevolutionary mechanisms would translate into the diversity of genome characteristics found in nature. Lynch and Conery (2003) have recently suggested that increases in genome size and complexity might evolve as a non-adaptive consequence of small effective population sizes. Although this hypothesis was recently supported by a study of ray-finned fish genomes (Yi and Streelman 2005), the generality of such mechanism is still controversial (Daubin and Moran 2004; Charlesworth and Barton 2004; Vinogradov 2004a, b).

A seminal study by Hinegardner and Rosen (1972) provided one of the few attempts to search for broad

patterns in genome evolution. In their study, information on genome size was compiled for 275 species of teleostean fish. One of the main hypotheses presented by Hinegardner and Rosen posited that species with small genomes might be relatively closer to the minimum number of genes necessary for the development of an adult fish, whereas species with larger genomes are relatively farther from this limit. Thus, in the former case, there should be a disproportionately greater chance that a mutation affecting genome size would be deleterious, an effect that would be increasingly less apparent as genome size increases. As a consequence, lineages with smaller genomes should display less variation in their genome sizes than lineages with larger genomes. Hinegardner and Rosen tested this corollary by correlating within-family mean genome sizes and their corresponding coefficients of variation (CV), and found significant support for their hypothesis. Given that our knowledge of fish genome size variation increased considerably over the past 30 years, it seems that the time is ripe for a reevaluation of the Hindegardner and Rosen (HR) hypothesis.

In addition to the expanded knowledge on fish genome size variation, another factor might also suggest that a reevaluation of the HR hypothesis is in order. The advent of modern comparative methods indicates that interspecific data cannot be analyzed using regular statistical methods because of phylogenetic non-independence, which can increase (often substantially) the probability of type-I errors (Felsenstein 1985; Harvey and Pagel 1991; Martins 2000). Therefore, a proper test of the HR hypothesis would require the use of appropriate techniques to control for phylogeny, such as the independent contrasts method (Felsenstein 1985; Díaz-Uriarte and Garland 1996).

One aspect of the evolution of genome sizes that was not considered by Hinegardner and Rosen is the shape of the distribution of genome sizes. When viewed over long timescales, the evolution of genome size of a lineage can be seen as a fluctuating random variable. If the dynamics underlying this random variable are based on multiplicative phenomena, such as polyploidy or the addition or deletion of entire chromosomes, then one could expect that interspecific variation in genome size should obey a log-normal distribution. On the other hand, if the main mechanisms responsible for the evolution of genome size are additive (e.g., small insertions and deletions), its distribution should follow a normal (Gaussian) curve (see May 1975). Therefore, a discrimination of these two alternatives can contribute to evaluate a leading hypothesis put forth in recent years to account for the vast differences in genome size found among organisms: the DNA loss hypothesis (Lozovskaya et al. 1999; Petrov et al. 2000; Petrov 2002). According to this hypothesis, differences in genome size may be driven largely by changes in the per nucleotide rate of DNA loss through small indels (Petrov 2002; see Gregory (2004a) for a critical review). As a consequence, if the DNA loss hypothesis is correct, one would expect that genome size variation should follow a normal distribution.

The objective of the present study is twofold. First, variation in fish genome sizes was fit to normal and log-normal distributions. Interestingly, although the fit to a log-normal distribution is clearly superior, the observed data remain skewed even after log-transformation, indicating a disproportionately high frequency of small genomes. Second, we test the HR hypothesis using a variety of linear regression techniques, including methods that control for phylogenetic non-independence. None of the analyses supported the HR hypothesis, suggesting that the evolution of genome sizes in fishes might be more complex than envisioned by the HR hypothesis. Moreover, these results indicate that genome size evolution in fish cannot be viewed as a simple homogeneous stochastic process, and either clade-level sorting or evolutionary biases might account for the disproportionate frequency of lineages with small genome size.

Material and methods

Information on fish genome sizes was obtained mainly from Gregory (2004b), as well as from additional sources (Chang et al. 1995; Carvalho et al. 1998, 2002; Fenerich et al. 2004; Appendix 1). Whenever more than one value was available for a given species, their average was used in the analysis. Average genome size (in pg) was computed for all fish families that had at least two species recorded in our database, totaling 1367 species (2050 records). Within-family variation in genome size was calculated using the CV. The fit of the distribution of genome sizes to normal and lognormal distributions of comparable means and standard deviations was evaluated using the Kolmogorov–Smirnov test (Sokal and Rohlf 1995).

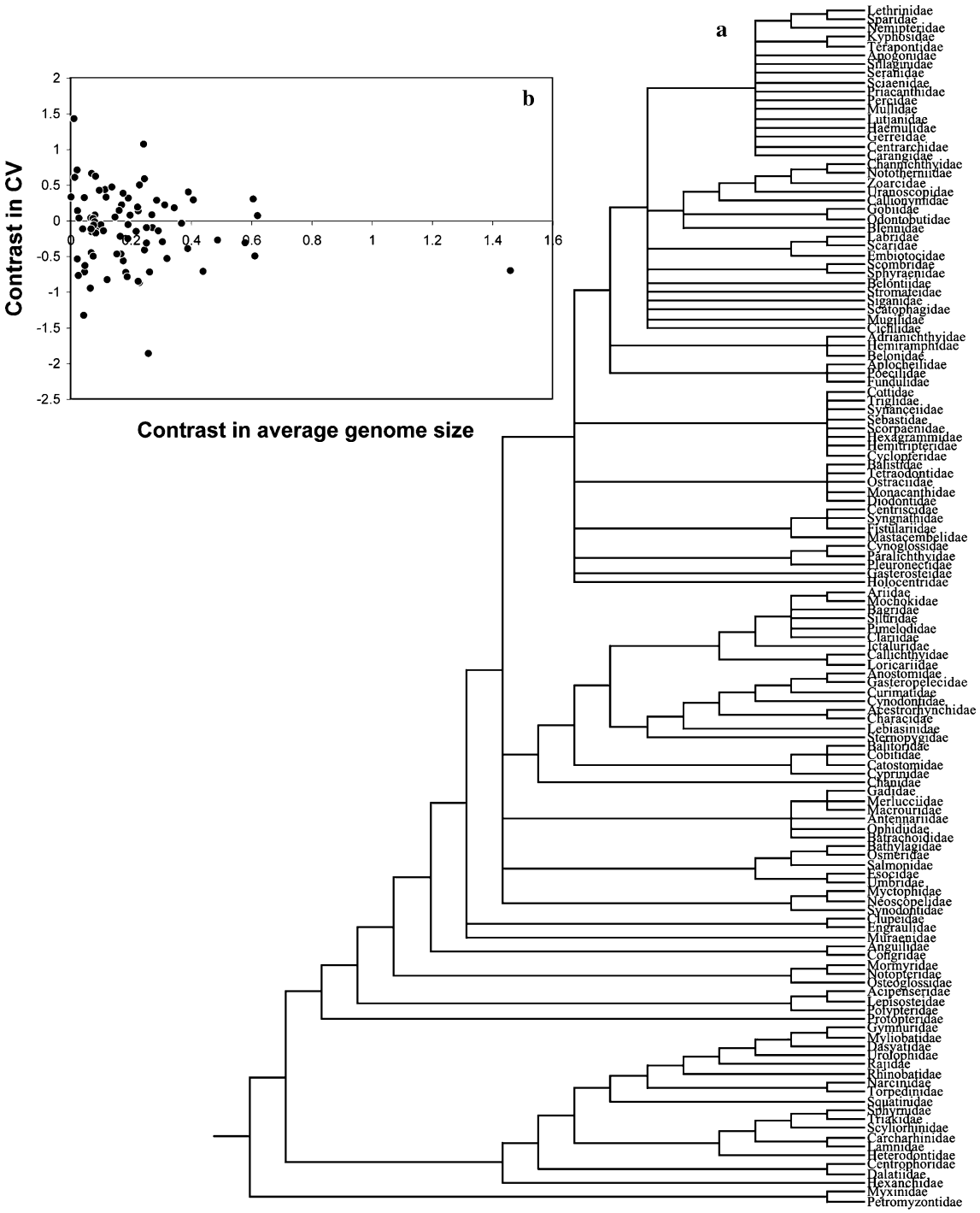
The HR hypothesis was evaluated by testing whether there is a negative association between average genome size within fish families and their respective CV. Initially, as in the original HR paper, the association between both variables was tested using standard linear regression techniques. Additional analyses were conducted to control for phylogenetic non-independence using the independent contrasts method

(Felsenstein 1985). Given that a complete fish phylogeny is not available, two approaches were used. First, the families in the dataset were arranged (to the extent possible) into composite phylogeny that was assembled from a variety of sources (Fig. 1a, see legend for references). A similar composite tree has been used recently in other studies (Mank et al. 2005; Mank and Avise 2006). All branch lengths were set to 1 prior to the analysis. Given the uncertainty regarding the phylogenetic relationships among some of the studied taxa, a second approach was taken by simulating 500 random phylogenies, repeating the independent contrasts test in each of them, and calculating an average slope of the regression among all simulated phylogenies. If the results are consistent regardless of the details of the topology used, the inference can be interpreted as robust. Tree manipulation was conducted using MacClade (Maddison and Maddison 2000) and TreeView (Page 1996). Independent contrasts test and tree simulation was implemented using the softwares CAIC 2.6.9 (Purvis and Rambaut 1995) and COMPARE 4.6 (Martins 2004), respectively.

Results and discussion

Linear regression analyses did not support a significant positive relationship between average genome size and CV (Fig. 2, $r^2 = 0.02$, $df = 128$, $P = 0.11$). Although the independent contrasts method initially indicated a marginally significant correlation (Fig. 1b, $r^2 = 0.05$, $N = 81$ contrasts, $P = 0.046$), this result was caused by the presence of an outlier with a very large contrast in genome size. The removal of that record caused the correlation to be non-significant ($r^2 = 0.02$, $P = 0.13$). Repeated analyses of 500 simulated trees (probability of speciation = 0.5, standard branching model) resulted in an average regression slope of –0.18 (±2.43, 95% confidence interval), confirming the poor correlation between the variables. One could suspect that certain families would have low CV simply because a small number of species have been sampled from the range of evolutionary lineages within the family. However, additional analyses (not shown) failed to find an association between CV and sample size in the dataset. In addition, the most frequently studied families (e.g., characids and cyprinids) have intermediate to low CVs, also indicating that this sort of bias would not affect our conclusions. Therefore, the results of the present study failed to support the HR hypothesis, suggesting that the complexity of the dynamics of genome size evolution has been underestimated and that their scenario for genome size evolution might be simplistic.

The fit of genome sizes to normal and log-normal distributions are shown in Fig. 3a. Contrary to the prediction of the DNA loss hypothesis, the Kolmogorov–Smirnov test indicated a poor fit to the normal distribution ($N = 130$ families, $D = 0.292$, $P = 4.744e-10$). Other studies have strongly criticized the DNA loss hypothesis, particularly its inability to operate at the rates necessary to produce observed interspecific differences (Gregory 2003, 2004a; Neafsey and Palumbi 2003). The present results cast further doubt on whether deletion bias is the predominant force driving the evolution of genome sizes as suggested by Petrov (2002). On the other hand, even though the Kolmogorov–Smirnov also rejected the normal distribution after log-transformation ($D = 0.1843$, $P = 0.0003$), a visual inspection of Fig. 3a indicates that a log-normal provides a reasonably good fit. This result suggests that multiplicative phenomena such as polyploidy, loss of whole chromosomes, fixation of accessory chromosomes, loss of large sections of heterochromatin and large duplications (John and Miklos 1988; Almeida-Toledo et al. 2000; Artoni and Bertollo 2002), as well as the expansion of transposable elements (San Miguel et al. 1998), play an important role in genome size evolution in teleostean fish, more so than additive phenomena. Normal distributions reflect additive combinations; whereas lognormal distributions reflect multiplicative combinations of random variables (see Maurer et al. 1992). However, the distribution of genome sizes remains skewed even after being log-transformed (Fig. 3b). A similar pattern has been known for the distribution of body sizes in vertebrates (e.g., Maurer et al. 1992) and has commonly been interpreted as a macroevolutionary bias towards smaller bodied organisms resulting any of three potential mechanisms: increased speciation rates in smaller organisms (Dial and Marzluff 1988), higher extinction rates in larger organisms (Cardillo and Bromham 2000), and/or a phyletic trend toward small body sizes (Hanken and Wake 1993). A similar argument could be made for the evolution of genome sizes. For instance, energetic constraints in the replication of large genomes could be a possible biasing mechanism. Also, preliminary analyses of genome size variation using character reconstruction methods suggests that a trend toward smaller genomes might be at work in the Characidae (Teleostei, Ostariophysi; V.M. Sass, R.A. Torres and M.L. Adam, unpublished results). It is important to note that the skew in the distribution of genome sizes cannot be attributed to stabilizing selection, given that it would only reduce the variance around the mean without producing the observed skew. Uncovering the mechanisms that are responsible for this skewed pattern of



genome size distribution, as well as an understanding of how prevalent this pattern is for other organisms, clearly merit further investigation.

Beginning in the early 1990s, a new branch of ecological studies was born which explicitly sought to investigate large-scale phenomena such as patterns of geographical range sizes and the relative abundance of species in local communities (Brown 1995). This field, known as macroecology, has rapidly matured into a prolific research area (see Gaston and Blackburn 2000; Blackburn and Gaston 2001, and references therein). The increasingly rapid rate of accumulation of genome information of a large range of organisms, as well as the results of the present study, suggests that an

◀ **Fig. 1** (**a**) Composite phylogeny of a subset of all fish families that was used in the present study to conduct the independent contrasts analysis. Relationships were based on a variety of sources: Shirai (1996), Adnet and Cappetta (2001), González-Isáias and Dominguez (2004), Carvalho et al. (2004), Geig et al. (2005), and Maisey et al. (2004) for the relationships within the Elasmobranchii clade, Inoue (2003) for several Actinopterygii relationships and Saitoh et al. (2003) for the Ostariophysan relationships, Albert and Campos-da-Paz (1998) for Gymnotiform families, de Pinna (1998) for Siluriform families, Brainerd et al. (2001) for Triacanthidae, Monacanthidae, Balistidae, Ostraciidae, Triodontidae, Molidae, Diodontidae, and Tetraodontidae, Carpenter and Johnson (2002) for Nemipteridae, Sparidae and Lethrinidae, Miya et al. (2003) for several teleost families, Ortí and Meyer (1997) for Characiform families, Carroll (1988), Nelson (1994), Froese and Pauly (2001) for Cottoidei, Beryciform and Hexagrammoidei families, Carroll (1988), Nelson (1994), Frickhinger (1995), Froese and Pauly (2001) for Scorpaenoidei, Mugiliform, Synbranchiform, Gadiform, Gasterosteiform and Pleuronectiforms families, Carroll (1988), Nelson 1994, Tyler and Sorbini 1996, Froese and Pauly 2001 for Tetraodontiform families, Carroll (1988), Nelson (1994), Ghedotti (2000), Froese and Pauly (2001), Lovejoy and Collette (2001) for Beloniform families. (**b**) Results from phylogenetically independent contrasts testing for an association between mean genome size and its corresponding coefficient of variation. Values were log-transformed prior to the analysis to bring them closer to a normal distribution. See text for details

analogous development in the field of genomics (a ''macrogenomics'') can represent an important underutilized tool to understand the dynamics of genome evolution.

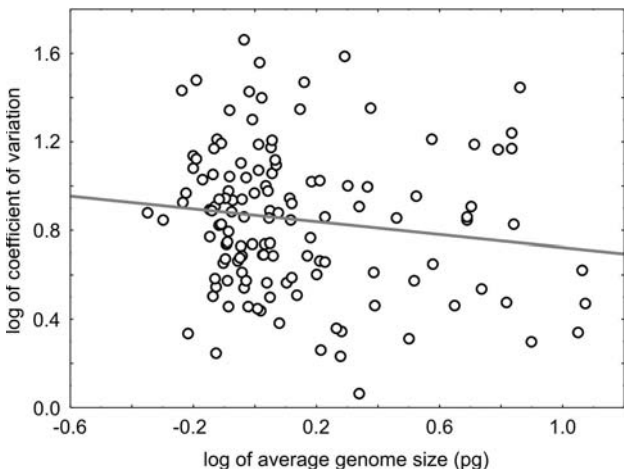


Fig. 2 Relationship between within-family average genome sizes and their respective coefficients of variation in teleost fishes (N = 130 families, r^2 = 0.02, t = –1.6248, P = 0.1067). Data were log-transformed to bring them closer to a normal distribution. An additional analysis with untransformed data showed similar results (not shown)

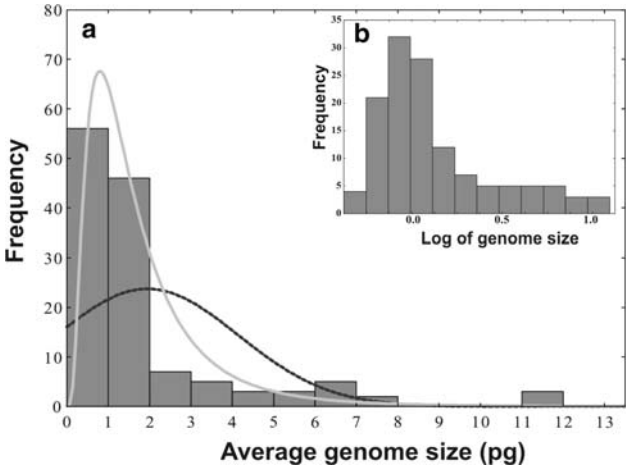


Fig. 3 (**a**) Distribution of fish genome sizes, including inferred expectations according to different underlying distributions; dotted dark gray line = normal distribution, light gray line = -log-normal distribution. (**b**) Inset shows the distribution of genome sizes after log-transformation, indicating an asymmetry towards smaller genomes

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Appendix 1

Family	Average (pg)	CV	# Species
Acanthuridae	0,904	4,128	8
Acestrorhynchidae	1,200	2,424	2
Acipenseridae	3,150	2,051	16
Adrianichthyidae	0,838	7,717	8
Anguilidae	1,401	22,427	2
Anostomidae	1,519	10,484	14
Antennariidae	0,898	5,401	2
Aplocheilidae	1,041	2,762	4
Apogonidae	1,013	2,808	3
Ariidae	2,367	22,738	3
Bagridae	1,026	11,888	6
Balistidae	0,671	10,801	8
Balitoridae	0,606	2,176	5
Bathylagidae	2,450	2,925	4
Batrachoididae	2,425	4,104	4
Belonidae	1,122	14,967	6
Belontiidae	0,745	3,548	10
Blennidae	0,788	4,519	18
Callichthyidae	1,883	1,722	24
Callionymidae	0,810	3,764	3
Carangidae	0,708	7,832	11
Carcharhinidae	3,779	4,507	14
Catostomidae	2,166	8,113	6
Centrarchidae	1,026	15,537	12
Centriscidae	0,500	7,071	2
Centrophoridae	6,825	17,549	2
Chaetodontidae	0,738	8,148	8
Chanidae	0,808	5,487	6
Channichthyidae	1,990	10,103	3

Appendix 1 continued

Family	Average (pg)	CV	# Species
Characidae	1,505	5,855	54
Cichlidae	1,112	7,777	23
Clariidae	1,130	11,415	2
Clupeidae	1,076	5,480	12
Cobitidae	1,630	1,834	15
Congridae	1,473	4,863	4
Cottidae	0,944	2,873	9
Curimatidae	1,624	10,636	12
Cyclopteridae	0,900	12,728	2
Cynodontidae	1,030	36,416	2
Cynoglossidae	0,915	3,497	2
Cyprinidae	1,361	3,261	189
Dalatiidae	11,502	4,209	13
Dasyatidae	4,869	7,036	15
Diodontidae	0,821	22,164	4
Embiotocidae	0,842	8,675	5
Engraulidae	1,682	7,284	3
Esocidae	1,171	12,487	5
Fistulariidae	0,753	16,372	2
Fundulidae	1,442	29,523	3
Gadidae	0,815	6,255	3
Gasteropelecidae	1,295	8,859	4
Gasterosteidae	0,630	13,748	3
Gerreidae	0,645	13,377	3
Gobiidae	1,115	3,158	17
Gymnuridae	6,560	3,012	2
Haemulidae	0,816	9,541	8
Hemiramphidae	0,903	4,883	4
Heterodontidae	11,200	2,200	2
Hexagrammidae	0,835	118,087	2
Hexanchidae	4,875	7,257	2
Holocentridae	0,877	4,649	2
Ictaluridae	1,046	25,355	2
Kyphosidae	0,920	7,319	4
Labridae	0,980	5,489	21
Lamnidae	6,155	14,753	2
Lebiasinidae	2,176	1,161	2
Lepisosteidae	1,310	8,421	2
Lethrinidae	1,306	7,085	5
Loricariidae	1,623	4,630	9
Lutjanidae	1,058	4,968	10
Macrouridae	0,824	11,131	5
Mastacembelidae	0,775	15,657	2
Merlucciidae	0,955	27,011	2
Mochokidae	1,085	10,088	4
Monacanthidae	0,580	8,447	8
Mormyridae	1,100	9,526	4
Mugilidae	0,800	8,835	4
Mullidae	0,595	9,369	4
Muraenidae	2,308	9,947	6
Myctophidae	1,950	39,000	3
Myliobatidae	5,154	15,572	10
Myxinidae	3,285	3,783	7
Narcinidae	7,870	1,996	4
Nemipteridae	0,935	3,778	2
Neoscopelidae	1,910	2,214	2
Notopteridae	1,190	7,650	2
Nototherniidae	1,263	3,681	2
Odontobutidae	1,163	13,152	2
Ophidiidae	0,760	6,718	2
Osmeridae	0,723	7,810	4

Appendix 1 continued

Family	Average (pg)	CV	# Species
Osteoglossidae	0,990	70,004	2
Ostraciidae	0,990	9,383	4
Paralichthyidae	0,798	4,734	6
Percidae	1,133	16,136	3
Petromyzontidae	1,578	4,039	10
Pimelodidae	1,113	5,556	4
Pinguipedidae	0,575	27,106	2
Pleuronectidae	0,710	5,949	17
Poecilidae	0,808	5,645	30
Polypteridae	5,040	8,076	4
Priacanthidae	0,893	4,807	3
Protopteridae	71,208	1,884	4
Rajidae	3,332	9,083	20
Rhinobatidae	4,424	2,899	9
Salmonidae	2,865	7,234	31
Scaridae	1,684	4,563	7
Scatophagidae	0,735	14,849	2
Sciaenidae	0,772	6,759	7
Scombridae	0,936	10,929	9
Scorpaenidae	1,138	4,869	5
Scyliorhinidae	6,896	6,728	4
Sebastidae	0,977	20,031	10
Seranidae	1,108	7,216	21
Siganidae	0,630	12,050	4
Sillaginidae	0,645	30,406	2
Siluridae	1,061	4,961	2
Sparidae	0,739	3,848	11
Sphyraenidae	0,815	2,883	4
Sphyrnidae	3,739	16,395	2
Squatinidae	11,837	2,983	3
Sternopygidae	0,993	172,050	3
Stromateidae	0,805	113,844	2
Synanceiidae	0,730	3,226	2
Syngnathidae	0,746	1,779	11
Synodontidae	1,310	3,907	5
Terapontidae	0,765	8,794	4
Tetraodontidae	0,448	7,650	16
Torpedinidae	7,232	28,006	4
Triakidae	5,436	3,445	7
Triglidae	0,890	6,293	2
Umbridae	1,830	2,303	4
Uranoscopidae	0,725	11,392	2
Urolophidae	6,825	14,849	2
Zoarcidae	1,087	3,689	5

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