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Article

The Magnitude of Global Marine Species Diversity

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Summary

Background: The question of how many marine species exist is important because it provides a metric for how much we do and do not know about life in the oceans. We have compiled the first register of the marine species of the world and used this baseline to estimate how many more species, partitioned among all major eukaryotic groups, may be discovered.

Results: There are ~226,000 eukaryotic marine species described. More species were described in the past decade (~20,000) than in any previous one. The number of authors describing new species has been increasing at a faster rate than the number of new species described in the past six decades. We report that there are ~170,000 synonyms, that 58,000–72,000 species are collected but not yet described, and that 482,000–741,000 more species have yet to be sampled. Molecular methods may add tens of thousands of cryptic species. Thus, there may be 0.7–1.0 million marine species. Past rates of description of new species indicate there may be 0.5 ± 0.2 million marine species. On average 37% (median 31%) of species in over 100 recent field studies around the world might be new to science.

Conclusions: Currently, between one-third and two-thirds of marine species may be undescribed, and previous estimates of there being well over one million marine species appear highly unlikely. More species than ever before are being described annually by an increasing number of authors. If the current trend continues, most species will be discovered this century.

Introduction

The most widely used metric of biodiversity is species richness, and much has been written about how many species may exist on land and in the sea [1–3]. Recent estimates of the number of extant described marine species vary from 150,000 to 274,000, and of those that may exist from 300,000 to over 10 million [4–14] (Table 1). Most of these estimates were made without the benefit of a global inventory of known marine species. The former estimates were based on experts' polls. The latter were based on extrapolation from past rates of description of species and higher taxa, proportions of undescribed species in samples, proportions that well-known taxa may represent of regional biota, and numbers of species in samples (Table 1). Here, we report on the near completion of such an inventory. The World Register of Marine Species (WoRMS) is an open-access online database created by an editorial board of 270 taxonomists from 146 institutions in 32 countries [15]. The first goal of WoRMS has been the compilation of a list of all taxonomically accepted marine species, commonly used synonyms, and key literature sources. Beyond complete taxonomic coverage, the longer-term aim is to provide or link to data on species distributions, biology, ecology, images, and guides to their identification. An important side benefit is that it facilitates communication within and beyond the taxonomic community, which can lead to increased rates of discovery of species and synonyms and a reduced rate of creation of new synonyms (and homonyms).

This collaborative database enabled the following set of marine biodiversity metrics to be compiled for the first time: (1) the number of nominal species, i.e., all species named, including those now recognized as synonyms due to multiple descriptions of the same species, and (2) the number of taxonomically accepted species, i.e., recognized species, excluding names that have been relegated to synonymy. In addition, we estimated the number of species that (3) have been collected but not yet described, (4) are undiscovered (unsampled), and (5) are molecular cryptics, i.e., only distinguishable by molecular analysis. Finally, we applied a statistical model that predicted how many more species might be discovered based on historical rates of species description and compared it with values from the above estimates. We omitted Bacteria and Archaea from our analysis because the species concept used for eukaryotes cannot be applied to these two taxa.

Our estimates of valid and nominal species are based on the WoRMS database as of February 17, 2012 and the literature on taxa for which WoRMS was not yet complete. The figures regarding species collected but not yet described, undiscovered, and cryptic are based on our own experience and that

Table 1. An Overview of the Estimated Numbers of Marine Species Described and Those that May Exist, as Published in the Literature

	Method	Reference (Year)
Number of Species Described		
150,000	expert opinion	van der Land [4] (1994)
160,000	expert opinion	Gordon [5] (2001)
204,000	expert opinion	Gibbons et al. [6] (1999)
222,000–230,000	inventory of 214,000 and expert opinion	present study
230,000	expert opinion	Bouchet [7] (2006)
250,000	literature and expert opinion	Winston [8] (1992)
274,000	expert opinion	Reaka-Kudla [9] (1996)
Number of Existing Species		
300,000	predicted based on description rate using WoRMS 2009	Costello et al. [10] (2012)
<500,000	proportion new species in samples	May [11] (1992)
320,000–760,000	predicted based on description rate using WoRMS 2012	stats model, present study
704,000–972,000	expert opinion	experts, present study
>1,000,000	expert opinion of proportions of undescribed species in regions of the world	Winston [8] (1992)
1,500,000	extrapolation from proportion of Brachyura in Europe	Bouchet [7] (2006)
2,200,000	extrapolation from rate of discovery of higher taxa	Mora et al. [12] (2011)
5,000,000	extrapolation from benthos samples off Australia	Poore and Wilson [13] (1993)
>10,000,000	extrapolation from deep-sea benthos samples	Grassle and Maciolek [14] (1992)

of other experts, considering information on numbers of undescribed species that we observed in samples and our knowledge of particular habitats and geographic areas that remain little explored. The rationales for these estimates are provided in Table S2 available online. We each limited our estimates to groups for which we have close working knowledge. To indicate areas of uncertainty, we applied minimum and maximum estimates. The expert-opinion approach to estimating the magnitude of unknown biodiversity has been endorsed, for example, by Gaston [16] and used by many others (e.g., [7, 8]; Table 1). It complements macroecological approaches involving extrapolation from surrogate taxa, habitats, and/or geographic areas (reviewed in [2]). Our collective estimates are less likely to be biased than previous estimates made by fewer experts because we are most familiar with our particular taxa [17]. The 270 editors in WoRMS are among the world's top taxonomists. They represent ~5% of the active marine taxonomists today (based on ~4,900 marine taxonomists publishing during the last decade) and are involved in nearly one-third of new marine species descriptions in the past decade [15]. However, estimates based on expert opinion are subject to bias based on scientists' individual experiences, accuracy of their recollections and beliefs (e.g., how endemic a taxon is), and concerns about the consequences of their estimates on perceptions of the importance of their taxon [18]. For example, expert estimates tend to be optimistic [18], and they may feel it prudent to overestimate rather than underestimate the number of species in a taxon. Estimates can be substantially improved by combining empirical data with expert judgment [19]. Thus, we complemented the expert-opinion approach by fitting a statistical model with confidence limits to the species description rate for accepted species in WoRMS as of February 17, 2012 [20] (Supplemental Experimental Procedures). This model accounts for variation between years and identifies taxa whose rate of discovery is too variable for such extrapolation.

Results

Accepted Species

We recognized that 222,000–230,000 accepted eukaryotic marine species have been described. Of these, ~7,600 species belong to Plantae, ~19,500 to Chromista, ~550 to Protozoa, ~1,050 to Fungi, and nearly 200,000 to Animalia. We were unable to give a more precise number for Animalia due to the uncertainty in the total number of gastropod species (Table 2; see also Table S2).

Unaccepted Synonyms

Of ~400,000 species names established, ~170,000 (~40%) were currently not accepted, i.e., were synonyms (Table 2). This means that on average, for every five species described as new to science, at least two had already been described. The level of synonymy was greatest among the most-studied organisms, such as cetaceans, where 1,271 names existed for only 87 valid species. Taxa of which over 70% of names were considered synonyms were Cetacea, Reptilia, Sirenia, Sipuncula, Siphonophora, Zoantharia, and Bacillariophyceae. Taxa with over 50% synonymy rates included Pisces, Mollusca, Myriapoda, Scleractinia, Asteroidea, Pennatulacea, Chaetognatha, and Larvacea. Of the 170,000 synonyms we were aware of, 57,000 were entered into WoRMS. These entries indicated that the proportion of recognized synonyms has been steadily decreasing since the early 20th century (Figure 1). Of species described in the first decade of the 20th century, 25% were now synonyms, from the 1950s 15%, and the 1980s 5%. Adjusting for the fact that about 33% of synonyms were in WoRMS, and if this synonym trend was only due to the time it takes to discover synonyms, then a further 42,000 species remain to be synonymized since 1900.

Estimated Total Global Species Richness

Based on Past Rates of Species Descriptions

The marine species description rate has increased since the 1750s, with a very high discovery rate around 1900 (Figure 2). It declined during the two world wars and has recovered from 1950 to present. The curve dipped in the 1990s but has sharply increased again since 2000, with more than 20,000 marine species (9% of those currently known) described in the last decade. The number of marine species described per year reached all-time highs in the past decade, with over 2,000 species described in each of four different years (Figure 2).

The statistical model predicted a total of 540,000 marine species, with a 95% probability interval of 320,000 to 760,000. When limited to the different taxonomic groups, the estimates were comparable to or less than the experts' estimates (Table 2). For several taxonomic groups (especially where the majority of species remain to be described), the rate of discovery was still rising and the model could not make a meaningful estimate of total species numbers. This was the case for Acanthocephala, Polychaeta, Hirudinea, Oligochaeta, Cumacea, Isopoda, Tanaidacea, Copepoda, Ostracoda, Bryozoa, Cephalorhyncha, Chaetognatha, Hexacorallia, Octocorallia, Hydrozoa, Gastrotricha, Gnathostomulida, Bivalvia, Gastropoda, Cestoda, Digenea, and Porifera (Table 2).

Even in taxa of large body size or high economic value, new species continued to be discovered and described. Between 1999 and 2008, 780 new crabs, 29 lobsters, and 286 shrimps (of a total of 1,401 decapods), 1,565 marine fish, 4 sea snakes, and 3 new species and 7 subspecies of cetaceans [15] were described.

Our data also showed that the number of authors describing new species each year has been increasing, to 4,900 authors in the past decade (Figure 3). Moreover, the number of authors has been increasing faster than the number of new species. The number of valid species described per author decreased from between three to six species per year before 1900 to less than two species per author per year since the 1990s (Figure 3).

Based on Expert Opinion

Our collective estimates suggested that global marine species richness was between 704,000 and 972,000, so that only one-third to one-fourth of marine species have been described. However, this proportion varied greatly between taxa (Table 2). Of this number, 58,000–72,000 species, or 25%–30% of the known marine diversity, were already represented in specimen collections waiting to be described (Table 2). The estimated number of undiscovered molecular cryptic species was ~9,000–35,000 (Table 2) for 49 taxa that have a total of ~80,000 accepted described species—i.e., 11%–43% of their known species. Cryptic species were predicted not to occur in 9 taxa, and for 32 of the 98 remaining taxa, the experts did not have a basis on which to make an estimate. The proportion of cryptic species was highest in taxa with few externally visible diagnostic characters, such as Radiozoa, Placozoa, Hydrozoa, Zoantharia, Mesozoa,

Table 2. Estimates of Known and Unknown Marine Species Diversity

			Total Known	Described (Accepted)	% Syn	Undescribed (Collected)	Undiscovered (Morpho)	Undiscovered (Molecular Cryptic)	Total Unknown (Experts)	Total Unknown (Model)	Total Estimated	% Known	New spp. (1999-2008)
Plantae			**7,593**							**2,500-3,600**	**22,798-22,803**	**33**	**632**
	Chlorophyta			1,300	19	?	1,200	-	1,200	-		52	
	Rhodophyta			6,150	49	?	14,000	-	14,000	-		31	
	Mangroves			75	29	?	0-5	-	0-5	-		94-100	
	Seagrasses			68	6	0	5	-	5	-		93	
Chromista			**19,444**							**3,500-4,200**	**77,930-93,923**	**21-25**	**790**
	Bigyra			76	?	?	75	-	75	-		50	
	Cercozoa			173	?	?	160	-	160	-		52	
	Ciliophora			2,615	39	?	1,058-4,648	3,173-14,526	4,231-19,174	-		12-38	
	Cryptophyta			86	?	?	150	-	150	-		36	
	Foraminifera			6,000	40	1,000	500	-	1,500	-		80	
	Haptophyta			241	?	?	100-150	-	100-150	-		62-71	
	Heliozoa			10	?	?	20	-	20	-		33	
	Myzozoa			2,686	?	?	575	-	575	-		82	
	Ochrophyta												
		Phaeophyceae		1,800	49	50	150-200	-	200-250	-		88-90	
		Bacillariophyceae		5,000	75	?	50,000	-	50,000	-		9	
		Chrysophyceae		51	-	?	1,000	-	1,000	-		5	
		Other Ochrophyta		263	?	?	160	-	160	-		62	
	Oomycota			43	?		225	-	225	-		16	
	Radiozoa			400	30	0	40	50-1,000	90-1,040	-		28-82	
Protozoa			**542**							**150-400**	**2,207**	**25**	**23**
	Amoebozoa			117	?	?	450	-	450	-		21	
	Apusozoa			3	?	?	15	-	15	-		17	
	Choanozoa			150	?	?	750	-	750	-		17	
	Euglenozoa			243	?	?	370	-	370	-		40	
	Excavata			29	?	?	80	-	80	-		27	
Fungi			**1,035**	1,035	10	200	14,800	-	15,000	**1,100-1,500**	**16,035**	**6**	**125**
Animalia													
	Acanthocephala		**450**	450	25	20	150	50-150	220-320	**	**670-770**	**58-67**	**30**
	Annelida		**13,721**								**26,011-37,096**	**37-53**	**841**
		Polychaeta		12,632	35	3,160	3,160	NB	6,320	**		67	
		Hirudinea		179	28	15-35	50-100	5-20	70-155	**		54-72	
		Oligochaeta		910	30	300	5,000-15,000	600-1,600	5,900-16,900	**		5-13	
	Arthropoda												
		Chelicerata	**2,685**							**2,700-3,000**	**5,335-7,066**	**38-50**	**340**
		Merostomata		4	-	1	0	NB	1	-		80	
		Pycnogonida		1,307	3	150-500	979-1,650	50-100	1,179-2,250	-		37-53	
		Acarina		1,218	-	100	1,220-1,830	150-200	1,470-2,130	-		36-45	
		Araneae		125	-	?	?	-	-	-		-	
		Pseudoscorpionida		31	-	?	?	-	-	-		-	
		Crustacea											
		Decapoda	**12,029**							**4,500-5,100**	**21,073-24,204**	**50-57**	**1,611**
		Dendrobranchiata		551	31	50	100	NB	150	-		79	
		Achelata		142	38	10	30-70	5-10	45-90	-		61-76	
		Chirostyloidea		206	2	250	580	10-55	840-885	-		19-20	

(*Continued on next page*)

Table 2. *Continued*

	Total Known	Described (Accepted)	% Syn	Undescribed (Collected)	Undiscovered (Morpho)	Undiscovered (Molecular Cryptic)	Total Unknown (Experts)	Total Unknown (Model)	Total Estimated	% Known	New spp. (1999-2008)
Galatheoidea		715	8	300	830	19-97	1,149-1,227	-		37-38	
Hippoidea		81	19	3	10	NB	13	-		86	
Lithodoidea		129	20	10	40	-	50	-		72	
Lomisoidea		1	0	0	0	-	0	-		100	
Paguroidea		1,106	17	150-200	400	NB	550-600	-		65-67	
Enoplometopoidea		12	20	0	2-7	1-3	3-10	-		55-80	
Glypheoidea		2	0	0	1-2	-	1-2	-		50-67	
Nephropoidea		54	24	1	10-28	2-5	13-34	-		61-81	
Brachyura		5,688	30	300	3,550-6,400	0	3,850-6,700	-		46-60	
Procarididea		6	0	0	2	NB	2	-		75	
Caridea		2,572	25	400	1,500	NB	1,900	-		58	
Polychelida		38	27	0	7-15	1-3	8-18	-		68-83	
Stenopodidea		68	16	10	50	NB	60	-		53	
Gebiidea		203	10	50	100	-	150	-		58	
Axiidea		455	10	50	200	-	250	-		65	
Peracarida	**17,115**							**	**132,297-228,231**	**7-13**	**2,275**
Amphipoda		6,947	-	?	20,000	-	20,000	4,000-4,300		26	
Bochusacea		5	0	0	10	NB	10	-		33	
Cumacea		1,444	2	45	6000	-	6,045	**		19	
Isopoda		6,345	2	3,400	60,000-120,000	0	63,400-123,400	**		5-9	
Lophogastrida		56	24	10	120	1-5	131-135	-		29-30	
Mictacea		1	0	0	0	0	0	-		100	
Mysida		1,180	32	80-100	2,000-4,000	10-20	2,090-4,120	340-450		22-36	
Tanaidacea		1,130	6	900	22,600-56,500	NB	23,500-57,400	**		2-5	
Thermosbaenacea		7	0	1	5	-	6	-		54	
Other Crustacea	**21,086**								**55,604-107,594**	**20-38**	
Branchiopoda		90	3	0	0	0	0	-		100	
Cephalocarida		12	0	0	10	NB	10	-		55	
Amphionidacea		1	-	0	0	0	0	-		100	
Euphausiacea		86	42	0	0	0	0	-		100	
Stomatopoda		468	19	52	200	-	252	-		65	
Leptostraca		49	2	50-100	200-600	-	250-700	-		7-16	
Branchiura		44	12	2-3	50-80	NB	52-83	-		35-46	
Copepoda		10,000	17	1,500-2,000	28,500-48,000	125	30,125-50,125	**		17-25	
Mystacocarida		13	0	1	10	NB	11	-		54	
Pentastomida		10	-	?	?	-	-	-		-	
Tantulocarida		36	0	60	1,000	NB	1,060	-		3	
Thecostraca		1,400	7	?	100-200	NB	100-200	-		88-93	
Ostracoda		8,853	7	1,000-2,000	1,625-32,000	NB	2,625-34,000	**		21-77	
Remipedia		24	4	8	20-50	5-9	33-67	-		26-42	
Hexapoda (Insecta and Collembola)	**2,037**	2,037	15	30-60	30-100	NB	60-160	110-250	**2,097-2,197**	**93-97**	**30**
Myriapoda	**61**	61	58	?	190	-	190	-	**251**	**24**	**2**
Brachiopoda	**388**	388	-	0	?		-	65-175	**388**	**?**	**21**
Bryozoa	**5,900**	5,900	9	?	2,450-4,250	350-950	2,800-5,200	**	**8,700-11,100**	**53-68**	**599**
Cephalorhyncha	**284**							**	**2,667-3,772**	**8-11**	**47**
Kinorhyncha		228	0	250-350	1,000-2,000	-	1,250-2,350	-		9-15	
Loricifera		32	0	123	1,000	-	1,123	-		3	

Table 2. *Continued*

		Total Known	Described (Accepted)	% Syn	Undescribed (Collected)	Undiscovered (Morpho)	Undiscovered (Molecular Cryptic)	Total Unknown (Experts)	Total Unknown (Model)	Total Estimated	% Known	New spp. (1999-2008)
	Nematomorpha		5	0	?	10-15	NB	10-15	-		25-33	
	Priapulida		19	-	?	?	-	-	-		-	
Chaetognatha		**129**	129	54	6-9	44	0-256	50-309	**	**179-438**	**29-72**	**11**
Chordata												
	Cephalochordata	**33**	33	-	?	?	-	-	-	**33**		
	Tunicata	**3,020**							2,700-4,300	**4,600-5,100**	**59-66**	**391**
	Ascidiacea		2,874	43	500	500-1,000	500	1,500-2,000	-		59-66	
	Larvacea		67	53	4	63	NB	67	-		50	
	Thaliacea		79	0	5	8	-	13	-		86	
	Pisces (incl. Agnatha)	**16,733**	16,733	49	500	4,200-4,300	200-300	4,900-5,100	6,700-10,700	**21,633-21,833**	**77**	**1,577**
	Mammalia	**135**							0-11	**137-143**	**94-99**	**3**
	Carnivora		44	14	0	0	-	0	-		100	
	Sirenia		4	89	0	0	0	0	-		100	
	Cetacea		87	93	0	1-5	1-3	2-8	-		92-98	
	Reptilia	**110**	110	82	?	20-30	-	20-30	-	**130-140**	**79-85**	**4**
	Aves	**641**	641	-	30-50	30-50	0	60-100	0-9	**701-741**	**87-91**	**1**
Cnidaria												
	Hexacorallia	**3,152**							**	**3,976-5,105**	**62-79**	**286**
	Actiniaria		1,093	25	?	?	NB		-		-	
	Antipatharia		250	11	50-75	50-100	NB	100-175	-		59-71	
	Ceriantharia		141	12	4-6	15-25	-	19-31	-		82-88	
	Corallimorpharia		47	15	?	?	NB	0	-		-	
	Zoantharia		101	78	30	180-380	60-760	270-1,170	-		8-27	
	Scleractinia		1,520	61	93	342	0-142	435-577	-		72-78	
	Octocorallia	**3,171**							**	**4,871**	**65**	**290**
	Alcyonacea, Helioporacea		2,951	18	100	1,500	NB	1,600	-		65	
	Pennatulacea		220	51	20	80	NB	100	-		69	
	Cubozoa	**37**	37	20	10-20	20-50	-	30-70	-	**67-107**	**35-55**	
	Hydrozoa (excl. Siphonophorae)	**3,426**	3,426	27	50-100	500-1,500	1,000-2,500	1,550-4,100	**	**4,976-7,526**	**46-69**	**304**
	Siphonophorae	**176**	176	74	50-60	50-60	0	100-120	-	**276-296**	**59-64**	
	Scyphozoa	**201**	201	1	38-80	77	22-25	137-182	-	**338-383**	**52-59**	
	Staurozoa	**48**	48	24	10-12	30-50	0-3	40-65	-	**88-113**	**42-55**	
Ctenophora		**190**	190	24	25-50	100-250	0-10	125-310	7-57	**315-500**	**38-60**	3
Cycliophora		**2**	2	0	3	10-125	-	13-128	-	**15-130**	**2-13**	1
Echinodermata		**7,291**							230-300	**9,617-13,251**	**55-76**	297
	Asteroidea		1,922	65	125-200	200-500	-	325-700	-		73-86	
	Echinoidea		999	37	20-50	45-150	306-1,080	371-1,280	-		44-73	
	Ophiuroidea		2,064	34	260-300	200-400	100-150	560-850	-		71-79	
	Crinoidea		623	32	20-30	50-100	-	70-130	-		83-90	
	Holothuroidea		1,683	29	200-400	800-2,600	-	1,000-3,000	-		36-63	
Echiura		**175**	175	14	5-10	30-40	-	35-50	12-44	**210-225**	**78-83**	5
Entoprocta		**193**	193	13	30	1,000	NB	1,030	16-57	**1223**	**16**	18
Gastrotricha		**434**	434	18	310	1,000-1,500	500-1,000	1,810-2,810	**	**2,244-3,244**	**13-19**	86
Gnathostomulida		**98**	98	10	15-20	200	NB	215-220	**	**313-318**	**31**	9
Hemichordata		**118**	118	7	10	?	-	10	0-2	**128**	**?**	4

(*Continued on next page*)

Table 2. *Continued*

		Total Known	Described (Accepted)	% Syn	Undescribed (Collected)	Undiscovered (Morpho)	Undiscovered (Molecular Cryptic)	Total Unknown (Experts)	Total Unknown (Model)	Total Estimated	% Known	New spp. (1999-2008)
Mesozoa (Orthonectida, Dicyemida)		134	134	1	40-50	500-1,000	100-500	640-1,550	84-305	774-1,684	8-17	34
Mollusca		43,689-51,689							**	135,887-164,107	28-36	4,022
	Bivalvia		9,000	55	2000	3,000	-	5,000	**		64	
	Caudofoveata		133	8	?	500	-	500	-		21	
	Cephalopoda		761	-	150	500	-	650	-		54	
	Gastropoda		32,000-40,000	69-75	35,000-45,000	50,000-60,000	-	85,000-105,000	**		23-32	
	Monoplacophora		30	-	3	50	-	53	-		36	
	Polyplacophora		930	52	50	50-100	-	100-150	-		86-90	
	Scaphopoda		572	33	55	500	NB	555	-		51	
	Solenogastres		263	21	20-30	320-480	-	340-510	-		34-44	
Myxozoa		700	700	7	100-250	6,300-8,400	71-468	6,471-9,118	600-1,200	7,171-9,818	7-10	93
Nematoda		11,400							-	61,400	19	295
	Nematoda, free-living		6,900	9	?	50,000	NB	50,000	-		12	
	Nematoda, parasitic		4,500	-	?	?	-	-	-		-	
Nemertea		1,285	1,285	20	200-400	500-1,000	-	700-1,400	170-320	1,985-2,685	48-65	85
Phoronida		18	18	56	0	0	-	0	-	18	100	0
Placozoa		1	1	0	18	0	10-100	28-118	-	29-119	1-3	0
Platyhelminthes		11,690							3,000-3,900	35,296-73,441	16-33	1,142
	Cestoda		1,393	31	300	2,000	-	2,300	**		38	
	Monogenea		1,626	-	200-300	10,000-15,000	500-5,000	10,700-20,300	2,300-2,700		7-13	
	Aspidogastrea		18	25	0	6	-	6			75	
	Digenea		6,000	20	600	4,000-8,500	400-900	5,000-10,000	**		38-55	
	Catenulida		12	0	5	20	-	25	-		32	
	Rhabditophora		2,641	9	500-700	5,000-28,000	75-420	5,575-29,120	820-1,130		8-32	
Porifera		8,553	8,553	22	2,300-3,000	15,000	NB	17,300-18,000	**	25,853-26,553	32-33	621
Rotifera		114	114	-	20	?	300-2,500	320-2,520	20-140	434-2,634	4-26	17
Sipuncula		150	150	90	3-5	10-25	30-200	43-230	2-20	193-380	39-78	0
Tardigrada		183	183		?	1,120	-	1,120	40-280	1,303	14	16
Xenacoelomorpha		401							250-360	4,501	9	74
	Acoela		391	35	100	4,000	NB	4,100	-		9	
	Nemertodermatida		8	20	?	?	NB	0	-		-	
	Xenoturbellida		2	0	0	?	NB	-	-		-	
Total		222,201-230,201			58,279-72,326	415,205-633,872	8,792-35,753	482,776-741,951		704,977-972,152		

The following data are listed: number of currently described and taxonomically accepted species, percent of all nominal species names considered subjective synonyms (% Syn), undescribed species in specimen collections, unsampled and undiscovered morphospecies, undiscovered molecular cryptic species (only distinguishable by molecular methods), total species unknown (undescribed + undiscovered based on expert opinions), total species unknown based on the statistical model, total estimated number of species (expert-based), estimated percent of all existing species that are currently described (% known), and number of new species published in the last decade (1999–2008; data from WoRMS). Names of taxonomic groups for which data are broken down further by subgroups are listed in bold. The following symbols are used: ?, not estimated; -, no data; NB, no basis for judgment; **, rate of discovery still rising, so no meaningful estimate of total species numbers can be made using the statistical model.

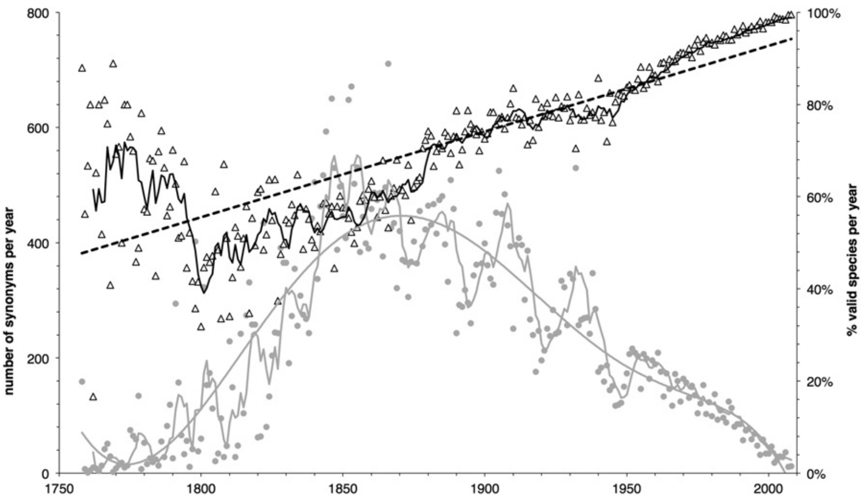

Figure 1. Number of Synonyms per Year of Original Description

The number of synonyms per year of original description (gray circles; solid gray lines: five-year moving average and sixth-order polynomial) and the percent of species that are now recognized as valid (black triangles; solid black line: five-year moving average; dashed black line: linear with r^2 = 0.638).

Rotifera, Sipuncula, Oligochaeta, and Remipedia. In contrast, there was no evidence that taxa such as Sirenia, Staurozoa, Siphonophora, and several Crustacea groups (including Brachyura and Isopoda, which are species rich) have any molecular cryptic species.

The Best-Known Taxonomic Groups. Based on the estimates of the authors, no new species were expected in some groups with few species already, namely marine mammals such as Sirenia (4 spp.) and Carnivora (44 spp.), Phoronida (18 spp.), and crustaceans such as Mictacea (1 sp.), Amphionidacea (1 sp.), Lomisoidea (1 sp.), Branchiopoda (90 spp.), and Euphausiacea (86 spp.). Only a few species may still be discovered in Cetacea (+2–8 spp.), Reptilia (+10 spp.), Merostomata (+1 sp.), Aspidogastrea (+6 spp.), Thaliacea (+13 spp.), and Nematomorpha (+10–15 spp.). Other well-known taxonomic groups that were >90% known but with hundreds of species were seabirds and, with over 2,000 species, marine Hexapoda (e.g., Insecta, Collembola). The marine vascular plants (mangrove species and seagrasses) were >80% known, but seaweeds and microalgae remained poorly known (Table 2).

The Least-Known Taxonomic Groups. Groups for which fewer than an estimated 20% of the species have been described included some taxa with few known species (i.e., Cycliophora, Loricifera, Placozoa, Tantulocarida, Leptostraca, Caudofoveata). However, most have hundreds (Myxozoa, Acoela, Kinorhyncha, Oligochaeta, Gastrotricha, Dicyemida, Orthonectida, and Entoprocta) to thousands (Bacillariophyceae, Ciliophora, Rhabditophora, Cumacea, Tanaidacea, Isopoda) of species. The largest numbers of undiscovered species may be in Isopoda (+63,150–123,600 spp.), Gastropoda (+85,000–105,000 spp.), Bacillariophyceae (+50,000 spp.), Nematoda (+50,000 spp.), Copepoda (+30,125–50,125 spp.), Ostracoda (+2,625–34,000 spp.), Rhabditophora (excluding Neodermata; +5,500–29,000 spp.), Tanaidacea (+21,900–24,900 spp.), Amphipoda (+20,000 spp.), Monogenea (+10,700–20,300 spp.), Porifera (+17,300–18,000 spp.), Ciliophora (+4,231–19,368 spp.), Oligochaeta (+5,900–16,900 spp.), and marine Fungi (+15,000 spp.) (Table 2).

Based on Undescribed Species in Samples Collected

Another approach to estimating how many species were undiscovered was to aggregate empirical data on the ratio of undescribed to described species in samples. Field studies on over 33,000 marine species in over 100 studies found an average of 37% (median 31%) of species were undescribed, primarily invertebrates from tropical and offshore environments (Table S1). The largest sample for which we had an estimate of unknown species was for the marine biota of New Zealand, estimated at 17,135 species of which 25% were undescribed and in specimen collections. Over all, Pisces and Echinodermata were below the median, but so were Scleractinia, Pycnogonida, Porifera, and free-living Nematoda as well. Taxa with a higher percentage of unknown species than the average included Oligochaeta, Polychaeta, Mollusca, Rhabditophora, and Peracarida (especially Tanaidacea and Isopoda). The proportion of unknown species was higher than average for studies from Australia (52%) but lower

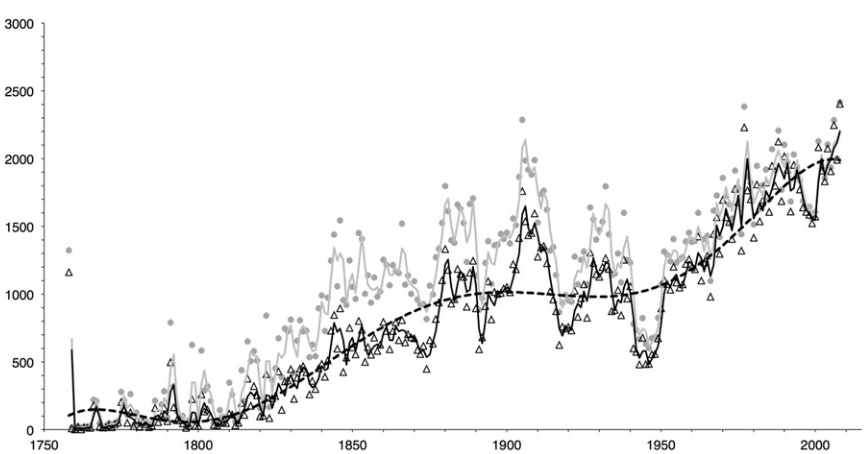

Figure 2. Number of Species Described per Year versus Number of Species Currently Recognized as Valid

The number of species described per year (gray circles, solid gray line) versus the number of species currently recognized as valid (black triangles, solid black line). Trend lines are two-year moving averages; the sixth-order polynomial for valid species (r^2 = 0.869, dashed black line) is also shown.

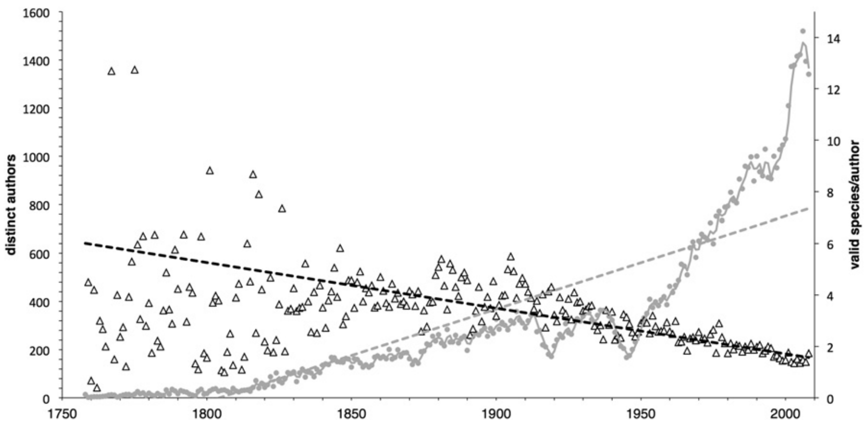

Figure 3. Number of Distinct Author Names per Year and Number of Valid Species per Author

The number of distinct author names per year (gray circles; solid gray line: two-year moving average; dashed gray line: linear with r^2 = 0.721) and the number of valid species per author (black triangles; dashed black line: linear with r^2 = 0.056).

than the median for New Zealand and the Southern Ocean (25% each). Averages for studies from Europe, deep sea, and tropics were close to the overall average (37%, 39%, and 33% respectively). These proportions can question estimates of total species richness. For example, the estimate of free-living nematode diversity reported here as 50,000 species suggests that 86% of the existing species remain to be discovered. Yet, field surveys have found only 6% to 56% undescribed species.

Discussion

Rate of Discovery

The description rate of marine species has been increasing steadily since 1955. Costello et al. [10] found a similar trend for marine and terrestrial (including freshwater) species, but the relative rate of description of marine species was higher than for terrestrial species. Evidently, the past decade has been the most productive period for marine species discovery. This may be due to more taxonomic effort, new technologies, exploration of new habitats and localities, use of molecular methods, or a combination of these factors.

Our analysis of temporal trends indicated a decreasing rate of species description (from six to two species per author per year) and an increased number of authors engaged in species descriptions. This increase in the number of taxonomists is likely to contribute to the continued high rates of species description. Other studies have similarly reported an increasing number of authors describing fossil North American mammals [21], marine fish [22], terrestrial vertebrates and plants in Brazil [23], flowering plants of the world [24, 25], cone snails, spiders, amphibians, birds, and mammals [25], as well as marine and nonmarine species globally [10].

The increasing number of authors publishing in taxonomy reflects the increasing number of scientists worldwide [26]. This has particularly been the case in Australasia and South America since the 1980s [27, 28]. The number of taxonomic publications has increased more than 8-fold from 1969 to 1996 [29]. Haas and Häuser [30] estimated there to be 5,000 professional and 35,000 amateur taxonomists worldwide. Our data suggest that this may be an underestimate. We found that 4,900 authors described marine species in the past decade alone, which accounted for about 12% of all species described. Although some of the marine taxonomists may also describe nonmarine species, this suggests that there are over 40,000 scientists involved in the taxonomic description of species. This number may be higher if the authors who could be considered taxonomists but have not recently described species are included, for example those who study taxa in well-studied geographic regions.

The change in the number of authors of species descriptions, a minimum indicator of authors involved in taxonomy, does not necessarily indicate increased taxonomic effort, because the individuals' effort may be declining. However, we found in WoRMS [15] that the proportion of authors who described only one species has been similar (42%–44%) over the past century. A previous study using WoRMS similarly found no trend in the proportion of the most prolific authors during that period [10].

The advent of scuba diving [31], deep-water tangle nets [32], submersibles, remotely operated vehicles (ROVs), and other technologies [22] has allowed sampling of previously unexplored habitats such as cold seeps, mud volcanoes, submarine canyons, and anchialine lakes and caves [33, 34] and of very fragile organisms previously unavailable to scientists [35]. For example, since 2002, the number of species of remipedes (crustaceans that live exclusively in coastal anchialine caves) has more than doubled from 11 to 24. The use of submersibles and deep diving resulted in the discovery of 30 new fish species around even such a highly studied area as the Galápagos Islands [22]. Thus, the greater number of taxonomists, the sampling of more remote geographic areas, and the use of a greater variety of sampling methods must all be contributing to the high rate of species description.

Molecular Methods and Cryptic Species

Estimating the diversity of cryptic species, i.e., species that remain unrecognized because of limitations of current morphotaxonomic methods, is a challenge because molecular surveys that most readily reveal them have been applied to only a fraction of marine diversity. For example, only 6,199 species (3% of all described) have been genetically "barcoded" by MarBOL (http://www.marinebarcoding.org, as of April 24, 2012). Furthermore, in all taxa except Placozoa (with only one species at present), these discoveries of "cryptic" species only apply to some of the presently known species, sometimes only within genera. For example, up to 18 cryptic species have been reported for parasite genera, but most (78%) only had one or two cryptic species [36]. It also needs to be considered that reports of cryptic species may be subject to sampling bias because these methods tend to be applied to taxa where positive findings are expected, and negative results may not be reported [36].

For two-thirds (in terms of described richness) of marine biota, experts were hesitant to provide, or indicated there was no good basis for, any estimate for the diversity of cryptic species, reflecting our poor understanding of this issue. For the remaining one-third, estimates ranged widely, reflecting the limited sampling and differences in the incidence of cryptic species among taxa. In some genera, molecular characters are more useful than morphological characters for distinguishing species (e.g., *Leptochonchus* gastropods [37]). In others, morphology is adequate to distinguish species, although molecular data can aid their classification. Thus in Pisces, a morphologically complex and visually communicating group of animals, the likely incidence of cryptic diversity is low, estimated here as ~1% of total diversity [38]. Most crustaceans have sufficient morphological characters to discriminate species, and so cryptic speciation may also be low (<5%) overall. Conversely, in Sipuncula, which have limited morphological complexity, cryptic species are estimated to represent between 10% and 55% of total diversity [39]. In some coral genera, molecular markers could better indicate the occurrence of cryptic species than reveal synonyms, because a lack of variation in one character does not necessarily suggest they are the same species [40]. Our knowledge is noticeably incomplete in the unicellular eukaryotes, where environmental sequencing is indicating that some of these groups may be more diverse than currently recognized based on conventional morphological taxonomy [41]. However, how this genetic diversity translates into species diversity is unknown.

Despite the uncertainty in the estimates of cryptic species, they help to illustrate the degree to which molecular methods may increase our knowledge of marine biodiversity, both in distinguishing and classifying species. Considering our numbers of cryptic species, molecular methods may add tens of thousands, rather than hundreds of thousands, of species to the currently accepted ~226,000 species. In a few cases, molecular methods have actually worked in reverse by assigning species to synonymy, though this is unlikely to have any more than a minor influence on total species numbers. Certainly, it is not valid to multiply up from examples of cryptic diversity discovered by molecular methods for a small group of species or genera to a phylum.

Synonyms

Our data showed that the proportion of described species that were later recognized to be synonyms of others was decreasing over time. This could be the result of fewer synonyms being created and/or could reflect the time it takes to discover synonyms. Taxa that had been studied more intensively tended to have more synonyms (e.g., fish, mollusks) but were also more likely to have had their taxonomy revised and thus more likely to have had such synonyms discovered. Even the same taxonomist can describe a species several times: for example, 9 of the sperm whale's 19 synonyms were by three authors, each naming the species three times [42]. With better access to publications and type specimens, improved communication among taxonomists, and the greater availability of systematic revisions, the introduction rate of synonyms should continue to decline.

Furthermore, molecular analyses complement morphological approaches and, where the latter are equivocal, have supported the raising of subspecies to species status [22]. For example, the killer whale and the common bottlenose dolphin have each been split into two or more species [43, 44]. WoRMS currently contains ~7,600 recognized infraspecific taxa (i.e., 3%). Molecular methods will also resurrect some names from synonymy. Assuming that pre-1900 names assigned to synonymy are mostly true synonyms, about 21,000 names of species described since 1900 were synonymized and another 42,000 may yet be synonymized due to the time delay in recognizing synonyms. It is highly unlikely that all 63,000 would be resurrected from synonymy by molecular methods. If all recognized subspecies and, say, 25% of synonyms were reestablished as accepted species, then the number of known species could increase by about 23,000.

The occurrence of as yet unrecognized synonyms is one of the most significant problems in estimating the true number of described species. Taxonomic revision may find more synonyms, but in some cases, often assisted by use of molecular methods, previously "sunken" species names may be found to be real. Although the significance of synonymy in biasing estimates of taxon and global species richness merits more in-depth study, action to reduce the reoccurrence of synonyms can be undertaken. This must include taxonomic revisions, rapid publication, open access to descriptions, online species identification guides, knowledge of where type specimens and genetic profiles are located, accessibility of taxonomic expertise, and continued revision of species inventories at global to local levels. An analysis of whether there is a trend of less time to discover synonyms could usefully clarify whether the creation of synonyms has been decreasing.

Global Species Richness

Both the sum of our individual estimates and the statistical analysis predicted that there were fewer than one million eukaryotic marine species on Earth. It was reassuring that the methods overlap, in contrast to most previous estimates, which have exceeded one million (Table 1). The estimates based on expert opinion were closest to ours, in the 1.0–1.5 million range. Winston [8] also considered the proportion of undescribed species in different geographic regions in her estimate of "over one million." This avoided extrapolation from one geographic area to the world, as was the case with the 5–10 million estimates. Local (α) diversity tends to overestimate regional (γ) diversity when few samples are available and thus spatial turnover (β diversity) is underestimated [45]. The relative species richness of higher taxa varies across geographic regions [46], although whether this is true or reflects variation in sampling and taxonomic effort is unclear. Further research is required before it can be assumed that the proportion that a higher taxon contributes to species richness in one region is the same as in other regions. Using the relationship of species richness in higher taxa to predict global species richness may compound several biases, including the changing proportions of species across higher taxa as classifications change, and dominance of richness by a few taxa. However, experts are not impartial [18]. They are subject to influence by such biases as the estimates of their peers and authority figures, widely reported hyperestimates, their personal experience and recollections, and not wishing to downplay the importance of their specialty. We have partly addressed this by independently eliciting experts by e-mail before exposing all experts to their peers' estimates. Experts were then asked to document their reasoning and review their numbers. This documentation was then compiled and circulated to experts, and they were asked to reconsider their estimates once again. Experts were not aware of the statistical model's predictions until a late stage in this process and thus did not consider them. By providing the rationale for our individual estimates (Table S2), we encourage them to be challenged as new data become available, as is the recommended best practice [19]. A future improvement on our approach may be to include direct discussion of all available data and opinions between experts at a workshop or video conference [17].

Recent estimates of the richness of insects and terrestrial species have also been more modest, on the order of six million, compared to the 30–100 million species proposed by some authors (reviewed in [1, 10]). The same model we used here predicted that only 0.3 million marine species may exist on Earth using an earlier version of WoRMS [10]. This model is sensitive to the period of highest species description. Because the data now show that the highest marine species description rates occurred in the past decade, the present study predicted 0.5 million species. Both estimates will be inflated by undiscovered synonyms. Future modeling may be improved by distinguishing the taxa and geographic regions that are well known and by quantifying the effects of taxonomic effort.

Some of our higher estimates of undiscovered species may be questioned. Findings of high local species diversity do not necessarily imply high global species diversity [45]. Species with life stages that are easily dispersed (e.g., due to small body size, as in microbes, Fungi, and meiofauna) and can survive conditions suboptimal for growth tend to be cosmopolitan and thus have low spatial turnover (β diversity) in species (discussed in [10, 45]). This may be the case for the high predictions of undiscovered species for Fungi and Nematoda [47]. Indeed, one analysis suggested that there were 10,000–20,000 free-living marine nematodes [48] rather than the 50,000 listed in this paper. The present estimate of undiscovered Fungi was back calculated from an estimate of 1.5 million species on Earth, suggesting that only 7% of species are described. This seems unlikely by comparison with other taxa, and if there were so many undescribed species, one might expect the current rate of description to be relatively higher than it is for other taxa, because species would be easier to discover. However, comparable easily dispersed life stages are not common in macroinvertebrate taxa such as Crustacea (especially Isopoda, Tanaidacea, Amphipoda, Cumacea, and Leptostraca) and Mollusca, where thousands of undiscovered species are predicted as well. Moreover, more cosmopolitan species also tend to be discovered first, and the remaining species of such taxa are likely to be geographically rare (i.e., endemic to small areas). Thus, a particular problem in estimating global species richness is the lack of understanding of geographic patterns. It is well known that most species are geographically rare, but whether all taxa show similar β diversity is not clear. For example, are there equal proportions of parasitic and nonparasitic copepods that are cosmopolitan, and does the spatial occurrence of parasitic and symbiotic species scale similarly with their hosts? If taxa do scale similarly, then this will aid prediction of both global species richness and sensitivity to extinction [45]. However, the present evidence suggests that taxa have contrasting geographies, with pelagic megafauna (mammals, birds, reptiles) and meiofauna being more cosmopolitan than benthic macroinvertebrates (reviewed in [10]). Consequently, taxonomic research into this spectrum of rare and endemic species is critical for scientific discovery and to inform the selection of conservation priorities.

Field studies found that most samples have less than 37% undescribed species (median 31%), suggesting that our estimate of two-thirds to three-quarters of species being undiscovered may be too high rather than too low. However, field studies document common species better than rare species, whereas undescribed species are proportionally better represented among rare species. Because of this, field studies undersample undescribed species, except when they are exhaustive at the species level, a level of sampling that has yet to be attained in species-rich localities (see e.g. [49]). Alternatively, these averages may be overestimates because (1) authors do not report when all species in samples have been described or (2) upon closer analysis, some may prove not to be new to science (but are perhaps new to the observer). Europe has probably the best-studied sea area in the world, but one-third of its biodiversity may yet be undescribed [2]. Consequently, the proportion of undiscovered species is likely between one-third and two-thirds of all described marine species. However, this is a global figure, and some taxa provide exciting opportunities for discovering many new species, notably Mollusca, Rhabditophora, Oligochaeta, Tanaidacea, and Isopoda.

If we further consider that the number of authors describing species has been increasing at a higher rate than the number of new species described, then it seems that it has become harder to find new species [10]. If the description curves for taxa have not reached an asymptote because of the increasing taxonomic effort, then the model will overpredict marine species richness as well as bias our personal estimates. Consideration of the increasing effort suggests that we should be conservative in our estimates of the number of undiscovered species.

Rates of marine species description have never been higher and are driven by the increasing number of taxonomists and their ability to sample geographic areas and habitats previously undersampled. If the rate of 2,000 new species per year can be maintained by continued taxonomic effort and focus on the least-known places, habitats, and taxa, then another 100,000 species will be described in the next 50 years, and the number of described species will be within the 95% confidence limits of our statistical predictions.

As more species are described, the skills to diagnose them will be increasingly in demand. This applies to both the large, easily identified species that may be important for food, conservation, and ecosystem functioning and the less conspicuous taxa with small body size, because they will include parasites and pathogens of other species, may become pests, and may have as yet unrealized roles in ecosystem function.

The open-access online World Register of Marine Species has set the stage for our estimates of marine diversity. Collaborative international initiatives such as WoRMS help increase our knowledge, promote standardization in taxonomy, and bring the community together in a more coordinated and, because of the shared responsibility of maintaining the database, more sustainable way. We call on other taxonomic communities to similarly collaborate to publish online databases of their species as a synthesis of current knowledge and vehicle for improved scientific collaboration. The present study provides a baseline of the diversity of marine species and higher taxa, which the taxonomic editors of WoRMS should revisit in 5 to 10 years' time in the light of future discoveries.

Supplemental Information

Supplemental Information includes two tables and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.09.036.

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