

What determines the likelihood of species discovery in marine holozooplankton: is size, range or depth important?

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The relationship between date of first description and size, geographic range and depth of occurrence is investigated for 18 orders of marine holozooplankton (comprising over 4000 species). Results of multiple regression analyses suggest that all attributes are linked, which reflects the complex interplay between them. Partial correlation coefficients suggest that geographic range is the most important predictor of description date, and shows an inverse relationship. By contrast, size is generally a poor indicator of description date, which probably mirrors the size-independent way in which specimens are collected, though there is clearly a positive relationship between both size and depth (for metabolic/trophic reasons), and size and geographic range. There is also a positive relationship between geographic range and depth that probably reflects the near constant nature of the deep-water environment and the wide-ranging currents to be found there. Although we did not explicitly incorporate either abundance or location into models predicting the date of first description, neither should be ignored.

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A negative relationship between the date of first description and body size, with larger species being described earlier, has been demonstrated for a number of terrestrial animals including British beetles (Gaston 1991), South American oscine passerine birds (Blackburn and Gaston 1995), some elements of the Australian and North American herpetofauna (Reed and Boback

2002) and Neotropical mammals (Patterson 1994). In the case of South American birds as a whole, Gaston and Blackburn (1994) have also shown that the most recently described species are smaller than would be expected if they were a random sample from the world avifauna. These data suggest that large species have a greater probability of description than small

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species, and support May's (1978) contention that our understanding of biodiversity is hampered by the fact that described species are not a random subset of all species.

Size is not the only factor that contributes to the likelihood of a species' description (Diamond 1985), and other attributes of "conspicuousness" have also been invoked. Foremost amongst these is geographic range, though altitudinal range and abundance (Blackburn and Gaston 1995), and geographic location (Allsopp 1997, Cabrero-Sañudo and Lobo 2003) have also been correlated with the date of first description.

All the foregoing studies have been conducted on land, and to our knowledge there has been no rigorous testing of these ideas in the marine environment. We aim to redress this imbalance here by focussing on the role of size as well as other potential measures of conspicuousness as predictors of the date of first description of marine holozooplankton. Holozooplankton are here defined as animals that remain within the plankton throughout their entire lifecycle, as opposed to meroplankton, which are members of the plankton for only portions of their lifecycle. The other predictors that we explicitly examine here are geographic range and depth of occurrence. The first of these has been widely tested in the terrestrial environment (Cabrero-Sañudo and Lobo 2003), and although the latter has its parallels in altitude (Blackburn and Gaston 1995) it is generally considered to be the last frontier in marine science. We would therefore anticipate that its role in predicting the date of first description would be significant.

Material and methods

The basic dataset we have used was compiled from literature sources summarised in Appendix A, validated and updated by the authors when possible. It is based on information published prior to 2002. It should be noted that a number of taxa were excluded from the analyses, either owing to poor information (Decapoda (Anomura and Natantia), Gammarida (Amphipoda), Ctenophora, Scyphozoa and Hydrozoa (but not Trachymedusae and Siphonophorae)), or to their low overall richness (<20 holoplanktic species: Pyrosomatida and Doliolida (Thaliacea), Monostilifera (Nemertina), Onychopoda and Ctenopoda (Branchiopoda), Biphragmormpha and Monophragmormpha (Chaetognatha), Harpacticoida (Copepoda), Nudibranchia (Gastropoda), Fauvelopsidae and Flabelligerida (Polychaeta)). We have followed Huys and Boxshall (1991) and recognised the copepod orders Poecilostomatoida and Cyclopoida as distinct.

Description dates reflect the date of first description ignoring taxonomic reshuffling (Patterson 1994). Length (mm) was used as an index of size, and the parameters measured reflect order-specific conventions (Boltovskoy 1999). A species' global geographic range was calculated as the number of 24 possible geographic bins it is present in (Fig. 1): the three oceans were each divided into eight (if applicable) latitudinal bands of 20° extent, and the Mediterranean and Red Seas were treated separately. The mean depth of occurrence was determined by assigning the following depths (m) to a species' vertical range: epipelagic only (100), mesopelagic only (600), bathypelagic only (2000), epi- and mesopelagic (350), meso- and bathypelagic (1300) and eurybathic (900).

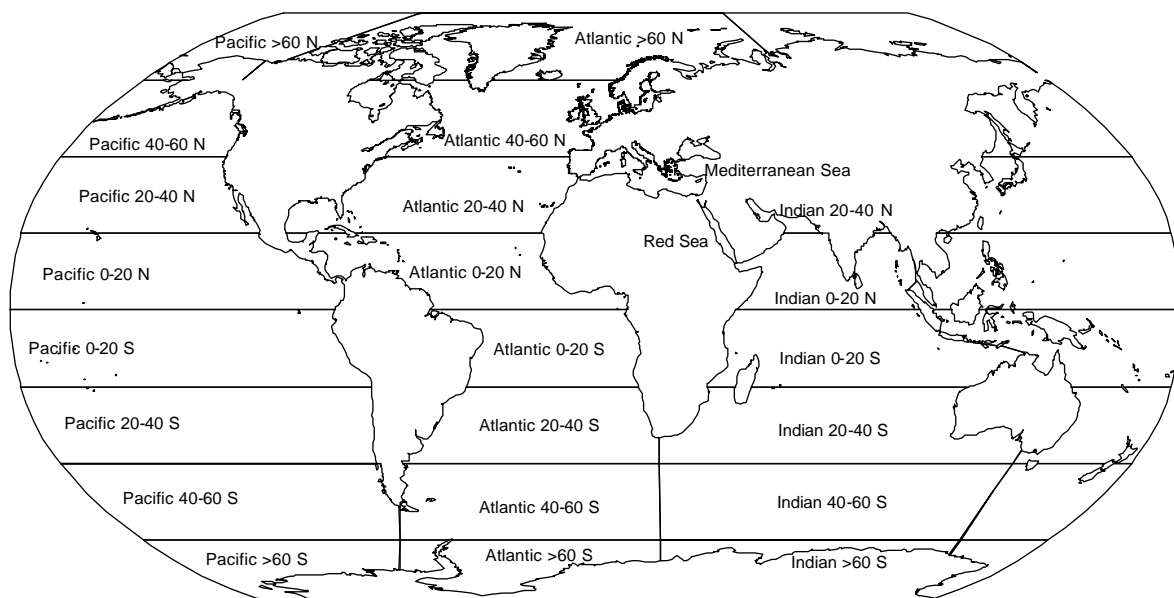


Fig. 1. Map of global ocean showing division into geographic bins.

Given the general interest in size data, we provide information on the skewness of the log-transformed size data, and indicate whether these are significant (i.e. if the absolute value of skewness divided by the standard error of skewness is greater than 2.0; Reed and Boback 2002). We have followed Gaston and Blackburn (1994) and assigned mean genus lengths to missing species' data in the case of Phyllodocida (Polychaeta). Only real data have been used in analyses examining the relationships between length and date of first description.

For each taxon, relationships between year of first description (response) and log size, range and depth (predictors) were identified using multiple regression. There were sufficient values of the response variable year of first description (226 values) and the discrete predictors range (24) and depth (7) to treat them as continuous. A visual assessment of residual and normal probability plots suggested that a linear multiple regression model with a normal error distribution provided an adequate description of the data. Partial regression coefficients, representing the correlation between year of first description and each of the predictors accounting for the other predictors by holding them constant, were calculated.

To identify general patterns across all taxa between when they were first described and their size, range and depth, the meta-analytical method of Worm and Myers (2003) and Worm et al. (2003) was used to combine individual partial correlation coefficients from the multiple regressions for each species. Although fixed-effects meta-analytic models (which assume effect sizes are the same for all correlation coefficients) were appropriate for some of our analyses, for the sake of brevity and consistency we chose to report only results from random-effects meta-analyses (which do not assume effect sizes are identical). This approach is more conservative than fixed-effects meta-analysis. Using a meta-analytic approach also has the benefit of minimising the problem of an inflated experiment-wise α -level associated with multiple hypothesis tests (Peres-Neto 1999). To aid interpretation of our results, we also examined interrelationships between the three predictors (size, range and depth) using a meta-analytic approach.

It should be noted that we have treated each holozooplankton order separately, and we assume that patterns in one order are independent of patterns in any other. Although we believe that such an assumption is not unrealistic given the likely age of zooplankton orders (Rigby and Milsom 2000), we accept that within any one order "...closely related species may share adaptations through common ancestry... [and that this]... may overestimate the actual number of times a trait or relationship has evolved" (Blackburn and Gaston 1995). Ideally, one should control for the effects of "identity by descent" (Blackburn and Gaston 1995), but we are not in a position to implement the necessary

"contrasts" owing to a general paucity of data (theoretical and actual). Therefore, to err on the side of caution we not only report results from the meta-analysis of all taxa, but also results on a selected subset of taxa that are only distantly related. This reduced meta-analysis was conducted on taxa from different phyla; where data on more than one taxon within each phylum was available, we selected the taxon with the most data. Thus the selected taxa were Calanoida, Aphragomorpha, Phyllodocida, Larvacea, Pelagica, Thecosomata and Calycophorae.

Results

Table 1 summarises the available data, and provides a useful vehicle to introduce the results. The first species of holozooplankton to be formally described was *Calanus finmarchicus* L 1756, which belongs to one of the most abundant groups of largely epipelagic marine organisms, the calanoid copepods. By contrast, the most recent of the orders (presented here) to be recognised was identified by the species *Pelagonemertes rollestoni* Moseley 1875, which belongs to a fairly rare group of largely meso- and bathypelagic organisms, the nemertines. At first glance then, the results would suggest that depth range and abundance are important indicators of the date of first description. However, *C. finmarchicus* grows to a length of ~ 3 mm and is now known to occur in only $\sim 8\%$ of the global ocean, whilst *P. rollestoni* attains a maximum size of 45 mm and can be found in over 70% of the ocean. These cursory results imply that size may play a limited role in predicting the date of first description, and that the relationship between geographic range and date of first description is positive.

Although 10 of the 15 orders (with sufficient data) exhibited right-skewed body size distributions after log-transformation, only five of these were statistically significant (Table 1). None of the left-skewed body size distributions were significant.

Before we assess the relationship between year of first description and geographic range, size and depth we first examine their degree of inter-correlation (Fig. 2). As size increases so too does depth of occupation; this is the case for all taxa except Poecilostomatoida and Mesogastropoda (Fig. 2a). Note that the correlations are considered significant if the 95% confidence intervals do not overlap zero. The random-effects meta-analysis confirms that there is a significant positive relationship between size and depth of occurrence across all taxa ($\bar{r}=0.24$, $Z=3.21$, $p<0.01$; Fig. 2a) as well as for the subset ($\bar{r}=0.29$, $Z=2.69$, $p<0.01$; Fig. 2a).

A species' range generally increases as size increases for almost all taxa except Larvacea and Phyllodocida (Fig. 2b). The meta-analysis confirms that there is a significant positive relationship between log size and

Table 1. Date of first description of the holozooplanktic taxa considered here, by order; median, and upper and lower quartiles also provided. The species diversity of each order, the mean geographic range and mean occupational depth are also shown, as is the mean size (\log_{10} mm) and the skewness of the \log_{10} size-frequency distribution (data in bold typeface are considered significant). No skewness data are supplied for Calanoida, Cyclopoida and Mysidacea owing to the large amount of missing data.

Order	First year	Lower quartile	Median	Upper quartile	No species	Mean range	Mean depth	Mean log size	Skewness
Aphragmophora	1828	1897	1930	1963	61	7.15	402	1.16	0.712
Calanoida	1756	1905	1949	1970	1688	7.27	674	0.52	
Calycephorae	1776	1885	1925	1954	102	12.64	599	1.10	0.265
Cyclopoida	1796	1908	1920	1977	54	7.75	109	-0.04	
Euphausiacea	1837	1883	1905	1911	85	8.30	479	1.33	0.838
Gymnosomata	1774	1886	1910	1942	55	7.07	242	0.93	-0.049
Hyperideae	1775	1879	1888	1925	233	9.84	581	1.03	0.699
Larvacea	1851	1887	1896	1937	58	11.28	208	0.25	0.501
Mesoga-stropoda	1758	1830	1852	1906	42	9.86	81	1.17	0.739
Myodocopa	1849	1906	1906	1977	188	8.38	1015	0.33	1.440
Mysidacea	1776	1913	1977	1977	991	2.39	589	1.03	
Pelagica	1875	1917	1934	1955	97	2.48	1026	1.28	0.236
Phyllocladida	1828	1885	1910	1947	102	8.73	674	1.09	-0.714
Physonectae	1775	1865	1932	1980	41	9.40	444	-0.01	0.657
Poecilostomatoida	1843	1891	1931	1977	176	10.73	518	1.38	-0.145
Salpida	1774	1819	1904	1955	43	12.84	129	1.68	-0.344
Thecosomata	1767	1832	1888	1979	77	9.25	300	0.91	0.536
Trachymedusae	1766	1893	1903	1913	51	6.29	1286	1.16	-0.353

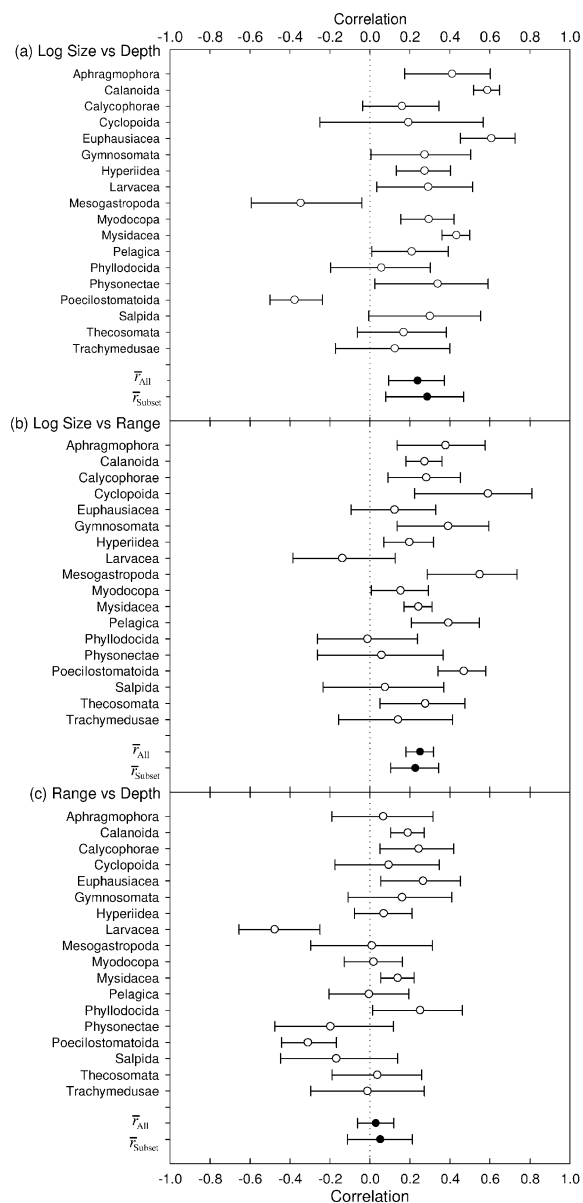


Fig. 2. Meta-analysis of bivariate correlations for (a) log size vs depth, (b) log size vs range and (c) range vs depth. Weighted mean correlations with 95% confidence limits calculated using the random-effects model for all taxa (\bar{r}_{All}) and a subset of seven taxa (\bar{r}_{Subset}) are also shown. Circles and bars represent correlation coefficients and 95% confidence intervals, respectively.

range across all taxa ($\bar{r}=0.25$, $Z=6.81$, $p<0.0001$; Fig. 2b) as well as for the subset ($\bar{r}=0.23$, $Z=3.57$, $p<0.001$; Fig. 2b).

The relationship between a species range and its depth of occurrence is very variable; many are slightly positive although two (Larvacea and Poecilostomatoida) are strongly negative. Overall, however, there is no relationship between range and depth across all taxa

($\bar{r}=0.03$, $Z=0.64$, ns; Fig. 2c) or a subset ($\bar{r}=0.05$, $Z=0.62$, ns; Fig. 2c).

All multiple regression models were significant, accounting for as much as 69% (Larvacea) and as little as 12% (Euphausiacea) of the variation in the description date data, with on average 40% of the variation explained. From the partial correlation coefficients, the year of first description was negatively related to log size, with 19 out of the 20 taxa yielding negative correlations (Fig. 3a). The one positive value observed (for Pelagica) was very close to zero. The meta-analyses of all taxa indicated that these negative relationships between year of first description and log size were significant overall ($\bar{r} = -0.24$, $Z = -6.14$, $p < 0.0001$; Fig. 3a). In terms of the subset of taxa from different phyla, similar results were obtained, although the correlation was weaker and only marginally significant ($\bar{r} = -0.16$, $Z = -2.92$, $p < 0.01$; Fig. 3a).

In terms of the range of each taxon, the year of first description was negatively related to range, with all 20 taxa yielding statistically significant negative correlations (Fig. 3b). Meta-analyses of all taxa indicated that these negative relationships between year of first description and range were highly significant overall ($\bar{r} = -0.49$, $Z = -12.73$, $p < 0.0001$; Fig. 3b). In terms of the subset of taxa from different phyla, even stronger results were obtained ($r = -0.56$, $Z = -7.50$, $p < 0.0001$; Fig. 3b).

In terms of the depth distribution of each taxon, the year of first description was positively related to depth, with 17 of the 20 taxa yielding positive correlations (Fig. 3c). The three negative correlations were close to zero and were non-significant. Meta-analyses of all taxa indicated that the generally positive relationships between year of first description and range were significant overall ($\bar{r}=0.27$, $Z=6.22$, $p < 0.0001$; Fig. 3c). In terms of the subset of taxa from different phyla, similar results were obtained ($r=0.27$, $Z=3.25$, $p < 0.001$; Fig. 3c).

Discussion

Most currently recognised species of holozooplankton in the orders studied here were described by 1952 (mean upper quartile). This date is in fair agreement with observations by Boltovskoy (1999), who suggested that 78% of all species currently known to occur in the South Atlantic Ocean were described before 1925. By contrast 71% of all South American oscine passerines had been described prior to 1890 (Blackburn and Gaston 1995). In addition, the median date of description of British Coleoptera (comprising ~4 000 species) is 1808 (Gaston 1991), whilst the earliest median date of first description for any order of marine holozooplankton is 1852 (Mesogastropoda, 42 species). Thus it is clear that our

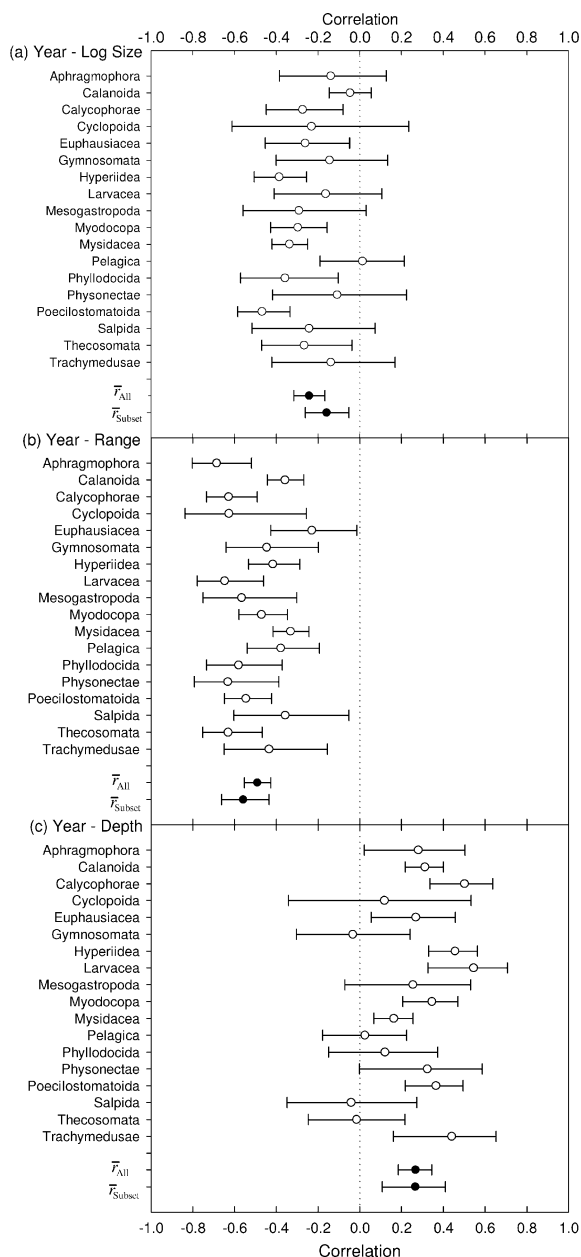


Fig. 3. Meta-analysis based on partial correlation coefficients between the year of first description and: (a) log size, (b) range, (c) and depth. Weighted mean correlations with 95% confidence limits calculated using the random-effects model for all taxa (\bar{r}_{All}) and a subset of seven taxa (\bar{r}_{Subset}) are also shown. Circles and bars represent correlation coefficients and 95% confidence intervals, respectively.

understanding of marine invertebrate diversity lags behind that of terrestrial invertebrate diversity. This may be because the collection of zooplankton at sea and especially in the open ocean is a costly and technology-rich method of obtaining specimens compared with landbased sampling techniques.

The size limits of an organism are thought to be set by design constraints (Stanley 1973), and most organisms show size distributions that are highly skewed to the right, even after log-transformation (Blackburn and Gaston 1994). In the case of the marine holozooplankton, only 30% of the orders are significantly right-skewed, whilst none are significantly skewed to the left (Table 1). These findings are at odds with the literature from terrestrial studies, and are reminiscent of the size distributions found at local, as oppose to "continental" or global scales (Burbidge and McKenzie 1989). A number of biases are known to affect the shape of size distributions including measurement errors, and known and unknown missing data (Blackburn and Gaston 1994). We have no information on the measurement error, and have corrected for known missing data by assigning a mean genus size to missing data. It is difficult to account for unknown missing data, however, which implies that taxa failing to show a right-skewed size distribution may be incompletely known, and that as more small species are discovered, the distribution will assume the predicted, right-skewed shape (Blackburn and Gaston 1994). It has recently been suggested that the number of species of holozooplankton still to be discovered is probably less than the number of species requiring synonymisation (Boltovskoy et al. 2002). This would imply that our current understanding of holozooplankton diversity is good, and that the relatively few species left to describe would likely contribute little new size data. Although advances are being made in the identification of cryptic zooplankton (Bucklin et al. 2003, Ortells et al. 2003), Boltovskoy et al. (2002) have suggested that the use of molecular techniques will provide insight to phylogeny but not taxonomy. Of course, the generally low number of species per order (Table 1) prevents the generation of statistically unambiguous size distributions, which in turn limits the conclusions that can be reached.

The present study suggests that geographic range is the most important indicator of date of first description, and that size and depth play important but lesser roles. Geographic range was the best predictor of the date of discovery of a species within an order. This is in agreement with the observations of Diamond (1985) and with the data collected by Blackburn and Gaston (1995) on South American oscine passerine birds.

The relatively weak size signal for holozooplankton contrasts with findings on British beetles (Gaston 1991) and South American birds (Gaston and Blackburn 1994), and can largely be attributed to the method in which plankton is collected. Specimens of terrestrial organisms tend to be collected on an individual basis, and under these circumstances small size often, but not always (Blackburn and Gaston 1995, Reed and Boback 2002), equates to inconspicuousness. Often small terrestrial organisms also require specialised collection tech-

niques, and they are harder to separate without the aid of optical equipment (Gaston 1991). The latter explanation clearly does not apply to zooplankton, which (owing to their relatively small size) have always been identified using optical equipment. By contrast with terrestrial organisms, zooplankton is caught as an entire assemblage using nets. As a consequence, visual conspicuousness is likely to have played little role in determining whether a specimen was caught or not, providing that the nets had a sufficiently small mesh size. Overall, there has been no significant change in mesh-size used since the first zooplankton samples were collected, though different types of net are used to quantitatively sample different components of the fauna (Harris et al. 2000, Wiebe and Benfield 2003).

Although there has been no appreciable change in the nets that are used to sample zooplankton, there has been a change in the capacity of vessels to sample in deeper water, and we are now able to sample much closer to the seabed than previously (Wiebe and Benfield 2003). And of course with the advent of submersibles we are now in a position to access the plankton of ocean trenches (Shushkina et al. 1991). These newer technologies have the advantage that they permit the collection of individual specimens, which is important if the material is delicate and prone to net damage (Harris et al. 2000). Thus, one of the most recently recognised families of holozooplankton, Lampoctenidae (Ctenophora, Tentaculata, Lobata), was described in 2001 from specimens of *Lampocteis cruentiventer* collected at >700 m depth off San Diego by Harbison et al. (2001), using the research submersible Alvin (interestingly, the most recently recognised order of holozooplankton, Thalassocalycida (Ctenophora, Tentaculata), was described in 1978 from a specimen, *Thalassocalyce inconstans*, collected by Madin and Harbison in the Sargasso Sea using another 20th century collection method; SCUBA, Madin and Harbison 1978). Although we have deliberately excluded such organisms from our database because of lack of information, the role of depth as a predictor of date of first description is nevertheless important (Fig. 3c).

The positive relationship noted between zooplankton size and geographic range has previously been observed for terrestrial birds and mammals, freshwater fish and stomatopods (reviewed by Gaston 1990), where it is thought to be a consequence of the scaling between minimum viable geographic range and body size (Brown and Maurer 1987). It has also been attributed to the vulnerability of smaller species to density-independent environmental changes (Lindstedt and Boyce 1985). Quite what it can be attributed to in the pelagos is open to speculation, though it should be realised that most endemic or range restricted species are likely to be neritic owing to the often more enclosed nature of coastal than oceanic circulation. Regardless of the actual

mechanism/s underpinning this relationship, it can be interpreted to mean that recently described species have small known ranges because they have only been recently described, so allowing little time for their ranges to be fully delineated. Unfortunately, it is difficult to fully counter this argument, because unlike South American oscine passerine birds, where recently described species are known to be truly localised (Blackburn and Gaston 1995), over 2.5% of the holozooplankton described since 1951 is now known to be found in over 91% of the global ocean (data not shown).

The relationship between body size and depth also reflects a general pattern. Strictly meso- and bathypelagic taxa tend to be bigger than epipelagic taxa within the same order for a number of possible reasons. The temperature of the deep sea is significantly less than that near the surface (on average), which implies that longevity is increased and that, in the case of taxa showing indeterminate growth, final size should also be increased (Jumars and Gallagher 1982; in Gage and Tyler 1991, pp. 196). Large size is also associated with lower relative food requirements, which is likely to be an asset in an environment that receives intermittent and reduced food input. Given that pelagic food chains are essentially size-based (Steele 1974), and that those in the meso- and bathy-pelagic ocean are dependent upon detritivory (faecal pellets, exuviae, marine snow and other flocculated material), and/or the direct export of surface production through the bodies of migratory secondary producers, the average size of individuals at each trophic level might be expected to be greater than in the epipelagic.

And finally the positive relationship between geographic range and depth has been noted by a number of authors, including Ekman (1953) and Boltovskoy (1999). It has been attributed to the near constant nature of the environment below 1000 m depth and to the truly global nature of deep-water circulation.

For practical reasons we have not been able to include abundance data in our analyses. However, it is likely that this too would be (negatively) linked to the date of first description as anecdotally suggested in the Results, and as shown by Blackburn and Gaston (1995) for South American oscine passerine birds. The relationship is unlikely to be simple, as abundance may not be correlated with geographic range or size; the largest and probably most abundant species of euphausiid *Euphausia superba* Dana 1850 measures 65 mm in length and occurs in just three geographic bins, whilst arguably one of the smallest and most ubiquitous cyclopoid copepods *Oithona similis* Claus 1866 measures less than 1 mm and can be found almost anywhere in the global ocean. On the other hand, abundance will be clearly linked to depth, as the desert-like nature of the deep-sea is such that their denizens are rare (Gage and Tyler 1991).

Neither have we explicitly incorporated geographic location into our model predicting the date of first description. The literature suggests that in the case of terrestrial organisms, the accessibility/proximity of a species' range to human exploration/settlement (and/or centres of taxonomic expertise) can play an important role in influencing its likelihood of description (Allsopp 1997, Cabrero-Sañudo and Lobo 2003). The reason we did not include geographic location in our models is that this information should be based on the type locality, and we did not have these data when we initially compiled the dataset. Although we might intuitively expect species in the temperate North Atlantic to have been described prior to those from around Antarctica, this relationship is unlikely to be simple as e.g. *Euphausia superba* (65 mm) was first described in 1850 from the southern ocean whilst *Meganctiphanes norvegica* (40 mm) was first described in 1857 from the North Atlantic. This pattern would be complicated further without recourse to information on the type locality, given the wide-ranging nature of most species of holozooplankton, which would tend to homogenise any locale-specific pattern in the median date of first description (Allsopp 1997).

An understanding of the factors that lead to the probability of a species being described contributes directly to our understanding of species diversity, primarily by highlighting the gaps and flaws in what is essentially a subjective human endeavour. In the terrestrial environment, where it has been suggested that our knowledge of (largely invertebrate) diversity is poor (May 1988, 1990), this knowledge allows us to focus our collecting efforts with respect to geography (Allsopp 1997) and size (Gaston 1991). The relationship between size and known diversity (May 1988) can be modified by an understanding of the relationship between size and description date to allow a more accurate prediction of overall diversity. Such efforts are especially important in the terrestrial environment given concerns about the escalating loss of biodiversity. In the present context, the results generated here would indicate that although size does play a role in influencing the date of first description it is generally limited, as too, surprisingly, is that last frontier to marine science, depth (though it should be realised that delicate meso- and bathypelagic gelatinous zooplankton have been ignored from our analyses). Rather, our efforts should be concentrated on more range-restricted and endemic (probably neritic) forms. Despite the contentions of Boltovskoy et al. (2002) that our understanding of overall zooplankton diversity is good, crypsis amongst widely distributed neritic species is likely to be high (Caudill and Bucklin 2004), and it is these self same environments that are most at risk from anthropogenic disturbance.

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Appendix A. Primary data sources used in construction of the basic spreadsheets, prior to validation. The responsible authors are indicated by their initials.

Order	Source 1	Source 2	Source 3	Source 4	Responsible author
Aphragmorpha	Bieri 1991	Casanova 1999	Pierrot-Bults and Nair 1991		ET
Calanoida	Mauchline 1998	Razouls 1995	Bradford-Grieve et al. 1999		MJG
Calycophorae	Pugh 1999	Totton 1965			PP
Cyclopoida	Razouls 1996	Bradford-Grieve et al. 1999			MJG
Euphausiacea	Mauchline and Fisher 1969	Mauchline 1980	Baker et al. 1990		MJG
Gymnosomata	van der Spoel et al. 1997				MJG
Hyperiid	Vinogradov et al. 1996	Vinogradov 1999			MJG
Larvacea	Fenaux 1998				GE
Mesogastropoda	van der Spoel et al. 1997				MJG
Myodocopa	Angel 1999				MA
Mysidacea	Mauchline 1980	Mauchline and Murano 1977	Murano 1999	Müller 1993	MJG
Pelagica	Gibson 1999	Gibson 1995			RG
Phyllodocida	Dales and Peter 1972	Day 1967	Fernández-Alamo and Thuesen 1999		MF-A
Physonectae	Pugh 1999	Totton 1965			PP
Poecilostomatoida	Razouls 1996	Bradford-Grieve et al. 1999			HI; RB-S
Salpida	Godeaux 1998				GE
Thecosomata	van der Spoel et al. 1997				MJG
Trachymedusa*	Kramp 1961	Bouillon 1999	Kramp 1968	Bouillon and Boero 2000	EB