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Marine Invertebrate Neoextinctions: An Update and Call for Inventories of Globally Missing Species

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Abstract: The register of global extinctions of marine invertebrates in historical time is updated. Three gastropod and one insect species are removed from the list of extinct marine species, while two gastropods, one echinoderm, and three parasites (a nematode, an amphipod, and a louse) are added. The nine extinct marine invertebrates now recognized likely represent a minute fraction of the actual number of invertebrates that have gone extinct. Urgently needed for evaluation are inventories of globally missing marine invertebrates across a wide range of phyla. Many such species are likely known to systematists, but are either rarely flagged, or if mentioned, are not presented as potentially extinct taxa.

Keywords: extinction; habitat destruction; co-extinction; species rediscovery

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1. Introduction

> *"The last fallen mahogany would lie perceptibly on the landscape, and the last black rhino would be obvious in its loneliness, but a marine species may disappear beneath the waves unobserved and the sea would seem to roll on the same as always."*
>
> —G. Carleton Ray

Carlton [1] introduced the concept of neoextinctions to refer to those species that have become globally extinct in historical time, as opposed to paleoextinctions over geological time. Carlton et al. [2] then summarized what was known about historical global extinctions in the sea, followed by brief updates by Carlton [3]. Additional reviews, which also included examples of regional marine extinctions ("neoextirpations," [4]) and endangered marine species, have included those of Dulvy et al. [5,6] and del Monte-Luna et al. [7].

I present here a revised and updated inventory of the current record of global marine invertebrate extinctions, as well as an appeal for the promulgation of lists of globally missing species. The threats to marine invertebrate diversity in highly vulnerable habitats that could lead to increasing numbers of extinctions in the 21st century, and the compelling rationales for understanding why extinctions matter, are not reviewed here, as these have been extensively discussed for the past two decades and more [8–13] (among many others). The burgeoning literature further flags the risks to specific threatened and endangered marine invertebrate taxa (for example, [14–23]).

2. Updated Assessment of Marine Invertebrate Global Extinctions

IUCN [24] defines a taxon as extinct "when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual." Notably, IUCN no longer suggests a specific length of time (such as 50 years [1,25])—a temporal line in the sands of the ocean—after which a species should be declared extinct, leaving consideration of what constitutes sufficiently exhaustive surveys, and thus when to "call it" for an extinction, to be somewhat subjective.

Nine species—of the millions of species!—of marine invertebrates are recognized as extinct (Table 1). Six of these are here newly formally treated as extinctions. An ectoparasite and an endoparasite of the extinct Steller's sea cow—one of the most famous losses in marine biodiversity—have long been mentioned in the literature, but not previously explicitly listed as extinctions. These, along with an ectoparasitic louse from the extinct Guadalupe storm petrel (Table 1), as well as the previously listed louse from the extinct Jamaican petrel, should be considered only as examples of the loss of endo- and ectoparasites of at least 10 additional extinct marine birds and mammals [3]. If each of these extinct marine vertebrates supported only one host-specific parasite, our current number of marine invertebrate extinctions would double. It is of note that there is no requirement that a species be described for it to be declared extinct [26–28]. Indeed, "dark extinction" [29] may play a significant role in future estimates of marine invertebrate extinctions, especially of soft-bodied species in extirpated coastal habitats.

Table 1. Marine invertebrate neoextinctions [1,2].

Species	Former Geographic Range	Last Known Living	Habitat	Cause of Extinction	Comments	References
Nematoda: Chromadorea (roundworms)						
Ascaridoidea?	Alaska: Commander Islands	1766	Endoparasite of extinct Steller's sea cow, *Hydrodamalis gigas*	Co-extinction of host		[30]
Mollusca: Gastropoda (snails)						
Lottiidae: *Lottia alveus* (Conrad, 1831) (eelgrass limpet)	Labrador to New York	1929	Restricted to blades of the eelgrass *Zostera marina* in marine waters.	Marine (but not estuarine) populations of *Zostera* died out in the early 1930s due to an eelgrass disease epidemic, and the limpet never re-appeared.	References to *Lottia alveus* as being still living in the Northeast Pacific Ocean refer instead to a distinct living species, *Lottia parallela* (Dall, 1921) [31].	[32]
Potamididae: *Cerithideopsis fuscata* (Gould, 1857) (horn snail)	California: San Diego Bay	1935	Estuarine mudflats	Habitat destruction		[1]
Dialidae: *Diala exilis* (Tryon, 1866)	California: San Diego Bay and San Francisco Bay	1860s (San Diego Bay); 1860s–1870s? (San Francisco Bay)	on "salt water grass" (77, for San Diego Bay)	Habitat destruction		[33,34]
Aplysiidae: *Phyllaplysia smaragda* Clark, 1977 (sea slug)	Florida: Indian River Lagoon	1982	Restricted to blades of the manatee grass *Syringodium filiforme*	Habitat destruction		[2,35–37]
Arthropoda: Crustacea: Amphipoda (amphipods)						
Cyamidae: *Cyamus rhytinae* (Brandt, 1846) (whale louse)	Alaska: Commander Islands	1766	Ectoparasite of extinct Steller's sea cow, *Hydrodamalis gigas*	Co-extinction of host	No other cyamid amphipods have been reported from sirenians.	[2,30]
Arthropoda: Insecta: Phthiraptera (lice)						
Philapteridae: *Saemundssonia jamaicensis* Timmerman, 1962 (Jamaican petrel louse)	Jamaica	1879	Ectoparasite of extinct Jamaican petrel, *Pterodroma caribbaea*	Co-extinction of host		[3,38]
Menoponidae: *Longimenopon dominicanum* (Kellogg and Mann, 1912) (Guadalupe storm petrel louse)	Guadalupe Island, Mexico	1912	Ectoparasite of extinct Guadalupe storm petrel, *Hydrobates macrodactylus*	Co-extinction of host		[38]

Table 1. *Cont.*

Species	Former Geographic Range	Last Known Living	Habitat	Cause of Extinction	Comments	References
			Echinodermata: Asteroidea (sea stars)			
Asterinidae: *Patiriella littoralis* (Dartnall, 1970)	Tasmania	1991	Intertidal, mixed soft and hard habitat	Habitat destruction		[39]

[1] As noted in the text, Gravili et al. [40] proposed that 10 species of hydrozoans in the Mediterranean Sea had a significant chance of being extinct. Four of these species are doubtfully valid or have doubtful records [40]. Of the remaining six, three were last seen in the 1960s, but it is unclear the extent to which they have been specifically searched for, nor over what seasons or lengths of time, in their last known locations. The last three are: (1) *Eucheilota maasi* Neppi and Stiasny, 1911, described as an endemic in the Adriatic Sea [40,41], last collected in 1914, and known only from its medusa. However, Batistic and Garic [42] report medusae identified as *E. maasi* from the Adriatic Sea based on 2011–2012 collections, indicating that, if correctly identified, it is still extant. (2) *Branchiocerianthus italicus* Stechow, 1921, also described as a Mediterranean endemic last collected in 1905 when it was dredged from 300 m in the Gulf of Naples [43]. (3) *Plumularia syriaca* Billard, 1931, last collected in 1929 and only known from the Gulf of Alexandrette, Syria, at 11 m deep or greater [44]. For these latter two species, it is also similarly not clear the extent to which species-specific searches have been conducted, either by deep-sea explorations in the Gulf of Naples, or at the appropriate depths off the Syrian coast. [2] As also noted in the text, Peters et al. [19] (2013) and Cowie et al. [20] considered five species of cone shells as of questionable status, or questionably or possibly extinct. All five species again reflect the challenges that have resulted in possibly underestimating neoextinctions. *Conasprella sauros* (Garcia, 2006), with only dead shells recovered from Texas, Louisiana, and Mexico, may or may not be a fossil species [45]. The Cape Verdes *Africonus bellulus* (Rolan, 1990) has either not been reported since the 1970s [19] or has been collected sometime since the 1990s [46]; Rolan [47] only cites a 1980 work as the basis for the knowledge of this species, without collection dates or habitat data. It is provisionally accepted as a good species [47]. *Conus colmani* Rockel and Korn, 1990, noted by Cowie et al. [20] as possibly extinct, is known from many specimens, none alive, from the Queensland coast of Australia through deep-water trawling [48]. It is not discussed by Peters et al. [19]. Marshall [49] notes that it needs taxonomic re-evaluation as part of a species complex. *Conus luteus* G. B. Sowerby I, 1833, a widespread Indo-Pacific and Hawaiian species, is noted by Peters et al. [19] as having not been reported since the 1970s, but appears to have been collected alive in recent years in a number of locations, including the Marshall Islands (http://www.underwaterkwaj.com/shell/cone/Conus-luteus.htm; accessed on 1 April 2023) and Papua New Guinea [50]. It is not treated by Cowie et al. [20]. Finally, a timeline of not having been re-collected in 20 years for *Conus splendidulus* G. B. Sowerby I, 1833, from the Indian Ocean, is potentially too short to permit judgment of its status. Overall, in none of these cases does there appear to be published information on the extent of targeted searches.

Previous marine extinction treatments (noted above) have flirted with the extinct, 22 mm long, Florida sea slug *Phyllaplysia smaragda*, but failed to formally list it, despite clear statements as to its status and despite it having once existed in a site that has been thoroughly explored and re-explored. The fifth, a tiny (circa 3 mm tall) snail (*Diala exilis*), long gone from the now highly modified but well-explored bays of the California coast, was flagged in a little-known paper [33]. O'Hara et al. [39] have recently and clearly outlined the evidence that the sixth species, the small Tasmanian sea star *Patierella littoralis*, with a radius up to 22 mm, is extinct. In all three of these cases, long-term explorations in the appropriate habitats and locations have failed to detect any living individuals.

While the data are too few to suggest any biogeographic patterns, ecologically all nine species have disappeared from shallow coastal waters, where the extinction of vulnerable marine vertebrates is expected, due to either direct or indirect human-mediated forces, or where shallow water habitats can be destroyed by human activity. The exception is the apparent non-human-mediated extinction of a marine limpet (*Lottia alveus*) from the Northwest Atlantic Ocean (Table 1), unless the slime mold disease agent that caused the demise of the limpet's host plant, the eelgrass *Zostera marina*, was introduced by a human-mediated vector.

Four species are here removed from the extinct or possibly extinct list (Table 2). Two of these are marine snails that have appeared in previous treatments of global marine extinctions [2]. One, the Chinese mangrove periwinkle *Littoraria flammea,* last believed to have been collected in 1855, was rediscovered in Singapore salt marshes in 2014; it is further likely a synonym of the widespread living Indo-Pacific species *Littoraria melanostoma* (Table 2). The other, a fossil species of California limpet, *Lottia edmitchelli*, was previously thought to have survived into the Holocene, represented by a single living specimen collected in southern California in 1861. This specimen has now been re-identified as an extant species, *Lottia scabra* (Table 2). A terrestrial snail, *Omphalotropis plicosa* from Mauritius, has been misinterpreted as a marine species (Table 2), while a southern California rocky intertidal beetle, *Bembidion palosverdes,* thought gone for nearly 50 years from a mainland site, was discovered alive in 2010 on an offshore island (a refugium?) (Table 2).

Table 2. Marine invertebrates no longer considered extinct, or erroneously listed as such.

Species	Geographic Range	Habitat	Comments and Reference
	Mollusca: Gastropoda (snails)		
Littorinidae: *Littoraria flammea* (Philippi, 1847) (periwinkle)	Indo-West Pacific	Mangrove and salt marsh communities	Formerly considered to have last been collected in 1855 in China, it was found living in 2014 in salt marshes near Shanghai, and may be the same as the widespread and abundant Western Pacific species *Littoraria melanostoma* (Gray, 1839) [51]
Lottiidae: *Lottia edmitchelli* (Lipps, 1966) (limpet)	Southern California	Rocky intertidal	Formerly considered to have last been collected alive in 1861 [1], the living specimen so identified is now considered to be the extant species *Lottia scabra* (Gould, 1846) [52]. *L. edmitchelli* is, further, now considered to have gone extinct by the Middle Pleistocene [52].
Assimineidae: *Omphalotropis plicosa* (Pfeiffer, 1854)	Mauritius	Tree trunks (terrestrial)	Listed as an extinct marine species by Kemp et al. [53] based on the IUCN Red List, this is a terrestrial snail, nor is it a salt marsh species (https://en.wikipedia.org/wiki/Omphalotropis_plicosa; accessed on 1 April 2023). It is not extinct [54].
	Arthropoda: Insecta: Coleoptera (beetles)		
Carabidae: *Bembidion palosverdes* Kavanaugh and Erwin, 1992 (shore beetle)	California: Santa Catalina Island	Rocky intertidal	Last seen in 1964 on the Palos Verdes Peninsula, Los Angeles County, California, and thought possibly extinct [55], it was rediscovered alive in 2010 on Santa Catalina Island [56].

3. Challenges with Assessing the Global Marine Invertebrate Extinction Record

The current record of global marine invertebrate extinctions is thus extraordinarily paltry. Why is that?

I highlight here three of a number of drivers [1,2,10,57] that may have led to our current embarrassing lack of knowledge of how many, and which, species of marine invertebrates have gone extinct. These drivers are a subset of the more general challenges of accurately assessing temporal and spatial changes in historical marine biodiversity (for example, [58–65]).

3.1. Reluctance to Declare a Species Globally Missing

The marine systematics literature is richly populated with species, especially those described in the 18th and 19th centuries, that cannot be reliably recognized today, often due to apparently insufficient diagnoses or lack of the availability of the original specimens. Terms often applied to such species are ***nomina dubia*** (for example, [66–69]) or ***incertae sedis*** (for example, [70–73]). The scientific names of such species—of which there may be thousands [74]—that cannot be confidently matched today to known species are often either simply set aside without disposition, or relegated to the probable synonymy of known species. Such names form part of the "taxonomic graveyard" noted by Bouchet and Strong (2010). In more than 50 years of reading the marine taxonomic and systematic literature across all major and many smaller phyla, I have seen no suggestions that any names now considered *nomina dubia* or *incertae sedis*, based on taxa first and last described centuries ago, might refer to extinct species.

As an example, and because the Mollusca are the best known phylum of marine invertebrates, thanks in large part to centuries of seashell collectors, I analyzed the extraordinary 1258-page monograph of Coan and Valentich-Scott [75] on the marine bivalve mollusks of the Tropical Eastern Pacific (TEP), which covers a 5000 km province from Isla Cedros, Baja California, Mexico to Piura in northern Peru. Of approximately 900 species treated, I tallied nine species that have not been found since the 1860s or earlier (Table 3), along with the suggestions (from Coan and Valentich-Scott [75] or other sources) as to why these species have not been seen again. These suggestions (Table 3) include that the species in question do not actually come from the TEP ("mislabeled," "mislocalized," "extralimital", or provenance uncertain), are difficult or impossible to recognize today from their descriptions or illustrations ("nomen dubium"), or are simply a mystery ("a significant unresolved question," or "not . . . recognized since"). Again, however, in no case is there a suggestion that any of these species may possibly be extinct.

Table 3. Missing bivalve species in the Tropical Eastern Pacific Ocean (data from Coan and Valentich-Scott [75], unless otherwise indicated).

Family	Species	Size (mm)	Last Known Location	Last Collected	Habitat	Possible Reason for Not Being Re-Discovered (Coan and Valentich-Scott, [75], Unless Otherwise Indicated)
Chamidae	*Chama producta* Broderip, 1835 [1]	93	Mexico: Gulf of Tehuantepec	1828–1830	Sandy mud, 18 m	"Possibly a mislabeled specimen from another province."
Veneridae	*Chinopsis crenifera* (G. B. Sowerby I, 1835)	37	Ecuador: Santa Elena; Paita, Peru	<1835	---	"This species is very uncertain"; known only from Ecuador (the type locality) and Peru (the latter based on 19th century material?; see Keen [76] p. 186.)
Veneridae	*Cytherea inconspicua* G. B. Sowerby I, 1835 [2]	25	Peru: Paita, Piura	<1835	Sandy, muddy bottom	Provenance uncertain (Panamic or Peruvian?)
Veneridae	*Pitar fluctuatus* (G. B. Sowerby II, 1851)	18	Ecuador: Santa Elena, Guayas	<1851	---	"We have not found additional specimens of this distinctive species, and the type locality might be mislocalized."
Petricolidae	*Petricola amygdalina* G. B. Sowerby I, 1834	---	Ecuador: Galapagos Islands	<1834	in pteriid valves, 6–11 m	Nomen dubium or extralimital
Solenidae	*Solen oerstedii* Morch, 1860	69	Costa Rica: Puntarenas	<1860	Subtidal in mud (Huber, 2010)	"not . . . recognized since" (Keen [76] p. 259)
Pandoridae	*Frenamya cristata* (Carpenter, 1865)	24	Mexico: Gulf of California	<1865	---	"Only known from the type locality in the Golfo de California, Mexico"
Pandoridae	*Pandora brevifrons* G. B. Sowerby I, 1835	22	Panama: Bahia Panama	<1835	---	"In spite of intensive collecting in Panama, this species has not been found since its description in 1835, and it is possible that the types were mislocalized. However, study of specimens from adjacent and far-reaching provinces has also not yielded any material of this species."
Periplomatidae	*Periploma excurva* Carpenter, 1856	---	Mexico: Mazatlan, Sinaloa	<1856	---	"A significant unresolved question"

[1] Cardoso et al. [77] report *Chama producta* from Peru, but their material is not that species (Paul Valentich-Scott, personal communication, May 2023). Huber [78,79], in a work not online and largely inaccessible to most workers, agreed with Reeve [80], (*Chama iostoma* Conrad, 1837) that Broderip's *Chama producta* from Mexico was the same as the Indo-Pacific species *Chama limbula* Lamarck, 1819, but neither Reeve nor Huber provided evidence for this. Bouchet [81,82] treats *Chama producta* and *Chama limbula* as distinct species. [2] Size and habitat data from Huber [78], who assigns it to the genus *Pitar* without explanation.

In short, nine "missing" marine bivalves, last encountered in the mid-19th century or earlier, can be tallied in one province, and these represent only one class of one phylum.

Given that there are 62 recognized marine provinces [83], this might suggest that the number of missing species across many phyla, including short-range provincial endemics [84], could be large.

Thus, while a standard assumption in the taxonomic and systematic sciences is that historical descriptions of species that cannot be clearly interpreted today likely largely represent coarse descriptions of still-extant taxa, if they can be recognized at all, "an alternative hypothesis is that some of these early descriptions represent the only known records of species that became extinct long ago" [3].

3.2. Reluctance to Declare Missing Species as Globally Extinct

Cowie et al. [85] have recently reviewed aspects of the hesitancy to declare a species extinct, including fear of committing the "Romeo Error"—a concern of declaring a species extinct when it is not. This fear may be reinforced by the regular stream of rediscoveries of rare species, some not seen for over 100 years (for example, [2,86–91], and Table 2, herein). Further reinforcement of the Romeo Error may arise from the discovery of living individuals of species previously known only from the fossil record—most famously the coelacanth, but also with cases continuing to be reported [92].

Cowie et al. [85] remarked that, relative to the IUCN criterion noted above of a requirement for exhaustive surveys, "For a very large proportion of described species, there will never be dedicated exhaustive fieldwork, at the appropriate time and over the appropriate timeframe because they are too numerous, and knowledge is too scarce to know the time-frame and even the range to be searched." The result of setting the bar potentially unachievably high, leading authors to "not dare to declare" species extinct, suggests that extinctions will be underestimated, perhaps markedly so [85].

The specter of the Romeo Error is deeply ingrained, and further casts a shadow on especially small and poorly known species. The tiny sea slug (sacoglossan) *Stiliger vossi* Marcus and Marcus, 1960, slightly more than one millimeter long in its preserved state, was last collected in 1958 among algae in shallow water in Biscayne Bay, Florida [93]. The late Kerry Clark, a sacoglossan specialist, searched for it assiduously, but failed to find it as of 1996 [2]. It remains unreported. While we consider another Florida sea slug of larger size, *Phyllaplysia smaragda,* extinct, *S. vossi* remains indefinitely suspended between the living and dead. The "smalls" rule of invasive species science (the smaller the species, the less likely it will be categorized as non-native) works against both additions to communities [94] and deletions.

Benovic et al. [95] identified a number of hydrozoan species not seen since 1910 and known only from the Adriatic Sea, but declared none of them permanently gone. Nearly 30 years later, a change in perspective led Gravili et al. [40] to suggest that some of these species were globally extinct, as discussed further below.

3.3. When Did You Miss Me? Time Lags in Recognizing Missing or Extinct Species

Boero et al. [96] commented that "The modern-day record demonstrates that even large, once-abundant species can simply disappear without notice, suggesting that documenting the disappearance of uncommon and smaller species is a fundamental challenge." Dulvy et al. [5] have discussed the phenomenon of delayed reporting, relative to both local and global extinctions. Clear examples emerge from the limited record of marine extinctions (Table 1). The once abundant eelgrass limpet *Lottia alveus* was last found living in 1929; its disappearance was first pointed out in 1991 [32]. The once common mudflat horn snail *Cerithidea fuscata* was last collected in San Diego Bay, California, in 1935, but its disappearance was not mentioned until 1981 [97].

In more recent times, the relatively large (up to 8 cm) and colorful sea slug (nudibranch) *Felimare californiensis* (Bergh, 1879) was once common along the rocky intertidal shores of southern California: the fact that it had been last detected there in 1977 was not pointed out until 2013 [98]; it remains extant elsewhere. The large (15 cm in length) mud shrimp *Upogebia pugettensis* (Dana, 1852) began steadily disappearing from many

North American Pacific coast estuaries in the 1990s, including wholesale extirpations from some embayments, with no remarks on its absence made by marine biologists, until its widespread demise (but not global extinction) was pointed out by Chapman et al. [99].

Most taxonomic monographs do not note when a given species was last collected or seen. Species long reported by our predecessors remain on lists, and as one generation of workers follows another, it may be difficult to notice that any one species has not been seen "recently." In the monographic work noted above of 900 species of marine bivalves in the Tropical Eastern Pacific, while a small number were flagged as not having been seen since the 19th century [75], we do not know for many of the remaining hundreds of species when in fact they were last collected or seen—which additional species might have gone missing in the last 75 to 100 years, versus those whose apparent lack of recent records is "simply because no one has sought them out again" [96].

Adding to the above list, then, of those drivers that have resulted in the discovery of few marine invertebrate extinctions is the lengthy time and effort to document the details of the history of any one species, including delving into old and often obscure literature in rare journals that may not be online, recognizing the earlier names under which a species may have appeared, tracking down museum holdings, and interviewing older workers who may be, or have been, familiar with a given species. An important caveat is that, while many museum collections can now be searched online, large swaths of material of what any given museum actually holds are not yet either catalogued or if catalogued not yet downloaded, meaning that for an accurate assessment of historical collections of a species, the appropriate museum collections must be visited in person. Very few workers may find investing large amounts of time in the 18th and 19th century literature and in wading through museum collections to be worthy of their time. Finally, all museums hold large amounts of unidentified material, requiring some level of taxonomic expertise to recognize that a target species of interest is in a collection but not yet identified (that, or convincing an expert taxonomist to come along in such explorations).

Nevertheless, recording "last seen" dates across the known historical range of a species may set the stage for a broader capture of species missing (and possibly extinct) globally, a task that I suggest below be profitably pursued.

4. A Call for Inventories of Globally Missing Marine Invertebrates

The IUCN Red List Categories and Criteria of Threatened Species [24] does not define "missing" in their nine-tiered classification system of species at risk of global extinction. Martin et al. [25] have proposed, for terrestrial vertebrates, that "lost taxa"—species not yet declared globally extinct—be defined as those "that have not been reliably observed in >50 years," resurrecting a temporal metric abandoned by the IUCN for extinctions.

Despite the challenges and limitations of attempting to tilt the missing and possibly extinct species windmills, none of these impediments, including fear of the Romeo Error, should prevent promulgating inventories of missing marine invertebrate species. Such inventories would have immediate and profound value that would serve to direct targeted search efforts. Lists of missing species harvested from the literature, or by interviewing experienced systematists, could capture species characterized (1) by being relatively taxonomically robust (ideally based upon examination of original specimens) but still including those taxa suspected of being a synonym of another species, (2) by having a reasonably firm handle on the last known records within Martin et al.'s [25] 50-year window, and (3) by having occurred in habitats highly susceptible to extraordinary levels of anthropogenic disturbance if not wholesale destruction, such as in bays, estuaries, lagoons, mangroves, marshes, supralittoral shores, and many intertidal shores [1,6].

While acknowledging the many threats to deep-sea biota (for example, [100,101]) generally excluded from such lists, at least initially, would be the many hundreds if not thousands of deep-water species that may have been collected only once, and often not since the 19th century, due to the vagaries of stochastic deep-sea exploration (but see [11], relative to endemic hydrothermal vent species).

In a rare example of an attempt to detect missing species, Gravili et al. [40] assessed the status of approximately 400 species of hydroids (Phylum Cnidaria, Class Hydrozoa) in the Mediterranean Sea. Of these, 53 species have not been reported in the literature for at least 41 years, and were thus considered candidates for analysis as potential extinctions. Gravili et al. [40] argued that "The choice of 41 years as a threshold to consider a species as missing was decided based on the rather intense study of hydrozoan species in the Mediterranean in the last four decades . . . " (and that) "Due to intensive sampling . . . if a previously reported species fails to be recorded chances are good that, at least, it is more rare than before." They then evaluated these 53 species with a formula for a "confidence of extinction index," proposed originally for paleobiology by Marshall [102], and adapted by Boero et al. [96] "to analyse cases of putative extinction in recent species."

The three variables in this formula are (1) the number of years since the species was last sighted, (2) the number of years between the original description and the last sighting (first framed in Boero et al. [96] as the years between the first record (the date of first collection) and the last sighting), and (3) the number of individual years in which there is a record. The probability of extinction in this formula is thus sensitive to the choice of the demarcation year after which a species is declared missing. The formula does not capture search efforts over a given length of time or area. The rationales for the failure for admitting any of Gravili et al.'s [40] 10 statistically extinct hydroid species to the register of global marine extinctions herein are outlined in footnote 1 of Table 1.

At a family and global level, Peters et al. [19] and Cowie et al. [20] examined the worldwide conservation status of cone shells (Class Gastropoda, Family Conidae). They considered five species as of questionable conservation status or as possibly extinct. As with Gravili et al.'s [40] Mediterranean hydroids, a series of taxonomic and sampling challenges impede admitting these species at this time to the register of global extinctions (footnote 2, Table 1).

The above attempts to seek out missing species in specific taxonomic groups illuminate both the value of detecting potentially lost species and the challenges of recognizing them as extinct, in the absence of dedicated multiyear and ideally species-specific searches. As noted above, these challenges are compounded if species thought to be missing occur or occurred in deeper waters, as illustrated in the examples in Table 1, footnotes 1 and 2.

5. Epilogue

I opened this essay with the same eloquent observation of G. Carleton Ray [103] as I did 30 years ago [1]. Little has changed. While Regnier et al. [104] concluded that "marine habitats seem to have experienced few extinctions, which suggests that marine species may be less extinction prone than terrestrial or freshwater species," and while this would be welcome news if so, such a conclusion remains premature [30] in light of the striking lack of investigation of the possible or probable number of marine extinctions.

The challenges to document and verify extinctions in the sea are many, but not insurmountable [8,10,40,85] and herein. In the early decades of the 21st century, even an approximate estimate of the number of marine invertebrate species that are globally extinct eludes us. Remarkably few scientists study extinctions of marine invertebrates [2], the most speciose group of ocean animals, nor are students typically introduced to the topic as a field of study. Nevertheless, that a notable number of marine invertebrate extinctions has not been documented is not evidence that they have not occurred—or are not now occurring. The study of marine invertebrate extinctions may be rare, but extinctions may not be.

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