HISTORICAL EXTINCTIONS IN THE SEA

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"The Frail Ocean"

—Wesley Marx, 1967 (79)

Monday, June 3, 1844
(*Date when the last Great Auks were seen alive, on the island of Eldey, Iceland*)

INTRODUCTION

Communities of organisms can change over historical (ecological) time in three ways: Species can be deleted (extinctions), added (invasions), or can change in relative abundance. In marine environments, while the latter two types of alterations are increasingly recognized (if not extensively studied), extinctions in historical time have received little recognition. This lack of attention to marine extinctions stands in striking contrast to the comparatively advanced recognition of the existence of extinctions, particularly of larger organisms, in terrestrial communities (7). Extinctions in historical time have been referred to as neoextinctions, and prehistoric extinctions as paleoextinctions (19), a distinction we follow here. Baillie & Groombridge (7) treat historical extinctions as those occurring in the past 400

years or less. Ehrlich et al (37) noted examples of birds that had become extinct "since 1776," noting that they had "chosen 1776 as our cutoff point somewhat arbitrarily, but reliable reports from before that point are few, museum specimens are rare, and documented extinctions are rarer still" (if this cutoff were to be extended beyond birds, it would not include the extinction of the Steller's Sea Cow, *Hydrodamalis gigas*, last observed in 1768).

We review the record of neoextinctions in the ocean and discuss these in terms of both temporal and spatial patterns. We further review the possible extent of underestimation of marine neoextinctions. Finally, we attempt to set the importance of what we do know about marine extinctions into a larger framework of the vulnerability of marine organisms to global deletion.

It is important to understand the diversity and number of extinctions in the oceans for a variety of reasons. At a general level, an understanding of marine extinctions provides a measure of the scale of susceptibility of the seas to human perturbations and alterations. More specifically, determining which species have become extinct can serve as a harbinger of further loss in particular habitats, providing both a rationale and an opportunity for increased protection of species guilds and habitats that may be most at risk. Knowledge of which species have regionally or globally disappeared is critical in understanding modern-day community and ecosystem structure and function. Energy flow, predator-prey networks, indirect interactions, and a host of other processes may change dramatically with the removal of a species—removals that have, by and large, preceded scientific study. Knowing which species were removed from communities in historical times is the sine qua non of understanding prealtered communities and how they evolved and functioned (20). Indeed, it is not impossible that some of our modern-day views and interpretations of the structure of many marine communities may be the result of species interactions that have been readjusted by means of unrecognized species deletions in ecological time.

Finally, there is a compelling value to knowing about extinct species in terms of evolutionary biology: Detecting species that have gone extinct but that are currently taxonomically buried and thus hidden in the synonymy of still-extant species may provide potentially important phylogenetic information.

SPATIAL AND FUNCTIONAL SCALES OF EXTINCTION

Extinction occurs at a variety of operative levels, in both spatial and functional terms:

Local extinction occurs when a population or populations of a species are displaced from a small area or habitat. This includes the local extirpation of a native species by an introduced species (that is, a reduction in the native species' fundamental niche). An example is the displacement of the native California mudsnail *Cerithidea californica* from open intertidal mudflats on San Francisco Bay, California, by the introduced American Atlantic mudsnail *Ilyanassa obsoleta*, resulting in *Cerithidea* being restricted to an upper intertidal refugium (105). We

discuss the California abalone *Haliotis sorenseni* below. Local extinctions may result in loss of distinctive genetic stocks.

Regional extinction occurs when a species is removed from parts of its "fundamental range" (to parallel niche theory terminology) and reduced to a "realized range." Examples include the extirpation of the gray whale *Eschrichtius robustus* from the North Atlantic Ocean (87), restricting modern-day populations to the North Pacific Ocean, and the removal of the sea otter *Enhydra lutris* from large parts of its former range in the Northeastern Pacific Ocean (69, 110). We discuss below the extirpation of the native mussel *Mytilus trossulus* from southern California. As with local extinctions, regional extinctions may result in loss of distinctive genetic stocks (which, as discussed below, could later be found to represent distinct species).

Global extinction occurs when a species completely disappears. For smaller marine organisms, there is no consensus as to how long a species must remain undiscovered in order to be declared extinct.

In addition to these spatial scales, *functional* extinction occurs when a species is so reduced in abundance that it no longer plays a quantitatively important role in the energy flow or the structuring (bioengineering) of the community. An example is the large-scale removal of baleen whales from the southern oceans and the subsequent increase of their former prey, euphausiacean crustaceans (krill) (70, 92).

Commercial extinction occurs when a species is so reduced by hunting (fishing) that exploitation pressure is reduced or ceases. Many finfish and most whale populations have been so overfished that hunting them is no longer economically viable; this results in the pursuit of other species (115, 116). We focus here largely on global extinctions, although other spatial and functional scales of extinction provide critical lessons, as we discuss.

GLOBAL MARINE NEOEXTINCTIONS

Challenges in Establishing a List of Extinct Species

Which marine organisms have become extinct in historical time? We discuss below the absence of data that obscures the true number of extinct species. Here we address three phenomena pertinent to establishing an actual working list of extinctions: one, the level of taxonomic resolution of the species in question; two, the ecological boundaries placed on the habitat definition; and three, the subjectivity, noted above, as to when to declare a taxon extinct in the wild. In this review we take a conservative approach in addressing these challenges.

We treat the extinction of "subspecies" as regional extinctions of allopatric populations of the stem species: Genetic studies (which may be still possible on museum material) may establish the uniqueness of the taxon in question. For example, it remains unclear if the Jamaican Diablotin (a petrel), *Pterodroma hasitata caribbea*, the Bonin Night Heron, *Nycticorax caledonicus crassirostris*, and the Japanese sea lion, *Zalophus californianus japonicus*, were distinct subspecific

TABLE 1 Status of additional marine birds and mammals listed as extinct in Norse (93) and Vermeij (138)

Taxon	Common name	Comment
Class Mammalia		
Order CETACEA		
Family Eschrichtiidae		
Eschrichtius robustus	Atlantic Gray Whale	Former Atlantic populations are now considered to be the same species as Pacific populations (87)
Class Aves		
Order PROCELLARIIFORMES		
Family Procellariidae		
Pterodroma jugularis	Petrel (Hawaiian Islands)	Prehistoric extinction (138)
Pterodroma hasitata caribbea	Jamaican Diablotin	Subspecific status uncertain (40) and extinct status uncertain (25)
Family Hydrobatidae		
Oceanodroma macrodactyla	Guadalupe Storm Petrel	Extinct status uncertain (7, 40)
Order CICONIIFORMES		
Family Ardeidae		
Nycticorax caledonicus crassirostris	Bonin Night Heron	Subspecific status uncertain (7)
Order ANSERIFORMES		
Family Anatidae		
Tadorna cristata	Crested Shelduck	Not extinct (7, 25)
Chendytes lawi	Flightless Duck (California)	Prehistoric extinction (138)

(genetic) taxa or only clinal variants of the stem species (Tables 1 and 2). Baillie & Groombridge (7) did not list the first two and did list the Japanese sea lion as an extinct subspecies. In contrast, Vermeij (138) listed the Canary Islands Oystercatcher (as the "Canary Islands Black Oystercatcher") under the trinomial *Haematopus ostralegus meadewaldoi*; however, Baillie & Groombridge (7) treated it as a full species (*H. meadewaldoi*), a designation that we follow here.

As further examples, we have also not treated as global extinctions two marine birds whose taxonomic status as valid species remains unclear: the Auckland Island Shore Plover, *Thinornis rossi*, and Cooper's Sandpiper, *Pisobia (Tringa) cooperi*. Cooper's Sandpiper is based on a single specimen of a shorebird collected on Long Island, New York, in 1833 (40). Cooper's Sandpiper has long been rejected as a valid species, being interpreted as either a hybrid of the White-Rumped Sandpiper, *Calidris fusicollis*, and the Pectoral Sandpiper, *Calidris melanotos* (40)—although no valid hybrid shorebird has been recorded from North America (81)—or as an aberrant specimen of one or the other (despite being placed in *Pisobia*, a different genus). Molecular genetic analysis could be done on the extant type specimen if

TABLE 2   Additional marine birds and mammals that may be extinct

Taxon	Common name	Comment
Class Mammalia		
Order CARNIVORA		
Family Otariidae		
Zalophus californianus japonicus	Japanese Sea Lion	Subspecific status uncertain (110, 138)
Class Aves		
Order PROCELLARIIFORMES		
Family Procellariidae		
Pterodroma sp.	Petrel (Mauritius)	Listed as extinct (7) with no further data
Order CHARADRIIFORMES		
Family Charadriidae		
Thinornis rossi	Auckland Island Shore Plover	Specific status uncertain (40, 49, 52)
Family Scolopacidae		
Pisobia (*Tringa*) *cooperi*	Cooper's Sandpiper	Specific status uncertain (40, 81)
Prosobonia leucoptera	White-Winged Sandpiper	Marine, maritime, or inland (see text)

harvestable DNA is present. The Auckland Island Shore Plover, *Thinornis rossi*, is also known from a single specimen collected in 1840. This individual differs from all known specimens of its congener, the New Zealand Shore Plover, *Thinornis novaeseelandiae*, itself a threatened species (7, 40, 49). Greenway (49) suggested that *T. rossi* may have been a distinct sibling ("sympatric") species. As with Cooper's Sandpiper, the still-extant type specimen may be worthy of molecular examination.

Vermeij (138) noted four taxa as being "marginally marine," but included them in a table of "recently extinct marine species." For the purposes of this review, we define a "marine organism" as one that relies for some or all of its life on ocean resources (such as food, breeding sites, or habitat). We omit, however, maritime taxa, such as the Pallid Beach Mouse (*Peromyscus polionotus decoloratus*) or the Dusky Seaside Sparrow (*Ammodramus maritimus nigrescens*). Unfortunately, precise habitat data are lacking for many extinct taxa, leading to further potential omissions from the list of extinct marine taxa. An example is the extinct White-Winged or Tahitian Sandpiper, *Prosobonia leucoptera* (32, 49, 81). Its habitat is unknown ("near small streams"; 52) and thus their proximity to or use of the ocean is also unknown. However, given that its only congener, *Prosobonia cancellata*, is a marine shorebird (52), *P. leucoptera* may also have been marine.

World Conservation Union criteria up until 1996 indicated that a species was considered extinct if it had "not definitely been located in the wild during the past 50 years" (50). In the 1996 "Red Book" (7), the arbitrariness of 50 years (19) was replaced with the criterion of when "exhaustive surveys . . . over a time frame

appropriate to the taxon's life cycle and life form." As discussed below, not finding a species may be due to inadequate exploration and incorrect identification. Thus, the Guadalupe Storm Petrel, *Oceanodroma macrodactyla*, returns to the "possibly alive" category (having been formerly considered extinct) because of the possibility of confusion with a related species and because all of its former island range has not been exhaustively surveyed (25, 40).

Marine Birds and Mammals Known to be Extinct

Treatments of marine vertebrate extinctions by Norse (93) and Vermeij (138) listed as extinct 10 and 13 species of birds and mammals, respectively. Setting aside two paleoextinctions (a flightless duck, *Chendytes lawi*, and a Hawaiian petrel, *Pterodroma jugularis*), Norse (93) and Vermeij (138) reported a total of 13 extinctions, with only a 62% overlap in their lists. The Guadalupe Storm Petrel, listed by both Norse (93) and Vermeij (138), may be extant, as noted above. The Korean Crested Shelduck, listed by Vermeij (138), is considered to be still living (Table 2). The Jamaican Diablotin, in Vermeij's (138) but not Norse's (93) list, is neither clearly a distinct taxon nor demonstrably extinct (Table 2). The Atlantic Gray Whale, listed by Norse but not by Vermeij, is not considered to be a distinct taxon (87).

We consider three mammals and five birds extinct, (Table 3). In Table 3, the date of record is the date the last individual(s) were actually seen (and usually killed), not necessarily when the species became extinct, but the last sighting can be considered an estimate of the date of *functional* extinction of the species. The status of seven other species of marine vertebrates discussed by Norse (93) and Vermeij (138) are summarized in Table 1, and five more species that may be extinct are listed in Table 2. We discuss below taxonomic, spatial, or temporal patterns in these extinctions.

Marine Invertebrates Known to be Extinct

There are, as discussed by Carlton et al (21) and Carlton (19), obstacles associated with assembling more than a rudimentary list of examples of extinct marine invertebrates. Comparison of pre-twentieth century accounts of marine invertebrates with museum collections (to detect sudden terminations in collections of specific taxa) or with modern faunal lists has not yet begun. In 1992, Carlton (19) suggested that four species of marine gastropods had become extinct, none of which has been found since then (Table 4). The data are too limited to resolve any patterns.

Clark (24, 25, and personal communication 1996) noted that the anaspidean seaslug *Phyllaplysia smaragda* was "possibly extinct." It was first described in 1977 and last collected in 1981, and only known from portions of the Indian River Lagoon system on the east coast of Florida. It may have specialized on the epiphytic algae growing on the basal stems of the seagrass *Syringodium*; this habitat was extirpated from the type locality of the slug, but remains widespread elsewhere in Florida and the Caribbean. Mikkelsen et al (89) reported specimens collected

TABLE 3   Marine birds and mammals extinct in historical time

Taxon	Common name	Geographic region (*)	Last known living (**)
CLASS MAMMALIA			
Order CARNIVORA			
Family Mustelidae			
Mustela macrodon	Sea Mink	NW Atlantic	1880
Family Phocidae			
Monachus tropicalis	West Indian Monk Seal	Caribbean, Gulf of Mexico	1952
Order SIRENIA			
Family Dugonidae			
Hydrodamalis gigas	Steller's Sea Cow	NW Pacific	1768
CLASS AVES			
Order PELECANIFORMES			
Family Phalacrocoracidae			
Phalacrocorax perspicillatus	Pallas's Cormorant	NW Pacific	ca. 1850
Order ANSERIFORMES			
Family Anatidae			
Mergus australis	Auckland Islands Merganser	SW Pacific	1902
Camptorhynchus labradorius	Labrador Duck	NW Atlantic	1875
Order CHARADRIIFORMES			
Family Charadriidae			
Alca impennis	Great Auk	NW/NE Atlantic	1844
Haematopus meadewaldoi	Canary Islands Oystercatcher	NE Atlantic	1913

*Region abbreviations: NE, Northeast; NW, Northwest, SW, Southwest.

**Final observations of living specimens:

Mustela macrodon: Day (32) stated that the last known specimen was taken in 1880 on an island in the Gulf of Maine; Campbell (16) stated it was taken at Campobello, New Brunswick, in 1894, but Waters & Ray (141) noted that the 1894 record is questionable. Vermeij (138) listed a date of "about 1900."

Monachus tropicalis: Knudtson (67) noted that the last authenticated sighting was in 1952 on Serranilla Bank in the western Caribbean. LeBoeuf et al (72) noted that surveys between 1973 and 1984 failed to discover it (thus Vermeij's (138) record of extinct "before 1973"). Solow (126) discussed the monk seal as an example of inferring extinction from sighting data (see also 82). In a prophetic statement, William T Hornaday wrote in 1913 (55) about West Indian monk seals, "... the Damocletian sword of destruction hangs over them suspended by a fine hair, and it is to be expected that in the future some roving sea adventurer will pounce upon the Remnant, and wipe it out of existence for whatever reason may to him seem good."

Hydrodamalis gigas: Vermeij (138) gave a date of 1750, and Day (32) a date of 1767; we follow Silverberg (121), Scheffer (118), and Rice (110) in using 1768.

Phalacrocorax perspicillatus: The date of "about 1850" is based on estimates made in 1882 of when the last birds were seen on a small island off the Komandorskiye (Commander) Islands (40, 49).

Mergus australis: Fuller (40) noted that the last pair of birds was collected in 1902. The dates of 1901 (49), 1905 (138), and about 1910 (32) appear to be either errors or speculations.

Camptorhynchus labradorius: A date of 1878 is occasionally cited, but Fuller (40) noted, this record cannot be verified, and added that "there is some doubt concerning the" date 1875 itself but did not elaborate.

Alca impennis (= *Pinguinus impennis*). The date of 1844 is widely agreed upon (32, 40, 49).

Haematopus meadewaldoi: Hayman et al (52) noted that the last "firm sighting" was 1913, but Fuller (1987) wrote the "black Oystercatcher was last seen on Tenerife in 1968." The 1968 date represents one of a series of sightings of "black oystercatchers" from regions such as the western Canaries (Tenerife) (in 1968 and 1981), and Senegal (in 1970 and 1975) where no oystercatchers, either the Canary Islands Oystercatcher or the African Black Oystercatcher (*H. moquini*) have ever been recorded. The temporal clustering of these records one decade could suggest a temporary expansion of the vagrant range of *H. moquini* (previously known only as far north as Angola, far to the south). Regardless, the long hiatus between 1913 and 1968, and the lack of reports since 1981 or 1975, compel us to use the date of 1913.

TABLE 4 Marine invertebrates extinct in historical time

Taxon	Common name	Geographic region	Last known living
PHYLUM MOLLUSCA			
Class GASTROPODA			
Lottia alveus alveus	Atlantic eelgrass Limpet	NW Atlantic	1929
"Collisella" edmitchelli	Limpet	NE Pacific	1861
Littoraria flammea	Periwinkle	NW Pacific	<1840s
Cerithidea fuscata	Horn Snail	NE Pacific	1935

in 1980 from the seagrass *Thalassia* in the Indian River Lagoon, but Clark, in Mikkelsen et al (89), felt that these may have been misidentified specimens of the related slug *P. engeli*. Clark (24, 25, and personal communication 1996) further noted that the sacoglossan seaslug *Stiliger vossi*, described in 1960 and known only from Biscayne Bay, in southeast Florida, has never been collected again, despite extensive searching, and he speculated that it was also extinct. Given the relatively recent discovery of these two seaslugs in the latter half of the twentieth century, and given that much of the Caribbean has not been thoroughly explored for rare opisthobranchs, we note these here as possible extinctions but do not formally admit them to Table 4 at this time.

Some other invertebrate species were thought possibly extinct:

- Wells et al (143) and Barnes (10) noted that the nudibranch seaslug *Doridella batava*, described from the Zuiderzee, Netherlands, may be extinct. Swennen & Dekker (130) demonstrated that this slug is *Corambe obscura*, described from North America and apparently introduced to Europe.

- Banks et al (8) speculated that the Kumamoto oyster, *Crassostrea sikamea*, "may be extinct in Japan" and thus survive only in the laboratory or in oyster culture in North America. Living specimens were recovered in 1996 in Japan (149).

- Runnegar (113) believed the Caribbean bivalve mollusk *Pholadomya candida* was extinct, but it was discovered living in Venezuela (45).

- Glynn & de Weerdt (47) reported that the hydrocoral *Millepora boschmai* had become extinct in its only known locality, the Gulf of Chiriqui, Panama, in the tropical Eastern Pacific Ocean. Glynn & Feingold (48) later reported the species had been rediscovered alive in 1992.

- Barnes (10) noted that the infaunal sea anemone *Edwardsia ivelli*, known only from a single lagoon in Sussex, England, "may...be extinct," as it had not been collected, despite searching, since 1983. However, as Barnes also notes, this is a small anemone of shallow soft mud bottoms, a habitat not

well explored for small invertebrates, and thus it "may well be living, unnoticed, in other localities."

- Edmondson (36) noted that the fiddler crab *Uca minor* was known only from and said to have been collected on the island of Oahu, Hawaiian Islands, in 1826–1827. It has never been found again in Hawaii (nor indeed were any species of fiddler crabs known from the islands). He speculated that it "may have become extinct here." Crane (28) believed the record, based upon the original description, represented mislabeled specimens of the widespread Indo-Pacific fiddler crab *Uca lactea*.

O'Clair & O'Clair (96) noted that the ectoparasitic cyamid amphipod crustacean (whale louse) "*Sirenocyamus rhytinae* was recorded from the Steller's Sea Cow, but that unfortunate marine mammal was driven to extinction in 1768 and its cyamid has not been seen since." No specimens were preserved, and cyamid amphipods are known only from whales and dolphins, and have never (since Steller) been recorded from sirenians. As Leung (73) noted, the species *Cyamus rhytinae* was resurrected by later workers based upon the assumption that a piece of dried skin discovered in St. Petersburg, Russia, was from the sea cow, and that the whale-lice attached to this skin were thus Steller's species. However, the specimens were *Cyamus ovalis*, a species well-known from the right whale *Balaena glacialis*. It was then assumed that the dried skin was that of a right whale. Leung (73) reported that *C. ovalis* is also known from the sperm whale, *Physeter catodon*, suggesting a third possibility for the skin's origin. As some cyamids are not host specific (73), it is possible that the cyamid found on Steller's sea cow was the same as a species found on North Pacific whales; arguing against this is a sirenian being an atypical habitat for a cyamid. Identifying this piece of dried skin by molecular means would thus be of interest.

Marine Fish, Marine Algae, and Marine Seagrass Neoextinctions

Although an increasing number of marine fish and marine plants are recognized as threatened and endangered, no fish, algae, or seagrasses are known to have become globally extinct in historical time. For seaweeds, this may reflect a taxonomic artifact, the difficulty of recognizing when poorly studied and systematically difficult taxa have disappeared.

Taxonomic, Geographic, and Temporal Patterns of Marine Vertebrate Neoextinctions

With only eight marine bird and mammal taxa unquestionably extinct, taxonomic, geographic, and temporal analyses are limited, but nonetheless offer some compelling insights. The eight extinct species represent five orders of mammals and birds, suggesting that extinction is not phylogenetically constrained. Three of the species occurred in the Pacific and five in the Atlantic-Caribbean. No Pacific

marine vertebrate has gone extinct since 1902, but Atlantic extinctions continued to 1952.

Eight extinctions from 1768 to 1952 means an extinction every 23 years. Aside from the first and last (1768 and 1952), these extinctions occurred from 1844 to 1913. A marine bird went extinct approximately every 12 years in the latter half of the nineteenth century and into the first decade of the twentieth century. This period of human history is coincident with rapidly increasing global exploration, colonization, and industrialization, and thus rapidly increasing hunting and habitat destruction. The most recent extinction, that of the West Indies monk seal, occurred in the Caribbean Islands suggesting that in areas with complex geography, it may be more difficult to locate and kill every individual of a larger organism than it is along more open coastlines or on individual islands.

UNDERESTIMATION OF MARINE NEOEXTINCTIONS

The small number of invertebrate and vertebrate marine extinctions recorded to date suggests that the true number may be underestimated. We argue below that this limited record is not due to marine life being relatively immune to extinction.

Two phenomena are primarily responsible for the poor record of marine extinctions in historical time (19): one, the rich pre-twentieth century literature on marine organisms remains largely uninvestigated (see also 20), and two, a decreasing knowledge of marine biodiversity, especially in those coastal waters most susceptible to human-induced destruction and perturbation. The combination makes it difficult to detect losses, even of once-abundant species. Carlton et al (21) demonstrated that the disappearance from the New England shore of a marine snail (a limpet) that was recorded in 1929 as occurring by the thousands on the eelgrass *Zostera marina* had been overlooked for more than 50 years.

Issues in systematics also contribute to overlooking extinctions (19). Sibling species—those that are so similar that they are considered to belong to a single species without corroborating genetic data—abound in the sea (66). The discovery of sibling species within even well-studied genera (e.g., the mussel *Mytilus*, and the snails *Littorina* and *Nucella*) (80, 84, 97; see 66 for additional examples) suggests that many additional widespread species may be complexes of two or more species, with the conservation status of each unknown. Similarly, phylogenetically distinct populations of single species may be seen in the context of conservation biology as evolutionarily significant units (ESUs), each with its own evolutionary trajectory (140). Considered in this manner, local populations may be the appropriate units of concern (90, 139). There is no evidence that many geographically restricted marine sibling species or ESUs have become extinct or are even endangered, but the question has not been systematically addressed. We discuss below examples of the impact of undetected sibling species extinction and the difficulty of recognizing ESUs.

Inadequately described species (especially those not collected since the nineteenth century or earlier and for which no museum material exists) are usually

assumed to be (*a*) completely unrecognizable taxa not assignable to a known species (but which, it is further assumed, could probably be so assigned if the description had been better), or (*b*) barely or questionably recognizable taxa that are placed in the synonymy of extant taxa based upon the best judgment of a systematist.

Extinct populations may have been of undescribed species; as suggested elsewhere in this review, this hypothesis is testable by molecular examination of museum material. The search should be for extinct populations that represented distant, peripheral, or end-of-range records or for extinct populations reported from habitats not typical of the species. As also noted by Carlton (19), undescribed parasites of extinct marine vertebrates and invertebrates can easily be overlooked. If undescribed species may go extinct before being collected or described, there is no way of knowing they ever existed.

We examine the question of extinction underestimation by reviewing the application of species-area relationship theory to coral reefs, a marine environment under global stress, and by reviewing molecular genetic analysis as a means of detecting now-extirpated sibling species and recognizable allopatric populations that, if rendered extinct, would result in genetic loss.

A Model System: Theoretical Estimations of Coral Reef Extinctions

It is possible to estimate species loss based on estimates of species diversity and documented range contraction and habitat loss. That species diversity is predictably related to the area of habitat in both continental and island faunas has been known empirically for over a century, and multiple regression studies in these environments have shown that area alone accounts for most of the variation in species number (30, 76).

Although early studies fitted the curve between species number and area in several ways, the most commonly accepted relationship now is that the logarithm of the number of species (S) is proportional to the logarithm of area (A) plus a constant (c), or $S = cA^z$ (11, 26, 76, 83, 145), where *c* depends upon the taxon, biogeographic region, and population density, and *z* is the rate of increase of species (log S) with area (log A). Of the *z*-values that have been determined empirically for beetles, ants, amphibians, reptiles, breeding birds, land vertebrates, land plants, freshwater diatoms, and crustaceans inhabiting coral heads, most cluster between 0.15 and 0.40 (76, 83, 122, 123, 147, 148). Although the reasons for slight variations in the parameters remain debatable, the fundamental relations between number of species and the area they occupy remains sound.

Particularly for marine environments, which are difficult to monitor for loss of species, the species-area curve can be useful in providing bracketed assessments of the numbers of species that should be present, and, given a documented or projected amount of habitat loss, how many species could go extinct. This approach has been used successfully, in consort with satellite imagery, to identify species loss

associated with the massive destruction of rainforests (38, 147). Except for a few studies (3, 119, 122) however, species-area relationships have received relatively little attention in the oceans, in part because there have been few studies of the number of species present in marine habitats.

The total number of marine species in several major marine environments, with a focus on the number of species on global coral reefs, was estimated by Reaka-Kudla (107) to be about 220,000 described coastal species, of which about 195,000 were tropical. These estimates were based upon an empirically determined total number of described marine species (about 274,000) and the areas of global coastal zones and tropical coastal zones, and employed several empirically based assumptions about the rate of change in species numbers with latitude, coastal versus open ocean environments, and complexity of the habitat. Although estimates of global reef area vary (65, 107, 127), it is likely that for purposes of assessing species diversity, the relevant global reef area is somewhere between 250,000 and 650,000 km^2, and that global coral reefs and reef-associated habitats support about 75,000–95,000 described species (M Reaka, unpublished observations).

Many of these species could be lost if recent estimates of loss of reef habitat are correct. Wilkinson (144) classified the status of the world's coral reefs as "critical" (severely damaged and in imminent threat of extermination if current levels of anthropogenic stress are not reduced), "threatened" (currently show signs of stress and threatened with collapse if stresses continue to increase at current rates), and "stable" (should remain stable unless large-scale anthropogenic processes introduce unforeseen impacts), based upon his own and other monitoring programs. These programs included data on observed or quantified live coral cover, existing populations of fishes and fishing pressure, and pollution and sedimentation near expanding human populations. Wilkinson hypothesized that 10% of global coral reefs already have been degraded beyond recovery, 30% are in a critical state and could be lost in the next 10–20 years, 30% are threatened and could disappear in the next 20–40 years, and another 30% are stable.

Bryant et al (13) mapped locations of human activity (size and density of urban areas, type of land clearing and agriculture, rainfall and watershed topography, ports, oil facilities, mining activities, shipping lanes, destructive fishing practices) and summarized these impacts as four threat factors: coastal development, marine pollution, overexploitation and destructive fishing, and inland pollution and erosion. They mapped the coral reefs where these factors would pose high, medium, or low threats. Reefs were regarded as under "high threat" if they were highly threatened from at least one of the four threat factors, under "medium threat" if they received medium threats from at least one of the four threat factors, and under "low threat" if all four of the threat factors posed a low threat to the reef. Under this categorization, 58% of the world's reefs were considered to be at risk (27% under high and 31% under medium threat); outside of the Pacific, however, these data indicated that 70% of all reefs were at risk. More than 80% of the reefs in both Southeast Asia (56% under high and 26% under medium threat) and the Atlantic (excluding the Caribbean) were considered to be at risk (55% under high and 32% under medium threat). More than 60% of the reefs in the Caribbean were

at risk (29% under high and 32% under medium threat). These figures are relatively consistent with Wilkinson's conclusions.

If one accepts the value that even 5% of the world's reef area has been degraded to a nonreef state, about 1,000 (1.3%) of the described species on global coral reefs would already have become extinct (984–1,200 if the original reefs occupied 2500,000 or 650,000 km^2 and $z = 0.25$; the latter figures are not intended to imply undue precision but simply to show that the calculations are robust relative to the estimated ranges of global reef area). If 30% of the world's reef area were to be lost in the next 10 to 20 years, almost 10% (approximately 6,000–8,000) of the world's described coral reef species could become extinct (M Reaka, unpublished observations).

Since the biota of the oceans is so poorly documented, however, estimates of the actual number of species (described plus undescribed), and their potential loss, on global coral reefs, would be of greater interest. The total number of global coral reef species (known plus unknown) has been estimated from reef area (about 6% that of global rainforests), assuming that coral reefs operate according to similar ecological principles as rainforests (107).

If rainforests contain 2 million species (an undoubtedly conservative number; 38, 147), global reefs would host between 750,000 and 950,000 total (known plus unknown) species (reef area $= 250,000$ to $650,000$ km^2, $z = 0.25$). If 5% of the area of these coral reefs were destroyed, 10,000–12,000 species would become extinct; if 30% of the area of global reefs were degraded to nonfunctional states, reefs could lose 65,000–85,000 of their total (known plus unknown) species. Since emerging consensus favors a figure of about 14–18 million species on Earth, it is reasonable to expect that global rainforests may support as many as 10 million species. Comparable calculations (reef area $= 250,000$–$650,000$ km^2, $z = 0.25$) showed that global reefs then would contain 3–4 million total (known plus unknown) species (M Reaka, unpublished observations). Of these, 50,000–60,000 species could become extinct if only 5% of reef area is destroyed and 300,000–400,000 species would be lost if 30% of the area of global reefs were destroyed (M Reaka, unpublished observation).

Model Systems: Regional Mussel Extinction and Snail Demise in California

Mussels of the genus *Mytilus* are common on intertidal and shallow-water hard bottoms worldwide. Three species comprise a sibling species group: *M. edulis* is native to the North Atlantic Ocean, *M. galloprovincialis* is native in the Mediterranean Sea, and *M. trossulus* is native in the North Pacific Ocean (68, 84). In southern California, *Mytilus galloprovincialis*, introduced from southern Europe, is abundant, and the native *M. trossulus* is rare or absent (84, 117, 129). In contrast, *M. trossulus* is abundant north of San Francisco Bay (84, 117, 129).

Collections and reports of living mussels in southern and central California in the twentieth and nineteenth centuries indicate there have been temporally continuous populations of mussels (18, 60, 64, 78, 111). Thus, the modern domination

of southern California by species thought to have been introduced in the twentieth century (18) suggests that a native species has been replaced. Geller (44) sequenced a portion of the mitochondrial 16S ribosomal RNA gene from dry mussels collected about 1900 from Santa Catalina Island, and in 1871 and 1884 from Monterey Bay. These three lots of mussels are *M. trossulus*, which proves that *M. trossulus* was present south of San Francisco Bay and later temporally overlapped *M. galloprovincialis*. This case illustrates how unrecognized species differences can obscure the regional extirpation of a member of a sibling species complex. It is not difficult to imagine the extinction of such a sibling species with a geographic distribution more restricted than in this example.

Could the decline of *M. trossulus* in southern California be a direct consequence of the invasion of *M. galloprovincialis*? Circumstantial evidence suggests interspecific competition as a contributing role: Environmental conditions in southern California may favor growth of *M. galloprovincialis* compared to *M. trossulus* (117). *Mytilus galloprovincialis* smothers another native mussel, *M. californianus*, in wave-protected areas in southern California (51, studying *M. galloprovincialis* under the name of *M. edulis*) and may exhibit similar behavior in patches of *M. trossulus*. *Mytilus galloprovincialis* is also a strong competitor in Europe, where it overlaps with *M. edulis*, having lower rates of predation by predatory snails, lower incidence of parasite infections, higher strength of attachment, and lower mortality rates (29, 42, 124, 146). In South Africa, invading *M. galloprovincialis* outcompetes a native mussel (*Aulacomya ater*) by overgrowth (54).

Cerithidea californica is a potamid mudsnail that is abundant on tidal flats in southern California. Populations also are known in northern California in San Francisco Bay, Bolinas Lagoon, Drake's Estero, and Tomales Bay, in marginal habitat at the upper fringes of salt marshes (17, 104, 105; J Byers, personal communication, JB Geller and JT Carlton, personal observation). Competition or egg-predation by invading snails (the Atlantic nassariid mudsnail *Ilyanassa obsoleta* and the Japanese potamid mudsnail *Batillaria attramentaria*) have had demonstrable impacts on the northern populations (104, 105; J Byers, personal communication). The northernmost population of *Cerithidea californica* known in the Eastern Pacific Ocean occurred in Bodega Harbor, 96 km north of San Francisco but went extinct in the late 1960s due to destruction of salt marsh habitat (17).

Emerging from these observations is a picture of large, robust populations in southern California and severely reduced and marginalized populations in northern California. Petryk (103) observed three mitochondrial haplotypes in a sample of 64 snails from southern California, in San Diego Bay, while only one haplotype (also found in San Diego) in a sample of 55 snails from Tomales Bay and San Francisco Bay. *Cerithidea* has no planktonic larva, and thus Petryk (103) concluded that gene flow between these two populations was absent or very low. Indeed, northern populations were once described as a separate species, *Cerithidea sacrata*, although the validity of the northern species is not widely recognized (1, but see 131). Regardless, Petryk's (103) work suggests that northern and southern

populations are isolated. The smaller northern populations may thus be considered as a unit of conservation concern or as an ESU, pending the recognition of diagnostic characters.

THE SUSCEPTIBILITY OF MARINE ORGANISMS TO EXTINCTION

Numerous workers have reviewed geological, ecological, and biological attributes that make species susceptible to extinction (19, 39, 53, 71, 85, 106, 109, 135–137). Carlton (19) argued that restricted geographic distribution, restricted habitat, and limited dispersal abilities may prove to be major factors that render marine invertebrates most prone to extinction. Vermeij (138) and Norse (93) noted that marine vertebrate species with both small and large aboriginal ranges have become extinct, although complicating this interpretation is the difficulty in distinguishing three types of ranges among extinct animals: the breeding range, the range occupied by adults throughout their lifetime, and the vagrant range.

The eelgrass limpet of the Northwestern Atlantic Ocean disappeared after most of its habitat, the eelgrass *Zostera marina*, was lost to disease (21). The invertebrates that have likely disappeared from southern California and Florida were largely taxa linked to shallow embayments that are easily destroyed by human activities. In reviewing the probable demise of the apparently endemic seahare *Phyllaplysia smaragda* in a Florida lagoon, Clark (24) noted that "reconnection of mosquito impoundments may have increased nutrient levels and decreased oxygen levels." This seahare fed on epiphytic algae growing at the base of the seagrass *Syringodium*. High densities of drift algae apparently excluded the epiphytes; in addition, the slugs' egg masses were deposited near the grass bases, and the lowered oxygen levels (a result of releasing impounded marsh peat) may have lowered the reproductive success of the slugs.

Human predation (for food, traditional medicines, the aquarium trade, decoration, or other reasons) on marine mammals, fish, invertebrates, and algae can be overwhelming. In speculating about the extinction of Steller's Sea Cow, Anderson (5) has argued that human predation on one species could lead to a cascading effect that could lead to the extinction of another species. Anderson notes that human extirpation of sea otters along the Arctic and Pacific coasts of America would have resulted in increasing populations of sea urchins in shallow water, leading, in turn, to the disappearance of nontoxic seaweeds and their replacement (from deeper waters) by phenolic-rich species. Anderson suggests that if the sea cows evolved in shallow waters, in the presence of large sea otter populations and eating nontoxic seaweeds, their foraging grounds may have been destroyed by such algal replacements mediated by sea otter reductions. This, Anderson argues, could explain the early demise of sea cows from the mainland (where aboriginal hunters would have reduced otter populations) and their isolation by the eighteenth century to uninhabited offshore islands. Discovery by eighteenth

century ship-borne hunters was the final blow to the reduced populations of the sea cow.

Few such complex relationships have been suggested in modern marine extinctions. Direct human hunting has severely affected edible species (9, 93, 99, 115, 116), and may imply that the twentyfirst century will witness vastly increased extinction rates. The number of species of marine mammals, turtles, and fish (7, 93, 116) that are now severely depressed appears to be unprecedented in human history. We review two case histories that illustrate how widespread marine organisms can quickly near extinction.

An Abundant Subtidal Mollusk Becomes Rare

The white abalone, *Haliotis sorenseni*, is a large herbivorous gastropod that ranged from Point Conception, California, to Isla Asuncion, central Baja California (86). White abalones occur mainly on low-relief rocky reefs at 26–65 m (31), deeper than the other seven Northeast Pacific species of *Haliotis*. Their populations were therefore largely ignored until other shallow-water species became rare from over-exploitation.

A fishery for white abalone began around 1965 and collapsed after 1977 (31, 132). When Tutschulte (134) surveyed the Channel Islands in southern California in the early 1970s after heavy commercial fishing had begun, white abalone population density averaged 10,000 per hectare ($1/m^2$). By 1980–1981, the density had dropped three orders of magnitude, to $0.0021/m^2$, and by yet another order of magnitude to $0.0002/m^2$ in 1992–1993 (31). Surveys in 1996–1997 at greater depths using a research submarine showed densities of about 1 per hectare in suitable habitat; there thus appears to be no relict white abalone populations in the deeper part of its range (G Davis, personal communication, 1998). There appear to be no other factors contributing significantly to the population decline during this period, and there is evidence that white abalone populations in Mexico have declined in parallel (31, 132). If population densities in the historic population center of this species, California's Channel Islands, are typical of the entire range, only 500–600 white abalone exist today.

White abalone can spawn as many as 10–15 million eggs and have planktonic dispersal, attributes that suggest that it would be difficult to render this marine snail extinct by overfishing. The last recruitment event of the white abalone occurred in the late 1960s, at the beginning of the most intensive eight years of the fishery (31). Sporadic recruitment might have been more than sufficient to sustain this species if the fishery had not reduced population densities by three to four orders of magnitude in prime habitat. As population density fell far below $1/m^2$, it became impossible for fertilization to occur, resulting in complete reproductive failure (31, 132). Many marine invertebrates are broadcast spawners, and when their population densities decline beyond a certain threshold, fertilization and recruitment fall sharply, a positive feedback mechanism called the Allee Effect that leads to extinction.

Trawling the Sea Floor and the Near-Extinction of the Barn Door Skate

A large proportion of the world's fish catch comes from continental shelves (114, 116). Fishing methods such as dynamite fishing, muro ami, poisoning, and use of mobile fishing gear such as otter trawls, beam trawls, scallop dredges, clam dredges, and St. Andrews' crosses are harmful because, in addition to killing target species and those incidentally brought on deck (bykill), they severely disturb the seabed and organisms that provide food and hiding places (33, 142).

Dragging (trawling and dredging) has a long history on smooth, shallow bottoms near industrialized nations, but with technological advances, such as diesel engines on fishing boats (in the 1920s) (74) it has spread. Dragging extended into continental slope waters as deep as 2000 m (88) as more continental shelf species were overfished. Starting in the 1980s, the widening use of roller, rockhopper, and streetsweeper gear, global positioning systems, precision depth finders, and more powerful engines led to dragging over rough and steep bottoms. By the end of the twentieth century, mobile fishing gear can be used on any bottom type on the continental shelf, upper continental slope, and seamounts from subpolar to tropical waters, penetrating ecosystems that had once served as de facto marine refuges. The effects of mobile gear on seabed biota resemble those of clearcutting in forests, removing the complex structures that are hiding and feeding places for many species (142).

Bottom trawling affects a greater area than any other benthic disturbance: Watling & Norse (142) estimated that an area equivalent to 14.8×10^6 km^2 is trawled annually. Worldwide, an area equaling the world's continental shelf is trawled every two years. Trawling effort is uneven; some spots are hit repeatedly, while others are missed randomly or because they are uneconomical to fish. For longer-lived species, repeated removal and physical disturbance on so large a scale can make extinction all but inevitable. The long-lived, large (1.5 m long) barndoor skate (*Raja laevis*), a Northwest Atlantic shelf-dwelling fish that was once common in trawl bykill (12), is now nearing extinction (22). Risk et al (112), Butler (41), and Fuller & Cameron (14) included anecdotal accounts that dragging is eliminating very long-lived cold-water shelf-dwelling gorgonian corals (*Primnoa* spp. and others). Large skates and five-meter tall corals are among the most conspicuous benthic species, and their loss would be noticed long before small bryozoans, amphipods, or polychaetes were missed. As in tropical forests, the disappearance of the most observable species is likely a strong indication of greater extinction.

CONCLUSIONS

That the sea is not immune to extinctions is demonstrated by the ubiquitousness of paleoextinctions and neoextinctions in the sea (4, 39, 57, 58, 106, 128, 138). That marine organisms are "immune" to extinction because of some perceived attributes

of a combination of having widespread populations, dispersal by ocean currents, or refugia from human predation is no longer a tenable position. Hudson (56) noted the "widespread and ingrained belief that some fishes are inherently resilient to extinction and will not disappear, however hard they are fished."

The unsurprising fact that more extinctions are not yet documented is a result of a number of factors. Few scientists work on marine extinction issues: data production on extinctions may be proportional to the number of investigators. As with the once abundant and widespread eelgrass limpet, the extinction of which went unremarked for more than five decades, the fact that these extinctions have not been documented is not evidence that they are not occurring.

The world ocean, covering 361×10^6 km^2 to an average depth of nearly 4 kilometers, constitutes more than 99% of the biosphere permanently inhabited by animals and plants (94). That most marine biota is not seen contributes to the belief that life in this vastness may be extinction-proof. In contrast, forests and woodlands cover 38×10^6 km^2 (102), or 7.5% of the Earth's surface. Because these terrestrial ecosystems are imperiled and are the best-studied wildlife habitat, much of the concern about biodiversity and habitat fragmentation (34, 133) came from studies in forests. Forest species are vulnerable, in part, because forest area is so limited that humans can eliminate, fragment, or simplify a very large proportion of it, eliminating species found only in forests and dramatically increasing extinction probabilities for species in forest remnants. It seems reasonable to assume that the sea's extent makes it less vulnerable than forests. However, the most productive marine ecosystems, hence the ones most heavily impacted by humans—the world's continental shelves—cover 28×10^6 km^2 (120), less than the area covered by forests. The most charismatic marine ecosystems, including coral reefs, kelp forests, seagrass beds, and mangrove forests, constitute a very small portion of the sea. Coral reefs, which are considered the marine equivalents of tropical forests, occupy only 0.6×10^6 km^2, or 0.1%, of the Earth's surface (107), a small fraction of the 12×10^6 km^2 of closed tropical forests (102). Widespread concern about the prospect of millions of extinctions in forests comes from calculations of how island biogeographic considerations of forest loss would affect numbers of species that forests could sustain (75), and we thus have reviewed above how comparable calculations might affect a portion of the sea.

In the two decades since Myers (91), Lovejoy (75), and Norse & McManus (95) announced that the loss of biological diversity is occurring on a scale without precedent in the last 65 million years, most concern about elimination of genetic, species, and ecosystem diversity has focused on the terrestrial realm. It is now clear that marine ecosystems are at equal risk, and that those marine ecosystems that receive the most sustained and unrelenting pressure from human activities—estuaries, coral reefs, intertidal shores, and continental shelves and slopes—are now at very serious risk (15). As the world human population grows and world marine populations decline, relying on a vast and deep ocean to be forever resilient will result in an ocean that in the twentyfirst century will see more extinctions than in all of human history.

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