

Neoextinctions of Marine Invertebrates¹

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SYNOPSIS. Historical or recent extinctions (here called neoextinctions) are rarely reported among marine and estuarine invertebrates. Four case histories of neoextinctions, using gastropod mollusks (snails) as examples, are reviewed: the periwinkle *Littoraria flammea* (last collected < 1840 in China), the rocky shore limpet “*Collisella*” *edmitchelli* (1861/3 in southern California), the eelgrass limpet *Lottia alveus* (1929 in Maine), and the marsh horn snail *Cerithidea fuscata* (1935, southern California) are all probably extinct. The central element in the demise of all four species may have been a vulnerable, extinguishable habitat. Three considerations suggest that neoextinctions among marine invertebrates have been generally overlooked: 1), hundreds of taxa have not been reported since the 18th and 19th centuries (these are treated by systematists as either unrecognizable, rare, or synonyms of known species); 2), species may have become extinct prior to their description; and 3), there has been a precipitous decline in systematics, biogeography, and natural history at the end of the 20th century—leaving too few workers to tell the story of neoextinction in the ocean. Searches in the literature and museums for overlooked neoextinctions would fruitfully focus on species reported from highly impacted, urbanized coastal habitats—saltmarshes, estuaries, lagoons, seagrass communities, and supralittoral (maritime) zones—habitats now largely obliterated on most coastal margins of the world.

“Monterey [California] as a collecting ground is already greatly injured, and will probably be nearly ruined before long, on account of the Hotel del Monte, the new town of Pacific Grove and the increased population of old Monterey, all the sewage of which is turned into the bay in front of the town. Beaches which formerly would afford several hundred species are now nearly bare, or offensive with stinking black mud. Old collectors will learn this with regret.”

—William Healey Dall, 1892

“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, 1988

INTRODUCTION

Modern day extinctions appear to be rare among marine and estuarine invertebrates. In this essay I refer to Recent (Holocene, historical, contemporary, modern-day) extinctions as neoextinctions, as opposed to paleoextinctions (pre-Holocene, geological, prehistoric extinctions). I review here, using shelled gastropods (snails) as examples, four cases of known or possible neoextinctions and I explore the reasons why we know so little about neoextinctions in the ocean. The following discussion is restricted to processes in shallow shelf (neritic) waters.

CASE HISTORIES OF MARINE INVERTEBRATE NEOEXTINCTIONS

The International Union for Conservation of Nature and Natural Resources (IUCN) and the Convention on the International Trade in Endangered Species

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TABLE 1. *Known or possible neoextinctions of marine mollusks.*

Species	Last known collection	Last known location	Total known range
<i>Lottia alveus</i> Atlantic Eelgrass Limpet	1929	Maine: Mt. Desert Island	Labrador–New York
“ <i>Collisella</i> ” <i>edmitchelli</i> Rocky Shore Limpet	1861/1863	California: San Pedro	San Nicolas Island (Pleistocene); San Pedro (Recent)
<i>Littoraria flammea</i> Periwinkle	<1840s ?	“China”	“China”
<i>Cerithidea fuscata</i> Horn Snail	1935	California: San Diego Bay	San Diego Bay

(CITES) definition of extinct—“species not definitely located in the wild during the past 50 years”—(McNeely *et al.*, 1990) is applied with great difficulty to marine invertebrates. While no review is available, there may be hundreds of “species” of marine invertebrates that have not been recorded since the 18th and 19th centuries. It is thus difficult to isolate distinctive cases of possible neoextinctions from this potentially vast field of candidates. As *examples* of such neoextinctions, I consider here four case histories of marine shelled gastropods from the Atlantic and Pacific Oceans (Table 1).

Atlantic eelgrass limpet *Lottia alveus alveus*

The small (12 mm long) marine limpet *Lottia alveus alveus* (Conrad, 1831) (= *Acmaea alveus*, = *Collisella alveus*) was known from Labrador to Long Island Sound, living only upon the narrow blades of the eelgrass *Zostera marina* (Carlton *et al.*, 1991; Vermeij, 1992). Nineteenth and early 20th century accounts record the Atlantic eelgrass limpet as abundant. Canadian naturalists noted that it was “very abundant on eel-grass at low water” at Grand Manan Island in the Bay of Fundy in 1890. In 1910 in the Boston region it was noted that “in certain places hundreds may be collected in a short time,” while in 1929 at Mt. Desert Island, Maine, William Proctor found “thousands of individuals readily accessible” at low tide (Carlton *et al.*, 1991). A search of museum collections, and field work from 1965 to 1990 from Labrador to New York, have revealed no further verified specimens since 1929. The conclusion is that this limpet is extinct in the North Atlantic Ocean (Carlton *et al.*, 1991).

Reconstruction of the limpet’s biology, as with all extinctions, is burdened with limitations. Nevertheless, it appears that, based upon the morphology of radulae recovered from museum material, *L. alveus* was a trophic specialist, feeding only upon the epithelial cells of the eelgrass (rather than upon diatoms or other epiphytes). Locality data and associated fauna indicate that the eelgrass limpet was likely restricted to fully marine waters. All other members of the genus *Lottia* have planktotrophic larvae (Carlton *et al.*, 1991); perhaps *L. alveus* had larvae which sought out and settled only upon eelgrass.

What happened? In the three year period between 1930 and 1933, approximately 90 percent of the eelgrass disappeared from the coastal waters of the Northwest Atlantic Ocean due to “wasting disease” (Short *et al.*, 1987, 1988). The slime mold *Labyrinthula zosterae* was identified as the causative agent in this disease (Muehlstein *et al.*, 1988, 1991). This eelgrass decline led to extensive reductions in migratory waterfowl populations and loss of commercial bay scallop fisheries.

Eelgrass lives in both marine and brackish water, while the slime mold appears to be restricted to marine, fully salt waters. Refugial eelgrass populations thus survived in low-salinity waters. This brackish water refugium was apparently outside of the limpet’s physiological range. It is of interest to note that there is another northwest Atlantic eelgrass specialist, the small sea slug *Elysia catulus*—a sacoglossan opisthobranch occurring in salinities as low as 17‰ if not lower. This slug did not become extinct.

Two subspecies of *L. alveus*, or perhaps distinct species, remain alive (as far as is known) in the North Pacific Ocean—one on

Sakhalin Island, Russia (but perhaps more widespread) and one in southern Alaska and northern British Columbia (Carlton *et al.*, 1991). If these two taxa are counted as part of the genetic remains of the *L. alveus* stock, then the demise of the Atlantic eelgrass limpet is an ocean basin, but not a global extinction. The decline of the eelgrass and thus the disappearance of the limpet do not appear to be linked to any human activity—unless the slime mold *Labyrinthula zosterae* was introduced by ships to the American Atlantic coast from Europe. While ships could have ballasted up infected eelgrass blades in Europe and released them in the United States, there were wasting diseases and mold-caused blights well back into the 19th century on aperiodic bases, but none apparently as extensive as the blight of 1930.

Rocky shore limpet “*Collisella*” *edmitchelli*

The rocky, mid-intertidal limpet “*Collisella*” *edmitchelli* (Lipps, 1966) was abundant in the late Pleistocene on what is now San Nicolas Island in southern California (Lindberg, 1984). The fossil terraces in which this limpet has been found are between $770,000 \pm 100,000$ years and $400,000 \pm 100,000$ years old (Lindberg, 1984). In 1983, David Lindberg discovered a museum specimen of this limpet (22 mm long), collected in either 1861 or 1863 on the southern Californian mainland shore at San Pedro, near Los Angeles. Dried mantle tissue on the muscle scar of this specimen indicates that it was alive when collected. Previous to this discovery, “*C.*” *edmitchelli* was the only limpet present in the Pleistocene of California that had not been found in the Holocene fauna.

As with two of the other species treated here, “*Collisella*” *edmitchelli* is not without its own modestly complex taxonomic history. Described as a Pleistocene species relatively late (Lipps, 1963, as *Acmaea mitchelli*), it was synonymized with “*Collisella*” *scabra* (Gould, 1846), another rocky shore limpet (Marincovich, 1976), but soon resurrected by Lindberg (1978). Had it not been for Lindberg’s recovery of this taxon, the existence of the single Recent specimen would have gone unnoticed. “*Collisella*” *edmitchelli* is closed related to “*Collisella*” *scabra* (Lindberg, 1978) and as such is a

member of the limpet family Nacellidae, rather than the Lottiidae, in which the genus *Collisella* resides. Both limpets belong to an undescribed genus, whose name, *Macclintockia*, was published by Kozloff (1987), but whose formal description awaits publication (D. Lindberg, personal communication, 1993).

The intertidal limpets of California have been extremely well collected for over 100 years (Grant and Gale, 1931; McLean, 1966; Lindberg, 1981). The San Pedro region itself was the subject of particularly intensive collecting at the end of the 19th century (Williamson, 1892; Monks, 1893)—a period of time when it is conceivable that remnant populations of this limpet could have persisted prior to the obliteration in the 20th century (Wicksten, 1984) of much of what remained of the natural shoreline. It is thus highly unlikely that any populations of this species remain extant and have been overlooked. The largest Pacific coast museums and the Smithsonian Institution contain no further Recent specimens of this species (Lindberg, 1984; D. Lindberg, personal communication, 1993), holdings that would reflect the field work of most of the prominent 19th century collectors. The absence of collections of “*Collisella*” *edmitchelli* after the 1860s suggests that the populations of this species that persisted into the mid 19th century were eliminated by the vast alterations of the California coastal zone that accompanied the rapidly increasing human population at that time (see prefatory quotation from Dall [1892], above). Chace (1917), for example, noted that the California cowry (gastropod) *Cypraea spadicea* “Years ago . . . was quite common at this point [in San Pedro], but continued collecting has nearly exterminated it,” while Burch (1943) noted the decline or disappearance of a number of species in San Pedro Bay due to human activities.

Although our modern understanding of this species is based upon only one specimen, I conclude that “*Collisella*” *edmitchelli* should be added to the list of marine invertebrate neoextinctions.

Periwinkle *Littoraria flammaea*

The periwinkle *Littoraria flammaea* (Philippi, 1847) was described from “China,”

with no more specific locality information (Reid, 1986). *Littoraria flammea* "is very rare in museum collections: all material seen dates from the early nineteenth century" (Reid, 1986). Reid (1986, p. 182) speculates that the species may occur on the shores of the East China Sea or the Yellow Sea, although the mollusks of the Chinese coast are generally well known, and it would appear unlikely that a snail of this size (16–20 mm) would be overlooked. As with two of the other snails considered here, coastal zone changes may have led to the demise of this species.

The habitat of this species is unknown. However, other members of the subgenus *Palustorina*, to which *L. flammea* belongs, live on mangroves or rocks. Reid (1986, p. 51) notes that littorinids from mangroves have distinctly different radular length : shell height ratios from littorinids living upon rocky shores. A potential indication of this species' habitat (and thus a target habitat for searching) could be obtained if dried tissue (and radulae) of the snail could be rehydrated from museum shells (present in the British Museum (Natural History), London and the Museum National d'Histoire Naturelle, Paris) and examined.

I conclude that this species should be added to the list of *possible* marine invertebrate neoextinctions.

Horn Snail Cerithidea fuscata
Gould in Gould and Carpenter, 1857

S. Stillman Berry's description in 1906 of the mudflat horn snail *Cerithidea sacrata hyporhyssa* (later to be recognized as a junior synonym of Gould's 1857 name, above) from San Diego Bay, California brought this taxon to the attention of shell collectors. A Gordian taxonomic history attends this snail. *Cerithidea sacrata* (Gould, 1849) was long considered (Bequaert, 1942) a junior synonym of *Cerithidea californica* (Halde- man, 1840). Berry's snail is thus more frequently referred to as *Cerithidea californica hyporhyssa*.

The specific status of *C. c. hyporhyssa*, as distinct from the stem species, has remained in doubt for many years (Grant and Gale, 1931; Bequaert, 1942; Burch, 1945), a situation reminiscent of the fate of the eelgrass

limpet *Lottia alveus*, whose failure to be recognized as a taxon distinct from *Tectura testudinalis* on the Atlantic coast was one of the reasons for a delay in its recognition as extinct (Carlton *et al.*, 1991). Berry (1906) noted that *C. c. hyporhyssa* was "smooth, or nearly so, and more tapering. It is quite heavy and solid, and in my specimens the callus of the aperture is of a lighter and browner tint than is usual, and the aperture is smaller and less inflated."

Berry (1906) believed *C. c. hyporhyssa* intergraded with *C. californica*, a comment that Bequaert (1942) paraphrases. Grant and Gale (1931) stated that *C. c. hyporhyssa* is "an individual variant or a pathologic form with very subdued sculpture and a higher spire. It is not a valid variety." Bequaert (1942) noted that *C. c. hyporhyssa* was "no more than an ecological form, characterized by the smooth or nearly smooth, flat whorls." Chace and Chace (1967) commented that *C. c. hyporhyssa* was "now considered only an ecologic form that was caused by factory waste contaminating the intertidal mudflats at that point" (the *C. c. hyporhyssa* morphology is, however, recognized in the Pleistocene of the San Diego region; D. Taylor, personal communication, 1973).

Burch (1945) noted that "This variety is generally ignored and placed in the synonymy [of *C. californica*]. However, it is a smooth form and I have collected thousands of them from San Diego Bay and they seem to be at least a different race of the species. I have never seen the same thing from any other locality . . . in any event they are not worn smooth. They are simply different. We have been discussing distinct species that differ less from others than this does in my opinion." Chace (1945), basing his remarks on material collected in 1914–1915, stated that "some shells . . . have very flat whorls and an almost straight line from apex to aperture, and do not have an eroded appearance. Other shells from the same collecting (*sic*) have rounded whorls and an eroded appearance. All are more slender than the usual form—*C. californica*."

In a checklist of the fresh and brackish water mollusks of California, Taylor (1981) presented a revision of the California *Ceri-*

thidea. He recognized three taxa: the northern *Cerithidea californica sacrata* (San Francisco Bay and north), the southern *Cerithidea californica californica* (Morro Bay and south), and *Cerithidea fuscata* (San Diego Bay only), the latter a senior synonym (according to Taylor) of *Cerithidea sacrata hyporhyssa*. The northern and southern populations of *Cerithidea californica* had previously not been recognized as taxonomically distinct, although the two subspecies (or species?) are readily separated and show no morphological intergradation (D. W. Taylor, personal communication, 1973). Taylor also newly recognized *Cerithidea fuscata* as a distinct taxon, although it had previously been treated as a strict synonym of *Cerithidea californica* (and had not been recognized as a prior name for Berry's *C. c. hyporhyssa*). Taylor provided no further details relative to this trichotomous splitting of the California *Cerithidea*.

Cerithidea fuscata has a smooth, slender, turritelliform shell with no axial ribs and with a few weak varices (Berry, 1906, ink drawing; Johnson and Snook, 1927, figure 581; Johnson, 1964, plate 11, figure 6). *Cerithidea californica* has numerous prominent axial ribs, also with weak varices (Abbott, 1974, figure 987; McLean, 1978, figure 16.1). Both *C. fuscata* and *C. californica* can exceed 45 mm in height. Despite Berry's (1906) remarks, there appears to be no evidence of intergradual forms between *C. fuscata* and *C. californica*.

Burch (1945) noted that *Cerithidea fuscata* (as "*C. c. hyporhyssa*") was restricted to the inner and southern portions of San Diego Bay ("south of Coronada and south of National City"). Taylor (1981) indicated that it occurred in "Eastern San Diego Bay" and was "narrowly localized." Both observations suggest an aboriginally limited distribution within the bay. Berry's (1906) and Chace's (1945) remarks suggest that *fuscata* may have co-occurred with *californica*, or at least the two species were in the same general regions of the bay (perhaps with microhabitat differences, similar to the middle intertidal populations of *Cerithidea albonodosa* [referred to by Taylor (1981) as *C. californica albonodosa*] versus the higher intertidal populations of *Cerithidea mazat-*

lanica described by Berry [1956] in the Gulf of California [see also Keen, 1971, page 419]).

Taylor (1981) noted that "no precise details" of the habitat of *Cerithidea fuscata* were recorded, but that it "presumably (occurred) on intertidal mudflats or in *Salicornia* marshes." Taylor states that *C. fuscata* was last collected in 1935 (presumably based upon examination of museum material), that "threats" to it were "pollution, dredging, and land fill" and, finally, that it is "possibly extinct."

Whether these three species are distinct taxa is potentially resolvable by molecular genetic studies (dried tissue of *C. fuscata* is presumably recoverable from specimens located in southern California museums). Based upon the characteristic morphology of *Cerithidea fuscata* and upon Taylor's species-level recognition of this taxon, I tentatively regard this snail as a distinct species. Genetic studies testing Taylor's hypotheses are planned (J. Geller, University of North Carolina, personal communication, 1993). It is possible that a distinct species of *Cerithidea* evolved from the stem species in Tertiary embayments of California, with a relict population persisting into the Holocene (similar to the persistence of the limpet "*Collisella*" *edmitchelli* into the southern California Holocene).

The San Diego Bay region has undergone vast changes (Emerson, 1970; Zedler, 1982; Carlton, 1979) and little remains of the original littoral environment. The extermination by human activity of a mid- to high-intertidal mollusk restricted to San Diego Bay is a probable scenario. Carlton (1976) noted that once-widespread populations of *Cerithidea californica* in San Francisco Bay had been severely restricted by the marginal filling of the bay. Museum material indicates, for example, that *Cerithidea californica* was abundant in Richardson Bay (a northwestern inlet of San Francisco Bay), at sites that are now landfill and roads. *Cerithidea* is extinct in all northern San Francisco Bay localities (J. T. Carlton, personal observations). Carlton (1976) also demonstrated that *Cerithidea* is susceptible to complete extinction within a bay. *Cerithidea californica* formerly occurred in Bodega

Harbor (Sonoma County), California (Bodega Harbor is shown on older maps as Bodega Lagoon; it is distinct from the outer Bodega Bay). While no museum material exists, the species occurred there commonly, in high intertidal pools among *Salicornia*, on June 6, 1944 ("D-Day"; R. Stohler, personal communication, 1974). The marsh site in the Harbor where *Cerithidea* occurred was destroyed about 1963 during road construction. *Cerithidea* is now extinct in the Harbor. The same site appears to have been the location of a clay bank in which the northernmost population of the scaled piddock *Parapholas californica* (Conrad, 1837) also occurred (Abbott, 1974, as "Bodega Lagoon"; McLean, 1978, as "Bodega Bay"). *Parapholas* is also now extinct in Bodega Harbor (J. T. Carlton and J. Standing, personal observations).

Cerithidea fuscata appears to have been restricted to a portion of San Diego Bay, and those shores have largely been destroyed. Based upon the reported absence of this species since 1935, its apparent absence from any other embayment, and the demonstrated ability of *Cerithidea* populations to be exterminated either entirely from embayments or within large portions of a bay, I conclude that *Cerithidea fuscata* is a neoextinction.

DISCUSSION

The identification of four known or possible neoextinctions among marine mollusks raises the question of additional neoextinctions among other invertebrate groups. It is no surprise that the only confirmed neoextinctions are among the shelled snails—by far the best known marine invertebrates in taxonomic and geographic terms. No other marine invertebrates have been reported as demonstrably extinct (Carlton *et al.*, 1991), despite the thousands of potential candidate species of other mollusks, crustaceans, annelids, flatworms, and other invertebrates in the same habitats from which the snails discussed here have disappeared.

In 1968 the American Malacological Union held a symposium on "Rare and Endangered Mollusks of North America." Keen (1970) considered the then-perceived

endangered status of the American Pacific coast saltmarsh snail *Algamorda newcomiana* (now known as *Littorina subrotundata* [see Taylor, 1981]), but the species is now recognized as widespread and relatively abundant throughout the Pacific Northwest (MacDonald, 1969; Berman and Carlton, 1991). Carlton *et al.* (1991) have earlier commented upon the status of Morrison's (1970) purported brackish water hydrobiid snail extinctions on the American Atlantic coast. Abbott (1970) concluded that no marine mollusks were in danger of extinction due to human activities, while Rosewater (1970) suggested that mollusk extinctions are "probably largely undetected." Wells *et al.* (1983) considered a wide variety of marine invertebrates as vulnerable, rare, or insufficiently known to be classified, but found none to be extinct or endangered (see Carlton *et al.* [1991] relative to their treatment of the nudibranch *Doridella obscura*). A tropical Pacific Panamic hydrocoral, *Millepora boschmai*, reported as extinct by Glynn and de Weerd (1991) has been discovered alive (Glynn and Feingold, 1992).

There remain two major possibilities: either there have been more neoextinctions and we have overlooked them, or there have not been many more neoextinctions.

There is perhaps a general belief among many marine ecologists and biogeographers that there have *not* been many neoextinctions, especially due to human perturbations, of marine invertebrates in the oceans. There is a certain sense of invulnerability of ocean life (particularly invertebrates, fish, and seaweeds) to extinctions that has pervaded the sciences for centuries. As Gould (1991) noted, Lamarck, in chapter 3 of his *Philosophie Zoologique*, wrote in 1809,

Animals living in the waters, especially the sea waters . . . are protected from the destruction of their species by man. Their multiplication is so rapid and their means of evading pursuit or traps are so great, that there is no likelihood of his being able to destroy the entire species of any of these animals.

Carlton *et al.* (1991) concluded that the eelgrass-dwelling and -eating *Lottia alveus* became extinct because of its stenotopic

habitat (which proved to be susceptible to destruction), physiological tolerances narrower than its host plant (which, when eliminated in part of its ecological range by a fungal disease, survived in low salinities), and by its limited geographic range. They further argued that "The fact that most marine invertebrates have large effective population sizes, often over broad ranges, may account . . . for their relative invulnerability to extinction in historical time. In contrast, small and geographically restricted populations of species (short-range endemics, for example) may be particularly vulnerable to extinction."

The demise of the limpet "*Collisella*" *edmittchelli* and the horn snail *Cerithidea fuscata*, both presumably due to human activity, appears to be directly related to their restricted ranges and extinguishable habitats, within which complete extermination was possible. In turn, both of these species may have been Pleistocene relicts in San Pedro Bay and San Diego Bay, respectively.

Vermeij (1993) reviewed the biogeographic patterns of neoextinctions in six strictly marine birds, two strictly marine mammals, and two marine invertebrates, the limpet *Lottia alveus* (Carlton *et al.*, 1991) and the hydrocoral *Millepora boschmai* (Glynn and de Weerdt, 1991); the latter, as noted above, has since been discovered alive. Vermeij divided these species into two groups: those of broad ranges (defined as encompassing two or more marine biogeographical provinces) and those of narrow ranges (defined as encompassing one biogeographical province). Based upon these definitions, *Lottia alveus* is a species having a "broad" range. Vermeij concluded that species with large ranges are susceptible to extinction, "contrary to the prevailing view that extinction is usually associated with a small range." *Lottia alveus* occurred in the boreal northwestern Atlantic Province (Labrador to Cape Cod), but as with a number of colder water western North Atlantic species, owed its presence south of Cape Cod to populations that barely entered the Virginian Province, that is, to populations in Long Island Sound.

Species that predominately occur in one

province but "slip over" to a second are perhaps best treated as a single province species, or treated in a separate, distinct category. Setting marine vertebrates aside, the data are too limited (even with the inclusion of the two new gastropod neoextinctions recognized here) to conclude whether narrow- or broad-ranged invertebrates are differentially, or equally, susceptible to extinction.

A sense of the invulnerable nature of marine invertebrates arises from the observation that thousands of species of marine invertebrates (and fish and algae) have very large ranges extending along thousands of kilometers of coastline. Many species often also occur over a wide variety of bottom types, and most have planktonic dispersal stages. Common examples in the northern hemisphere would be species occurring from Alaska to Mexico, from Sakhalin Island to China, from Nova Scotia to Florida, and from Scandinavia to Spain. Here a working assumption is that nothing short of ocean-wide alterations can eliminate species in these broad regions, although there is little argument that populations can be decimated (local, or ecological, extinction). In turn, one conclusion is thus that centuries of such decimation (directly by fishing or indirectly by habitat destruction) of invertebrate populations in coastal habitats appear to have consistently *not* lead to species-level extinctions. Coastal destruction and overharvesting have led to scores of documented cases of extinct populations of marine invertebrates (Wells *et al.*, 1983)—and thus, no doubt, some loss of genetic diversity (genetic extinction). Extermination and decimation of individual populations of species are so universal, and so ancient at the hands of human endeavor, however, that it is easier to focus on the ultimate (as Pimm [1991] has remarked, "nothing concentrates the mind quite like extinctions do"). Further, it may be argued that if many neoextinctions have been occurring, the two groups of marine invertebrates best known taxonomically and geographically—mollusks and decapod crustaceans (that is, the crabs, shrimps and lobsters) would be the best "indicator" taxa. Such groups are not necessarily more sus-

ceptible to the causative agents of destruction and extinction of marine organisms (as listed, for example, by Wells *et al.* [1983] and Norse [1991]), but the finer details of their historical distributions are far better known than any other group of invertebrates. With the exceptions of the snails treated here, there have been no reports of extinctions in either of these groups.

Alternatively, perhaps we have in fact overlooked—or are overlooking—extinctions. There are three considerations critical in this regard:

First, what of the many (hundreds of?) “species” reported in 18th and 19th century monographs—species of mollusks and crustaceans and annelids for example—that have never been collected again? We can divide these “missing” taxa into two categories: those for which specimens still exist, and those for which the type specimens, or any subsequent material, have been lost. It must be noted, of course, that many of these descriptions are such that the species (and sometimes even the type of organism!) is unrecognizable (such names are often referred to by taxonomists as *nomena dubia*). For species with no extant specimens, a common assumption is that these taxa are only forms (sexual, ontogenetic, phenotypic, or otherwise) of species that still exist. For species with extant specimens (indeed perhaps only one or two known examples) we assume that, even if the species has not been found for over 100 years, it is more the fault of biologists than of the species. Biologists are comparatively rare, one might argue, and thus we must not expect too much of our collections to interpret the status of any given species. This argument appears to be substantiated on a regular basis by the “rediscovery” of supposedly long-lost, or indeed even purportedly extinct, species (Gibson-Smith and Gibson-Smith, 1981; Carlton *et al.*, 1991; Glynn and Feingold, 1992). Such rediscoveries shore up the general belief, perhaps, in the vastness (and thus invulnerability) of the oceans.

It seems certain that among these “missing” we have overlooked extinctions. There is, unfortunately, no list of “missing” species (except perhaps in the minds of systematists) for any group of marine inverte-

brates. Such lists would be of extraordinary value and would provide the foundation for taxon-specific and site-specific searches. The complex taxonomic histories of three of the four snails considered here, wherein each was at one time considered a synonym of another extant species, underscores the potential difficulties in the discovery and resurrection of such taxa.

Second, we may assume that most species of marine invertebrates—even in shallow shelf waters—remain undescribed. Thus, as with tropical arthropod neoextinctions (McNeely *et al.*, 1990) many extinctions may go undetected. This would be especially true in the more poorly explored regions of the world. The concomitant extinct and endangered status of many marine invertebrate systematists at the end of the 20th century suggests that little near-term improvement in this arena can be expected.

Third, while we note the vast size of the undescribed biota, it may be observed that the described biota are receiving no better attention in many parts of the world. A measure of this comes from the phenomenon of biological invasions—the introduction of non-indigenous species into coastal waters (Carlton, 1987, 1989). On the Massachusetts and Connecticut coasts, for example, a European seasquirt, *Ascididiella aspersa*, has become abundant in fouling communities since it appeared about 1985. I would judge that not six biologists on the Atlantic coast of North America know that this species is now present in shallow-water encrusting communities. If we do not see the invasions of abundant animals and plants, how will we see the disappearance of rare ones?

Restricted geographic distribution, restricted habitat, and limited dispersal abilities may, separate or combined, prove to be major attributes that would render marine invertebrates prone to extinction. The center piece may be the extinguishable habitat: if the habitat disappears throughout the range of a species (whatever the distance) then so goes the species ultimately and subtly linked to that habitat. The eelgrass limpet met all of these criteria: it occurred in a small portion of the northwestern Atlantic Ocean, it was restricted both to a host and further to a subset of the

host's population, and although it had planktonic larvae, these proved of little value for dispersal to a habitat that was disappearing or no longer existed. Extinguishable habitats were likely the cause of the demise of the horn snail and the rocky shore limpet, and such may have been the case for the Chinese (mangrove?) periwinkle as well.

Given this, and given the destructive potential of humans relative to coastal zones of the world (Norse, 1991), where might searches prove productive for overlooked neoextinctions? Geographically or ecologically disjunct environments adjacent to intense human coastal developments are obvious high profile habitats to search the literature and museums for potential neoextinctions. Wetland habitats—lagoons, salt-marshes, and upper estuarine shores—are perhaps the first candidates. Eelgrass and other seagrass communities have been similarly fundamentally altered on a global basis. And one of the perhaps most overlooked littoral habitats, the high-intertidal maritime zone (also called the wrackline, the driftline, the strand, and the supralittoral), with a fascinating array of species peculiar to this narrowest ecotone—lycastopid nereid worms, enchytraeid and other oligochaetes, talitrid amphipods, ghost crabs, pseudoscorpions, insects, and spiders—has been simply removed from many shores. Where the supralittoral zone once existed we now often find bulkheads, retaining walls, condominiums, and parking lots. Thoroughly scholarly work in these arenas will predictably lead to the discovery of additional neoextinctions.

Two additional domains may prove of value in this search for cryptic extinctions. While we lament the loss of entire populations of marine invertebrates, almost without exception we assume that the same species survives elsewhere. Museum material often exists of such extinct populations—and some of these, especially those that represented distant and disjunct populations, would now bear reexamination, to examine the hypothesis of assumed conspecificity, by molecular genetic techniques. In addition, species-specific parasites of extinct marine vertebrates may have been lost as well; careful examination of museum

material for mummified ectoparasites appears never to have been made.

At the end of the 20th century, one of the major crises in global marine invertebrate conservation is not so much that invertebrates are becoming extinct at a rapid rate (although they may be)—the crisis is that we do not know, that our understanding of this process is dismal. We may have lost many more species than we suspect; centuries of human alterations may have dipped deep into the resilience that the ocean seems to project. With biodiversity as a watchword for the environment in the 1990s, we are ill positioned to argue the relationship between our obliteration of coastal zone habitats and the obliteration of our coastal biota. The future historians of science may well find that a crisis that was upon us at the end of the 20th century was the extinction of the systematist, the extinction of the naturalist, the extinction of the biogeographer—those who would tell the tales of the potential demise of global marine diversity.

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REFERENCES

- Abbott, R. T. 1970. Eastern marine mollusks. *Malacologia* 10:47–49.
Abbott, R. T. 1974. *American seashells*. 2nd ed. Van Nostrand Reinhold Co., New York.

- Bequaert, J. 1942. Random notes on American Potamididae. *Nautilus* 56:20–30.
- Berman, J. and J. T. Carlton. 1991. Marine invasion processes: Interactions between native and introduced marsh snails. *J. Exper. Mar. Biol. Ecol.* 150: 267–281.
- Berry, S. S. 1906. Note on a new variety of *Cerithidea sacrata* Gld., from San Diego, Cal. *Nautilus* 19: 133.
- Berry, S. S. 1956. A tidal flat on the Vermilion Sea. *J. Conch.* 24:81–84.
- Burch, J. Q. 1943. Tellinidae. *Min. Conch. Club So. Calif.* 25:11–13.
- Burch, J. Q. 1945. [On *Cerithidea californica*]. *Min. Conch. Club So. Calif.* 54:34–35.
- Carlton, J. T. 1976. Extinct and endangered populations of the endemic mudsnail *Cerithidea californica* in northern California. *Bull. Amer. Malacol. Union* for 1975:65.
- Carlton, J. T. 1979. *Chlamydoconcha orcutti* Dall: Review and distribution of a little-known bivalve. *Veliger* 21:375–378.
- Carlton, J. T. 1987. Patterns of transoceanic marine biological invasions in the Pacific. *Bull. Mar. Sci.* 41:452–465.
- Carlton, J. T. 1989. Man's role in changing the face of the ocean: Biological invasions and implications for conservation of near-shore environments. *Conserv. Biol.* 3:265–273.
- Carlton, J. T., G. J. Vermeij, D. R. Lindberg, D. A. Carlton, and E. C. Dudley. 1991. The first historical extinction of a marine invertebrate in an ocean basin: The demise of the eelgrass limpet *Lottia alveus*. *Biol. Bull.* 180:72–80.
- Chace, E. P. 1917. Shell collecting at San Pedro. *Lorquinia* 1:42–44.
- Chace, E. P. 1945. [Note on *Cerithidea californica hyporhyssa*]. *Min. Conch. Club So. Calif.* 54:48.
- Chace, E. P. and E. M. Chace. 1967. *Conchological reminiscences. Recollections of Emery P. Chace and Elsie M. Chace*. San Diego Society of Natural History, San Diego, California.
- Dall, W. H. 1892. [Letter to Editor]. *Nautilus* 6:48.
- Emerson, W. K. 1970. Symposium on rare and endangered mollusks: Discussion of Dr. Keen's paper. *Malacologia* 10:52–53.
- Gibson-Smith, J. and W. Gibson-Smith. 1981. The status of *Pholadomya candida* G. B. Sowerby, I, 1823. *Veliger* 23:355–356.
- Glynn, P. W. and J. S. Feingold. 1992. Hydrocoral species not extinct. *Science* 257:1845.
- Glynn, P. W. and W. H. de Weerd. 1991. Elimination of two reef-building hydrocorals following the 1982–83 El Nino warming event. *Science* 253: 69–71.
- Gould, S. J. 1991. On the loss of a limpet. *Natural History* 100:22–27.
- Grant, U. S., IV and H. R. Gale. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. *Mem. San Diego Soc. Natl. Hist.* 1:1–1036.
- Johnson, M. E. and H. J. Snook. 1927. *Seashore animals of the Pacific coast*. The Macmillan Co., New York.
- Johnson, R. I. 1964. The Recent Mollusca of Augustus Addison Gould. *Bull. U.S. Natl. Mus.* 239:1–182.
- Keen, A. M. 1970. Western marine mollusks. *Malacologia* 10:51–53.
- Keen, A. M. 1971. *Sea shells of tropical West America*. Stanford University Press, Stanford, California.
- Kozloff, E. N. 1987. *Marine invertebrates of the Pacific Northwest*. University of Washington Press, Seattle.
- Lindberg, D. R. 1978. On the taxonomic affinities of *Collisella edmitchelli* (Lipps) (Gastropoda: Acmaeidae) a late Pleistocene limpet from San Nicolas Island, California. *Bull. So. Calif. Acad. Sci.* 77:65–70.
- Lindberg, D. R. 1981. *Acmaeidae Gastropoda Mollusca. Invertebrates of the San Francisco Bay Estuary System*. Boxwood Press, Pacific Grove, California.
- Lindberg, D. R. 1984. A Recent specimen of *Collisella edmitchelli* from San Pedro, California (Mollusca: Acmaeidae). *Bull. So. Calif. Acad. Sci.* 83: 148–151.
- Lipps, J. 1963. A new species of *Acmaea* (Archaeogastropoda) from the Pleistocene of San Nicolas Island, California. *Sci. Contrib. Los Angeles Co. Mus.* 75:1–15.
- MacDonald, K. B. 1969. Molluscan faunas of Pacific coast salt marshes and tidal creeks. *Veliger* 11: 399–405.
- Marincovich, L. 1976. Late Pleistocene molluscan faunas from upper terraces of the Palos Verdes Hills, California. *Sci. Contrib. Los Angeles Co. Mus.* 281:1–28.
- McLean, J. H. 1966. West American prosobranch Gastropoda: Superfamilies Patellacea, Pleurotomariacea, and Fissurellacea. Ph.D. Diss., Stanford University, Stanford, California.
- McLean, J. H. 1978. *Marine shells of southern California*. Science Series 24, Rev. ed. Natural History Museum of Los Angeles County, Los Angeles.
- McNeely, J. A., K. R. Miller, W. V. Reid, R. A. Mittermeier, and T. B. Werner. 1990. *Conserving the world's biological diversity*. International Union for Conservation of Nature, Switzerland.
- Monks, S. P. 1893. San Pedro as a collecting ground. *Nautilus* 7:74–77.
- Morrison, J. P. E. 1970. Brackish water mollusks. *Malacologia* 10:55.
- Muehlstein, L. K., D. Porter, and F. T. Short. 1988. *Labyrinthula* sp., a marine slime mold producing the symptoms of wasting disease in eelgrass, *Zostera marina*. *Mar. Biol.* 99:465–72.
- Muehlstein, L. K., D. Porter, and F. T. Short. 1991. *Labyrinthula zosterae* sp. nov., the causative agent of wasting disease of eelgrass, *Zostera marina*. *Mycologia* 83:180–191.
- Norse, E. A. 1991. Conserving the neglected 71%: Marine biological diversity. *Species* (Newsletter of the Species Survival Commission, IUCN), 16:16–18.
- Pimm, S. L. 1991. *The balance of nature?* The University of Chicago Press, Chicago.

- Ray, G. C. 1988. Ecological diversity in coastal zones and oceans. In E. O. Wilson and F. M. Peter (eds.), *Biodiversity*, pp. 37–50. National Academy Press, Washington, D.C.
- Reid, David G. 1986. The littorinid molluscs of mangrove forests in the Indo-Pacific region. The genus *Littoraria*. *Brit. Mus. (Nat. Hist.) Bull.* 978:1–227.
- Rosewater, J. 1970. Symposium on Rare and Endangered Mollusks: Discussion of Dr. Abbott's paper. *Malacologia* 10:49.
- Short, F. T., L. K. Muehlstein, and D. Porter. 1987. Eelgrass wasting disease; cause and recurrence of a marine epidemic. *Biol. Bull.* 173:557–562.
- Short, F. T., B. W. Ibelings, and C. den Hartog. 1988. Comparison of a current eelgrass disease to the wasting disease in the 1930s. *Aquat. Bot.* 30:295–304.
- Taylor, D. W. 1981. Freshwater mollusks of California: A distributional checklist. *Calif. Fish Game* 67:140–163.
- Vermeij, G. J. 1992. Time of origin and biogeographical history of specialized relationships between northern marine plants and herbivorous mollusks. *Evolution* 46:657–664.
- Vermeij, G. J. 1993. Biogeography of recently extinct marine species: Implications for conservation. *Conservation Biology* 7. (In press)
- Wells, S. M., R. M. Pyle, and N. M. Collins. 1983. *The IUCN invertebrate red data book*. IUCN, Gland, Switzerland.
- Wicksten, M. K. 1984. Early twentieth century records of marine decapod crustaceans from Los Angeles and Orange Counties, California. *Bull. So. Calif. Acad. Sci.* 83:12–42.
- Williamson, M. B. 1892. An annotated list of the shells of San Pedro Bay and vicinity. *Proc. U.S. Natl. Mus.* 15:179–219.
- Zedler, J. B. 1982. The ecology of southern California coastal salt marshes: A community profile. FWS/OBS-81/54. U.S. Fish and Wildlife Service, Biological Services Program, Washington, D.C.