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Near extinction of an exploited marine invertebrate

Marine extinctions within historical times are thought to be rare[1–3]. Of 1321 taxa on the United States federal listing of threatened or endangered organisms (as of Ref. 3), only six have marine or estuarine phases in their life cycle, and none is a wholly oceanic finfish. Carlton[1] describes four recent extinctions of non-exploited marine invertebrates; their commonality appears to be coastal habitats vulnerable to human impact – salt marshes, estuaries, lagoons, seagrass communities, and supralittoral zones. Although there are reasons to question the perception of fewer extinctions in the ocean[2], the implication is that species inhabiting offshore marine habitats buffered from degradation and manipulation are more likely to be endangered by overexploitation[3].

In a 1994 fisheries review, Jamieson[4] found no marine invertebrates to be threatened with global extinction resulting from overexploitation, despite many examples of severe depletion or disappearance of local populations. Indeed, marine invertebrates are often considered to be resistant to overfishing owing to broad ranges, high fecundities, larval dispersal and, for most benthic species, limited mobility and scattered concentrations that may provide for refuge populations. A new report by Davis *et al.*[5] of the near extinction of the white abalone (*Haliotis sorenseni*), a prosobranch gastropod subjected both to commercial and to recreational harvest, suggests that a re-evaluation of management policies for certain fisheries is long overdue.

Abalones – highly prized shellfish – are found in predictable and accessible locations near stands of their macroalgal food; movement is minimal[6,7]. They are slow growing, long-lived, and have unpredictable recruitment; as a result, size-frequency distributions tend to be skewed with an accumulation of older individuals. Historically, white abalones ranged over about 8° of latitude from Point Conception, California, USA to Punta Abreojos, Baja California, Mexico. Adults are found in the open, on rocky habitat with understory kelp from depths of 26 m to at least 65 m (Ref. 5); the difficulties of stock assessment for benthic species with patchy distributions are exacerbated by this depth range where diving safety considerations minimize bottom time.

The deepest living of the five commercially exploited abalone species in Southern California, *H. sorenseni*, was harvested after the decline of the more available shallow water species, but its tender meat yielded premium value[5]. This resulted in an intense but short-lived fishery in which 95% of commercial landings took place in just nine years, 1969–1977. Davis and colleagues recently censused Channel Island sites in the Southern California Bight that had been surveyed in the 1970s and 1980s, and found two to three order-of-magnitude decreases in abundance. They found only three white abalones in 3.06 ha of prime habitat in 1991–1993, habitat that had supported 6120–30 600 animals 20 years earlier[5].

Abalone shells offer information about population structure and sources of mortality[7]; 119 white abalone shells collected during the 1991–1993 surveys were predominantly large animals and only one was a recent mortality. While mortality caused by handling sub-legal animals may have caused some of the deaths, a number of the shells were larger than commercial minimum legal size. Davis *et al.* conclude that the last major recruitment to the population was probably spawned in the late 1960s or early 1970s, and that the population is approaching extinction from natural causes. The three live animals found in the most recent survey were collected for captive breeding; unfortunately all are male.

The decline of this species appears to derive from a combination of fishery and biological considerations. The high economic value of abalones has justified extensive commercial search effort for many years, and the abundance of legal-sized animals in even distant Channel Island populations is often quite low[7,8]. The return to commercial fishermen for red abalones (*H. rufescens*), the only remaining fishery in Southern California, was US $450 per dozen animals in February 1996 (K. Henderson, pers. commun.). Recreational diving pressure is extensive and under no economic

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constraints on search effort. Management relies almost completely on minimum legal size to protect spawning stock; while the size limits appeared to provide for adequate egg production[7], this practice does not take into account spatial dispersion, variability in recruitment, or other biological factors.

Abalones are dioecious broadcast spawners that require high concentrations of sperm and thus aggregations of adults for successful fertilization (reviewed in Ref. 9). Some species are known to aggregate for spawning, but lose that ability as densities decline to low levels. Thus, the effective population size, the number of individuals making more or less equal contributions to subsequent generations, declines more rapidly than the true population size as density declines[10]. Whether the zone of effective fertilization is less than a meter[5] or slightly larger[9], it is apparent that the reduction in density caused by fishing led to lowered reproductive potential. There are doubtlessly a few white abalones left in the wild, but it seems unlikely that reproduction will be successful without human intervention[5]. Shepherd and Brown[10] estimated the minimum viable population size of an Australian abalone species to be more than 800 individuals for a local population.

Mexican waters are unlikely to provide a refuge; details of Baja California stocks are sketchy, but Guzman del Proo[11] presented no white abalone density data after 1970 nor a minimum legal size in his review of the Mexican fishery. Furthermore, abalone larval dispersal is relatively limited under average environmental conditions (reviewed in Refs 8 and 9); stock replenishment by distant, less impacted sources, as might be expected for species with longer lived larvae, is not a realistic prospect over multi-decadal timescales.

Disease can have potentially devastating implications for depleted stocks (e.g. Ref. 12). Withering syndrome, an apparent disease, led to the collapse of black abalone (*H. cracherodii*) populations in the Southern California Bight over the past decade[13], and it is possible that disease contributed to the decline of white abalones. One of us (M.J.T.) collected 20 freshly-dead, adult white abalone shells that had no predator marks, from Farnsworth Bank offshore of Santa Catalina Island (CA, USA) in July 1990 (unpublished data). Davis *et al.*'s[5] collection of adult shells also indicates that the last few large animals were not fished. However, they argue convincingly that 'harvest in the mid-1970s reduced adult densities to the point that reproduction was insufficient to produce recruits regularly. If disease played any role in this population collapse, it may have only delivered the *coup de grâce* to an already depleted and struggling population'[5].

For most fisheries, population depletion leads either to management closing the fishery or to densities that are so low that further fishing is uneconomical before the situation becomes critical. White abalones exhibit most of the traits that Jamieson[4] suggests would characterize species vulnerable to near extinction and range reduction from overfishing: relatively large size, occurrence in a relatively restricted geographic range near human settlement, exceptional market demand to justify exploitation at very low stock densities and, associated with their typically large size, a relatively long lifespan and, consequently, normally low annual recruitment. White abalones are certainly not intertidal or shallow subtidal to facilitate capture, but their high value has apparently overridden any refuge potentially afforded by their deep distribution. Diving is an extremely efficient harvesting method on open substrate types[7] and poaching appears to be a serious problem in Southern California[8]. On the basis of Davis *et al.*[5], the California Department of Fish and Game closed the commercial and recreational fisheries for white abalone on 1 March 1996.

Within Southern California, white abalones were predominantly found on the Channel Islands; it is unlikely that pollution or habitat alterations have been factors in their decline. Nor are abalones extreme trophic specialists or dependent on a narrow habitat range like the Atlantic eelgrass limpet (*Lottia alveus*) now presumed extinct[1] or several rare ascoglossan molluscs of the Florida Keys[14]. There is no evidence that introduced species or hybridization, factors frequently cited as causes of extinction for freshwater fishes[15], have affected white abalones. We note, however, that Anderson[16] has recently reported that an introduced asteroid (*Asterias amurensis*) may have rendered the spotted handfish (*Brachionichthys hirsutus*) virtually extinct in estuaries of southern Tasmania. Intensive fishing pressure has certainly altered the structure of nearshore communities, and while it is possible that such alterations have affected white abalones, there are no documented cases where exploitation of a wild population of any marine species has resulted in extinction or severe population depletion of another species[4]. Thus, we must agree with Davis *et al.*[5] that overfishing has driven the white abalone to the verge of global extinction.

Protection of natural stocks of remaining abalone species will require going beyond dependence on minimum size limits to ensure the survival of brood stocks at appropriate densities through periods of poor recruitment. Marine reserves or harvest refugia offer many potential benefits, but management via abalone fishery closure was not sufficient to protect a coastal population in Los Angeles County, CA, USA, from apparent poaching[8]. Furthermore, because of limited larval dispersal, a large number of refugia would be required to conserve or enhance abalone stocks[8,10]. Spatial management, where harvest levels are based on stock assessments within individual areas, is expensive and time-consuming. Whether resources are adequate enough to provide the levels of assessment and protection necessary to prevent extinction of small stocks of luxury foods in densely populated regions like Southern California is a conundrum of the 20th century.

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Longevity in the deep

Perhaps as part of our general biophilia, we have a general fascination for longevity. Maximal human lifespan seems to be about 120 years, and some turtles exceed this by 50%. Many people are aware of the bristlecone pines (*Pinus aristata*) as being the oldest living plants, for there are several specimens thought to be approximately 5000 years old. Now Druffel and her colleagues[1] present some fascinating data on colonial sea anemones that demonstrate that these organisms live almost as long; of the order of at least 2000 years. This puts even Methuselah and his kin in the shade.

The organisms studied by Druffel *et al.* belong to the genus *Gerardia*. These colonial zoanthid sea anemones were once thought to be kin of the black corals; they look like twiggy bushes[2] with 'buds' of yellow tentacles along the greenish-brown 'branches'; they grow up to 2 m or so with a 'trunk' of up to several centimetres. They are unusual in the marine world because the trunk is proteinaceous rather than calcareous. The protein is somewhat like collagen, being rich in glycine and alanine, but while collagen contains large amounts of hydroxyproline, the *Gerardia* skeleton is rich in histidine. Such a structure seems to be unique.

Druffel *et al.* collected several specimens of *Gerardia* from the Florida Straits (27°N, 79°W) in October 1982 using the deep-sea submersible *Alvin* at a depth of 620 m. Cross sections of pieces of 'stem' indicated apparent growth rings of 5–10 μm. If these rings can be assigned as annual growth rings, which is not unreasonable since there are good reasons to expect seasonal differences in food supply for these creatures, then cross sections suggest an age of 1350–2700 years!

Rather stronger evidence comes from radiocarbon dating. The 'growth rings' could not be peeled individually, but layers some 1 mm thick were collected by careful dissection, and analyzed for radiocarbon to assess their age. Surface layers were rich in ^{14}C, indicating that at least the very outer layers had been synthesized since the advent of hydrogen bombs. The remarkable finding was that the interior layers were very old; the corrected ^{14}C age of the central layers of one branch was 2420 years. While this is still only a fraction of the apparent age of the remarkable cryptoendolithic photosynthetic organisms that inhabit Antarctic deserts[3], it is getting close in age to the bristlecones.

Gerardia may thus be an unheralded sentinel of changes in the marine environment, given its long life and potentially reliable annual resolution. Archives of similar resolution are kept in tree rings whose carbon is procured from the atmosphere[4], and in corals whose carbon is procured from inorganic carbon dissolved in sea water[5]. Unlike corals, *Gerardia*'s carbon carries the isotopic signature of the particulate organic matter on which it feeds. This organic matter was originally produced in surface euphotic zones and its composition stores indicators of the environment of the overlying ocean mixed layer. These chemical and isotopic indicators might be used to reconstruct the past behavior of the Earth's climate system, which may hold clues to future changes[6], which are of intense current interest fueled by the prospect of global warming. *Gerardia*'s indicators could thus add to the cadre of paleo-indicators, from ^{18}O in glacial ice, indicating paleo-temperature[7], to ^{13}C in Patagonian peat, indicating paleo-CO_2 concentrations[8]. Whether or not there are enough *Gerardia* to perform this task remains to be seen.

Another interesting aspect of the longevity of *Gerardia*, and its relatively small size, is that it is obviously a very slowly growing organism. This can presumably be blamed on a relatively sparse diet, suggesting a relatively slow metabolic rate. It is noteworthy that the other longevity record holders, the bristlecones and the desert cryptoendoliths, are also rather slow growers. These organisms are photosynthetic, and they seem limited more by environmental factors such as water availability, than by food *per se*. Nevertheless, a common feature of all these ancient organisms is that their growth is limited by the supply of food in its broadest meaning. This is reminiscent of the situation in many laboratory animals, where restricting caloric intake by 30–35% from what would be *ad libitum* feeding can extend an animal's lifespan (50% survival) by a similar amount[9]. While there are numerous hypotheses to explain this phenomenon[9], all lead to the rather depressing notion that longevity and a good time are inversely correlated.

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