The IUCN Species Survival Commission

The Conservation Biology of Molluscs

Edited by E. Alison Kay

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The Conservation Biology of Molluscs

Proceedings of a Symposium held at the 9th International Malacological Congress, Edinburgh, Scotland, 1986.

Edited by E. Alison Kay

Including a Status Report on Molluscan Diversity, written by E. Alison Kay.

IUCN/SSC Mollusc Specialist Group.

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Foreword

The Mollusc Specialist Group is one of several specialist groups established to provide advice and data to the Species Survival Commission (SSC), and through it, to the International Union for Conservation of Nature and Natural Resources (IUCN). An Action Plan is mandated of each Specialist Group by the Species Survival Commission and is the means by which Specialist Groups provide input into an overall SSC Action Programme, which is in turn used to develop the IUCN "Conservation Programme for Sustainable Development," the thesis of which is that the conservation of resources relies on sustainable development.

Recognizing the importance of molluscs in the life of humankind and the significant roles they play in ecosystems, the Mollusc Specialist Group (MSG) believes that continuing loss of mollusc diversity is detrimental not only to ecosystems around the world, but, in the long run, to the welfare of humankind itself. In an effort to ameliorate the increasing loss of diversity suffered by molluscs worldwide, this volume has been developed to provide a resource on the conservation status of molluscs today and some suggestions for the conservation of molluscan diversity in the future. There are two parts: 1) a series of papers summarizing the current status of molluscs presented at a Symposium on Endangered Molluscs at the 9th International Malacological Congress, held in Edinburgh, in September 1986; and 2) a status report on molluscan diversity worldwide.

The Symposium on Endangered Molluscs was commissioned by Resolution of the 8th International Malacological Congress, held in Budapest in September 1983:

"Recognizing that all biotic diversity is changing in a dramatic manner as a result of increasing pressures of man, and recognizing the need for the enunciation of priorities if we are to develop a world strategy which will insure the survival of species and genetic diversity, be it resolved that the Unitas Malacologica encourage and support the activities of the Species Survival Commission on Invertebrates of the International Union for Conservation of Nature, and in particular the work of the Species Survival Commission on Mollusca.

Be it further resolved that the Unitas Malacologica encourage and support a climate for research and education in such areas of concern as those of economically important species like the giant clam *Tridacna,* of endangered species such as the achatinellid snails of the Hawaiian Islands, and of areas of high molluscan diversity such as in the Madeira Islands.

And, be it further resolved that a meeting on the conservation of molluscs be organized for the 9th International Congress in Edinburgh in 1986."

The eight papers and five abstracts from the symposium are arranged in Section 1 in four chapters: 1) the keynote address, a synthesis of what we know and what we do not know about current pressures on molluscs; 2) a group of papers that address the pressures on especially vulnerable groups of Mollusca, namely those found in island habitats; 3) several papers dealing with the current status of molluscs on continents; and 4) a final paper representing a major statement on the economics of the shell trade, a continuing source of pressure on marine molluscs.

Section 2 presents a report on molluscan diversity. This status report focuses on the diversity of molluscs on continents, on islands, in freshwater, on coral reefs, as economic resources, as alien species, and as model systems. Five major actions are proposed for the conservation of molluscan diversity:

1) the acquisition and management of threatened habitats on islands, in aquatic ecosystems, on continents and on coral reefs;
2) the development of a data base necessary for knowledge of molluscan diversity;
3) the prevention of the introduction of alien species that have negative impacts on native mollusc species and control and eradication of those exotic species where such introductions have already occurred;
4) the establishment of self-sustaining captive populations of endangered mollusc species and support of their eventual re-introduction into their native habitats;
5) the promotion of public awareness and concern for molluscan conservation programmes.

E. Alison Kay
Mollusc Specialist

Editors Note:
The publication of the Proceedings of the Symposium held at the 9th International Malacological Congress, Edinburgh, Scotland, on 31 August - 6 September 1986 was subject to a number of delays. Because of the lateness of publication, authors of the papers making up the report of the proceedings were given an opportunity to check their original text and correct errors which appeared in the orginal text (which may have come to light after the text was submitted). Authors were specifically asked to refrain from updating their text with new information, but were invited to refer to sources of updated information if they wished, in a separate section to be inserted just after their original text.

SECTION 1: PROCEEDINGS OF THE SYMPOSIUM

Chapter 1: Keynote address

Which molluscs for extinction?

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Abstract

Molluscs, along with other animals and plants, are undergoing an unprecedented rate of extinction. Does the record show differentially threat-prone groups of molluscs among major taxonomic categories? A data base of about 1130 species (and subspecies) considered threatened, endangered, rare and/or recently extinct was compiled from sources around the world. Three patterns emerge. The list is essentially geographically restricted to North America (the United States), Australia-New Zealand, and Europe. Ninety-eight percent of the species are freshwater and terrestrial molluscs, and 61% of the list is from nine families. The common characteristics of these "threat-prone" molluscs include late maturity, relatively great longevity, low fecundity, restricted distribution, and specialized habits and habitats. In contrast, there are molluscs which are "successful": the giant African snail, *Achatina fulica,* the carnivorous snail *Euglandina rosea,* and the freshwater bivalve *Corbicula fluminea* have nearly legendary reproductive and dispersal potentials; they are opportunistic, rapidly exploiting vacant niches; and they adapt to a wide range of habitats. If these ecological successes are the only survivors of the present extinction crisis, will the world of molluscs eventually be reduced to a few common species?

Introduction

Molluscs are among the most ancient of animals on earth today. They appear in the oldest Cambrian deposits, more than 500 million years BP. Molluscs are also among the most successful of all animals, and are second only to insects in numbers of species. As with other organisms however, the fossil record does not show the continuous presence of all families and genera through time. Groups at various taxonomic levels have appeared, radiated and disappeared: the rudists, ammonites and belemnites are among the best known molluscs of the fossil record but all were extinct by Tertiary time. There are innumerable local records—in the Eocene and Miocene of the Paris Basin, in the Pleistocene of the eastern coast of North America, and in the Miocene and Plio-Pleistocene deposits of Pacific islands — of genera and species which are now extinct.

In recent years it has become increasingly apparent that molluscs along with other animals and plants are undergoing yet another period of extinction. The current extinction differs from that in geological time in that it is occurring much more rapidly and is largely the result of human activities rather than of natural causes. Where the Permian and Cretaceous extinctions occurred over periods of a million or more years, the present extinctions of species occur in time spans of less than ten years. In the Hawaiian Islands before human colonization, the extinction rate for molluscs may have been on the order of one species per million years. With settlement by the Polynesians, it increased to perhaps one species per 100 years. Since 1778, the year Captain Cook discovered Hawaii for the western world, the extinction rate for molluscs has reached a rate of between one and three species a year (Kay and Schoenberg-Dole 1990). On Moorea in French Polynesia, eight species and subspecies of *Partula* became extinct in a period of less than 10 years, following the introduction of the carnivorous snail *Euglandina rosea* (Clark, *et al.* 1984; Murray, *et al.* 1988).

The problem

There is now an enormous literature on the present period of extinction, much of that literature published within the last decade. There are many generalizations about organisms which appear to be extinction-prone, among them: 1) the "basket cases," animals and plants enroute to extinction as a result of natural causes; 2) k-selected species, that is, those with long lives and low fecundity; 3) species which live on islands; 4) species with small geographical ranges; 5) species near the top of the pyramid of biomass or at the end of a food chain; 6) species with little or no power of dispersal; 7) species with large body size; 8) species requiring climax vegetation; 9) species with small populations; and 10) species with specialized niches.

The listed characteristics, which emerge from a variety of studies of rare and endangered species, serve as a profile for each group of organisms. In this review I analyze the molluscs in terms of that profile. Does the record show differentially threat-prone groups among major taxonomic categories? If so, this selectivity may tell us a great deal about what will become extinct in the near future.

To answer the question, a data base of about 1130 species (and subspecies) was compiled from national and international sources of mollusc species considered threatened, endangered, rare and/or recently (within the last 200 years) extinct, and the molluscs on the

Table 1.1 Molluscan families with estimated numbers of threatened species and subspecies.

	Number of species threatened		Number of species threatened
GASTROPODA			
PROSOBRANCHIA		**STYLOMMATOPHORA**	
Aciculidae	2	Acavidae	1
Assimineidae	10	Achatinellinae*	51
Bithyniidae	1	Amastridae	13
Hclicinidae	2	Ammonitellidae	1
Hydrobiidae	128	Arionidae	3
Hydrocenidae	1	Bradybaenidae	1
Melaniidae	2	Bulimulidae	73
Muricidae	1	Camaenidae	5
Neritidae	5	Caryodidae	2
Pleuroceridae	79	Cerionidae	1
Pomatiasidae	2	Charopidae	36
Pomatiopsidae	1	Clausiliidae	11
Potamididae	3	Cochliocopidae	1
Ranellidae	1	Diplommatinidae	9
Turbinidae	1	Elonidae	1
Valvatidae	3	Endodontidae	12
Viviparidae	5	Enidae	4
		Haplotrematidae	1
OPISTHOBRANCHIA		Helicarionidae	43
Corambidae	1	Helicidae	29
		Helicodiscidae	6
BASOMMATOPHORA		Helminthoglyptidae	48
Acroloxidae	1	Limacidae	4
Anyclidae	9	Megaspiridae	1
Glacidorbidae	3	Oleacinidae	1
Lymnaeidae	7	Oreohelicidae	13
Physidae	14	Partulidae	23
Planorbidae	20	Polygyridae	23
		Punctidae	12
BIVALVIA		Pupillidae	16
Hyatellidae	1	Rhytididae	56
Hyriidae	2	Sagdidae	1
Margaritiferidae	6	Streptaxidae	3
Mytilidae	1	Subulinidae	8
Pteriidae	2	Succineidae	5
Sphaeriidae	17	Testacellidae	1
Tridacnidae	7	Vallonidae	5
Unionidae	158	Vertiginidae	18
		Zonitidae	22
		* = Subfamily	

list are examined for taxonomic composition, geography and their biological characteristics. The list was derived from lists circulated by the International Union for the Conservation of Nature (IUCN), the United States Office of Endangered Species, individual states in the United States, individual countries in Europe, and from compilations such as those of Basch (1963), Bogan and Parmalee (1983), Coppois and Wells (1987), Clarke (1976), Hubricht (1981), Solem, *et al.* (1982), Stansberry (1971), and Taylor (1980).

The mollusc data base

The results of simple computerized sorting of the database suggest three patterns.

1) There is a noticeable geographical skew among the items in the data base (Table 1.1), and the list is virtually restricted to North America (the United States) (40% of the list), Australia and New Zealand (19%) and Europe (16%). About 33% of the molluscs are species from oceanic islands.

2) The list (Table 1.1) is biased toward non-marine molluscs: about half the list consists of freshwater molluscs (prosobranchs and bivalves), and half are land snails (Stylommatophora). Only 22 (2%) of the 1130 molluscs on the list are marine molluscs.

3) Taxonomic groups are affected differently (Table 1.1): 61 percent of the list is derived from nine families. Among the prosobranchs, the Hydrobiidae and the Pleuroceridae bear the greatest species burdens: 83% of the prosobranchs on the list are in these two families. In the Stylommatophora, 69% of the 62 families include threatened species. Except for the Helminthoglyptidae of western North America with 20% of the species listed, the families occurring on islands are among the most heavily encumbered, that is, the achatinelline, amastrid and partulid land snails of Pacific islands, the Bulimulidae of the Galapagos Islands, and the Rhytididae of New Zealand. Only eight families of bivalves are on the list, and 81% of the 197 bivalves are unionids.

Characteristics of threat-prone groups

The foregoing summaries indicate that threat-proneness does not occur randomly among molluscs but that it is associated with certain groups of molluscs. A survey of the characteristics of the threat-prone families shows the following:

1) The families on the list represent for the most part actively evolving groups of molluscs averaging six species per genus.

2) Body size (Table 1.2) is relatively large in six of the seven groups. In the Bulimulidae, Rhytididae, and Unionidae body size is on the order of 100 mm in length; in the Helminthoglyptidae, shells are 20-30 mm in diameter. Only in the Hydrobiidae are the shells small, usually less than 10 mm in greatest dimension.

3) Virtually all species on the list have restricted distributions (Table 1.2). In the Hydrobiidae and in the Pleuroceridae, 62 of 85 (73%) and 67 or 82% listed from the United States are, respectively, known only from single states. In the Helminthoglyptidae, all 52 species listed are from a single state and most are from single localities, sometimes a single rock pile. The epitome of short range and restricted distribution is on islands. In the Pacific, the achatinellines and Amastridae of Hawaii, Partulidae of Tahiti and Guam, and Bulimulidae of the Galapagos are, for the most part, single island endemics, and in some cases found only on single mountain ridges or in a single valley.

4) The molluscs on the list are specialists in habitat and food habits (Table 1.2). The Hydrobiidae are found in single drainage basins, springs, caves and other subterranean habitats where there are often impressive radiations (see Ponder, this volume; Ponder and Clark 1990). The Pleuroceridae and Unionidae are specialists in the shoal waters of the rivers of the United States where nearly all the rich freshwater fauna of central and southeastern North America evolved in or adjacent to a riffle or shoal habitat (Stansberry 1971). The Hawaiian achatinellines live in trees where they feed on fungal filaments on leaves. *Partula* of French Polynesia are similarly specialized, and include one species which is carnivorous (Cowie, 1992), and others which are humidity sensitive (Bloxam, *et al.* 1983). The Rhytididae of New Zealand have radiated into a variety of habitats from lowland forests to alpine grasslands, and are found deep in acidic leaf mould where they feed on earthworms and millipedes (Meads, *et al.* 1984).

5) The species for which there are data on reproduction show many similarities (Table 1.3). Threat-prone molluscs are relatively late in maturing: one and a half years in the pleurocerids, four to six years in the achatinellines, and 15 years in the rhytidid *Powelliphanta.* Many of the species are relatively long-lived: some pleurocerids live at least three years; achatinellines live 6 to 11 years, and *Powelliphanta* in New Zealand is thought to live at least 40 years. A record of 67 years for a unionid (Stober 1972) may be overly optimistic, and its life span is more probably 10-15 years (Dudgeon and Morton, 1981). Despite their long lives, fecundity is low: the achatinellines produce one to four offspring per year and no more than 60 eggs per year are known in the Helminthoglyptidae.

Table 1.2 Characteristics of molluscan families and subfamilies with major numbers of threatened and recently extinct species.

FAMILY/SUBFAMILY	**SIZE**	**% RESTRICTED DISTRIBUTION**	**Hydrobiidae**
Hydrobiidae	Small: <10mm	**93%**	Habitat
Pleuroceridae	Large: 30-50mm	**83%**	Habitat
Achatinellinae	Large: >20mm	100%	Habitat/Food
Bulimulidae	Large: >50-70mm	100%	Habitat
Helminthoglyptidae	Large: 15-30mm	100%	Habitat
Rhytididae	Large: >90mm	100%	Habitat/Food
Uionidae	Large: >70mm	**70%**	Habitat/Larvae/Fish Host

In the Unionidae and Hyriidae the life cycle is complicated by the insertion of the glochidium stage in the life history, and the water-borne larva must attach to a fish host.

Molluscs that are successful

Not all molluscs are on threatened and endangered lists. Many species are well known for large population densities and broad geographical ranges. Among these "successful" molluscs are the giant African snail, *Achatina fulica* and the carnivorous snail *Euglandina rosea* both of which are now widespread on Pacific islands, and the freshwater bivalve, *Corbicula fluminea,* which made its way through rivers and streams from California to the Rio Grande drainage of Texas between 1956 and the early 1960's and then to the eastern seaboard by 1972 (McMahon 1983).

The dispersal of these molluscs is clearly associated with human activity. They also have in common early maturation, high fecundity, considerable interpopulation variability, and they are easily dispersed and highly adaptable. They are representatives of

Table 1.3 Reproduction characteristics of some threatened and "successful" molluscs.

TAXON	**AGE 1ST REPRODUCTION** (YEARS)	**LONGEVITY** (YEARS)	**FECUNDITY**	**REFERENCES**
THREATENED MOLLUSCS				
GASTROPODA				
Achatinellinae				
Achatinella mustellina	7	11	1	Hadfield and Mountain 1980
Partulina redfieldii	4	11	1-4	Hadfield 1986
Partulina proxima	5-7	18-19	6.2	Hadfield and Miller 1989
Partulidae				
Partula spp.	.8-1.5	16-17	16-19	Murray and Clarke 1966
Bulimulidae				
Liguus fasciatus	4	6	~19	Voss 1976
Rhytididae				
Powelliphanta/Paryphanta	15	40	3-20	Meads, et al. 1984; O'Connor 1946
Helminthoglyptidae				
Helminthoglyptids	3-5	5-10	60	Walton 1963;Roth, pers. comm.
BIVALVIA				
Margaritiferidae				
Margaritifera margaritifera	12-15	70-100	3-4 million (glochidial larvae, fish hosts)	Young and Williams 1984a, 1984b
"SUCCESSFUL" MOLLUSCS				
GASTROPODA				
Achatinidae				
Achatina fulica	0.5	5-6	1200	Mead 1961
Oleacinidae				
Euglandina rosea	<1	1-2	100-200	Chiu and Chou 1962
BIVALVIA				
Corbiculidae				
Corbicula Fluminea	<1	1-2	8,000 (lab) 68,678 (field) (veligers)	McMahon 1983

families which are evolutionarily conservative, usually with only one to three genera in the families.

The reproductive and dispersal potential of all three molluscs are legendary. *Achatina fulica* was transported from its native Africa to Asia for food in the 1920's, and since then has been hand carried, transported in mud on jeep tires during World War II, and carried in flower pots, across the Pacific and even to Florida (Mead 1961). The giant African snail is reported to mature in less than a year (Pawson and Chase, 1984) and may produce 300 eggs per clutch with clutches deposited four times a year. Mead (1961) calculated the potential offspring from a snail of this sort could number about seven billion in three years. *Euglandina rosea* also matures in less than a year (Chiu and Chou 1962), and is highly fecund and capable of building up large populations within a short period of time. Population studies in Hawaii indicate that following the release of about 600 snails in 1955, the population tripled within two years, and numbered some 12,000 snails within three years (Davis and Butler 1964). Initially released in the lowlands where *Achatina fulica* infestations were significant, *Euglandina* was recorded in the Koolau mountains of Oahu in 1967 and in the Waianae range in 1969 (van der Schalie 1969). On Moorea, in French Polynesia, *E. rosea* was similarly introduced to control the giant African snail in 1977, and spread within a year from its point of introduction into the adjoining forests. By 1980 its range covered approximately 4 km , nearly a third of the island (Clarke *et al.* 1984), and by 1987 it was found at or near the top of every mountain crest on the island (Murray *et al.* 1988).

The small bivalve, *Corbicula fluminea*, an Asian immigrant to North America, is similarly invasive. Eurytopic and seemingly unaffected by changes in temperature, pH and siltation, *Corbicula* matures in less than a year and produces enormous numbers of offspring: one individual can release perhaps as many as 68,670 juveniles per year (McMahon 1983). A European counterpart, *Dreissena polymorpha*, which spread from the Black and Caspian Seas to London docks in 1824 (Morton 1969), has since become a pest in the reservoirs and water systems of India, Hong Kong, southern China, and the United States.

The spectrum of life history

The life histories and habits of all organisms lie on a spectrum of time and strategy. What emerges in this analysis is a profile in which threat-prone molluscs are at one end of the spectrum and the successes on the other. Those molluscs which are actively evolving, specialized, late maturing, and which have low fecundity are at one end; they are found on the east coast of the United States, in southern Europe, on oceanic islands and in isolated lakes. The opportunists and the generalists which mature early and have a high fecundity are at the other end of the spectrum. In addition to the successes that do not appear on the list, there are a variety of other molluscs with life histories and habits which do not qualify them for the extinction-prone list. The basommatophorans such as *Lymnaea* fall on the spectrum near the "successes": they survive drought and flood, grow quickly, mature early, and can produce large numbers of offspring. Most marine molluscs are not on the list by virtue of their habits and physiology: they are easily dispersed, have wide ranges and are highly fecund. Those which are on the list, for example, the giant clam *Tridacna*, have a restricted distribution, extremely large size and long period of growth (Yamaguchi 1977).

The model proposed above is consistent with the model for land snail diversity proposed by Solem (1984). Indeed, if Solem's model were expanded to include freshwater molluscs the two models would be entirely congruent.

Which molluscs will survive?

There remain two questions. What is the impact of the present burst of extinction on mollusc families? Which molluscs will survive?

There are about 90 families of non-marine molluscs. More than 80% percent of the families are represented on the list. Within those families, the species on the list represent 57% of the 200 species of North American Hydrobiidae, 52% of the 150 species of Pleuroceridae; more than 85% of the 190 species of Unionidae; 59% of the 41 species of Hawaiian achatinelline snails; more than 30% of the 48 species of the Rhytididae of New Zealand; and more than 50% of the 57 species of Galapagos Islands' Bulimulidae. More of the molluscs not now on the list will undoubtedly be added to it. Among these molluscs are the Bulimulidae of South America, the Camaenidae of the Philippines, the South Australian cowries with restricted ranges and direct development and the highly endemic element of marine molluscs in the Red Sea.

The survivors will form the nucleus of a vastly reduced pool of species. In the case of the Mollusca, those species which survive are the opportunistic species which can rapidly exploit vacant niches by making widespread use of food resources, which are relatively short-lived with high rates of population increase, which are adaptable to a wide range of environments, and which prosper in disrupted habitats, especially those habitats which have been impacted by humans.

A useful distinction has been made between short term or ecological success and long term or evolutionary success (Hickman 1982). This distinction can serve both for interpretation of the geological record of the past and predictions for the future. The geological record of the Pleurotomariidae (Figure 1.1) may serve as a model. As a family the Pleurotomariidae was diverse in Jurassic time, but suffered bottlenecks of extinction in the Triassic and Paleogene. Some members of the family survive today but they are few in number and far less diverse in habit and form than they were in the Jurassic (Hickman 1984). If the ecological successes among the molluscs of today are the only survivors of the present extinction will they become evolutionary successes, or will the world of molluscs be reduced to a few common species?

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Literature cited

BASCH, P.F. 1963. A review of the recent freshwater limpet snails of North America (Mollusca: Pulmonata). *Bulletin of the Museum of Comparative Zoology,* Harvard University, 129: 399-461.

BLOXAM, Q.E., S.J. TONGE, R. HORTON. 1983. A preliminary account of the history and management of populations of endangered Moorean tree snail *Partula* spp. at Jersey Wildlife Preservation Trust. *Dodo, Journal Jersey Wildlife Preservation Trust* 20: 73-79.

BOGAN, A.E. AND PARMALEE, P.W. 1983. *Tennessee's Rare Wildlife,* Volume II: *The Mollusks.* Tennessee Wildlife Resources Agency, Nashville, Tennessee, 123 pp.

CHIU, S-C. AND CHOU, K-C. 1962. Observations on the biology of the carnivorous snail *Euglandina rosea* Ferussac. *Bulletin of the Institute of Zoology, Academia Sinica,* 1: 17-24.

CLARICE, A.H. 1976. Endangered freshwater mollusks of north-western North America. *Bulletin of the American Malacoogical Union.* 1976: 18-19.

CLARKE, B., J. MURRAY, AND M.S. JOHNSON. 1984. The extinction of endemic species by a program of biological control. *Pacific Science,* 38: 97-104.

COPPOIS, G. AND S. WELLS. 1987. Threatened Galapagos snails. *Oryx,* 21: 236-241.

COWIE, R.H. 1992. Evolution and extinction of Partulidae, endemic Pacific island land snails. *Phil. Trans. R. Soc.* Lond. B 335: 167-191.

DAVIS, C.J. AND G.D. BUTLER. JR. 1964. Introduced enemies of the giant African snail, *Achatina fulica* Bowdich, in Hawaii (Pulmonata: Achatinidae). *Proceedings of the Hawaiian Entomological Society,* 18: 377-389.

DUDGEON, D. AND B. MORTON. 1983. The population dynamics and sexual strategy *oiAnodonta woodiana* (Bivalvia: Unionacea) in Plover Cove Reservoir, Hong Kong. *Journ. Zool. London* 201: 161-183

HADFIELD, M.G. 1986. Extinction in Hawaiian achatinelline snails. *Malacologia* 27: 67-81.

HADFIELD, M.G. AND B.S. MOUNTAIN. 1981 [for 1980]. A field study of a vanishing species, *Achatinella mustelina* (Gastropoda, Pulmonata), in the Waianae mountains of Oahu. *Pacific. Science* 34: 345-358.

HADFIELD, M.G. AND S.E. MILLER. 1989. Demographic studies of *Partulina proxima. Pacific Science* 3: 1-16.

HICKMAN, C. 1982. The single helix: successful gastropods or successful paleontologists? *Third North American Paleontological Convention Proceedings,* 1: 237-242.

HICKMAN, C. 1984. *Pleurotomaria*: pedigreed perseverance. In: Eldredge, N. and S.M. Stanley *(Eds.), Living fossils.* Springer-Verlag, New York. 291 pp.

HUBRICHT, L. 1981. The endangered land snails of the eastern United States. *Bulletin of the American Malacological Union,* 1981: 53-54.

MCMAHON, R.F. 1983. Ecology of an invasive pest bivalve. *Corbicula.* In: W.D. Russell-Hunter (Ed.), *The Mollusca,* Vol. 6. pp. 505-561. New York: Academic Press.

MEAD, A.R. 1961. *The Giant African snail. A Problem in economic malacology.* Univ. of Chicago Press. 257 pp.

MEADS, M.J., WALKER, K.J., AND G.P. ELLIOTT. 1984. Status, Conservation, and management of the land snails of the genus *Powelliphanta* (Mollusca: Pulmonata). *New Zealand Journal of Zoology,* 11: 277-306.

MORTON, B. 1969. Studies on the biology of *Dreissena polymorpha* Pall. I. General anatomy and morphology. *Proceedings of the Malacological Society of London,* 38: 301-321.

MURRAY, J. AND B. CLARKE. 1966. The inheritance of polymorphic shell characters in *Partula* (Gastropoda). *Genetics* 54: 1261-1277.

MURRAY, J., E. MURRAY, M.S. JOHNSON, AND B. CLARKE. 1988. The extinction of *Partula* on Moorea. *Pacific Science* 42: 150-153.

PAWSON, P.A. AND R. CHASE. 1984. The life-cycle and reproductive activity of *Achatina fulica* (Bowdich) in laboratory culture. *Journal of Molluscan Studies* 50: 85-91.

PONDER, W.F. AND G.A. CLARK. 1990. A radiation of hydrobiid snails in threatened artesian springs in western Queensland. *Records Australian Museum* 42: 301-363.

VAN DER SCHALIE, H. 1969. Man meddles with nature - Hawaiian style. *The Biologist* 51: 136-146.

SOLEM, A.G. 1984. A world model of land snail diversity and abundance. In: A. Solem and A.C. Van Bruggen, (Eds.), *World-Wide Snails.* E.J. Brill/ Dr. W. Backhuys, Leiden. 289 pp.

SOLEM, A.G., E.-L. GIRARDI, S. SLACK-SMITH, AND G.W. KENDRICK. 1982. *Austrassiminea letha,* gen. nov., sp. nov., a rare and endangered prosobranch snail from south-western Australia (Mollusca: Prosobranchia; *Assimineidae). Journal of the Royal Society of Western Australia,* 65: 119-129.

STANSBERRY, D.H. 1971. Rare and endangered freshwater mollusks in eastern United States. In: S.E. Jorgenson and R.W. Sharp, *Proceedings of a Symposium Rare and Endangered Mollusks (Naiads) of the U.S.* U.S. Dept. of the Interior Fish and Wild Life Service Bureau of Sport Fisheries and Wildlife Region 3.

STOBER, Q.J. 1972. Distribution and age of *Margaritifera margaritifera* in a Madison River (Montana, U.S.A.) mussel bed. *Malacologia* 11:343-350.

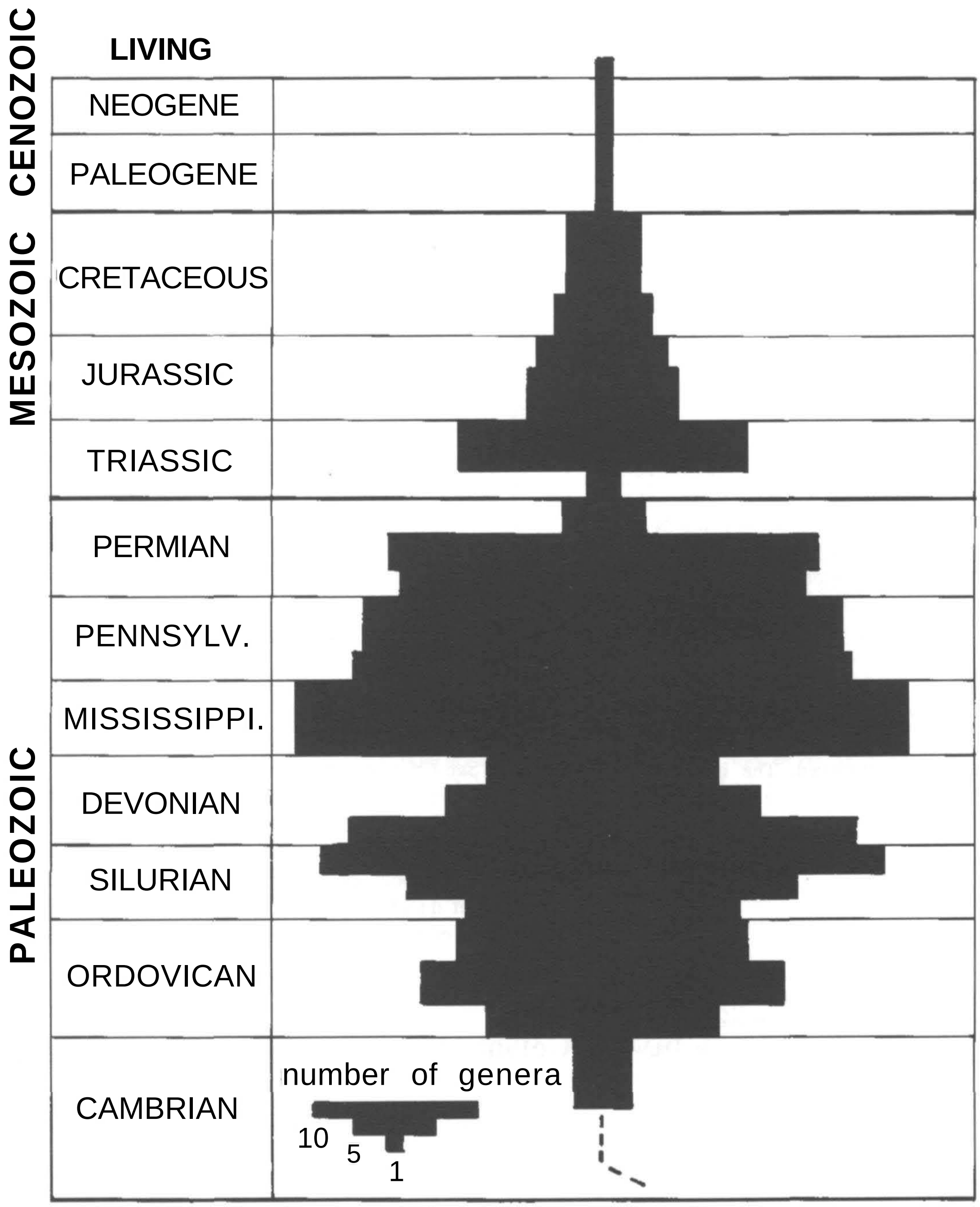
TAYLOR, D.W. 1980. Endangered and threatened freshwater mollusks of Armagosa drainage, California-Nevada. In: Williams, J.E., G.C. Kobelich and C.T. Benz (Eds.), *Management Aspects of Relict Populations Inhabiting the Armagosa Drainage.* University of California Press, Berkeley.

VOSS. G. 1976. Observations on the ecology of the Florida tree snail *Liguus fasciatus* (Muller). *Nautilus* 90: 65-69.

WALTON, 1963. Length of life of west American land snails. *Nautilus* 76: 127-131.

YAMAGUCHI, M. 1977. Conservation and cultivation of giant clams in the tropical Pacific. *Biological Conservation* 11: 13-20.

Figure 1. Generic diversity of the Pleurotomariidae over geological time. (Adapted from Hickman 1984).



Chapter 2: The vulnerability of "island" species

Threatened galapagos bulimulid land snails: an update

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Abstract

The Galapagos malacofauna is largely dominated by the Bulimulidae (90% of the species present). Many species of these endemic gastropods have, or had, their natural habitat in areas where local residents are developing their settlements. These areas are considered "colonised zones", excluded from the National Park, and legislation relating to environmental protection does not apply in these zones.

Human activities have contributed to the reduction in distribution of the bulimulids and are responsible for the extinction of many species. The original vegetation has been destroyed or altered in some areas through the introduction of exotic plants, and forests have suffered from heavy grazing by introduced goats, pigs and cattle. Other human activities, such as road building, fire-wood collection and setting intentional or accidental fires, may also result in localised but drastic changes in the biotope which lead to the elimination of entire populations of bulimulids. Introduced predators such as the little fire ant (*Wasmannia auropunctata*), and the black rat (*Rattus*) have great impact on the native biota. Potential competitors, for example, *Subulina octona* and *Deroceras* sp., have also been introduced. The influence of climatic changes is discussed with special reference to the consequences of the Nino event of 1982-1983.

Introduction

The Galapagos fauna has provided abundant material for the study of speciation and adaptive radiation. The groups most studied are the vertebrates, such as the tortoises (*Geochelone elephantopus*) and the well known finches (Geospizinae) used by Charles Darwin (1859) to support his theory of evolution. Among the invertebrates, land snails in the Bulimulidae also underwent a spectacular speciation process within the archipelago. With about 65 described species and several subspecies or forms, totalling 93 taxa, the Galapagos Bulimulidae far outnumber Darwin's finches.

The morphological diversity shown in the Galapagos bulimulids is surprising: the general shape of the shell, the shape of the aperture and of the umbilicus, the sculpture of the umbilicus, colour and size vary from one species to another. Smith (1966) noticed that "no where else has so large a number of species been found within an equally limited area; and nowhere else do they exhibit so great a variation in so many different particulars". The Galapagos bulimulids are adapted to a wide range of climatic conditions and habitats: some species live in near-desert conditions, others are found only in humid forests with a more temperate climate.

All bulimulid species found in the Galapagos are endemic. They are represented on almost all sizable islands of the Archipelago, but are not found on Wolf or Darwin (which are isolated far north of the central group of islands), or on Marchena, Genovesa (Tower), Seymour Norte or Baltra. Species generally differ from one island to another and few species are found on more than two or three islands. Usually there is higher diversity on the elevated islands where a marked vegetal zonation parallels the climatic gradient from the arid coastal zones to humid highlands and where habitats are more diversified. For instance, Santa Cruz (altitude 864m) has the greatest diversity with 23 species (Coppois and Glowacki 1982; Coppois 1984), and is the island with the most varied vegetation. One exception is Pinta (altitude 777m) which has only one species.

Many species were described at the end of the 19th century from Floreana, San Cristobal and Santiago, but most of these are now extinct. Specimens in various museums around the world testify to their former existence, but they cannot be found in the field today. Furthermore, many of the remaining species are now endangered (Coppois and Wells 1986). In this review, two main categories of threats are considered: that resulting from human colonisation of the Galapagos, and that due to natural climatic changes.

Colonisation of the Galapagos Islands

Human colonisation of the Galapagos began early in the 19th century with a small settlement on Floreana (Hickman 1985). The first arrival, in 1807, was an Irishman, Patrick Watkins, who stayed involuntarily for two years only, growing vegetables to survive. He was followed by Ecuadorian settlers led by General Villamil who established an important penal colony on Floreana after the islands were annexed in 1832. The Ecuadorians introduced many domestic animals and brought land into cultivation. In 1835, the year Charles Darwin visited the Islands, the human population of the Archipelago numbered only 200 at most. After the failure of their "orchilla" industry (collecting dyer's moss, *Rocella* *tinctoria*), the settlers moved to San Cristobal around 1847. Santa Cruz was neglected for a long time, and colonized only after 1920. This is certainly the reason why so many bulimulid species are still found on Santa Cruz: unlike the three other inhabited islands, the effect of colonisation has not yet become so destructive.

The situation has changed over the last two decades: from 3500 people in 1973, the human population of the Galapagos is now more than 12,000. On Santa Cruz alone, the local population (Ecuadorian colonists and a few foreign families) rose from 850 in 1973 to more than 4500 in 1986. More than 20,000 tourists visited the Galapagos in 1986, although their direct impact on bulimulid habitat is negligible.

Habitat Destruction

It is important to realize that the National Park does not include all the Galapagos. People are allowed to settle in what are termed the "colonized zones". These zones include villages along the coasts where most people live, as well as wide areas in the highlands where farms have been established. Huge areas of native forest were cleared for agriculture and transformed into grassland for cattle and horses. Unfortunately, these zones with a humid and temperate climate and *Scalesia* forests were also the most suitable habitat for many land snail species. Entire populations were exterminated. For example, *Bulimulus (Naesiotus) blombergi* was, when it was described, a common tree snail on Santa Cruz at an altitude of 250-400m. The remaining living populations inhabited relic forests along the road between the villages of Bellavista and Santa Rosa, at "Occidente". Although the forests survived, the microclimate was modified by clearing of the surrounding areas for sugar cane plantations, and *B. blombergi* disappeared in 1975. Similar examples can be found on all of the inhabited islands.

On Floreana, the habitat has been greatly changed as the native forests were destroyed and replaced by crops, orange trees, and guava trees (*Psidium guajava*, Myrtaceae). The exotic guava is spreading rapidly on all islands where it has been introduced, replacing the local vegetation. Such changes in habitat are fatal to the malacofauna and other native invertebrates. Only two bulimulid species (*B. nux nuciformis* and *B. ustulatus*) are still found in remnants of the native forest near the base of Cerro Pajas, the top of Floreana. Not more than 15 years ago, another fast growing tree, *Cinchona succirubra* (Rubiaceae), was introduced on Santa Cruz,and is modifying the highland region (Eliasson 1982).

Uncontrolled fires sometimes spread out of the colonisation zones and cause drastic habitat destruction. The last one of a long list was disastrous enough to attract the attention of the mass media around the world. It lasted for at least four months (from late February to June 1985 (Anon. 1985a, 1985b)), and destroyed many populations of three bulimulid species on Sierra Negra Volcano (behind Villamil) from an altitude of 200m to the rim. Some populations of these species still survive in other places on the southern slopes of Sierra Negra but their chance of survival is reduced as most of them are located in the colonised zone. This catastrophic fire originated from a fire to burn rotten coffee trees.

Since transport has always been a problem on the inhabited islands, roads have now been built. Although destruction was localised, entire hills have been destroyed, both within and without the National Park, in order to obtain gravel. In one place at least, on Cerro Maternidad (Santa Cruz), gravel pits destroyed a sizable part of the very limited habitat of *B. cavagnaroi* and altered the microclimate on the slope of the hill where the remaining population lived.

Introduced animals

Habitat destruction is sometimes not intentional but is a consequence of other activities, such as the release of goats or other domestic animals on deserted islands. The first known case of the introduction of exotic animals into the Galapagos was reported by Captain David Porter (1822) from the U.S. frigate *Essex:* in 1813 four goats were lost on Santiago, where they had been dropped for grazing. More recently, in 1954 on Pinta, local fishermen released goats to provide fresh meat when they returned for the next fishing trip. Feral goats reproduce rapidly and they soon became one of the major threats to Galapagos wildlife. They have had an extremely destructive impact on the vegetation of at least nine islands, and have caused severe erosion which has resulted in the loss of land snail habitat. *B. darwini* is one of the goats' victims and must now be considered extinct. The last live specimens were seen in 1975 (pers. observ.).

Bulimulids have a few natural predators such as the mockingbird (*Nesomimus parvulus*), the woodpecker finch (*Camarhynchus pallidus*) and the Galapagos centipede (*Scolpendra galapagensis*). Predation by mockingbirds on *B. reibishi* and *B. wolfi* has been seen in the "transition zone" of Santa Cruz. The body of the snail was seized in the beak and the shell knocked against a stone until it broke. The woodpecker finch used the same method to pick up specimens of *B. deridderi* in the valley of Cerro Coralon (Santa Cruz highlands, altitude 650m); as no stones were available, the shell was shaken against the twigs of bushes, mainly *Sida rhombifolia* on which *B. deridderi* was common. Such observations have not previously been reported and are worth mentioning. As the land snails are rarer in these areas now, their disappearance will affect the finches' diet. Predation by the centipedes has never been observed directly, but, in the centipedes' hiding places under lava blocks, broken shells are common, and careful observation of the hiding places has shown that there are no other possible predators. Observed prey of centipedes are *B. tanneri* and *B. wolfi* in the arid and transition zones on Santa Cruz. Other possible natural predators are endemic rice rats, but these are now extinct on Santiago, Floreana and Santa Cruz. Only two species of rice rat are still living, one on Fernandina (*Nesoryzomys narboroughi*) and one on Santa Fe (*Oryzomys bauri*). Characteristically broken shells were collected on Santa Fe and support the idea that endemic rats effectively prey on land snails, but no other information is available. All these natural predators had a very limited impact on snail populations, unlike the introduced predators such as fire ants (*Wasmannia auropunctata*), black rats (*Rattus rattus*) and mice (*Mus musculus*), although little is known of the impact of the last mentioned in the Galapagos as no studies have been carried out.

The little fire ant, *Wasmannia auropunctata,* was introduced to Santa Cruz less than half a century ago, between 1924-1934 (Kastkalen 1982; Clark *et al.* 1982; Lubin 1984, 1985). It is now common on all inhabited islands and also on some of the uninhabited islands, often around the landing places. Although only 2mm long, the fire ants outcompete other ant species and prey on other invertebrates. In areas of high densities of *Wasmannia*, bulimulid populations are low or even absent. Direct attack of *Wasmannia* has been observed on land snails on rare occasions, and these ants can inflict a painful sting even on humans. A possibly greater threat than the direct attack on adult snails is predation by the ants on juveniles and eggs. Bulimulids often lay their eggs in empty shells which are also used by the ants as nests. So far, no successful methods for eliminating fire ants have been found.

The other main introduced predator, the black rat (Clark, D.A. 1980, Clark, D.B. 1980), is widespread and was already established on some of the islands by the time of Darwin's visit (Patton 1984). In the El Junco area on San Cristobal, it is difficult to find any intact snails: on most shells of *B. nux incrassatus,* the apex is chewed. The snail may survive if just the tip of the shell has been removed, but empty broken shells are found along the "rat paths" in the vicinity of rat burrows. Similar observations have been made on other islands, such as Santiago (*B. darwini*), Sierra Negra volcano (*B. albemarlensis, B. tortuganus*) and Santa Cruz (*B. ochsneri, B. cavagnaroi, B. wolfi, B. deridderi* and many other species) where broken shells are common in some places.

I should also mention that two molluscs were introduced in some places (mainly the inhabited colonised zones): *Subulina octona* and a slug, *Deroceras* sp. However, there is no evidence of competition between these molluscs and the bulimulids. In one place, along the occasional stream from El Junco lake to Fresh Water Bay on San Cristobal, *S. octona* is the only live snail to be found; all bulimulids, including *B. achatellinus* (Smith, 1971), had disappeared by the beginning of the century, probably because of habitat destruction.

Natural climatic changes

The El Nino event of 1982-1983 (Robinson and del Pino 1985) had a catastrophic impact on many bulimulid populations. El Nino is the name of an abrupt change in the weather that usually begins around December and causes a rapid rise in sea water temperature and heavy rainfall. Since 1940, there have been 10 El Nino events, but none of them had as serious an impact on Galapagos wildlife as the El Nino of 1982-1983. Using coral aging techniques, Peter Glynn (pers. comm.) showed that the previous El Nino event of comparable importance in the Galapagos could only have happened 160 years ago; similar measurements in Panama suggest 190 years.

In early 1983, sea water temperature rose from 4 to 8°C above the average temperature. These high temperatures persisted long enough to destroy or alter the populations of many marine organisms on which other animals depended, such as the marine iguanas, birds and sea lions (Merlen 1985). Rainfall was ten times higher from December to July than the average for the previous 17 years: 3223mm of rain was recorded at the Darwin Station (arid coastal zone, altitude 2m, south Santa Cruz) between December 1, 1982 and July 31,1983; the average precipitation recorded for the same eight month period from 1965 to 1982 (inclusive) was 345mm. No precise data are available to show how bulimulid land snails responded to these unusual conditions. In fact, it seems that many bulimulid species benefited from the abundance of water, particularly in the arid zones (Andre De Roy, pers. comm.). However, in the *Scalesia* forests, the trees began to rot and subsequently fell, causing major modification of the land snails' habitat.

Scalesiapedunculata trees are 10 to 15m high and form a closed canopy which provides continuous shade for the undergrowth where the bulimulids live, in a protected and temperate microclimate. After the El Nino of 1982-1983, few trees remained, and the herb and shrub layer was exposed directly to the sun. The habitat would have become rapidly drier once the heavy rainfall ceased. Unfortunately, the years 1984 and (mainly) 1985 were unusually hot and dry, and many bulimulid species living in these forests died from excessive drought. At the Darwin Station, a total of 2768.9 mm precipitation was recorded in 1983, 146.9mm in 1984, but only 62.8mm in 1985. The annual average from 1965 to 1982 was 386.5mm. However, the *Scalesia* forest is already recovering and young trees, 1.50m high, are now abundant (August 1986) but need ten more years to reach the size of those that fell.

It is still too early to know how many bulimulid species survived the El Nino event and the subsequent dry years. I had the opportunity to visit only a few sites in July and August 1986, and in many places on Santa Cruz, only empty shells were found. Some species with restricted distributions are obviously extinct because of these drastic climatic changes. However, this does not mean that all species disappeared and it can be assumed that at least for some, relic populations will survive, unless other adverse factors intervene. On Sierra Negra volcano where fire had already reduced their numbers, *B. albemarlensis* and *B. tortuguanus* were still common in some areas. These species were even found on introduced vegetation (*Kalanchoe pinnata* and *Pothomorpha peltata*), an observation which is quite uncommon.

Discussion and conclusions

About one half, and possibly even two-thirds, of the Galapagos bulimulid species are now extinct, including *Bulimulus nux* Sowerby, 1832, the first species to be described. Bulimulids were major victims of human colonisation of the islands, and suffered from habitat destruction and introduced predators. Some were victims of the drought after the dramatic 1982-1983 El Nino event. After previous similar El Nino events, bulimulids survived and entered a spectacular speciation. In fact, the survival of isolated populations after such an event could be a factor in bulimulid speciation. But, for many populations, the chances of surviving such an unusual event were certainly reduced by the destruction and changes brought about by human colonisation, resulting in the extinction of many species which might have survived if the 'human factor' had not been present. Numerous bulimulid species occurred on Santa Cruz until recently, often in high densities. Most of these disappeared in a relatively short period after the colonisation of the island. Similar processes took place on other inhabited islands at the beginning of this century. In colonised zones, the habitat was modified and there were microclimatic changes. Modification of the habitat in these places could also have altered the climate in surrounding areas, outside the colonised zone, although this is difficult to prove.

It has been suggested that the climate has become drier over the last 50 years (Kastdalen 1982), which could explain the extinction of certain species, such as *B. planospira* from Champion, where no human interference has been noticed. In fact, objective meteorological data only exist for the last 25 years; and they do not indicate any special trends. Colinvaux (1972) and Colinvaux and Schofield (1975) have shown from palynological studies that the Galapagos climate was drier between 34,000 and 10,000 years ago, and that the present humid climate has been stable over 10,000 years. However, at the scale of a land snail's lifetime, one or two years of severe drought would be sufficient to destroy the entire population. Moreover, it is almost impossible to separate the influence of human activities from possible long term natural climatic changes. In a previous paper, Coppois (1984) reported that bulimulid populations disappeared for no obvious reason from the *Scalesia* forests of Santa Cruz in 1974, before the El Nino event. Is this extinction the result of a natural although undetected change in the climate, or the effect of some unknown factor, or is it the consequence of human activity? The question is still to be answered.

W.H. Dall (1896) wrote almost a century ago, "May it not be hoped, therefore, that someone will undertake to make a thorough and complete survey of the malacology of these islands *the Galapagos* before it is too late. The study of development of specific forms can never be made complete in the Hawaiian Islands, because the sheep and goat have preceded the investigator. There is still a chance to study the problem in the Galapagos Islands, and it should not be lost." Unfortunately, it is possible that we are once again too late to study the adaptive radiation shown by an insular group of land snails, and that Galapagos bulimulids will slowly go extinct if no conservative action is taken immediately.

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Literature cited

ANON. 1985a. Ordeal by fire and water. *Noticias de Galapagos* 41: 1-2.

ANON. 1985b. The great fire on Isabela. *Noticias de Galapagos* 42: 4-5.

CLARK, D.A. 1980. Age and sex dependent foraging strategies of a small mammalian omnivore *Rattus rattus. Journal of Animal Ecology* 49: 549-564.

CLARK, D.A. 1982. Foraging behaviour of a vertebrate omnivore *Rattus rattus* meal structure sampling and diet *bieadth, Ecology* 63: 763-772.

CLARK, D.B. 1982. Population ecology of *Rattus rattus* across a desert montane forest gradient in the Galapagos Islands, Ecuador. *Ecology* 61: 1422-1433.

CLARK, D.B., GUAYASAMIN, C, PAZMINO, OL, DONOSO, C, DE-VILLACIS, Y., 1982. The tramp ant *Wasmannia auropunctata* autecology and effects on ant diversity and distribution on Santa Cruz Island, Galapagos, Ecuador. *Biotropica* 14 196-207.

COLINVAUX, P.A. 1972. Climate and the Galapagos Islands. *Nature* 240: 17-20.

COLINVAUX, P.A. and SCHOLFIELD, E.K. 1976. Historical ecology in the Galapagos Islands. I. A Holocene pollen record from El Junco lake, Isla San Cristobal. *Journal of Ecology* 64: 989-1012.

COPPOIS, G. 1984. Distribution of bulimulid land snails on the northern slope of Santa Cruz Island, Galapagos. *Biological Journal of the Linnean Society* 21: 217-227.

COPPOIS, G. and GLOWACKI, C. 1982. Bulimulid land snails from the Galapagos: 1. Factor analysis of Santa Cruz Island species. *Malacologia* 23: 209-219.

COPPOIS, G. and WELLS, S. 1987. Threatened Galapagos snails. *Oryx* 21: 236-241.

DARWIN, C. 1859. *The origin Species by Means of natural Selection, the Preservation of favoured Races in the Struggle for Life.* John Murray, London. 458 pp.

ELIASSON, U. 1982. Changes and constancy in the vegetation of the Galapagos Islands. *Noticias de Galapagos* 36: 7-12.

HICKMAN, J. 1985. *The Enchanted Islands. The Galapagos Dis-covered.* Anthony Nelson, Oswestry, England. 169 pp.

KASTDALEN, A. 1982. Changes in the biology of Santa Cruz Island between 1935 and 1965. *Noticias de Galapagos* 35: 7-12.

LUBIN, Y.D. 1984. Changes in the native fauna of the Galapagos Islands following invasion by the little red fire ant *,Wasmannia auropunctata. Biological Journal of the Linnean Society* 21: 229-242.

MERLEN, G. 1985. The 1982-83 El Nino: some of its consequences for Galapagos wildlife. *Noticias de Galapagos* 41: 8-15.

PATTON, M.J. 1984. Genetical process in the Galapagos. *Bio-logical Journal of the Linnean Society* 21: 97-111.

PORTER, D. 1822. *Journal of a cruise made to the Pacific Ocean by Captain David Porter in the United States Frigate Essex in the years 1812,1813,1814.* Philadelphia. New York.

ROBINSON, G. and DEL PINO, E. 1985. *El Nino in the Galapagos Islands, the 1982-83 event.* Publ. Charles Darwin Foundation for the Galapagos, Quito. 534 pp.

SMITH, A.G. 1966. Land snails of the Galapagos. In: Bowman, R.I. (Ed.). *The Galapagos.* Proceedings of the Symposia of the Galapagos International Scientific Project. University of California Press, Berkeley, pp. 240-251.

SMITH, A.G. 1971. New record for a rare Galapagos land snail. *Nautilus* 85: 5-8.

Demographic studies on Hawaii's endangered tree snails

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Abstract

Members of the pulmonate subfamily Achatinellinae are endemic to the Hawaiian Islands. Species of these large (15-25mm), colourful tree snails have been going extinct over the last 80-100 years, and remaining populations are found only in high-altitude stands of native forest. In spite of the massive collections of shells that have been accumulated by the world's museums, only meagre, anecdotal information has been collected on achatinelline biology and life history. *Partulina proxima* is one of the four achatinelline species currently under study, using mark-recapture techniques to assess major life history parameters. The study area is on the island of Molokai at an elevation of 1200m. Three single-bush populations have been visited bi-monthly for two years, and all snails found on each visit have been marked, measured and released. Average numbers of snails in the three bushes were 10, 14, and 30, and there was no evidence of significant immigration. Thus population fluctuations appeared to result from birth and death alone. Numbers of reproductively mature adults were only 2, 2, and 6 (about 15% of the snails present) in the three bushes, and each of these adults produced 4-6 offspring per year. Early mortality (and/or out migration) was extremely high, but adult longevity is probably great. The life history traits observed for *P. proxima* (large birth size; slow growth; late maturity; low fecundity; and long life) are similar to those of closely related species in this sub-family studied by the author, but differ in specific details. A life history pattern of this type can only exist in the virtual absence of predation on adult snails. Causes of extinction will be discussed.

Mound spring snails of the Australian Great Artesian Basin

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Abstract

Many of the springs associated with the Great Artesian Basin of Australia contain rare flora and endemic fishes and invertebrates, including at least 24 species of hydrobiid snails in five genera, three of them endemic. Numerous springs have become extinct in the last hundred years because of water extraction from the Great Artesian Basin, and most of the remaining springs are threatened.

Introduction

The central problem in most conservation issues is the protection of habitats. Once these are adequately protected, the survival of the species contained in those habitats is much more likely. Other issues, such as the introduction of exotic competitors, predators or diseases, are secondary, although often very serious, problems.

Situations most difficult to resolve are those in which man's needs for a particular resource conflict with the conservation of that resource. Proper management measures involve controlled access, often resulting in a reduction in utilization which may affect an individual's income or livelihood. The access to water in arid lands is one of the fundamental rights that anyone utilizing such lands might expect but, in arid Australia, the use of artesian water is central to the continued existence of at least 38 species of aquatic invertebrates which live in unusual and biologically unique springs.

Artesian springs

Springs fed from artesian waters are known in several parts of the world and, particularly in arid areas, often contain relict and endemic biota (Cole 1968). The Great Artesian Basin (GAB), one of the largest artesian systems in the world, occupies about 22% of the Australian continent, or about 1.76 million square kilometres, extending through western Queensland to the south-eastern corner of the Northern Territory, north-eastern South Australia and north-western New South Wales (Habermehl 1980). Numerous artesian springs lie on the fringes of this basin (Figure 1), and, because they are a source of permanent water, are of considerable significance in this generally arid area.

Active and extinct spring-formed mounds are distinctive features of the arid landscape in northern South Australia and parts of western Queensland and it is for this reason that the springs are usually called "mound" springs. They are sometimes conspicuously vegetated but often appear as almost bare, white hills.

Calcareous deposits (travertines) are often important in mound formation. Wind-blown sand and accumulated plant debris, as well as mud, sand and gravel carried up with the water, also assist in forming mounds. Some groups of springs mounds are composed predominantly of sand or clay; others are mostly calcareous. Some larger, hill-like formations represent an accumulation of mounds that have welded together. Many artesian springs, however, particularly the more active ones, have not developed a mound and lie at ground level.

There are in excess of 600 springs and spring groups associated with the GAB. They range from damp areas to actively flowing, some with large pools and outflows several kilometres long. The total discharge from all of the GAB artesian springs is estimated to be about 1500 litres per second (Habermehl 1980). Available information is reviewed by Ponder (1986), Zeidler and Ponder (1989) and Boyd (1990).

Climate

The climatic regime in which the springs in South Australia and western Queensland lie, has temperature fluctuations from below zero to well in excess of 40° C. This can have a major impact on the spring biota because, in many spring outflows, the water is only a few millimetres deep and closely follows air temperature (Ponder 1986). Rainfall over most of the GAB is erratic with yearly averages in the 125-250mm range in South Australia and the most western part of Queensland but in the 250-500mm range in the rest of Queensland. Severe flooding occasionally occurs. In some parts of Queensland floods are an annual event but, in the area around Lake Eyre, they occur only about once every 8-10 years. All water courses in the region are ephemeral drainage channels. The larger ones may contain waterholes, many of which are maintained by groundwater seepage. Some springs also occur in water courses and are thus flooded periodically.

A typical spring comprises a vent, an outflow often forming a channel, and a tail which may form an extensive marsh in large springs. A pool is sometimes formed at or near the vent.

Springs may occur in groups associated with the same local fault system. Larger aggregations of springs or spring groups are termed Spring Complexes. Geographically related spring complexes form larger groupings or Supergroups, of which eleven can be recognised around the GAB (Habermehl 1982; Ponder 1986). These are listed and identified on the map in Figure 1. For information on the geology of these springs see Habermehl (1982).

Hydrology

Habermehl (1980) has summarised the chemical composition of artesian water throughout the GAB and Williams (1967) has reviewed the available information on the chemistry of the spring water flowing from the basin.

Total dissolved solids in the springs generally range around 2000 - 4000 mg/1, those in the Lake Eyre Supergroup from about

2000 - 10,000 mg/1 and Dalhousie Springs 650-2000 mg/1. The pH varies from about 7 to nearly 10.

Temperatures taken at the vents range from near air temperature to about 45°C, and the water in the more active springs is typically warm to hot. Paralana Spring, on the eastern side of the Flinders Ranges, which is probably fed at least in part from the GAB, is 62°C and is also radioactive. The temperature in most thermal springs remains remarkably constant. The large warm pools of Dalhousie springs remain very constant but in most springs, particularly the smaller ones, the water rapidly approaches air temperature as it moves away from the vent.

The rate of water flow varies from small seepages to flows of 14.3 megalitres per day from one of the Dalhousie springs. The flow from Dalhousie Springs is the greatest of all the spring groups, being about 6701/sec (Williams 1979; Williams and Holmes 1978; Habermehl 1982).

The spring biota

The flora

Most springs (in all supergroups) contain a luxuriant growth of sedges (usually species of *Cyperus*) which helps to stabilize the sediments and provide shelter for the aquatic fauna. Green and blue-green algae are usually conspicuous. *Phragmites* and, more rarely, *Typha,* form dense stands around the head of some springs. Some of the larger, cooler pools contain aquatic macrophytes.

Only one plant, the button grass *Eriocaulon carsonii* is considered to be endemic to artesian springs. It is found in a few springs near Hermit Hill, in two groups near the northern end of the Flinders Ranges and in Elizabeth Springs in western Queensland (Ponder 1985). Very recently it has also been found living in a few small springs in northern New South Wales. A few other rare plants are also found associated with the springs (Fatchen 1984; Symon 1984,1985).

The fauna

The fauna of the GAB springs includes a number of endemic invertebrates and fishes. Studies on the fishes in the South Australian springs have been in progress since the 1960's (Glover 1973, 1979, 1982; Glover and Inglis 1971; Ivantsoff and Glover 1974; Glover and Sim 1978a, 1978b) but the rich fauna of invertebrates in these same springs, with one exception, were first collected by W. Zeidler in 1974. A comprehensive survey was carried out in 1978 by a team from the Nature Conservation Society of South Australia and included studies on the limnology of the springs (Mitchell 1985). A considerable amount of additional work on the endemic invertebrates has been done subsequently by W. Zeidler and the writer but the results are largely unpublished to date.

Fishes

Little information is known about fishes of the Queensland springs but nine species are said to inhabit the South Australian mound springs (Glover and Sim 1978b; Glover 1979; Crowley and Ivantsoff 1990), although recent electrophoretic evidence suggests that this number may be larger. Most of the fishes found in the South Australian springs also occur in other water bodies, only two species apparently restricted to springs. The introduced Mosquito Fish (*Gambusid*) is common in some of the Queensland springs and, because it is a predator, may pose a threat to the survival of endemic animals.

Molluscs

Small prosobranch snails of the family Hydrobiidae are known to speciate in arid zone springs in the Americas (e.g. Taylor 1966; Hershler 1985) but few other examples have been reported. The hydrobiids found in springs in South Australia and Queensland are often very abundant. There are two major radiations of these snails in South Australia, one in the Lake Eyre Supergroup, the other as yet unnamed, in the Dalhousie Supergroup. In a study of the Lake Eyre radiation (Ponder, Hershler and Jenkins 1989) taxa were conservatively separated morphologically. This study recognises two endemic genera (*Trochidrobia* and *Fonscochlea*) and ten species with four or five species coexisting in most springs. One species (*Fonscochlea zeidleri*) is amphibious, and two groups of congeners, one about half the size of the other, are aquatic. The aquatic species have speciated geographically but *F. zeidleri,* which is much more resistant to desiccation, has not. One or two species of *Trochidrobia* are found in most of the springs and are aquatic and photopositive, differing in behaviour from species of *Fonscochlea* which tend to retreat from light.

The snails in Dalhousie Springs appear to be a single radiation of a genus related to the most speciose of the genera of the Lake Eyre Supergroup. There is good geological evidence (Kreig 1989) to show that Dalhousie Springs developed in the Pleistocene. The speciation of the hydrobiids (Ponder and Colgan, from work in progress) does not appear to have stabilized. There are two sympatric species in the large pools of a few springs, but in most other habitats only one or the other of these species is found. Unlike the snails in the Lake Eyre springs the taxa are not clear-cut and considerable variation occurs within some populations. Different morphotypes occur in different parts of the spring, sometimes separated by long areas of outflow in which only non-endemic snails (*Lymnaea* and *Thiara*) occur. Observations suggest that there is differentiation in response to a number of physical differences in the springs - e.g. spring size, type of water body, speed of current and in particular, water temperature. There is also, apparently, a response to predation by catfish. Snails appear to be larger and thicker-shelled where they coexist with catfish than when they live in similar habitats that lack these fish. Another species belonging to *Fluvidona,* a genus found widely in S.E. Australia, is found in some outflows and seeps at Dalhousie Springs.

The hydrobiid snail radiation in the Lake Eyre Supergroup shows the greatest diversity, and the sympatric taxa currently recognized are readily differentiated. The ranges of some of the taxa are considerable, several found in widely separated spring groups. Morphologically such populations are essentially indistinguishable, although small differences exist in many cases the total number of endemic hydrobiid taxa that are currently recognised in the Lake Eyre Group is 10 (Ponder *et al.* 1989), but recent electrophoretic studies indicate that subdivision of some taxa is necessary.

In any one spring complex in the Lake Eyre Supergroup, the same fauna is found in virtually every type of active spring, whereas at Dalhousie Springs physically different springs, or parts of springs, contain morphologically distinct snails. These observations suggest that different selection pressures are important in driving the speciation in these two supergroups.

Additional species of hydrobiid snails have also been found in the Springvale Supergroup and the Eulo Supergroup in Queensland and the Lake Callabonna springs of the Lake Frome Supergroup (South Australia). Only a single species (genus *Jardinella*) occurs in all of the Queensland localities but in Edgbaston Springs in the Barcaldine Supergroup, there are six sympatric species of *Jardinella* and a bithyniid, as well as an additional allopatric species of *Jardinella* (Ponder and Clark 1990).

Other invertebrates

The crustacean spring fauna includes several interesting endemics. A phreatoicid isopod, *Phreatomerus latipes,* is widespread and abundant in the springs of the Lake Eyre Supergroup and belongs to a monotypic genus and subfamily (Nichols 1943). Species of *Austrochiltonia,* a gammarid amphipod, live in the Lake Eyre, Dalhousie and Barcaldine Supergroups.

An ostracod, *Ngarawa dirga,* is very abundant in many of the Lake Eyre springs and is endemic to this Supergroup. Like the isopod, it has been placed in a monotypic subfamily (DeDeckker 1979). Other undescribed endemic ostracods occur in GAB springs. An unpigmented, blind amphipod lives in some of the seeping mounds at Dalhousie Springs (Zeidler, 1991). A tiny flatworm (Macrostomida) found in the Lake Eyre Supergroup is only one of two records of this order from Australia (Sluys 1986) and a new (undescribed) genus of oligochaete has also been found. No doubt, with careful collecting, additional minute animals will be discovered that will prove to be spring endemics.

Other possible endemic invertebrates in the springs include atyid prawns (Caridina sp.) which have been recorded from Coward and Elizabeth Springs in the Lake Eyre Supergroup (Mitchell 1985) and another atyid, Caridina thermophila, which occurs in springs in the Barcaldine Supergroup. Although this latter species was described from a bore drain it was located near these springs and probably evolved in them. A freshwater crayfish (Charex sp.) may also be endemic to Dalhousie Springs (Sokol, 1987).

Origin and evolution of the spring fauna

The presence of endemic animals, including endemic genera and subfamilies, in some artesian springs suggests that these animals have been isolated in this environment for a considerable period of time. It is probable that at least some of the spring endemics may represent relicts of a more ubiquitous fauna from a generally wetter climatic period in the late Tertiary or early Pleistocene, or they may be a much older fauna that has been associated with artesian springs through much of the Tertiary. The little fossil evidence does not particularly favour either view (Ponder 1986). The two endemic hydrobiid genera in the Lake Eyre Supergroup are found in Pleistocene mounds in that area, indicating that the fauna was diverse then. No older fossil mounds are known.

The springs can be likened to aquatic islands in an arid sea, with each Spring Group a small island group and a Spring Complex an archipelago. Under these circumstances one might expect to see differentiation in populations several kilometres apart as the level of gene flow must be very small. Somewhat surprisingly, observations on the fauna in the springs of the Lake Eyre Supergroup have shown that, at least at the morphological level, marked differentiation does not appear to occur within Spring Groups and Spring Complexes. The hydrobiid snails show the greatest speciation and interpopulation differentiation/variation but even these can show some large ranges, in some cases the same taxon occurring in widely separated spring groups (Ponder *et al,* 1989). Preliminary results of electrophoretic studies on the hydrobiids, crustaceans and fishes indicate, however, that the diversity is greater than indicated by morphological studies.

Hydrobiid snails and crustaceans are absent or reduced in diversity in isolated springs (Ponder *et al.,* 1989; Zeidler 1984;). These observations have important management implications indicating that it is important to maintain a number of springs in a group rather than attempt to salvage only one.

The majority of springs in the northern and eastern areas of the basin do not appear to support endemic faunas (with one notable exception). The eastern springs (see fig 2.1) are in wetter areas with large rivers and contain essentially the same fauna found in other water bodies in the area. The artesian springs in western Queensland are, in many cases, in areas subjected to regular catastrophic flooding. Some of the springs in the Lake Eyre Supergroup that lack fauna are near Lake Eyre south and are occasionally flooded.

Whereas flooding may be an important dispersal agent, especially for fishes, the evidence suggests that flooding can cause extinction or severe depletion of the spring fauna. This, however, is a natural phenomenon whereas termination of spring flow through the interference of humans immediately exterminates the fauna.

Conservation and management

Because the mound springs were, until recently, the only sources of water in some of the arid parts of Australia, they were extremely important to wildlife. Numerous artifacts associated with almost all springs indicate their importance to aborigines and the early explorers used them as stepping stones on their route to the interior (Harris 1981).

Many of the early pastoralists fenced the springs to protect them from stock damage but, with the introduction of artesian wells and bores late last century, the dependence on the springs ceased and the fences were allowed to fall into disrepair. Trampling and fouling of the springs by stock has caused considerable degradation of many of them, affecting both the flora (Symon 1985) and the fauna (Ponder 1985,1986).

Most of the area in which the springs are found is suitable only for sheep and cattle grazing and this industry, like the towns in the area, is dependent on artesian water. About 211 megalitres of water per day is removed from the basin in South Australia alone, compared with 83 megalitres for all of the springs in that state (Boucat and Beal 1977). The heavy usage of artesian water in the last century has been the cause of the extinction of many springs and with them, their aquatic biota. All but one very small group of the once numerous springs in north western New South Wales are now dry, as are many in Queensland, particularly in the western, northern and southern parts of the basin. In some areas the few remaining springs are so reduced in flow that they are highly vulnerable to stock damage and extinctions appear to be inevitable in these instances.

Some pastoralists modify the springs by damming or digging them out, usually resulting in the extinction of the endemic invertebrate fauna (Ponder and Hershler 1984).

Habermehl (1980) has suggested that the GAB has achieved a new steady state condition in which total recharge and discharge are approaching equilibrium again provided no new, major developments occur. Some of the enormous waste that is occurring from free-flowing stock bores is being reduced by the bore capping and control programs being undertaken by the Queensland and South Australian governments but one major development, the bore field supplying water to the Olympic Dam uranium mine (Kinhill Stearns Roger 1982; Kinhill Stearns 1983, 1984), is located near an important group of South Australian springs.

Although overlooked until recently, the conservation of mound springs is now considered to be a matter of importance (Casperson 1979; Harris 1981, 1992; Ponder 1985, 1986; Ferguson 1985; Murphy 1985). It must, however, be appreciated that many of the springs still in existence have been drastically altered since late last century and need to be properly rehabilitated.

The recent incorporation of Dalhousie Springs in a National Park is a long overdue recognition of the importance of that spring group and reflects a growing concern in that State for these unique habitats. Similar protection of other spring groups is essential but must be coupled with proper management and conservation of artesian water if their continued existence and the survival of their endemic biota are to be assured.

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Literature cited

BOUCAT, W.R.P. and BEAL, J.C. 1977. Great Artesian Basin in South Australia, importance of rehabilitation of the uncontrolled flowing wells. Department of Mines of South Australia, Report Bk 77/109.

BOYD, W.E., 1990. Mound springs. In: *Natural History of the North East deserts.* M.J.Tyler, C.R. Twidale, M. Davies and Wells C.B. (Eds.) Royal Society of South Australia, Adleaide. 107-118.

CASPERSON, K.C., 1979. Mound springs of South Australia. Part 1 - Physical features, history, biota and conservation requirements. Department of Environmental Planning of South Australia (unpublished report).

COLE, G.A., 1968. Desert limnology. In: G.W. Brown, Jr. (Ed.) *Desert Biology* 1: 423-486. Academic Press, New York.

CROWLEY, L.E.L.M. and IVANTSOFF, W., 1990. A second hardyhead, *Craterocephalus gloveri* (Pisces: Atherinidae) from Dalhousie Springs, Central Australia. Ichthyol. Explor. Freshwaters 1(2): 113-122.

DEDECKKER, P., 1979. Ostracods from the mound springs area between Strangways and Curdimurka, South Australia. *Transactions of the Royal Society of South Australia* 103: 155-168.

FATCHEN, T.J., 1984. Vegetation. *In: Supplementary environmental studies - mound springs,* Kinhill Stearns, Adelaide, pp. 4-1- 4-23.

FERGUSON, D., 1985. The mound springs: lens on a looming tragedy for Australia's desert lands. *Habitat* 13: 32-33.

GLOVER, C.J.M., 1973. Adaptations of a central Australian gobiid fish. *Bulletin of the Australian Society of Limnology* 5: 8-10.

GLOVER, C.J.M., 1979. Studies on central Australian gobiid fish. *Bulletin of the Australian Society for Limnology* 5: 8-10.

GLOVER, C.J.M., 1982. Adaptations of fishes in arid Australia. Paper 26 *In:* Barker, W.R. and Greenslade, J.M. (Eds.) *Evolution of the flora and fauna of Arid Australia,* pp. 241- 246. Peacock Publications, Frewville, South Australia.

GLOVER, C.J.M. and INGLIS, W.G., 1971. Freshwater fish of South Australia. *South Australian Yearbook:* 27-34.

GLOVER, C.J.M. and SIM, T.C., 1978a. Studies on central Australian fishes: a progress report. *South Australian Naturalist* 52: 35-44.

GLOVER, C.J.M. and SIM, T.C. 1978b. A survey of central Australian ichthyology. *Australian Zoologist* 19: 245-256.

HABERMEHL, M.A., 1980. The great artesian basin, Australia. *B.M.R. Journal of Geology and Geomorphology* 5: 9-38.

HABERMEHL, M.A. 1982. Springs in the Great Artesian Basin, Australia - their origin and nature. B.M.R. Report 235 (unpublished).

HARRIS, C.R., 1981. Oases in the desert: the mound springs of northern South Australia. *Proceedings of the Royal Geographical Society of Australasia, South Australian Division* 81: 26-39.

HARRIS, C.R., 1992. Mound springs: South Australian conservation initiatives. *Rangelands Journal* 14: 157-173.

HERSHLER, R. 1985. The systematics and evolution of the hydrobiid snails (Gastropoda: Rissoacea) of the Cuatro Cienegas Basin, Coahuila, Mexico. *Malacologia* 26: 31-123.

IVANTSOFF, W. and GLOVER, C.J.M., 1974. *Craterocephalus dalhousiensis* n.sp., a sexually dimorphic fresh water teleost (Atherinidae) from South Australia. *Australian Zoologist* 18: 88-98.

KINHILL-STEARNS ROGER, 1982. Olympic Dam project: draft environmental impact statement, prepared by Kinhill Stearns for Roxby Management Services Pty Ltd. 103 pp.

KINHILL STEARNS, 1983. Olympic Dam project. Supplement to the Draft Environmental Impact statement. Prepared for Roxby Management Services by Kinhill Stearns Pty Ltd.

KINHILL STEARNS, 1984. Olympic Dam Project. Supplementary Environmental Studies - Mound Springs. Prepared for Roxby Management Services by Kinhill Stearns Pty Ltd.

KRIEG, G.W. 1989. Geology. In Zeidler, W. and Ponder, W.F. (Eds.) Natural History of Dalhousie Springs, South Australia Museum, Adelaide. XIV + 138pp.

MITCHELL, B.D., 1985. Limnology of mound springs and temporary pools south and west of Lake Eyre. In: Greenslade, J., Joseph, L. and Reeves, A. Eds.) *South Australia's mound springs.* Nature Conservation Society, South Australia. pp. 51-63.

MURPHY, D., 1985. Mound springs: threatened cutback ecosystem. *Australian Conservation Foundation Newsletter* 17 (8): 8.

NICHOLS, G.E., 1943. The Phreatoicoides. Part 1. The Amphisopidae. *Papers Proceedings of the Royal Society of Tasmania* (1942): 1-145.

PONDER, W.F., 1985. South Australian mound springs. Relict faunas in the desert. *Australian Natural History* 21 (8): 352-355.

PONDER, W.F. 1986. Mound springs of the Great Artesian Basin. In: DeDecker, P. and Williams, W.D. (Eds.) *Limnology in Australia,* pp. 403-420. CSIRO, Melbourne, and W. Junk, Dordrecht.

PONDER, W.F. and CLARK, G.A., 1990. A radiation of hydrobiid snails in threatened artesian springs in western Queensland. Records of the Australian Museum 42: 301-363.

PONDER, W.F. and HERSHLER, R., 1985. Hydrobiid studies. In: Supplementary environmental studies - mound springs. Kinhill Stearns, Adelaide, pp. 5-1 - 5-16.

PONDER, W.F., HERSHLER, R. and JENKINS, B. 1989. An endemic radiation of Hydrobiidae from artesian springs in northern South Australia; their taxonomy, physiology, distribution and anatomy. *Malacologia* 31: 1-140.

SLUYS, R. 1986. First representative of the Order Macrostomida from Australia (Platyhelminthes, Macrostomidae). *Records of the South Australian Museum* 19: 400-404.

SOKOL, A. 1987. Yabbies at Dalhousie Springs, northern South Australia: morphological evidence for long term isolation. *Transactions Royal Society of South Australia* 111: 207-209.

SYMON, D.E., 1984. A checklist of plants of Dalhousie Springs and their immediate environs. *Journal of the Adelaide Botanic Gardens* 7 (1): 127-134.

SYMON, D.E., 1985. Botanical notes on mound springs and bores. In: J. Greenslade, L. Joseph and Reeves, A. (Eds.). South Australia's mound springs, pp. 78-83. *Nature Conservation Society of South Australia, Adelaide.*

TAYLOR, D.W. 1966. A remarkable snail fauna from Coahuila, Mexico. *The Veliger* 9: 152-228.

WILLIAMS, A.F., 1979. Sampling and measurement of mound springs, Great Artesian Basin, South Australia. Progress Report no. 3 Warrina, Oodnadatta, Billakalina, and Curdimurks sheets. Geological Survey of South Australia Report Bk 79/66 (unpublished).

WILLIAMS, A.F. AND HOLMES, J.W., 1978. A novel method of estimating the discharge of water from mound springs of the Great Artesian Basin, South Australia. *Journal of Hydrology 38: 263-272.*

WILLIAMS, W.D., 1967. The chemical characteristics of lentic surface waters in Australia - a review. *In:* Weatherby, A.H. (Ed.) *Australian inland waters and their fauna.* Australian National University Press, Canberra. pp. 18-77.

ZEIDLER, W., 1984. *In:* Other fauna studies. Supplementary environmental studies - mound springs. Kinhill Stearns, Adelaide. pp. 6-1 - 6-6.

ZEIDLER, W., 1991. A new genus and species of phreatic amphipod (Crustacea: Amphipoda) belonging in the "Chiltonia" generic group, from Dalhousie Springs, South Australia. *Transactions of the Royal Society of South Australia.* 115: 117-187.

ZEIDLER, W. and PONDER, W.F., 1989. Natural History of Dalhousie Springs. South Australia Museum, Adelaide. XIV + 138pp.

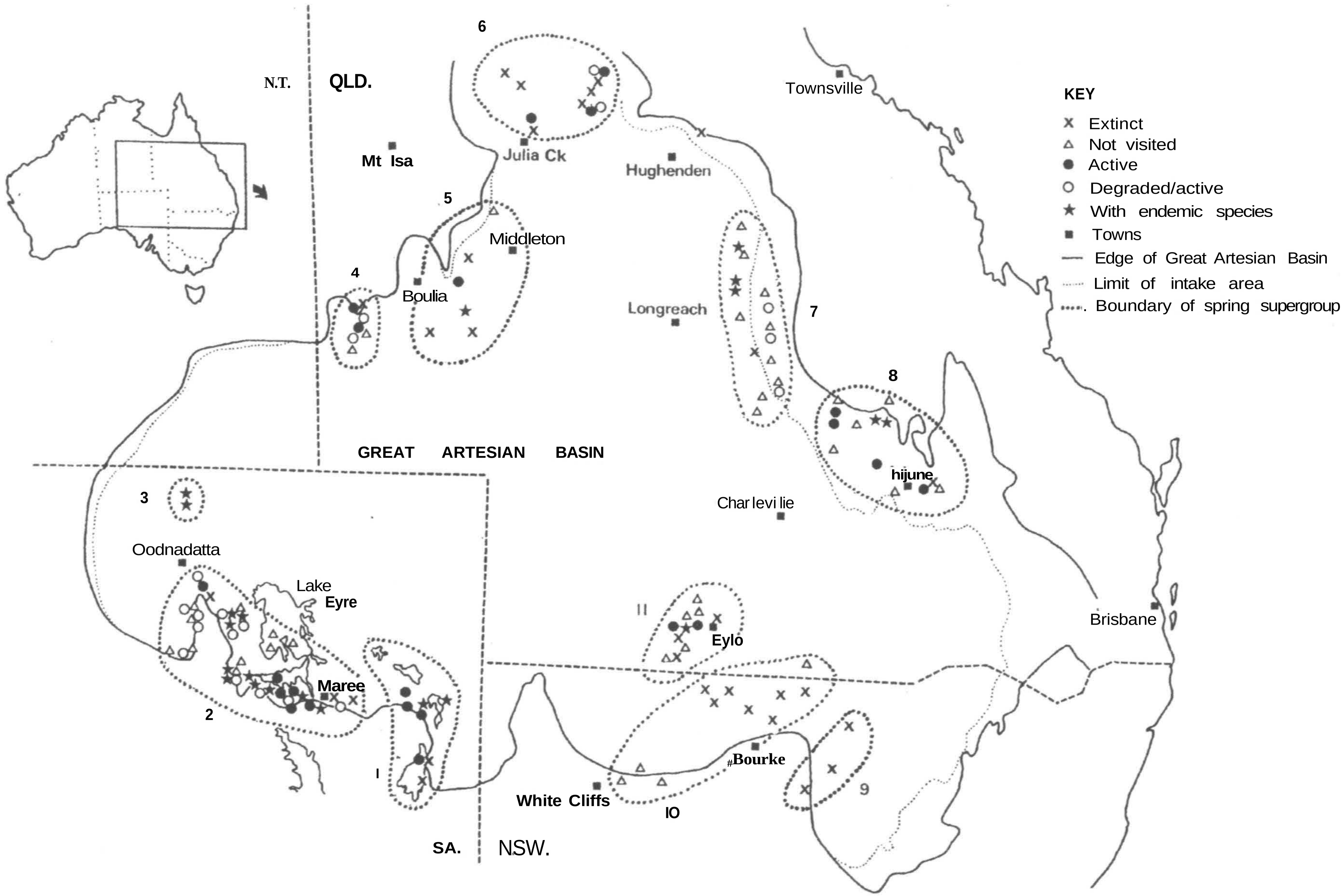

Figure 2.1. The Great Artesian Basin showing the locations of the spring supergroups. The springs are indicated by a variety of symbols (explanations given on diagram). The outline of the GAB is shown by a heavy line and the approximate limits of the recharge areas indicated by dotted lines. Redraw from Ponder (1986). The spring Supergroups are numbered from 1 to 11 and are named as follows:

I. Lake Frome Supergroup; 2. Lake Eyre Supergroup; *3.* Dalhousie Supergroup; *4.* Mulligan River Supergroup; 5. Springvale Supergroup; 6. Flinders Supergroup; 7. Barcaldine Supergroup; 8. Springsure Supergroup; 9. Bogan River Supergroup; 10. Bourke Supergroup; 11. Eulo Supergroup.

Endangered species of land molluscs in Sweden and Madeira

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Abstract

The threat situation for land molluscs in Sweden and Madeira is reviewed. Sweden and Madeira offer highly contrasting examples of topography, climate, human impact and the composition of their respective molluscan faunas. In both cases the molluscan faunas are fairly well known, and long historical records permit an estimate of declining trends and disappearance of species.

Of the 113 species recorded from Sweden, one species may have become extinct in recent years. A further 24 species are subject to threat (e.g. from forestry practices), including species which are highly endangered and species which are still relatively widespread but which may be declining and require special attention. None is endemic to Sweden.

In Madeira the number of indigenous species and subspecies is now estimated to be 190, of which 164 are endemic. Of these, 17 species have not been seen during the last 100 years. A further 55 species are subject to threat of varying degree. Together these species correspond to 33% of the indigenous molluscan fauna, and 36% of the endemic element. Most of the vanished or threatened species are confined to the remnants of the original damp, leafy woodland, and are unable to endure the effects of human impact. The remnants of extremely shell-rich fossil deposits, mainly of Pleistocene age, in the Madeiran islands must also be preserved.

Introduction

In 1968 a symposium on rare and endangered molluscs of North America was held at Corpus Christi, Texas. As far as the author knows, this was the first meeting of its kind. Very pessimistic views of the future of molluscs were expressed by the convenor (Clarke 1970) and most of the participants. Since then, the topic has been studied systematically, and a listing of endangered and threatened molluscs in the United States has been compiled (U.S. Fish and Wildlife Service 1984, 1986). What is the situation in other parts of the world? Examples will be given here from two quite different regions of the Old World.

Sweden and Madeira provide strongly contrasting examples of the problems of preservation of land molluscan faunas. Both in Sweden and Madeira the land molluscs are fairly well known, and a rather long historical record permits an estimate of trends in decreasing numbers and disappearance of species.

Sweden is a wide, sparsely settled country with a climate and vegetation of the northern type. It is, however, impacted by technically advanced industries. The moderately rich mollusc fauna is composed of, in most cases, widely distributed species, none of which is endemic. Madeira, on the other hand, is a small archipelago of oceanic islands, with very pronounced topography, a subtropical climate, and a dense human population exerting a strong pressure on fairly limited natural resources. The mollusc fauna is extremely rich, largely endemic, and of great interest from the scientific point of view. The basic problem in both cases, however, is the same: maintenance and protection of habitats.

Endangered species in Sweden

Sweden encompasses an area of about 450,000 km of which about 55% is woodland. In addition, there is a considerable amount of wetland, alpine area and other wilderness. The climate varies from subarctic to central European cool-temperate. The country is sparsely populated, with an average of 18.5 inhabitants per km, but over much of central and northern Sweden there are fewer than three people per km.

The land molluscan fauna

A total of 113 species of land molluscs have been recorded from Sweden (Walden 1984a). Some of these apparently occurred only accidentally and then disappeared, or exist only in extremely sheltered conditions, e.g. in greenhouses.

None of the estimated 93 "natural" species is endemic to Sweden, although a few have their main distributions restricted to this country and adjacent Norway. For the majority of species, their presence in Sweden represents only a minor part of an extensive distribution in Europe, or the Holarctic as a whole. The question in Sweden, therefore is not that of preserving species from total extinction, but of maintaining species as part of the fauna at the national level, and so far as is possible, to maintain them in reasonably extensive and vigorous populations. For some species, now nearly extinct outside Scandinavia, the situation for protecting populations is particularly favourable in Sweden. This implies a national responsibility to protect these species.

Endangered species

Beginning in 1975 an extensive survey was carried out to identify the endangered species of all groups of terrestrial invertebrates in Sweden. The survey includes information on type and intensity of threat, and the measures required for preservation of species. For molluscs, the survey was essentially based on the extensive and detailed material resulting from the faunistic survey of the Natural History Museum of Gothenburg (see Walden 1965, 1986), in the course of which nearly 20,000 mollusc localities were investigated.

A total of 768 species of invertebrates, of which 25 are terrestrial molluscs, have been placed on a national "Red Data List" (Andersson *et al.* 1987). Most of these molluscs are woodland species, and are treated more thoroughly in a recent publication (Ehnstrom and Walden 1986).

One species, *Vallonia enniensis,* seems to have died out in recent years at its only known site. Four species, known from single or very few sites, are regarded as directly endangered, five as vulnerable, 10 as rare, and a further five are listed as sensitive and of special concern in the context of forestry practice. In addition, there are at least 10 species which will probably never become endangered at the national level, but which are showing decreasing abundance over much of the country, and may become rare if present land use practices persist. They are not listed here, but include, e.g. *Acanthinula aculeata* (Muller) and *Clausilia cruciata* Studer.

Ecological considerations

Most of the species fall into three habitat categories: old woodland species, stenotopic calcareous fen species, and species of dry, steppe-like habitats.

Old woodland species depend on stability and little disturbance. Like certain beetles, they are particularly useful indicators of old woodland. About half of the species are of this type, although some also occur in other habitats. Characteristic species are *Spermodea lamellata, Ena montana,* some of the clausiliids, and, in several provinces, *Acanthinula aculeata* (which is not included on the national list).

Twelve species can be included among the stenotopic calcareous fen species, although, again, some can also occur in other habitats as swampy woodlands. The need for habitat protection is particularly urgent for this group. The rate of destruction of calcareous fens is very rapid. In the province of Ostergotland, about 50% of the fens were drained between 1970 and 1980. In the province of Scania 97% of the wetland, of which a significant part was distinctly eutrophic or calcareous, was drained over a hundred year period. Most species in this group are in the Succineidae and Vertiginidae.

Dry, steppe-like habitats are, to a considerable extent, remnants of a former more open and grazed landscape, and are today dependant on active management for their continued existence. Species characteristic of dry, steppe-like habitats are all more or less pronounced calciphiles. A few are sometimes also found in dry, open woodland on calcareous soil. Characteristic are the *Truncatellina* and the Helicellinae species.

Main threats

In Sweden the greatest threat to land molluscs undoubtedly is from forestry, a consequence of the importance of woods in the country's economy. Not only is the woodland fauna threatened, but so also is the fauna of pastures and glades, as well as the fens, which are drained, and then planted with trees. These habitats are also seriously threatened in farming districts where they have nearly disappeared along with the small deciduous spinneys and swamp woods in hollows, which formerly supported a varied flora and fauna. This landscape is now dominated by monocultures. Other impacts include construction work for roads, buildings, tourist facilities, etc. and the effects of pollution and acid rain. Intensified tourism and recreation cause considerable disturbance to the environment from which even protected areas are not exempt.

Conservation measures

Much of the pressure to which the fauna and flora is now subjected can only be mitigated within the framework of a general coordinated environmental policy. Management of nature reserves must be better adjusted to the requirements of endangered species, as well as to mollusc life in general. It is also important to influence forestry practice so that greater consideration is given to molluscan habitats: marginal vegetation must be spared along shores, in ravines, on slopes and on rough ground in general, so that molluscs can find refugia and survive. Considerable emphasis is laid on such practical recommendations by Ehnstrom and Walden (1986).

Compared with habitat protection, legislation to prohibit collecting is unnecessary in the Swedish context, with the exception of a few, very special cases. No cases of disastrous over-collecting have been reported for molluscs so far (whereas this seems to be a real threat for certain Coleoptera), but it is recommended that the precise sites for certain rare species should not be published.

Endangered species in Madeira

The Madeira archipelago covers a very small area compared to that of Sweden, only ca. 800 km^2. The islands are extremely rugged, with mountain heights up to 1861m. Only small remnants of the original extensive woodland exist today, mainly on the northern slope of the main island of Madeira. The climate is sub-tropical, but varies greatly between islands and at different altitudes. Parts of the main island are very wet. The human population is dense, with an average of 340 inhabitants per km , and land use is intense, particularly with terraced agriculture.

The land molluscan fauna

The mollusc fauna is extremely diverse. 194 recent indigenous species and subspecies have been reported and there are also at least 43 introduced species. Of the indigenous molluscs, 171 or 88% are endemic . The richness of the land molluscan fauna of Madeira is particularly remarkable when compared with the fauna of central and northern Europe where some 280 native and naturalized species are known from an area of about 2.5 million km^2 (Kerney *et al.* 1979). Very few are endemic to the area.

The most striking feature of the Madeiran fauna is its pronounced relict character. Most of the endemic taxa belong to genera or subgenera which are now either extinct in Europe or have evolved from ancestors in Europe. The colonization of Madeira seems to have taken place largely in the mid-Tertiary and was probably facilitated by the presence of now sunken islands between Madeira and the Iberian Peninsula (Pastouret *et al* 1980). Thus Madeira can be considered a living museum for a Tertiary molluscan fauna now extinct elsewhere.

The land molluscs of Madeira were first described in a series of classic works by Lowe (1831, 1852, 1854, 1860) and Wollaston (1878), with contributions from Albers (1854) and Paiva (1867). When these authors were describing the fauna, considerably more woodland existed than is present today, particularly on the southern slope of Madeira proper. The only remaining evidence for several species described in the 19th century is in the collections and published works of the authors.

Census 1986 (Unpublished). The figures deviate from those given in previous papers (Walden, 1983, 1984), owing to recent discoveries and taxonomic revision, and also becuse the present census is restricted to living taxa, whereas the previous figures included extinct forms.

Extinct and endangered species

The current status of the Madeiran molluscan fauna should be assessed in relation to the early studies. Of the endemic taxa, 17 species have not been seen for 100 years despite the collecting efforts of many workers throughout this period, but especially in recent years. These molluscs may now be extinct, or near extinction, although surprising re-discoveries are still possible, such as the recent finding (Hemmen and Groh 1984) of *Idiomela subplicata.*

A further 22 species are very rare; several are restricted to single populations or small areas, and are clearly endangered or vulnerable. There are also 25 rare, though at present not threatened, species. Except for two of the last mentioned, all these threatened species are endemic to the Madeiran archipelago. In all 64 species are concerned.

The figures correspond to 33% of the indigenous taxa and 36% of the endemic taxa. Several species and subspecies, restricted to small, inhabited islands where no threat is discernible, have not been included in the list. Local subspecies of relatively widespread species are also omitted if the species as a whole is not endangered, even if some of the subspecies are highly endangered. There are also some other species for which there have been no records for a long time, but it is uncertain to what extent this is due to insufficient searching. If these actually or potentially threatened species are included, then about 40% of the indigenous species of molluscs can be considered threatened.

Ecological aspects of endangered species

Eleven of the presumed extinct species were confined to damp laurel woodland, and 12 species in the other categories are also found in this or other wooded habitats. Twenty-one species of all categories live in dry, open habitats, a few on Madeira proper, the remaining on the smaller, generally dry islands. In addition there are 20 species which have more specialized modes of life, such as on flushed, mossy precipices or in rocky terrain, although these habitats can occur as mosaic elements in wooded or open terrain.

Main threats

The most serious threat to the land molluscs of Madeira is the destruction of damp laurel woodland. Except for a few species, which can survive in other habitats, the endemic mollusc fauna is virtually totally eliminated when an area of laurel woodland is cleared. Most of this woodland was destroyed in the centuries immediately following human settlement, and it is probable that a number of species had already disappeared when scientific study began in the 19th century. The secondary woodland, largely of pines and *Eucalyptus,* is colonized mainly by introduced species, with a few relatively catholic native species (in particular some large vitrinids).

Other serious threats to the Madeiran molluscan fauna include overgrazing by cattle and construction work for purposes of industry, military activity, and tourism. The establishment of nature reserves for recreational purposes can sometimes conflict with preservation interests.

In contrast to the fauna of laurel woodland, many Madeiran species live on lower levels in dry or mesic habitats, and they appear to have a remarkable ability to survive the impact of man and his animals. Some species seem almost to flourish under these conditions and have even been favoured by the clearing of the former dry, open bushwood. Several species use man-made habitats, such as gardens, terraces and stone walls.

Conservation measures

The conservation of the endemic, relict land molluscan fauna of Madeira must be regarded as a high priority for international conservation action. The question is, however, how such action can be implemented, given the heavy population pressure and the need for improving the standard of living. A project for comprehensive protection and management has been established in the National Park of Madeira (cf. Bramwell *et al.* 1982), and will eventually obtain financial support from international sources. The following measures are necessary with regard to the molluscan fauna:

1) Reserve management must ensure suitable conditions for species sensitive to environmental change. In particular, the impact of tourism - the demands of which the reserves are also intended to satisfy - must be monitored, and encroachment into vulnerable habitats and vegetation must be prevented.

2) The localities of the narrowest endemics should be identified and strictly protected. Threats can be very direct, as is already apparent from construction work, quarrying, plantations, etc. Fortunately, the reserves which have been proposed mainly for botanical reasons coincide fairly closely with the areas where endangered land mollusc species live.

Subfossil deposits

There are extensive Pleistocene and Holocene deposits with land mollusc shells in Porto Santo and easternmost Madeira (Ponta Sao Lourenco). These deposits are of interest not only because they extend the background of the local fauna, but also for evolutionary and ecological reasons. Today the larger part of the deposits has been removed and used for various construction purposes, and preservation of the remaining deposits is now an urgent need.

Addendum

The preceeding article is accordant with the presentation at the IX International Malacological Congress, 1986. Data given and opinions expressed are unchanged. However, during the past nine years extensive further evidence has accumulated, which to a considerable degree is the result of intentional search for threatened species, carried out from 1987 and onwards.

Instead of modifying the original text the current situation is presented in this addendum. - Publications, which were not available when the original manuscript was compiled, are indicated by asterisks in the literature list.

Sweden

A program for systematic inventory of the till then insuffícently known northern regions was launched in 1987. From 1987 through 1994 a further 989 localities were investigated here. Local surveys have also been carried out in certain tracts in southern Sweden. These surveys have considerably extended the knowledge on distribution and ecology of several of the endangered species. A consequence to this is that some species have been moved to lower threat categories. An updated Red Data List for Invertebrates was published in 1993 (Ehnstrom *et al.),* which included 1876 species (Categories 0-4), compared with 768 species in the first edition (Andersson *et al.* 1987). The increase mainly refers to groups whose threat situation had not yet been adequately surveyed at the time of the first edition.

The present threat situation for Swedish terrestrial molluscs is summarised in Table 2.1.

Regarding the number of sites four species have a major part of their extant distribution in Sweden, *viz. Vertigo angustior, genesii* and *geyeri,* and *Catinella arenaria.* These are also placed on the International Red Data List of IUCN (1990) and specifically addressed in the report of Wells & Chatfield (1992). For these species Sweden has an international preservation responsibility.

Madeira

Madeira has attracted increasing interest by malacologists in recent years. Further evidence has been published e.g. by Cook *et al.* (1990), Hemmen & Groh (1985), and Holyoak & Seddon (1986), Hutterer & Groh (1993). A preliminary list of endangered species was published in the report by Wells & Chatfield *(ibid).* However, several taxonomical complexes are still badly understood and revision work is ongoing, and some figures in the present census are uncertain.

In a new census (1994) the number of indigenous recent species and subspecies is estimated to be 203, of which 167 are endemic. The number of introduced species is estimated to be at least 36, of which several have become naturalized and are now widespread.

According to the present census 11 species are now presumed to have become extinct during the last more than 100 years, 48 species (including two which are possibly subspecies) fall in the categories 1-3. A further 15 rare species have not been seen for a long time, but evidence is too uncertain to allow any judgement (category K). Some may even be extinct. Finally there are at least 7 species, still relatively widespread but which must be regarded as potentially threatened (category 4). In the report of Wells & Chatfield (*ibid.*) concern is expressed for the long-term survival of a further 12 species, but these are all well established; some are even among the most common species in the archipelago.

Summing up, six species which a few years ago were supposed to be extinct, have been refound alive, but otherwise the survival situation for the threatened endemic species must now be regarded as more critical than in 1986.

Table 2.1 Degree of threat to terrestrial molluscs in Sweden.

Probable Category 0 (=Ex) species	**Habitat**	**Category 3 (=R) species**	Habitat
Vallonia enniensis (Gredler)	F	*Catinella arenaria* (Bouch.-Chant.)	F
		Vertigo extima (Westerlund)	F,S
Category 1 (=E) species		*Vertigo geyeri* Lindholm	F
Vertigo moulinsiana (Dupuy)	F	*Vertigo genesii* (Gredler)	F
		Spermodea lamellata (Jeffreys)	W
Category 2 (=V) species		*Clausilia dubia* Draparnaud	W,S
Acicula polita (Hartmann)	W,F	*Trochoidea geyeri* (Soós)	D
Cochlicopa nitens (Gallenstein)	F	*Perforatella bidentata* (Gmelim)	F,W
Ena montana (Draparnaud)	W	= 8 species	
Laciniaria plicata (Draparnaud)	S		
Bulgarica cana (Held)	W	**Category 4 (=S) species**	
Oxychilus glaber (Rossmässler)	S	*Succinea oblonga* (Draparnaud)	F,S
= 6 species		*Columella columella* (v. Martens)	F,S
		Truncatellina cylindrica (Férussac)	D
		Truncatellina costulata (Nilsson)	D
		Vertigo angustior Jeffreys	F.W.S
		Lauria cylindracea (Da Costa)	W,S
		Macrogastra ventricosa (Draparnaud)	W
		Balea biplicata (Montagu)	W,S
		= 8 species	

Legend for Tables 1 and 2: W = woodland, F = fen, D = dry habitat, S = special habitat
The Categories of Threat correspond to the pre 1994 IUCN Red List Categories.

Table 2.2 Degree of threat to terrestrial molluscs in Madeira.

Possible category 0 (=Ex) species	**Habitat**	**Category 2 (=V) species**	**Habitat**
Leiostyla simulator (Pilsbry)	W	*Craspedopoma lyonnetianum* (Lowe)	W
Leiostyla abbreviata (Lowe)	W	*Leiostyla filicum* Holyoak & Seddon	W
Leiostyla cassida (Lowe)	W	*Amphorella melampoides* (Lowe)	D
Leiostyla lamellosa (Lowe)	W	*Amphorella cimensis* Waldén	D
Leiostyla gibba (Lowe)	W	*Cylichnidea ovuliformis* (Lowe)	W
Discus guerinianus (Lowe)	W	*Celilioides nyctelia* (Bourguignat)	S
Geomitra coronata (Deshayes)	S	*Geomitra moniziana* (Paiva)	S
Geomitra delphinuloides (Lowe)	S	*Caseolus commixtus* (Lowe)	D
Caseolus galeata (Lowe)[2]	W	*Caseolus subcalliferus* (Reeve)	S
Discula lyelliana (Lowe)	D	*Caseolus calculus* (Lowe)	D
Pseudocamphylaea lowei (Férussac)	S	*Caseolus leptostictus* (Lowe)	D
= 11 species		*Disculella spirulina* Cockerell	D
		Actinella actinophora (Lowe)	W
Category 1 (=E) species		*Actinella obserata* (Lowe)	W
Leiostyla concinna (Lowe)	W	*Actinella armitageana* (Lowe)	S
Leiostyla heterodon (Pilsbry)	W	*Actinella giramica* (Lowe)	W
Leiostyla laevigata (Lowe)	W	*Actinella anaglyptica* (Reeve)	D
Leiostyla corneocostata (Wollaston)	D	*Discula leacockiana* (Wollaston)	S
Leiostyla degenerata (Wollaston)	W	*Discula oxytropis* (Lowe)	D
Lauria fanalensis (Lowe)	W	*Discula turricula* (Lowe)	D
Geomitra tiarella (Webb & Berth.)	D	*Leptaxis portosancti* (Lowe)	W
Geomitra spec. nov[3]	D	*Leptaxis furva* (Lowe)	W
Actinella effugiens (Waldén)	D	*Idiomela subplicata* (Sowersby)	S
Discula tabellata (Lowe)	D	= 23 species	
Discula testudinalis (Lowe)	D		
Leptaxisnivosawollastoni(Lowe)	S	**Category 3 (=R) species**	
= 12 species		Leiostyla vincta (Lowe)	S
		Leiostyla laurinea (Lowe)	W
Species of uncertain status (=K)		*Leiostyla ferraria* (Lowe)	S
(very rare, some possibly extinct, but adequate observations lacking)		*Boettgeria obesiuscula* (Lowe)	S
		Balea perversa (Linnaeus)	S
Leiostyla relevata (Wollaston)	D	*Spirorbula squalida* (Lowe)	S
Leiostyla loweana transiens (Wollaston)[4]	W	*Caseolus calva* (Lowe)[5]	S
Ceciliodes eulima (Lowe)	S	*Actinella laciniosa* (Lowe)	D
Amphorella iridescens (Lowe)	D	*Actinella carinofausta* Waldén	S
Amphorella producta (Lowe)	D	*Discula cheiranthicola* (Lowe)	S
Geomitra grabhami (Wollaston)	S	*Discula bulweri* (Wood)	S
Actinella robusta (Wollaston)	W	*Discula tectiformis* (Sowerby)	D
Discula tetrica (Lowe)	D	*Lampadia webbiana* (Lowe)	S
In addition 7 species living in the marine epilittoral		= 13 species	
= 8+7 species			
		Category 4 (=S) species	
		Craspedopoma trochoideum (Lowe)	W
		Leiostyla monticola (Lowe)	S
		Boettgeria crispa (Lowe)	W
		Janulus stephanophora (Deshayes)	S
		Spirorbula latens (Lowe)	W
		Discula michaudi (Deshayes)[6]	W
		Discula albersi (Lowe)	S
		= 7 species	

Footnotes to table 2.2:

[1] Recent record doubtful.

[2] Syn. *Lemniscia galeata* (Lowe).

[3] Figured by Hemmen and Groh (1985, Fig.6) as *G. moniziana* (Paiva). Possibly a distinct species.

[5] Syn. *Lemniscia calva* (Lowe).

[6] Syn. *Lemniscia michaudi* (Deshayes).

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Literature cited

Note : * indicates that the paper was not available at the date of the original manuscript (1986), and not mentioned in the original version.

ALBERS, J.C. 1854. *Malacographia maderensis sive enumeratio molluscorum quae in insulis Maderae et Portus Sancti aut viva extant aut fossilia reperientur.* Berlin, 94 pp.

ANDERSSON, H., COULIANOS, C.C., EHNSTROM, B., HAMMARSTEDT, O., IMBY, L., JANZON, L.A., LINDELOW, A. AND WALDEN, H.W. 1987. Hotade evertebrater i Sverige. (With English abstract). *Entomologisk Tidskrift* 108: 65-75.

BRAMWELL, D. MONTELONGO, V., NAVARRO, B. AND ORTEGA, J. 1982. Informe sobre la conservation de los bosques y la flora de la isla de Madeira. Mimographed report. I.U.C.N., 13 pp.

CLARKE, A.H. 1970. Foreword. Symposium on the rare and endangered mollusks of North America. *Malacologia* 10 (1): 3.

* COOK, L.M., CAMERON, R.A.D. AND LACE, L.A. 1990. Land snails of eastern Madeira: speciation, persistence and colonization. *Proc. R. Soc. Lond.* B239: 35-79.

* EHNSTROM, B., GARDENFORS, U. AND LINDELOW, A. 1993. Rodlistade evertebrater i Sverige 1993. Databanken for hotade arter Press. 69 pp.

EHNSTROM, B. AND WALDEN, H.W. 1986. *Faunavard i skogsbruket. Del 2 - den lagrefaunan.* (With English summary: The protection and management of endangered and declining invertebrate species in Swedish woodlands). Skogsstyrelsen Publishers, Jonkoping. 351 pp.

HEMMEN, J. AND GROH, K. 1984. Die Gattung *Idiomela* stat. nov. auf Porto Santo (Mollusca: Pulmonata: Helicidae). *Courier Forschungs Institut Senckenberg,* 71: 17-26.

* HEMMEN, J. AND GROH, K. 1985. Eine neue Art der Gattung *Geomitra* SWAINSON auf Porto Santo. *Arch. Moll.* 116, 2/3: 73-80.

* HOLYOAK, D. H. AND SEDDON, M. 1986. An undescribed Leiosfy/a (Gastropoda, Pupillidae) from Madeira. *J. of Conch.* 32: 191-193.

* HUTTERER, R. AND GROH, K. 1993. A review of Macaronesian *Truncatellina* (Gastropoda: Vertiginidae) with description of four new species. *Bocagiana.* No. 151, 19 pp.

KERNEY, M.P., CAMERON, R.A.D. AND RILEY, G. 1979. *A field guide to the land snails of Britain and North-west Europe.* Collins Ltd., 288 pp.

LOWE, R.T. 1831. Primitiae faunae et florae Maderae et Portus Sancti. *Transactions of the Cambridge Philosophical Society* 4: 5-66.

LOWE, R.T. 1852. Brief diagnostic notices on new Maderan Land Shells. *Ann. Mag. Nat. Hist.* Ser. 2, 10: 112-120 and 275-279.

LOWE, R.T. 1854. Catalogus Molluscorum Pneumatorum Insularum Maderenseium. *Proceedings of the Zoological Society of London* 28: 161-218.

LOWE, R.T. 1860. The Cyclostomas of Madeira belonging to the genus *Craspedopoma* of Pfeiffer: with description of four new Madeiran and one new Canarian species. *Annals and Magazine of Natural History* Ser. 3, 6: 114-118.

PAIVA, CASTELLO DE, 1867. *Monographia molluscorum terrestrium, fluviatilum, lacustrium insularum maderensium.* Lisboa, 168pp.

PASTOURET, L., AUZENDE, J.-M., LE LANN, A. AND OLIVET, J.-L. 1980. Temoins des variations sur le Banc de Gorringe (Atlantique du Nord-Est). *Palaeogeography, Palaeoclimatology, and Palaeoecology* 32: 99-118.

U.S. FISH AND WILDLIFE SERVICE. 1984. Endangered and threatened wildlife and plants; review of invertebrate wildlife for listing as endangered or threatened species. *Federal Register* 49 (100): 21664-21675.

U.S. FISH AND WILDLIFE SERVICE. 1986. *Endangered and Threatened Wildlife and Plants.* Washington, D.C., 30 pp.

WALDEN, H.W. 1965. Terrestrial faunistic studies in Sweden. *Proceedings of the First European Malacological Congress:* 95-109.

WALDEN, H.W. 1983. Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. With an annotated checklist. *Annales Zoologici Fennici* 20: 255-275.

WALDEN, H.W. 1984a. Sveriges landmolluker - en artlista med kommentarer. (With English summary: an annotated check-list of the Swedish land Mollusca with remarks on their investigation and comparisons with the other Nordic countries). *Fauna och Flora* 79: 29-43.

WALDEN, H.W. 1984b. On the origin, affinities, and evolution of the land Mollusca of the mid-Atlantic islands, with special reference to Madeira. *Boletim Museum Municipal du Funchal* 36 (158): 51-82.

WALDEN, H.W. 1986. The 1921-1981 survey on the distribution and ecology of land Mollusca in southern and central Sweden. *Proceedings of the Eighth International Malacological Congress:* 329-336.

* WELLS, S.M. AND CHATFIELD, J.E. 1992. Threatened non-marine mollusc species of Europe. *Nature and environment, No. 64. Council of Europe Press.* 163 pp.

WOLLASTON, T.V. 1878. *Testacea Atlantica or the Land and Fresh-water shells of the Azores, Madeiras, Salvages, Cape Verdes and Saint Helena.* L. Reeve and Co., London, 588 pp.

Chapter 3: Endangered Mollusca and methods of conservation

The extinction of endemic snails (genus *Partula*) in French Polynesia: is captive breeding the only solution?

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[Update: Since this paper was written, the seven species of *Partula* endemic to Moorea have become extinct in the wild although several species still exist in captivity. Further information is available in *(a)* Murray, J., Murray, E., Johnson, M.S. and Clarke, B.C. 1988. The extinction of *Partula* on Moorea. *Pacific Science* 42:150-154 and (b)Pearce-Kelly, P. and Clarke, D. (Eds). 1992. *Partula* '92. Proc. Annual Meeting of the *Partula* Propagation Group, August 1992. Zoological Society of London.]

Abstract

Seven species of *Partula* are endemic to the island of Moorea in the Society Islands, French Polynesia. They have been the subject of intensive genetics research since the 1960s, providing an example of microgeographical differentiation that is quoted in many text books on evolution and population dynamics. As a result of fairly continuous fieldwork, they provide a unique case history of species apparently doomed to extinction in the wild as a result of a programme of biological control. In 1977, the carnivorous snail *Euglandina rosea* was introduced to Moorea in an attempt to control the agricultural pest, the giant African snail, *Achatina fulica. E. rosea* is estimated to be spreading through the island at 1.2km a year, eliminating the native *Partula* in its path. One species and one subspecies are considered to have become extinct in the wild since 1981. The ranges of the remainder are rapidly diminishing; one species is probably restricted to a single valley. There appears to be little hope of preserving the species *in situ* at present and efforts are therefore being focused on breeding colonies in captivity. This case history provides an example of the ease with which terrestrial molluscs may go extinct.

Introduction: the Moorean Partula

The land snails of the genus *Partula* are widespread on high volcanic islands in the Pacific, reaching their greatest diversity in the Society Islands of French Polynesia, where 65 species are found. Although little is known about the ecology and general biology of most Pacific land-snails, *Partula* has been studied in detail. It was the subject of three classic monographs by Crampton (1916, 1925, 1932), describing the species from the islands of Tahiti, Guam and Moorea, respectively. The species from Moorea, in the Society Islands, have been further investigated by Clarke and Murray (1969), Johnson *et al.* (1977), Murray and Clarke (1980), and Murray *et al.* (1982). There are two species complexes on the island, one with two species (*P. taeniata* and *P. exigua*) and one with four (*P. suturalis, P. aurantia, P. tohiveana and P.mooreana*). Within the complexes there are frequent cases of local hybridisation and introgression between species. The two complexes are linked through *P. mirabilis*, which hybridises with *P. taeniata* on the southern slopes of Mt. Rotiu, and with *P. aurantia* and *P. tohiveana* in the laboratory. At any particular place on the island, however, as many as four taxa may coexist without interbreeding, remaining clearly distinct in their genetics, morphology and behaviour.

Partula's unique combination of ovoviviparity, low mobility, short generation time, and extensive polymorphism, combined with the comparative ease of its culture in the laboratory make it ideal material for the study of ecological and evolutionary genetics.

Moorea, lying about 20km northwest of Tahiti, is the caldera of an extinct volcano. It has high mountainous ridges (with a maximum altitude of 1207m) dividing the island into a series of steep-sided valleys, the upper parts of which usually support forest that is habitable for *Partula.* The lower ridges are often covered by dense ferns that form barriers to the dispersal of the snails. The Moorean *Partula* are arboreal, found on shrubs and on the trunks of *Hibiscus tiliaceus,* the commonest forest tree. They feed predominantly on epiphytic fungi and algae. Distinct ecological differences have been found between sympatric species. For example, *P. taeniata* predominates on shrubs between two and five metres in height, *P. suturalis* favours the trunks of *Hibiscus,* whereas *P. tohiveana* is most often found on the leaves of the climbing pandanus, *Freycinetia demissa.*

The impact of the introduced predator *Euglandina rosea*

Regular visits to Moorea by Clarke, Murray and Johnson have provided a unique history of the extinction of species by an introduced predator (Clarke *et al.* 1984; Tillier and Clarke 1983). In 1977 the carnivorous snail *Euglandina rosea* was introduced at Paopao, Moorea, with the approval of the Service de l'Economie Rurale and the Division de Recherche Agronomique, in an attempt to control the spread of the agricultural pest *Achatina fulica,* the giant African snail. A second introduction was made later in the northwest of the island. Estimated to be spreading at the rate of 1.2km a year, *E. rosea* now occupies most of the island. Although the giant African snail has declined since 1978, the decline may have had little to do with *E. rosea,* since there was a similar decline on the island of Huahine, where *E. rosea* has not been introduced.

Despite its uncertain effect on *Achatina, E. rosea* has had a devastating impact on *Partula.* With one possible exception, the endemic species are entirely absent within the range of the predator. All seven *Partula* species have been eliminated from the greater part of the island. P. *aurantia* has not been found since 1981 and is probably extinct. *P. mirabilis, P. tohiveana* and *P. olympia* (now considered a geographical race of *P. tohiveana*) are probably also extinct (Clarke *et al.* 1984). It is just possible that *P. mirabilis* may still occur in one isolated valley, but, if so, it is unlikely to survive the year.

P. exigua, which was restricted to the northeast of the island, appears to be exceptional in that a few individuals were found in 1982, within the range of *E. rosea,* although all other *Partula* had been eliminated. It is uncertain whether *P. exigua* still persists. It seems likely that all the remaining species will be extinct within about two years.

Introductions of *E. rosea* to other islands should be prevented. *Partula* in Tahiti, Guam and Saipan are already under threat. *E. rosea* was introduced to Tahiti in 1974, is currently spreading, and appears to have eliminated all the *Partula* in its path. *E. rosea* and two other carnivorous snails, *Gonaxis quadrilateralis* and *G. kibweziensis,* have been introduced to Guam and Saipan and it is thought that there is little hope for the malacological fauna on those islands. In Hawaii, where *E. rosea* has also been introduced, the plight of the subfamily Achatinellinae is already well known, and it is thought to be unlikely that the group will survive much longer in the wild (Hadfield 1986).

Captive breeding

Partula

The only hope of survival for the Moorean *Partula* seems to be captive breeding. Seven species are being bred at universities in Nottingham (United Kingdom), Charlottesville (U.S.A.), and Perth (Western Australia).

Stocks are generally stable but occasionally succumb to what is presumed to be an unidentified disease. Following experiments at Nottingham, the snails there are fed a diet consisting of a finely ground mixture of the following: 3 tsp native chalk, 3 tsp grass, 1.5 tsp trout pellets, 3 tsp oats, 20mg Vitamin E and 0.25 tsp dog food 'Stress'. The addition of Vitamin E seemed to produce an improvement in reproductive success, especially among *P. tohiveana* but the same treatment produced no noticeable improvement in the University of Western Australia stocks. These are breeding reasonably well, with the exception of *P. aurantia,* but survival to adulthood is not very good.

At the University of Virginia in Charlottesville, *P. suturalis* and *P. taeniata* are doing particularly well. Like the Perth snails, they are kept in plastic boxes (12 x 12 x 2.5cm) with moistened toilet paper on the floor, and are fed twice weekly with a few flakes of rolled oats and a dusting of powdered natural chalk. Lettuce is fed occasionally. The boxes are cleaned at each feed. The addition of Vitamin E to the diets of the Charlottesville snails seems to have had little impact. All species of *Partula* need a fairly rapid cycle of wet and dry conditions, rather than a constantly humid regime which is harmful. Temperatures above 26°C also seem to be harmful. It is curious that snails from a tropical rainforest should be susceptible to high humidity and high temperatures.

In 1981, a captive breeding colony of five taxa was established at the Jersey Wildfowl Preservation Trust (JWPT) with the financial support of the Fauna and Flora Preservation Society (Bloxam *et al.* 1984; Bloxam and Tonge 1986). After initial problems, these are doing fairly well and in 1986 there were nearly 400 individuals. Breeding of *P. mirabilis* has been particularly successful but *P. tohiveana* proved difficult and one remaining individual was returned to Nottingham recently. Numbers fluctuate, apparently regardless of husbandry. The current diet of the snails at Jersey is porridge oats, cuttle bone and baby food (8:8:1). At Edinburgh Zoo, a colony derived from individuals supplied by the JWPT had similar problems and the snails had died by 1987. Early efforts at London Zoo were abandoned, but another attempt is being made.

Problems in the captive breeding of invertebrates

Over the centuries, invertebrates have been bred in captivity for food, other economic reasons (e.g. silkworms *Bombyx mori* for silk), for research and for educational purposes, but there are few instances where the main purpose has been to preserve the species (Cooper 1986). The captive breeding of endangered vertebrates, however, is a fully accepted technique of conservation, high among the goals of an increasing number of zoos (Seal 1986). Soule *et al.* (1986) suggest that about 2000 species of large terrestrial animals may have to be kept in captivity for 500 to 1000 years in order to prevent their extinction. Species such as Pere David's Deer *Elaphurus davidianus* and Przewalski's Horse *Equus przewalskii* have already become extinct in the wild, and survive only because of captive breeding programmes. Attempts at reintroduction are now under way for several species of mammals, including the Arabian oryx *Oryx leucoryx,* which was re-introduced to Oman and which is now successfully breeding in the wild (Stanley Price 1986), and many birds, including the well-known case of the Hawaiian goose or nene, *Branta sandvicensis* (Fyfe 1977).

The bias towards vertebrates in efforts to conserve species may lead us to overlook the ease with which invertebrates can be bred. They can often be reared in small spaces, and they may not require costly equipment or housing. They tend to have short generation times, so that breeding success can easily be monitored. They can provide valuable models for the study of problems relevant to other endangered species, such as the problems of inbreeding depression, epizootic disease, and strategies of release.

An explosive growth of butterfly houses in the United Kingdom illustrates how successful programmes can be for breeding and rearing invertebrates. Although butterfly houses are often primarily commercial, their educational role in conservation is important. They have the potential to play an active role, by directing efforts towards rare species, or by initiating field projects (Collins 1986).

The medicinal leech *Hirudo medicinalis* is being bred in captivity because it is heavily in demand for various medical applications, and for research. There is hope that eventually world demand can be met from captive-bred specimens and that the pressure on the dwindling wild population will be reduced (Wells and Coombes 1987).

At present the only real interest in the captive breeding or 'farming' of snails is in Europe, where progress is being made in cultivating *Helix aspersa* to meet an increasing demand for luxury food and, in certain areas, for traditional local food. The breeding of the Roman snail, *H. pomatia,* has met with less success.

Unfortunately there is no commercial incentive to breed the endangered species with which this paper is concerned. Snails such as *Partula* lack the glamour that is generally required in zoo animals. Generally the attention and finance devoted to animals is proportional to their position on the evolutionary scale. Twenty five million dollars have been spent on the captive breeding of the California condor, but there have been difficulties in raising even one hundredth of one percent of that figure for the captive breeding of *Partula.*

Nevertheless, there is scope for a captive breeding programme. 'Snailaria' could be established by more zoos and wildlife collections, either in existing facilities for endangered species (for example, in the New York Zoological Society's St. Catherines Island centre), or in the increasingly popular 'ecosystem exhibits' (for example those illustrating tropical forests). Some zoos already have 'insect houses', and some allocate space in their aquaria to terrestrial as well as to aquatic forms. Berlin Zoo has a specially designed 'Insectarium' (Klos and Lange, 1986).

Some of the Pacific snails are very colourful, and they would make an attractive and educational exhibit. The story of *Partula* is, after all, a unique lesson in island biology and in the fragility of island ecosystems. Commercial butterfly houses, which are anxious to be involved in conservation, often have general invertebrate exhibits. Some already display the giant African snail. They may have the potential to be involved in a captive breeding programme for snails.

There is already a growing awareness that captive breeding can play a valuable role in insect conservation. Morton (1983) proposed the establishment of a "Captive Breeding Institute" for insects. A code of practice for the re-establishment of insect populations (or their reintroduction) has been produced (Joint Committee for Conservation of British Insects 1986) and many of the ideas embodied in this could be extended to other invertebrates. In any case, closer collaboration between field workers, private collectors, laboratories and zoos is clearly needed (Cooper 1986). This is particularly true of *Partula,* where breeding has been successful in research laboratories, but the techniques of culture have only recently been passed on to a few zoos. The IUCN Captive Breeding Specialist Group provides an international forum for the development of collaborative plans for captive breeding programmes (Seal 1986) and is currently considering developing a plan for *Partula.*

Reintroduction to the wild

The ultimate aim of most captive programmes is the reintroduction of endangered species into the wild. Invertebrates are perhaps better known in the context of unwelcome introductions, whether they be accidental, such as that of the giant African snail, or intentional, such as that of *Euglandina rosea,* which was introduced as an agent of biological control. However, there are already a few cases where threatened invertebrates have been successfully re-established, or translocated to a safer habitat. They may provide useful models for future projects. At Woodwalton Fen in Britain, for example, a free-living population of the Dutch race of the Large Copper Butterfly, *Lycaena dispar batavus,* is supplemented annually by specimens reared in captivity (Duffey 1968). The Large Blue Butterfly, *Maculinea arion,* which went extinct in Britain in 1979, was reintroduced experimentally in 1984 using Swedish individuals. So far, the trials have been successful (Regan 1986).

Several species of the threatened New Zealand endemic land snail *Placostylus* have been successfully translocated to islands that are free of predation, and other such translocations have been recommended (Ogle 1979). Molluscs may prove easier to re-establish than many vertebrates. Their low mobilities should facilitate monitoring of introduced populations, although this advantage may sometimes be outweighed by their cryptic habits. Several introductions may be necessary before a population becomes established.

If breeding colonies of *Partula* can be maintained successfully, and if *E. rosea* dies out on Moorea (as could happen through food shortage and cannibalism, although this is perhaps more possible rather than probable), a reintroduction programme could be initiated for *Partula.* For such a programme to be successful, Moorea must continue to provide a suitable habitat. Unfortunately, although it has long been considered one of the most beautiful of the Pacific islands, and although the scientific interest in its fauna and flora is well documented, there have been no local attempts to deal with conservation issues, and no integrated approach to terrestrial research. Natural forests at low altitude have largely disappeared and the remaining vegetation is under pressure from expanding agriculture and a variety of introduced species (Holyoak 1974). Tourism is now a mainstay of the economy. Although still largely restricted to the coast, it may well expand inland, capitalising on the dramatic beauty of the interior.

Much of the remaining endemic fauna and flora is now restricted to the steepest and most inaccessible patches of forest, and is relatively safe. Nevertheless such areas are shrinking. If a reintroduction programme were to be initiated, a firm guarantee of the long term survival of the forest would be required. Holyoak (1974) has called for the protection of the entire mountainous interior, and for its management to cater for the demands of the developing tourist industry. Moorea would be suitable for the creation of a multiple-use reserve, such as a Biosphere Reserve, a form of protected area developed by Unesco's Man and the Biosphere Program. Biosphere Reserves are designed with zoning systems which include core areas that protect natural ecosystems and genetic diversity, areas reserved for traditional uses, experimental areas and rehabilitation areas. The reserves aim to involve local communities in programmes of research and education within their confines. The reintroduction of *Partula* into a reserve created along these lines would provide the necessary framework for the continued protection of the species.

As Conway (1986) points out, preserving segments of habitat without their key species, be they condors, gorillas or snails, is like saving a husk without a kernel: 'Captive propagation of endangered species is to do with kernels'. If the captive breeding and reintroduction of *Partula* is not pursued, there are few other options. Future research may provide techniques for preserving zygotes and embryonic cells, and for regenerating viable individuals, but this will take many years (Soulé *et al.* 1986). There is also a strong case for preserving the DNA of endangered species, a procedure that is relatively simple and cheap, and that retains a large amount of important scientific information, but does not save the animals themselves. At present it must be recognised that *Partula* and its Pacific relatives will be better 'bred than dead'.

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Literature cited

BLOXAM, Q.M.C., TONGE, S. AND HORTON, R. 1984. A preliminary account of the history and management of populations of endangered Moorean tree snails *Partula* spp. at the Jersey Wildlife Preservation Trust. *Dodo, Journal Jersey Wildlife Preservation Trust,* 20: 73-79.

BLOXAM, Q.M.C. AND TONGE, S. 1986. Breeding programmes for reptiles and snails at Jersey Zoo: an appraisal. *International Zoo Yearbook,* 24/25: 49-56.

CLARICE, B.C. AND MURRAY, J. 1969. Ecological genetics and speciation in land snails of the genus *Partula. Biological Journal of the Linnean Society,* 1: 31-42.

CLARICE, B.C., MURRAY, J. AND JOHNSON, M. 1984. The extinction of endemic species by a program of biological control. *Pacific Science,* 38 (2): 97-104.

COLLINS, N.M. 1986. Conservation and exploitation of terrestrial invertebrates. In: *Exotic Animals in the Eighties.* Proceedings of the 25th Anniversary Symp. British Veterinary Zoological Society. April 1986: 111-115.

CONWAY, W.G. 1986. The practical difficulties and financial implications of endangered species breeding programmes. *International Zoo Yearbook,* 24/25: 210-219.

COOPER, J.E. 1986. Captive breeding of invertebrates. *International Zoo Yearbook,* 24/25: 74-76.

CRAMPTON, H.E. 1916. Studies on the variation, distribution and evolution of the *genus Partula.* The species inhabiting Tahiti. *Carnegie Institution of Washington Publication,* 228: 1-311.

CRAMPTON, H.E. 1925. Studies on the variation, distribution and evolution of the genus *Partula.* The species of the Mariana Islands, Guam and Saipan. *Carnegie Institution of Washington Publication,* 228A: 1-116.

CRAMPTON, H.E. 1932. Studies on the variation, distribution and evolution of the genus *Partula.* The species inhabiting Moorea. *Carnegie Institution of Washington Publication,* 410: 1-335.

DUFFEY, E. 1968. Ecological studies on the large copper butterfly *Lycaena dispar* Haw. *batavus* Obth. at Woodwalton Fen National Nature Reserve, Huntingdonshire. *Journal of Applied Ecology,* 5: 69-96.

FYFE, R.W. 1977. Reintroducing endangered birds into the wild: a review. In: Temple, S.A. (Ed.), *Endangered Birds: Management Techniques for Preserving Threatened Species.* Univ of Wisconsin Press, Croom Helm Ltd.

HADFIELD, M.G. 1986. Extinctions in Hawaiian Achatinelline Snails. *Malacologia,* 27(1): 67-81.

HOLYOAK, D.T. 1974. Les oiseaux des îles de la Societé. *L 'Oiseau et la Revue Francaise d'Ornithologie,* 44: 1-27,153-184.

JOINT COMMITTEE FOR CONSERVATION OF BRITISH INSECTS. 1986. Insect re-establishment - a code of conservation practice. *Antenna,* 10 (1): 13-18.

JOHNSON, M.W., CLARKE, B. AND MURRAY, J. 1977. Genetic variation and reproductive isolation in *Partula. Evolution,* 31:116-126.

KLOS, H.-G. AND LANGE, J. 1986. The modernisation of the aquarium at Berlin Zoo. *International Zoo Yearbook,* 24/25: 322-332.

MORTON, A.C. 1983. Butterfly conservation - the need for a captive breeding institute. *Biological Conservation,* 25:19-33.

MURRAY, J. AND CLARKE, B. 1980. The genus *Partula* on Moorea: speciation in progress. *Proceedings of the Royal Society B,* 211:83-117.

MURRAY, J., JOHNSON, M.S. AND CLARKE, B. 1982. Microhabitat differences among genetically similar species of *Partula. Evolution,* 36: 316-325.

OGLE, C.C. 1979. Critical status of *Placostylus* and *Paryphanta* land snails in the far north. *Fauna Survey Unit Report 14,* New Zealand Wildlife Service.

REGAN, S. 1986. The large blue comes home. *Butterfly News,* 8: 8.

SEAL, U.S. 1986. Goals of captive propagation programmes for the conservation of endangered species. *International Zoo Yearbook,* 24/25: 174-179.

SOULÉ, M., GILPIN, M., CONWAY, W. AND FOOSE, T. 1986. The millenium ark; how long a journey, how many staterooms, how many passengers? *Zoo Biology,* 5 (2): 101-113.

STANLEY PRICE, M.R. 1986. The reintroduction of the Arabian oryx *Oryx leucoryx* into Oman. *International Zoo Yearbook,* 24/25:179-188.

TILLIER, S. AND CLARKE, B.C. 1983. Lutte biologique et destruction du patrimoine genetique: le cas des mollusques gasteropodes pulmones dans les territoires Francais du Pacifique. *Genetique, Selection, Evolution,* 15 (4): 559-566.

WELLS, S.M., PYLE, R.M. AND COLLINS, N.M. 1983. *The IUCN Invertebrate Red Data Book.* IUCN, Gland and Cambridge.

WELLS, S.M. AND COOMBES, W. 1987. Status of and trade in the medicinal leech. *Traffic Bulletin,* 8 (4): 64-69.

Conservation of marine molluscs in the British Isles

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Abstract

With a long and varied coastline, broad continental shelf, and long stretches of continental slopes, the seas around the British Isles are exceptionally rich in habitats for marine molluscs. Moreover, their situation at the interface between Boreal and Lusitanian faunas provides interesting examples of distributions limited by climate-related factors. Offshore, the sea bed is typically characterised by sediment communities with such infaunal bivalves as *Venus, Abra* and *Nucula,* while commercially exploitable stocks of scallops and queens (*Pecten, Chlamys*) occur on the surface. Because the waters around the British Isles have good water circulation due to strong tidal streams, pollution is not a significant problem offshore, but there is increasing evidence of damage to benthic populations through use of heavy fishing gear.

Inshore, there are local problems from water pollution from domestic and industrial sources, from oil spills and from anti-fouling paints. Land reclamation schemes and commercial dredging provide additional pressures, as does usage of the coastline for recreation, food and bait collection, field classes, etc. Areas particularly at risk appear to be sediment habitats in estuaries, and the sea inlets or rias such as occur in southwest England.

In the United Kingdom, some progress has been made towards designation of statutory Marine Nature Reserves to include both the intertidal zone and shallow water offshore. Some half a dozen voluntary marine conservation areas have also been established.

Introduction

The British Isles are favourably placed to support a wide variety of marine, brackish and estuarine communities, in which molluscs frequently play an important part. The total coastline of Great Britain and Ireland exceeds 20,000km; that of England and Wales together is estimated at 4415km (Steers 1976), while the much more dissected coastline of Scotland, with its many islands, is estimated at 10,200km (Countryside Commission for Scotland 1978).

Coastlines

The coasts are of varied character, depending on the local geology, past history of changing sea levels and glaciation, and degree of exposure to wave action. In Great Britain they range from the rocky coasts which predominate in the west to low-lying sandy coasts, often associated with dunes and salt marshes, on the east coast, or backed by machair pastures as in the Outer Hebrides. In Scotland there are many sea lochs, and in southwest England their counterparts are the drowned valleys or rias which contain a particularly rich fauna and flora under sheltered and fully marine conditions. In some sheltered inlets, particularly in parts of Scotland and at Lough Ine in Ireland, tidal rapids occur, supporting a diverse fauna and flora on current-swept substrata (Lewis 1964). Estuaries of many types occur, but lagoonal systems are restricted in extent, the best examples being the Fleet in southern England and the brackish sea lochs of the Uists and Benbecula in the Outer Hebrides.

On rocky shores the nature of the substratum is of importance: where this is slaty it is likely to provide crevices which harbour a varied interstitial fauna (Morton 1954), where of limestone, soft sandstone or clay a suitable habitat is provided for borers, notably pholad molluscs. Granite shores have few crevices, and rock pools may be scarce.

Biogeography

The British Isles lie at the boundary of the Boreal and Lusitanian provinces (as was recognised over a century ago by Edward Forbes (Forbes and Godwin-Austen 1859)), many Lusitanian species showing a limited penetration into the south and west of the region (Earll and Farnham 1983). For such reasons, numbers of species are very much higher in the west and southwest than on North Sea coasts. Offshore, the British Isles are surrounded by a broad continental shelf linking them on the one side to the continent of Europe, and on the other to the slope and deep-sea communities of the eastern Atlantic. The shallow-water zone below low tide mark, previously poorly known, has been revealed through the use of SCUBA equipment, adding much to our knowledge of the species and communities, both of rock and sediment (Earll and Erwin 1983).

Offshore shelf

Farther offshore, the shelf typically supports sediment communities characterised by such infaunal bivalves as *Venus, Abra,* and *Nucula,* with commercially exploitable stocks of scallops (*Pecten maximus* (L.)) and queens (*Chlamys opercularis* (L.)) occurring on the surface. To the north and west of Britain the continental shelf gives way to the slope extending to 2000m and beyond, inhabited by a different suite of species (le Danois 1948).

Numbers of molluscs

It is difficult to arrive at an exact figure for the numbers of species of molluscs in the waters adjacent to the British Isles, as this must depend on the limits chosen. As a guide, the following figures for British marine molluscs are based on Seaward (1982):

Gastropoda:			
Aplacophora	8	Prosobranchia	245
Polyplacophora	14	Opisthobranchia	215
Lamellibranchia	223	Pulmonata	4
Cephalopoda	32	Scaphopoda	5
		Total species:	746

The effects of fishing and pollution

Fishing

Because the waters around the British Isles have a vigorous water circulation due to strong tidal streams, pollution is seldom a significant problem offshore, and on the continental shelf the effects of man's activities are chiefly limited to those of fishing gear, and engineering structures such as oil and gas rigs and associated pipelines.

Trawls employing heavy chain groundlines for catching soles, and scallop dredges, are likely to cause considerable damage to the bottom fauna. Scallop dredges have a low catching efficiency, of around 10%, but it seems that, in addition, a similar proportion of the scallops are damaged without being taken (Gruffydd 1972; Caddy 1973; Noel 1982). Trawls and dredges also tend to damage burrowing invertebrates (de Groot 1984), or bring them to the surface where they are rapidly consumed by predators (Caddy 1973; Meyer *et al.* 1981). In addition, such operations break up and destroy hydroids and Bryozoa (notably *Cellaria* spp.) rooted in the bottom. These normally form attachment surfaces for young stages of both queens and scallops (Pickett and Franklin 1975; Pickett 1977), stocks of which are likely to suffer should these attachment surfaces be reduced.

One mollusc which seems particularly susceptible to damage by towed fishing gear is the fan-mussel, *Pinna fragilis* Pennant, which lives vertically in the sediment with its top protruding above the surface. It was formerly common off parts of the Cornish coast, where specimens were brought up entangled in fishing lines or hooks (Couch 1841). However trawls and dredges are likely to have inflicted far more damage to the populations, and today this species is rare, possibly surviving only where the ground is 'rough' and unsuitable for trawling or dredging (cf. Hignette 1983, who describes threats to the Mediterranean fan-mussel from both divers and fishing gear).

In the English Channel fishermen have recently learned to 'jig' for squid (*Loligo forbesi* Steenstrup) when these come inshore to spawn in the late autumn. This exploitation, and intensive bottom trawling for this species which attracts a higher price than many prime fish, seems to have markedly reduced stocks of squid off Plymouth in recent years.

Pollution

In coastal regions there are a variety of threats to molluscs, as to other forms of marine life. These include pollution from industrial and domestic sources, by oil and measures employed to combat it, and from antifouling paints. For example, the deleterious effects of tributyltin, leached from antifouling paints, on the common shore gastropod *Nucella lapillus* (L.) have been identified in a recent paper by Bryan *et al.* (1986). Even concentrations of tin (as tributyltin species) as minute as 1 ng/1. have been found to affect this species, which results in the acquisition of imposex features (male characteristics) by females. These authors have shown that populations of this species have been affected to a varying degree around almost the entire coastline of southwest England, with a very high degree of imposex near harbours and marinas where pollution from tributyltin is likely to be greatest. In the Fal estuary and Helford River *Nucella* is now absent at a number of sites where it was formerly common. Tributyltin was already known to affect spatfall and shell development in *Crassostrea virginica* (Gmelin) (=*gigas*) (Alzieu and Portmann 1984; see discussion by Stebbing 1985); to what extent are other forms of marine life threatened at such low concentrations of this pollutant?

Land reclamation schemes and commercial dredging for aggregates for building provide additional threats (de Groot 1979), as does dumping of sewage and other forms of solid waste. Fish farms are another source of pollution, and there is the possibility that exotic species of clam cultivated in shellfish farms could become naturalised, with effects on the native fauna. Many of these forms of pollution , combined with other pressures (e.g. usage of the coast for recreation SCUBA diving, food and bait collection, field classes) tend to be concentrated in localised areas often around seaside towns or in estuarine and other inlets. Such sites are consequently paricularly at risk.

Population declines

The decline of the native oyster, *Ostrea edulis* L., in British waters over the past 150 years or so has been well documented, and in recent years the sporozoan *Bonamia ostreae* has seriously affected stocks in certain areas (Bucke *et al.* 1984). But to what extent has there been a general decline in our molluscan fauna? The situation is complicated by the large fluctuations which regularly occur in populations from year to year. This seems to be found particularly in certain opisthobranchs. Bivalve species also, notably *Donax,* are well known to have a successful spatfall only exceptionally, so that populations may be very high over a period of years while a single year's brood grows up, followed by a drastic fall to low levels until another spatfall occurs. Other changes appear to be more long-lasting. Thus the bivalve *Spisula subtruncata* (da Costa) virtually disappeared from the Clyde at the end of the last century, and has not subsequently recovered to a significant degree (Barnett and Watson, in press).

An example of extension of the range of a species occurred about 19 years ago when the clam *Mya arenaria* L. suddenly appeared in estuaries in southwest England, where it had not previously been found. Efforts to conserve particular species seem to be fraught with problems when one is faced with such fluctuations in 'natural' populations, but there seems to be a good case for affording protective status to coastal areas having particularly important habitats, or where there are serious threats to the area.

Conservation efforts

Statutory marine reserves

In Great Britain, initiative for the setting up of statutory marine nature reserves (MNRs) has been taken by the Nature Conservancy Council (for progress in the Republic of Ireland and in Northern Ireland see papers in Jeffrey 1984). The groundwork for conservation measures was carried out through two working parties (NCC/NERC1979), and with the passing of the *Wildife and Countryside Act* 1981, it became possible for the first time to establish reserves which extended below tidemark (Gibson 1984). NCC plan to have seven Marine Nature Reserves (MNRs) designated in the next few years, and progress is well advanced for the first two, in Lundy and Skomer, which will be followed by Bardsey and the Menai Straits in Wales and Loch Sween and St. Abb's Head in Scotland (Figure 3.1).

Voluntary conservation areas

There can be no doubt that voluntary conservation areas are much more easily and quickly set up than those with statutory designation - only time will tell how effective voluntary measures can be. Statutory designation allows for the control or prohibition of such operations as trawling, dredging, and spear-fishing (although discharge of any substance from a ship is not unlawful), whereas in voluntary reserves only moral pressures can be brought to bear.

A number of voluntary marine conservation areas or reserves have already been established (Figure 3.2) (Holme 1983; Gubbay 1986). One example of a voluntary reserve is the Roseland Marine Conservation area, set up to conserve a variety of habitats in the outer part of the Fal estuary in Cornwall. The area is threatened by a proposed container terminal on the opposite side of the estuary at Falmouth (Deeble and Stone 1984). The Conservation Area includes intertidal flats with a rich and varied fauna living under sheltered and fully marine conditions, a *Zostera* bed, and the most extensive bed of living calcareous red seaweed ('maerl') in England. There are in addition rocky shores, with varying degrees of exposure to wave action, and the Duchy of Cornwall oyster beds in the Percuil River. To my mind this blend of rich and unique habitats, subject to a potential threat, makes a more powerful case for conservation measures than some of the isolated islands and associated areas, under no particular environmental pressures, which are being considered for designation as Statutory MNRs. The Roseland Marine Conservation Area is listed as a threatened community in the IUCN Invertebrate Red Data Book (Wells *et al.* 183).

The nearby Helford River is another drowned valley or ria, having both rocky shores and intertidal sand and mud flats, with an extensive *Zostera* bed at Helford Passage. The River has a particularly rich molluscan fauna, some 189 species of molluscs having been listed from the River up to the year 1910 (Holme and Turk 1986), with many more having been recorded subsequently.

There is, however, evidence of a decline in the marine life of the River in recent years, which has resulted in a proposal to make the River a conservation area. Because of uncertainties as to the cause of the deterioration, it was decided as a preliminary move to make a 12-month survey of the River, with particular emphasis on the environmental pressures to which it is exposed. This study has been financed by the World Wide Fund for Nature. Pressures on the River include the traditional 'trigging' or raking for shellfish on Good Friday, and the work of Bryan et al. (1986) has shown that tributyltin pollution has resulted in the disappearance of Nucella from the River. Whether either of these have been major factors contributing to the general decline remains to be discovered.

The areas listed for statutory designation and those already established as voluntary marine conservation areas form but a negligible amount of the coastline of Great Britain. Clearly there is a need for conservation measures to be applied to much more extensive areas of coastline than is covered by present plans.

Acknowledgment

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References

Note that in several instances a single reference has been cited to give a lead in to the extensive literature on a particular topic.

ALZIEU, C. & PORTMANN, J. E. 1984. The effects of tributyltin on the culture of *Crassostrea gigas* and other species. *Proceedings of the Fifteenth Annual Shellfish Conference,* 15-16 May 1984, 87-100. Shellfish Association, London.

BARNETT, P. R. O. AND WATSON, J. in press. Long-term changes in some benthic species in the Firth of Clyde, with particular reference to *Tellina tenuis* da Costa. *Proceedings of the Royal Society of Edinburgh, B.*

BRYAN, G. G., GIBBS, P. W., HUMMERSTONE, L.G. & BURT, G.R. 1986. The decline of the gastropod *Nucella lapillus* around south-west England: evidence for the effect of tributyltin from antifouling paints. *Journal of the Marine Biological Association of the United Kingdom,* 66, 611-640.

BUCKE, D., HEPPER, B., KEY, D. & BANNISTER, R. C. A., 1984. A report on *Bonamia ostreae* in *Ostrea edulis* in the U.K. *International Council for the Exploration of the Sea,* Paper CM. 1984/K:9.

CADDY, J. F. 1973. Underwater observations on traces of dredges and trawls and some effects of dredging on a scallop ground. *Journal of the Fisheries Research Board of Canada,* 30.173-180.

COUCH, J. 1841. *A Cornish Fauna, being a Compendium of the Natural History of the County. Part II. Containing the Testacecous Mollusks.* Royal Institution of Cornwall, Truro.

COUNTRYSIDE COMMISSION FOR SCOTLAND 1978. *Scotland's Scenic Heritage.* The Countryside Commission for Scotland.

DANOIS, E. LE 1948. *Les Profondeurs de la Mer. Trente Ans de Recherches sur la Faune sous-marine au large des Cotes de France.* Payot, Paris.

DEEBLE, M. & STONE, V.1984. A port that could threaten marine life in England's Fal estuary. *Oryx,* 19(2): 74-78.

EARLL, R. & ERWIN, D.G. (EDS). 1983. *Sublittoral ecology. The ecology of the shallow sublittoral benthos.* Clarendon Press, Oxford.

EARLL, R. & W. FARNHAM. 1983. Biogeography. pp. 165-208 in R. Earll and D.G.Erwin (eds) *Sublittoral Ecology. The ecology of the shallow sublittoral benthos.* Clarendon Press, Oxford.

FORBES, E. & GODWIN-AUSTEN, R. 1859. *The Natural History of European Seas.* Van Voorst, London.

GIBSON, J. 1984. Marine nature reserves. *Journal of Planning and Environment Law,* October 1984, 699-706.

de GROOT, S. J. 1979. The potential environmental impact of marine gravel extraction in the North Sea. *Ocean Management,* 5, 233-249.

de GROOT, S. J. 1984. The impact of bottom trawling of benthic fauna of the North Sea. *Ocean Management,* 9,177-190.

GRUFFYDD, LL.D. 1972. Mortality of scallops on a Manx scallop bed due to fishing. *Journal of the Marine Biological Association of the United Kingdom,* 52, 449-455.

GUBBAY, S. 1986. *Conservation of Marine Sites. A Voluntary Approach.* Marine Conservation Society, Ross-on-Wye, 18 pp.

HIGNETTE, M. 1983. Croissance de *Pinna nobilis* Linne (Mollusque Eulamellibranchie) après implantation dans la reserve sous-marin de Monaco. Rapports et procés-verbaux des Reunions. *Commission Internationale pour I'Exploration scientifique de la Mer Mediterranee.* 28(3), 237-238.

HOLME, N.A. 1983. Marine nature reserves. *Journal of the Devon Trust for Nature Conservation,* 4, 56-61.

HOLME, N.A. AND TURK, S.M. 1986. Studies on the marine life of the Helford River: fauna records up to 1910. *Cornish Biological Records,* 9, 26 pp.

JEFFREY, D.W. (ED). 1984. *Nature Conservation in Ireland. Progress and Problems. Proceedings of a seminar 24-25 February 1983.* Royal Irish Academy, Dublin.

LEWIS, J.R. 1964. *The Ecology of Rocky Shores.* English Universities Press, London.

MEYER, T.L., COOPER, R.A. AND PECCI, K.J. 1981. The performance and environmental effects of a hydraulic clam dredge. *Marine Fisheries Review,* 43(9), 14-22.

MORTON, J.E. 1954. The crevice faunas of the upper intertidal zone at Wembury. *Journal of the Marine Biological Association of the United Kingdom,* 33,187-224.

NOEL, S. 1982. The scallops that get away... or do they? *Fishing News International,* 21(8), 42-43.

NCC/NERC 1979. *Nature Conservation and the Marine Environment.* Nature Conservancy Council/ Natural Environment Research Council, 65 pp.

NERC 1973. Marine Wildlife Conservation. *Natural Environment Research Council Publications Series B,* 39 pp.

PICKETT, G.D. 1977. Artificial collection of pectinid spat: preliminary experiments in Start Bay, S.W. England, 1975-1977 *International Council for the Exploration of the Sea,* Paper CM. 1977/E:49, 10 pp.

PICKETT, G.D. AND FRANKLIN, A. 1975. Techniques for surveying queen scallop populations: experiments off south-west England in May-June 1974. MAFF Technical Report, 14, 19 pp.

SEAWARD, D.R. (ED), 1982. *Sea Area Atlas of the Marine Molluscs of Britain and Ireland.* Nature Conservancy Council, London.

STEBBING, A.R.D., 1985. Organotins and water quality - some lessons to be learned. *Marine Pollution Bulletin,* 16, 383-390.

STEERS, J.A. 1976. *The Coastline of England and Wales/* (2nd). Cambridge University Press, London.

WELLS, S.M., PYLE, R.M. AND COLLINS, M. 1984. *The IUCN Invertebrate Red Data Book.* International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland

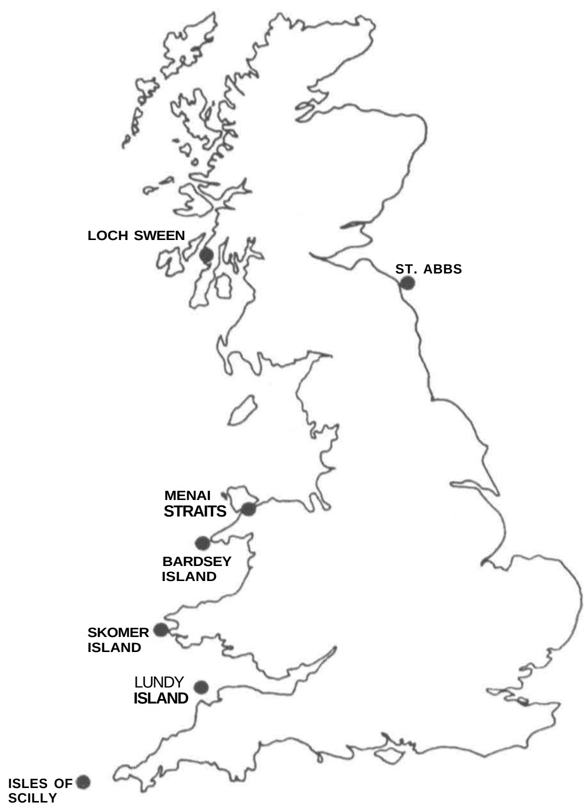

Figure 3.1 Proposed statutory Marine Nature Reserves in Great Britain (from Gubbay, 1986).

Figure 3.2 Location of voluntary Marine Reserves in Great Britain and Northern Ireland (from Gubbay, 1986).

Exploitation and conservation of marine molluscs in India

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[UPDATE: An updated and detailed version of the Status Report on Mollusca by the author appears in *Conservation of Biological Diversity in India* compiled and edited by the Indian Institute of Public Administration, New Delhi (In press).]

Abstract

In recent years shell fisheries have come to occupy a significant place in the Indian economy. Some of the species are collected for their utility as food while many are used in the preparation of ornaments and curios. The present level of exploitation of the marine shell resources does not indicate any rational approach to prevent the depletion of the natural stock. Some of the well known gastropods like *Trochus niloticus, Turbo marmoratus* and *Turbinella pyrum* are not as common today as these used to be a decade ago. *Ancilla ampla* which was once very common on the sandy beach at Digha, on the east coast of India, has now become scarce due to overcollecting for use in curios. The bivalve *Meretrix meretrix* is extensively used in the manufacture of poultry feed and lime and is collected by the tonne from the Subarnareka River in Orissa. These examples point out the need for a judicious exploitation of various species of molluscs. Conservation of some of the commercially important molluscs is suggested.

Conservation projects for the freshwater pearl mussel *Margaritifera margaritifera* in the Federal Republic of Germany

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Abstract

Since the beginning of the 19th century, a decrease in the occurrence of mother of pearl mussels has been observed in central Europe. Later in the century, when interest in mother of pearl subsided, so did the attention paid to the decreasing populations of the mussels. It was not until after World War II that interest focused on loss of mother of pearl mussel habitats in central Europe. The process was induced by Hertel's (1959) report in which he documented the diminution in the Saxon Vogtland which had been the centre of the pearl fishery in Germany. In subsequent years, publications repeatedly reported the disappearance of habitats of the mother of pearl mussels in the German Uplands and other habitats in Europe. By the end of the sixties, comprehensive studies were undertaken at several locations in Germany to investigate the occurrence, biology and population development of the mother of pearl mussel.

In spite of the fact that scientists have studied the pearl as a pearl mussel supplier for several centuries, the life cycle of this mussel is still largely unknown. In the literature, it has always been assumed that the life cycle is comparable to that of other naiads. Investigations recently undertaken in Hanover, Giessen/ Heidelberg and Bayreuth have largely elucidated the life cycle of the mussel, especially in connection with the species conservation project run in the Lüneburg Heath (cf. Jungbluth 1986). These studies provided for the first time hints of the actual extent of the decrease in mussel populations in central Europe. The publication of the first results raised interest in further extensive investigations and initiated other species conservation projects.

Finally, in 1985-1986, (Jungbluth *et al.* 1985a, 1986) a complete inventory and analysis of the situation of the mother of pearl mussel was undertaken nationwide . The results have not yet been published. At the same time, species conservation projects have been intensified and carried on. It is intended that an overall concept of species conservation be prepared. The project will cover all of the Federal Republic of Germany, and interlink ongoing individual projects.

Introduction

As elsewhere, successful species conservation projects for invertebrates have been rare in the Federal Republic of Germany for several reasons. For one thing, interest in studying the local invertebrate fauna on a general level has been decreasing since World War II, and especially since the end of the sixties. For another, systematics and taxonomy at German universities have been in a desperate condition. This state of affairs affects conservation of endangered species in several ways: the required basic biological knowledge, especially of population processes, is often lacking, and the data available on occurrence, density and distribution are, for the most part, many decades old. Frequently, the development of areas and consequent changes in the distribution of species cannot be completely reconstructed because recent records are mostly missing. Due to the continuous splitting-up of landscapes by human settlements and progressing land use, the missing data can no longer be secured. Another problem characterizing species conservation projects is, in general, insufficient financial support from the institutions promoting research in combination with a lack of understanding that species conservation is a long-term matter: in most cases it takes years or, depending on the species, even decades, before a conservation project will yield visible success. Added to this is the frequent need for preceding basic biological research to identify and define the way of life, behaviour, propagation and population development of the species of interest. Generally speaking, species conservation projects are extremely complex with diversified tasks which require not only a very large staff but also sufficient working possibilities (in the field and laboratory), if they are to be successful.

Mother of pearl mussel projects

Stimulated by repeated reports on continuous decreases in populations and losses of areas of mother of pearl mussels (*Margaritifera* (L.), Figure 3.1) in central Europe, W. D. Bischoff (Bischoff 1971; Bischoff and Utermark 1976) was the first to start measures for the conservation of mother of pearl mussel populations left in the Lüneburg Heath in the second half of the sixties. Subsequently, the author began another conservation project in the Vogelsberg/Hesse (Uplands region) (Jungbluth 1980), and since the beginning of the eighties, a third conservation project has been initiated in the Fichtel Mountains (Bauer 1979; Bauer and Eye 1986). All three projects concentrated on individual sites or regions, but from the very beginning, communication among the scientists was excellent, so that initial errors could be prevented. Two of the three projects are established projects today; the third was abandoned because the number of specimens was too small.

Securing chorological data

Each of the three conservation projects was preceded by more or less comprehensive regional inventories which provided insight into two essential facts:

1) The surveys revealed that the biological data contained in the literature were neither correct nor complete.

2) Despite the fact that amateurs and scientists had studied the occurrence of mother of pearl mussels in central Europe for several decades, not all sites of occurrence were known to them (Heuss 1962). Moreover, the distribution data are generally old, particularly for specimens in museum collections, but also in the literature.

Another drawback is the lack of computerized information services which could facilitate the reconstruction of distribution patterns. Because of these limitations, the species conservation projects never went beyond the local level. An overview of the distribution of the species is lacking to this day, and its realization may be very difficult in view of the jurisdictions of the federal and the regional governments.

Reports on the disappearance of populations and losses of habitat as well as species conservation efforts finally led to the first mother of pearl mussel inventory in Bavaria (Bauer 1979). After several attempts, it was finally possible, in 1985, to launch a nationwide analysis of the situation in the Federal Republic of Germany (Figure 3.2). The Project Group of Mollusc Mapping/ FRG (supervised by the present author) is responsible for the execution of the project, and it can refer to comprehensive data bases and literature data banks (Jungbluth *et al.* 1985a). This nationwide analysis of the condition of the mother of pearl mussels in our country will be completed by the end of 1987.

The objectives of the project include:

1. Mapping of the recent mother of pearl habitats and localities in the Federal Republic of Germany;
2. Investigation of the composition of the populations (age structure, number of individuals and density);
3. Analysis of the biotic and abiotic habitat conditions.

To accomplish these objectives, all data known from the literature on the occurrence of the mother of pearl mussels are being checked, as are locality data documented by specimens in private and museum collections. An estimate of the total number of examined pearl creeks amounts to more than 300 [in 1987].

The goal of the investigations is the development of an overall species conservation concept for the region covered by the Federal Republic of Germany.

Securing Biotopes

The results so far obtained from the project supply clear evidence of the necessity of comprehensive biotope conservation as an indispensable prerequisite to successful species conservation in invertebrates. This requirement has been taken into account in the current species conservation projects in that attempts have been made to secure appropriate sections of running water as nature conservation areas. Utilization of these areas is limited, alterations are not permitted, and access is prohibited to the extent necessary. Biotope improvement measures such as re-naturalization of the water sections and bank vegetation have also been instituted.

Securing populations capable of reproduction

Since the existing mussel populations are mostly over age and juvenile animals have not appeared for years or even decades, the most urgent task is to develop populations capable of reproduction. Generally, this means that the individuals still existing, yet dispersed over large sections of running water, have to be concentrated in selected creeks or trenches.

Securing propagation.

To secure propagation, a sufficient number of host fishes has to be made available for the larvae (glochidia) during the phase of their discharge from the gills of the mother. In central Europe, the only known host is the brown trout (*Salmo truttafario* L.). Development from the larval stage to the independently viable juvenile mussel on the river trout has been observed repeatedly and documented (Jungbluth and Utermark 1981).

Since development of mussel larvae on the host fish is usually longterm, extending over the winter period (July/August to May/June), provisions must be made to make sure that the host trout will neither migrate nor be fished. These provisions will further ensure that the juvenile mussels will be concentrated and grow up in the selected water section (Wächtler 1986).

This work must be accompanied by studies in which particular attention is paid to the site where the juvenile mussels are developing during their first four years, in order to fill gaps still existing in knowledge of these aspects of life history. Today it must be assumed that the majority of juvenile mussels die during this phase in the hyporheic interstitial — most probably because of unsuitable abiotic living conditions.

Securing populations

The populations in the test facilities and areas require many years of observation and control if populations with a balanced age structure are to be restored. Suitable measures for this are half-artificial fish host infections under laboratory and field conditions (cf. Wellmann 1943). The test periods to be fixed for these species conservation projects are decades, not years.

Results

Since the end of the 1960's, several species conservation projects have been launched in the Federal Republic of Germany for preventing extinction of the mother of pearl mussel. The studies cited above helped to clarify most of the questions pertaining to the life cycle of these mussels. At the same time, critical phases of the life history of the mussels were identified. These provide timetables for the commencement of the conservation projects. Finally, the species protection projects prepared the ground for the realization of a nationwide situation analysis (1985/1987). Among other purposes, the results of this analysis will be used for developing an overall species conservation concept including and interlinking the individual projects hitherto underway. Nearly 20 years of continuous efforts of species conservation have also resulted in a comprehensive documentation of the literature on the mother of pearl mussel (Jungbluth *et al.* 1985b).

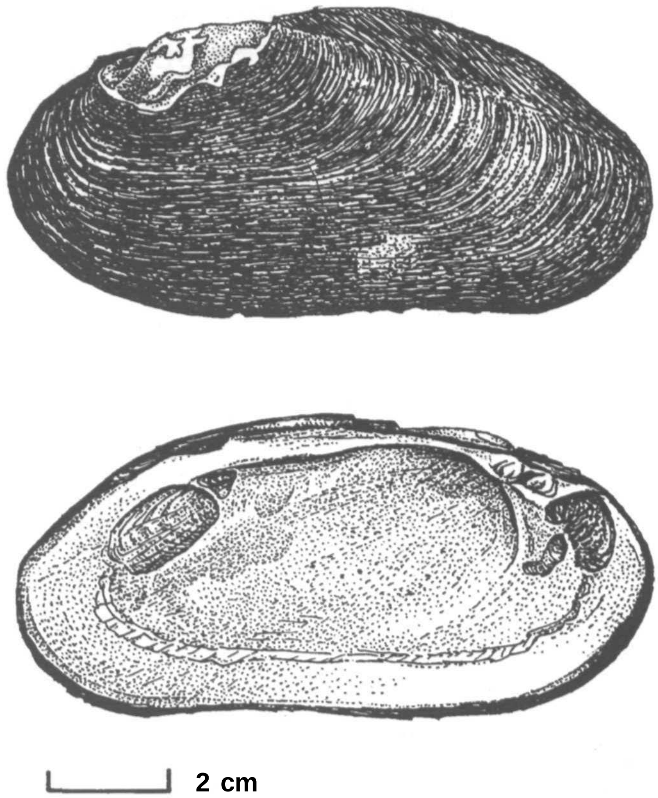

Figure 3.1 *Margaritifera margaritifera* (L.) Ellersbach - "Am Wald" E Rixfeld/ Vogelsberg/ Upper Hesse - Germany. In Coll. J.HJungbluth; Drawing: Helmut Stocker.

Literature Cited

BAUER, G. 1979. Untersuchungen zur Fortpflanzungsbiologie der Flusperlmuschel (*Margaritana margaritifera*) im Fichtelgebirge. *Archivfur Hydrobiologie* 85, 152-165.

BAUER, G. AND EICKE, L. 1986. Pilotprojekt zur Rettung der Flussperlmuschel *(Margaritifera margaritifera* L.). *Natur und Landschaft* 61, 140-143.

BISCHOFF, W.-D. 1971. Die Flussperlmuschel in der Lüneburger Heide - ein Versuch ihrer Erhaltung. *Mitteilungen der deutschen malakozoologischen Gesellschaft 2,* 303-305.

BISCHOFF, W.-D. AND UTERMARK, W. 1976. Die Flussperlmuschel in der Lüneburger Heide, ein Versuch ihrer Erhaltung. 30 *Jahre Naturschutz und Landschaftspflege in Niedersachsen* 1976, 190-204.

HERTEL, R. 1959. Die Flussperlmuschel (*Margaritana margaritifera* L.) in Sachsen. *Abhandlungen und Berichte des Staatlichen Museums für Tierkunde Dresden* 24, 57-82.

HEUSS, K. 1962. Ein neues Flussperlmuschel-Vorkommen in der Röhn. *Mitteilungen der deutschen Malakozoologischen Gesellschaft* 1, 22.

JUNGBLUTH, J.H. 1980a. Biotopschutz-Projekte zur Bestandssicherung gefährdeter Arten am Beispiel der Flussperlmuschel [*Margaritifera margaritifera* (L.)]. *Verhandlungen der Gesellschaft fur* Ökologie 8 (Weihenstephan), 321-325.

JUNGBLUTH, J.H. 1980b. Probleme und Möglichkeiten des Arten-und Biotopschutzes bei Muscheln. *Natur und Landschaft* 55, 9-12.

JUNGBLUTH, J.H. and UTERMARK, W. 1981. Die Glochidiosis der Salmoniden in Mitteleuropa: Infektion der Bachforelle *Salmo trutta fario* L. durch die Glochidien der Flussperlmuschel *Margaritifera margaritifera* (L.). *Fisch und Umwelt* 10, 153-165.

JUNGBLUTH, J.H., BÜRK, R. NESEMANN H. and SCHEURIG, A. 1985a. Flussperlmuschel Erfassung in den Mittelgebirgen. Neckarsteinach und Mainz [unveröffentlichtes Gutachten über die rezenten Vorkommen in sechs Bundesländern].

JUNGGLUTH, J.H., COOMANS, H.E. AND GROHS, H. 1985b. Bibliographic der Flussperlmuschel *Margaritifera margaritifera* (Linnaeus 1758) [Mollusca: Pelecypoda]. *Verslagen en Technische Gegevens, Instituut voor Taxonomische Zoölogie* (Zoölogisch Museum) Universiteit van Amsterdam 41, XXXI, 220 s.

JUNGBLUTH, J.H., BÜRK, R. and GROH, K. 1986. Flussperlmuschel-Erfassung in Bayern. Neckarsteinach [unveröffentlichtes Gutachten über die rezenten Vorkommen in Bayern.

WÄCHTLER, K. 1986. Zur Biologie der Flussperlmuschel *Margaritifera margaritifera* (L.). *Entwicklung, Gefährdung, Aussichten. Naturwissenschaften* 73, 225-233.

WELLMANN, G. 1943. Fischinfektionen mit Glochidien der *Margaritana margaritifera.* Z. Fisch. 41, 385-390.

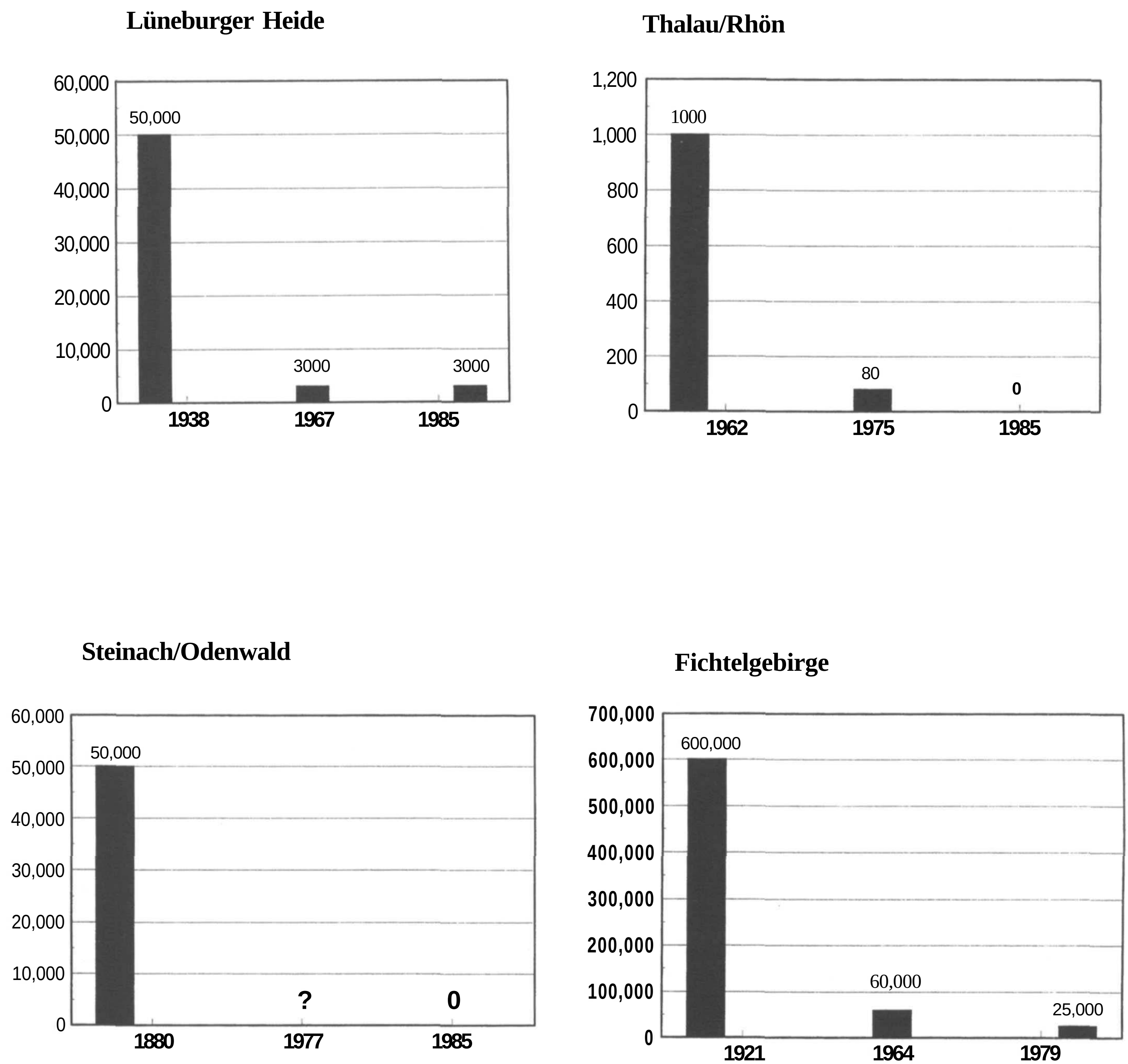

Figure 3.2 The decline of populations of the Mother of Pearls in Germany.

The freshwater pearl mussel, a protected but endangered species in Finland

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Abstract

The freshwater pearl mussel (*Margaritifera margaritifera* (L.)) has been protected in Finland since 1955. In 1978, the World Wildlife Fund in Finland and the Zoological Museum of the University of Helsinki established a working group to study the distribution, ecology and protection of the species.

At the beginning of this century, there were about 200 rivers with this mussel in Finland. At this moment only 25% of these rivers have a population of the species. Decades ago, heavy collection, timber floating, and water pollution threatened the populations of *Margaritifera.*

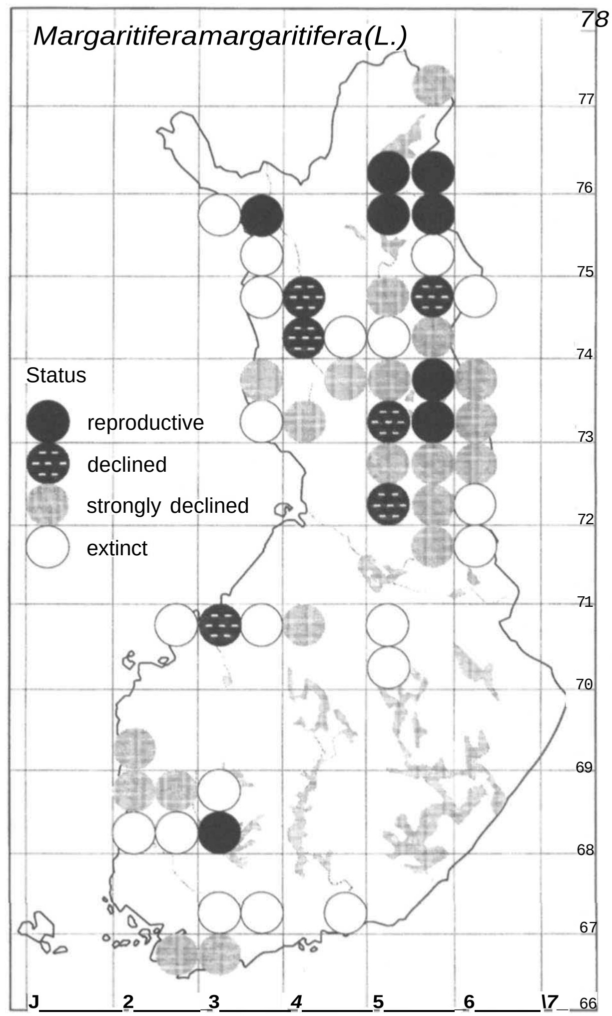
The problem now is loss of proper environment for the species. This is caused by a variety of factors: deepening and straightening of water-courses for preventing flood damage during ice cover in the spring; building of power stations; daily regulation of water levels; pollution of water by agriculture, industry or settlement wastes; and pollution of river bottoms with organic matter during the drainage of peat-moors.

During the last eight years the "Margaritifera" group has checked about 60 rivers. The species is on the verge of extinction in southern and western Finland and in western Lapland. In this area it has been found in only ten rivers, and breeds in only three of these rivers.

In eastern Lapland, between 65°N and 67°N, the species is more common, and there are rivers with populations exceeding 100,000 mussels with densities exceeding 100 specimens/m^2. However, the populations are endangered here as well, mainly because of drainage of peat-moors.

Because of engineering works, about 4000 mussels have been transferred from one place to another in the same river, or from one river to another. After seven years the success rate is 80-90% in the same river and 50% at best in transfer to another river.

The "Margaritifera" group has carried out morphological and ecological baseline work as well. Growth of the shell is 25% slower in Lapland than in southern Finland. Morphological features are so typical in different rivers that it is possible tell the origin of a population, even to name the river of origin. Correlation analyses of water quality, humus content, vegetation, bottom quality, and the rate of water flow have been carried out in rivers from which the species has disappeared, in rivers where it no longer breeds, and in rivers where populations remain. Heavy metals have also been analyzed. Because of their long lifespan, the freshwater pearl mussel can be used as an indicator species of river quality over long periods of time.



A proposal for placing three Slovak molluscs on the IUCN Red Data List

J. Stêffek

Update: Readers are referred to the following references for more recent information on Slovakian molluscs:

LOŽEK, V. 1989. Z ïervené knihy našich mekkyšº - relikt z konce doby ledové. Živa (Praha), 37 (6): 270.

LOŽEK, V. 1990. Z ïervené knihy našich mêkkýšº - alpská v¡etenatka na V¡áïniku. Živa (Praha), 37 (2): 78.

LOŽEK, V. 1991. Z ïervené knihy našich mêkkýšº - k osudu skalnice *Chilostoma rossmaessleri.* Živa (Praha) 39 (2):79.

ŠTEFFEK, J. 1987. Some Slovakian molluscs entered in the International Red Book. Pamiatky a priroda (Bratislava) 18 (2): 68-69. (In Slovak).

ŠTEFFEK, J. 1987. Endangered, rare and important mollusc species in Slovakia. Ochrana prirody (Bratislava) 8: 43-52. (In Slovak).

ŠTEFFEK, J. 1992. In: Wells, S.M. and Chatfield, J.E. (Eds.). Threatened non-marine molluscs of Europe. Nature and environment 64. Council of Europe Press, Strasbourg. 164pp.)

Abstract

Whenever animal or plant species are exposed to danger, their rarity and significance can only be judged from knowledge of their ecology, distribution, and possible threats in the area of their distribution. The incessant growth of pollution and other negative impacts in the landscape implies that the word "protect" will have to be gradually superseded by the word "save".

This paper deals with an assessment of the current status of molluscs in Slovakia. V. Ložek, Vl. Hudec, J. Brabenec, S. Mácha, L. Lisický, V. Kroupová, and V. Pfleger have provided the information on exposure to danger, rarity and significance of each species.

The molluscs of Slovakia

Two hundred and forty six species of molluscs are known in the territory of Slovakia. Not considered are species that may have been imported with exotic plants or by aquarists and which live only in hothouses, aquaria, or thermal springs (for example, *Melanoides tuberculata, Helisoma trivolvis, Gulella io, Zonitoides arboreus, Pseudosuccinea columella,* etc.).

On the basis of the size of the area of distribution, number of localities of occurrence, and origin, the molluscs of Slovakia are classified into four groups:

1. Endemic *species: those occurring only in* a *small part of* Slovakia.
2. Species with wide distribution: those with distribution within the boundaries of Slovakia either at one or several localities.
3. Early Recent species: molluscs which have a patchy distribution.
4. Species with rapidly declining stocks, or in which the number of localities has recently declined either because of chemical pollution or habitat disruption or destruction.

Molluscs may also be categorized with respect to their degree of exposure to danger:

1. Critically threatened species: molluscs occurring at present in Slovakia at one or several localities, but which, if not protected, are in danger of extinction.
2. Threatened species: species found with declining frequency, in localities which are vanishing, or for which fewer than ten localities are known.
3. Rare species: species with their limits of distribution within Slovakia.
4. Significant species: species which, though not immediately threatened, nevertheless may be associated with endemics or which are important in terms of zoogeography.

Molluscs suggested for inclusion in the Red Book

Three mollusc species in Slovakia are proposed for inclusion in the IUCN Red List.

Spelaeodiscus tatricus Hazay, 1883, is endemic to the Belianské Tatry Mountains where it occupies a small area of the Tatra Basin in the area of the Suchá dolina Valley. It is neither abundant nor directly threatened. However, its entire distributional area coincides with that of the Tatra National Park, an attractive area for tourists, and thus it is a good candidate for inclusion with other rare species.

Cochlodina fimbriata remota Ložek, 1952, is endemic to the northern part of Vtáïnik Mountain. It occurs in a very small area in the neighbourhood of the Bystrý potok Brook. Its territory is in a flood valley between two rivulets in a sylvan environment within the Ponitrie Protected Landscape Area, a locality affected by the exhausts from nearby factories. The effect of these exhausts has not been monitored. Placing it on the register would protect it from clear felling which will change both climate and habitat conditions.

Alopia bielzi clathrata Rossmässler, 1857, is an endemic of the Slovak Karst. Its territory is that of the slopes of the Zádielska Dolina Valley and adjacent rocky biotopes. Its entire area of distribution is part of the Slovenský Kras Protected Landscape Area, which is further protected through its designation as a state nature preserve. The single potential threat to the area is the presence of a cement factory near the valley mouth. The effect of the exhaust from the cement factory has not been monitored.

Other endemic molluscs such as *Chondrina tatrica* Lozek, *Chilostoma cingulella* (*Rossmässler, 1837*), *C. rossmaessleri(L.* Pfeiffer, 1842), and *Sadlerianapannonica* (*Frauenfield,* 1865) are not proposed for protected status because of the many locations from which they are known and their relatively abundant populations.

Genetic aspects of mollusc conservation *(Nautilus)*

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Abstract

Fishermen presently harvest large numbers of *Nautilus pompilius* in the Philippines for the specimen shell trade. Overfishing has resulted in marked decreases in abundance of this species in some areas and population recovery is prevented by continued exploitation of these long-lived, K-selected cephalopods. Economic factors appear to prevent over-exploitation elsewhere as few fishermen are prepared to undercut the present price of approximately U.S.$1 per shell in the Philippines. Recent genetic studies by the author show that there are at least five or six other species of living *Nautilus;* these species and their ranges will be described. The conservation status of the rare *N. scrobiculatus* will be discussed.

Chapter 4: Sustainable utilization

The shell trade: a case for sustainable utilization

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Abstract

The scale of international trade in ornamental shells has recently become a subject of considerable concern: more than 5000 species may be involved and international trade in unworked ornamental shells amounts to thousands of tonnes annually. The Philippines are a major exporter of shells; the United States and Japan are major importers. Major concerns are those of over-exploitation and the fear that ecological balance in some localities may be upset by depletion of species that play a key role in ecosystem function. The impact of commercial collecting on most of the species involved in trade is unknown. No marine shells are presently threatened with extinction because of over-collection, although some rare shells with restricted geographical distribution are subject to local depletion. A variety of management strategies are possible, including protection of vulnerable species, introduction of fishery quotas, and establishment of fishery and non-fishery zones. Unfortunately, little is known about the biology and distribution of many species.

Introduction

Marine molluscs are used by man for a variety of purposes and are also of considerable indirect benefit because of their role in food chains and their contribution to secondary production. Throughout the world there is an enormous food fishery, especially for gastropods, bivalves and cephalopods, amounting to millions of tonnes annually. In this study we concentrate on the use of molluscs for their shells.

This report is concerned primarily with molluscs which are valued for their aesthetic appeal. Most of these molluscs are tropical species. Despite their importance, particularly in developing countries, they have received little scientific attention compared with species valued as food. A number of terrestrial molluscs are involved in the ornamental shell trade, but these are outside the scope of this paper.

It is difficult to categorise shells satisfactorily according to their uses, as many are collected for several purposes. The main categories are shown in Table 4.1. With certain species, for

Table 4.1 Some uses of mollusc shell and examples of molluscs involved.

	EXAMPLE OF MOLLUSCS	OUTLETS/PRODUCTS
ORNAMENTAL SHELLS	Mostly large, colourful, relatively cheap, plentiful. Mostly gastropods*, some bivalves, including giant clams.	Whole shells used as 'souvenirs' and decorations. Trade; private collections.
'RARE' OR SPECIMEN SHELLS	Few in trade; expensive; mostly narrow endemics and/or deep water gastropods*.	Collectors' items. In trade; private collections.
SHELLCRAFT	a) *Strombus gigas*, *Cassis* spp., *Cypraea* spp. b) *Placuna* spp. (window-pane oysters) c) Small shells such as cowries, dove shells, cockles d) *Turbinella pyrum* (chanks)	Cameos, lampshades etc. as in c) Lampshades, windchimes, boxes. Handbags, jewellery, other decorative 'souvenirs'. Bangles, jewellery.
MOTHER OF PEARL OR COMMERCIAL SHELL	*Trochus niloticus* (commercial trochus), *Turbo marmoratus* (green-snail), *Pinctada maxima* (gold-lip pearl shell), *P. margaritifera* (black-lip pearl shell)	Buttons, inlay work, jewellery, shellcraft.
INDUSTRIAL SHELL	Giant clams (Tridacnidae)	Constituent of pottery glazes; manufacture of floor tiles.

*Families of molluscs particularly popular with shell collectors include cones (*Conus spp.*), cowries (*Cypraea spp.*), ceriths (*Cerithium spp.*), strombs (*Strombus spp.*), murexes (*Murex spp.*) and augers (*Terebra spp.*).

example, spider shells, *Lambis* spp., the queen conch, *Strombus gigas*, and giant clams, Tridacnidae, both shell and flesh can be used. Whether or not this happens depends on demand and relative values: in the Caribbean the meat of the queen conch is in great demand, and shells are often discarded; similarly, demand for the meat of giant clams in Southeast Asia is generally higher than for the shells, although the shells are also of great value, especially in the Philippines (Munro 1988, Munro and Heslinga 1983).

Shells of some species have several alternative uses. For example, the entire giant clam shell is used in the ornamental trade while broken pieces are used for jewellery. Ground up giant clam shell is used as a constituent of pottery glazes and in the manufacture of floor tiles. Some gastropods and bivalve shells are collected primarily for 'mother of pearl', and are traded as whole shells for ornamental purposes.

The number of species in trade is very large: 5000 species may be involved (Abbott 1980), about a quarter of the estimated world total of marine gastropod species. About 1000 species appear in Philippine trade alone (Anonuevo *et al.* 1982) with at least 139 'commercially viable species' used in the shellcraft industry. Of these species, 80 are common and widely used, 24 uncommon and sometimes used, and 35 rarely used.

Volume of trade

A clear picture of the volume of trade in shells is difficult to obtain for several reasons:

a) shells are often combined with other goods or marine products (especially corals) in official statistics;

b) trade statistics seldom differentiate between species, except for 'commercial' or mother of pearl species, and it is difficult to calculate the relative volume of each species in trade, or the numbers of individuals involved; and

c) international trade statistics do not include domestic trade (e.g. through gift shops in the country of origin) so that export figures cannot necessarily be equated with total exploitation.

Detailed records of catches are rarely kept for miscellaneous marine products such as shells, as the fisheries are often artisanal. FAO statistics considerably underestimate production. For example, annual production of *Trochus* shell is known to be about 6000 tonnes (Bouchet and Bour 1980), yet FAO statistics for 1985 give a figure of only 892 tonnes (Anon 1986). Nor do FAO statistics give a detailed species breakdown.

Shell exporters

Trade in ornamental shells is centred on the Philippines (Wells 1981, 1982) (Table 4.2), and has been important for many years. Fisheries statistics for the Philippines show exports of shells from 1955 to 1970 to be less than 1000 tonnes per year (643t [1955]; 670t [1960]; 451t [1965] and 990t [1970]). Trends after this are shown in Figure 1: exports of "other shells" rose to over 4000 tonnes in 1973, remained between 3000 and 4000 tonnes until 1980, but then declined to about 1000 tonnes in 1985.

Indonesia (Figure 4.2), Thailand, Singapore and Taiwan are also major suppliers, but a part of the Singapore and Taiwan totals may be re-exports. India is another important supplier, although the most recent figures (April 1984-March 1985) show a decline (Table 4.3). It is one of the few countries to record some species separately, in this case cowries. Exports of cowries have declined over the years from a peak of 45 tonnes in 1977. The Maldives also list cowries separately, and exports remain fairly high. In the 1960s 20-60 tonnes were exported annually, and in 1985,17 tonnes were exported. At one time India exported substantial quantities of chanks, *Turbinellapyrum*, but exports declined from 55 tonnes in 1976 to 3 tonnes in 1981, just over one tonne in 1983, and none in 1984, when it had become illegal to export chanks in their natural state.

Import statistics for the United States suggest that Mexico and Haiti supply significant quantities of shells to the world market. Export statistics for the two countries are not available, but exports from these two countries to the United States have declined in recent years (Figure 4.3).

Table 4.2 Major producers and exporters of mollusc shells and estimated exports for 1985 (from export statistics unless otherwise stated).

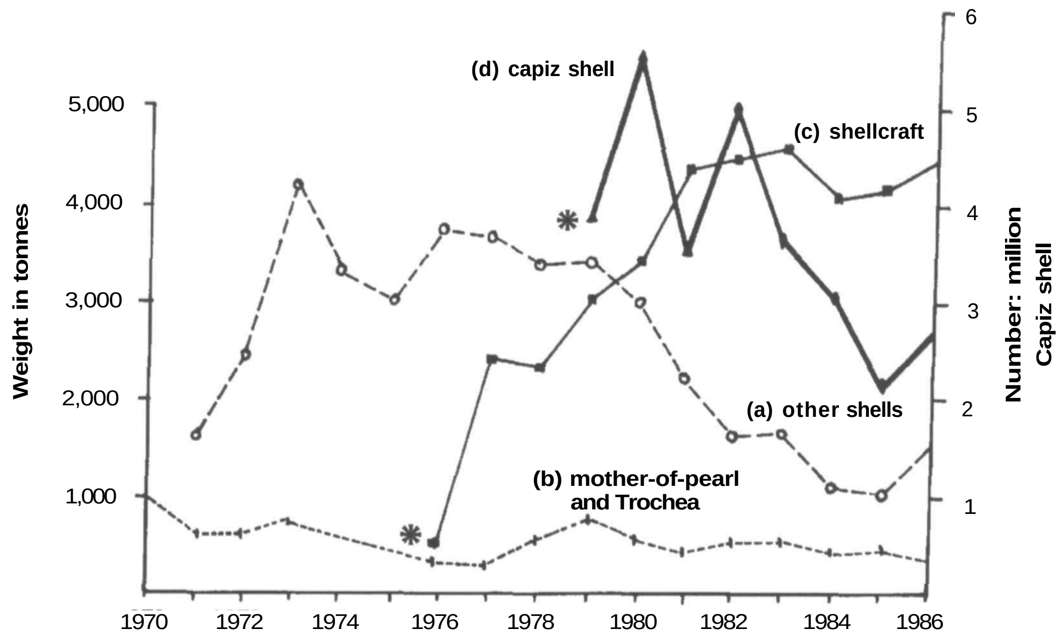
COUNTRY	TONNES
Japan	2668[1]
Philippines	1067
United States	1016[2]
Singapore	846[3]
Taiwan*	361[3]
Indonesia**	228
Thailand	122
Mexico	[94][4]
Haiti	[69][4]
India	43

Notes
* estimate only, based on 1986 figure
** estimate only, based on 1984 figure
[1]probably includes shells of pearl oysters
[2]total exports 'marine shells crude' minus exports to Japan (see text)
[3]may include re-exports
[4]from United States import statistics.

Table 4.3 Exports in tonnes of unworked shells from India.
Totals are annual figures, April-March, e.g. 1985 figure is from April 1984 to March 1985.

	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
SHELLS	55	66	150	465	166	138	240	128	147	41
COWRIES	40	45	?	?	3	3	5	12	2	-

Figure 4.1 Exports of shells (unworked) and shell articles from the Philippines (1970 -1986)



(a) 'other shells' (Wt: tonnes)

(b) Trochea shell': 'mother-of-pearl (shell) unworked' (Wt: tonnes)

(c) 'lamp shades, chimneys, globes and other light fittings, of shell' and 'other manufacture of animal shell' (Wt: tonnes)

(d) 'worked capiz shells' (window-pane oyster) (Number of articles: million)

* This commodity not included in Philippine Customs export statistics prior to date shown

Figure 4.2 Exports of marine shells from Indonesia (1970 -1986). Source of data: Indonesia Customs Export Statistics.

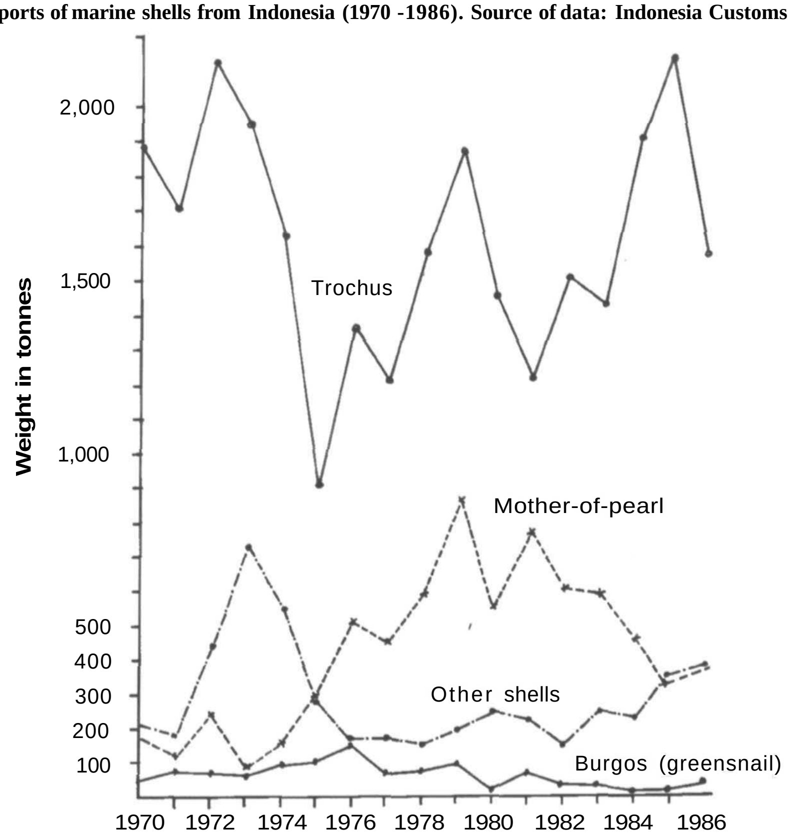
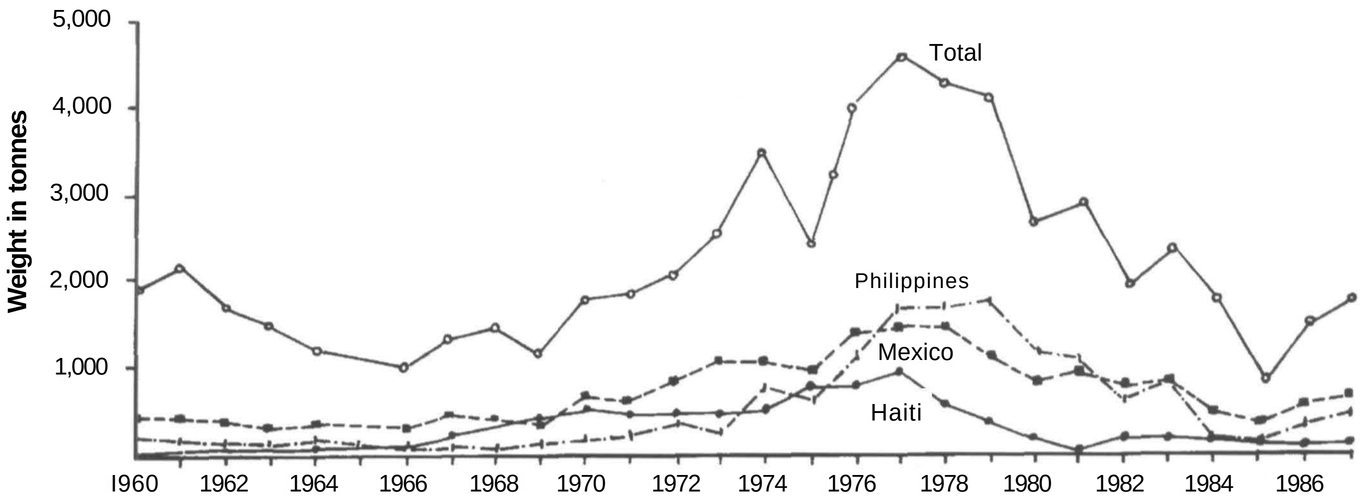


Figure 43 Imports of 'other shells' into the United States 1960 -1986.



Malaysia, Kenya, Sri Lanka and Australia are undoubtedly important suppliers of shells, but statistics for shells and their waste are combined with corals. Also, in the case of Malaysia, some of the figures are conflicting. For example, their export statistics for 1985 give a total of 344 tonnes of 'unworked coral, shell, powder and waste of shells' of which 56 tonnes went to Singapore. In the same year, Singapore trade statistics list imports of 7949 tonnes from Malaysia under the same category — a discrepancy of 7893 tonnes. The amount of 'ornamental' shell involved is difficult to ascertain. However, in 1982, when Singapore listed corals and shells separately, 23 tonnes of unworked shells were imported from Sabah, and 10,672 tonnes of powder and waste shells from Peninsular Malaysia. It is likely that the recent large imports to Singapore from Malaysia consist primarily of powder and shell waste destined for 'industrial' rather than 'ornamental' purposes.

Exports of corals, shells and their wastes from Kenya have increased fairly steadily from 85 tonnes in 1979 to 165 tonnes in 1984. Exports of chanks and their wastes from Sri Lanka are around 60 tonnes annually, while exports of other shells are in the region of 100 tonnes. According to the commodity description in trade statistics, both categories also include corals. Exports from Australia in the 1980s have been around 500 tonnes annually; in 1985 the figure was 460 tonnes.

Although the United States and Japan record large exports of marine shells in the categories 'marine shells' and 'shells of shellfishes' respectively, other evidence suggests that these quantities are not predominantly ornamental shells. A large proportion of the United States exports are dispatched to Japan, and are reported to consist primarily of freshwater pearl mussels (Abbott 1980). In 1985, 86% of the 'marine shells' (7370 tonnes) from the United States went to Japan, suggesting that possibly only about 1000 tonnes were ornamental shells. Japanese exports may also include pearl oysters: in 1985, 60% of exports went to the Republic of Korea, and 31% to Taiwan, both countries involved in pearl culture.

Shell importers

The main importer of ornamental shells is probably the United States (including Hawaii) followed by Japan, Taiwan, Canada and Europe (Table 4.4). The high figure recorded for Japan is a result of the inclusion of freshwater molluscs imported from the United States, as mentioned above. As indicated in Table 5, the United Kingdom is one of the largest European importers, followed by Italy and Spain. Imports in the United States reflect a trend similar to that of the Philippine exports: imports have risen from 1000-2000 tonnes a year in the 1960s to nearly 5000 tonnes in 1977 before dropping to around 1000 tonnes since 1983 (Figure 4.3). The United States has an estimated 1000 shell dealers; Florida alone has 5000-10,000 retail outlets such as gift shops, hotels and department stores (Abbott 1980).

Commercial shell

Fisheries for 'commercial' shell exist in many Southeast Asian and Pacific countries and in most cases are well documented. The main suppliers are listed in Table 6, and trends in Indonesian exports shown in Figure 4.2. World exports for 1985 were an estimated 4500 tonnes, compared with 5300 tonnes in 1978 (for the same countries). *Trochus niloticus* is the most important species and an annual demand of 6000 tonnes for this species alone was estimated by Bouchet and Bour (1980).

The main importers of commercial shell are listed in Table 7. Southeast Asia is the centre of the mother of pearl and button industry. Taiwan exports around 30 tonnes of worked mother of pearl and 200 tonnes of mother of pearl articles annually, and Japan has similarly large exports (Table 4.8). The Philippines are also important, exporting 13,149 articles of worked mother of pearl in 1985, probably from domestic supplies.In the Philippines, mother of pearl is also incorporated into shellcraft (see over the page).

Table 4.4 Major importers and estimated imports of unworked shells for 1985, from import statistics unless otherwise noted.	
DESTINATION	**TONNES**
Japan	7935
United States	759
Taiwan*	792
Canada	[738][1]
Europe	[453][2]
Central/South Africa	[13][1]
South Korea	[76][3]
India and Pacific	[71][4]

Notes

*estimate only

[1]from United States' export statistics

[2]from United States', Japan's, Philippines', and Thailand's export statistics

[3]from United States' and Philippines' export statistics

[4]from Philippines' export statistics

Table 4.5 Imports of marine shells into Europe during 1985. Major importers and exporters only.				
IMPORTING COUNTRY	**EXPORTING COUNTRIES Weight of marine shells in tonnes**			**TOTAL IMPORTS**
	United States	**Philippines**	**Japan**	
United Kingdom	46	53	3	102
France	5	24	-	29
West Germany	16	-	-	16
Netherlands	-	20	-	20
Spain	-	45	-	45
Italy	-	50	4	54
Greece	-	23	-	

Figure 4.4 Value of United States imports of'articles of shells' 1961 - 1987.

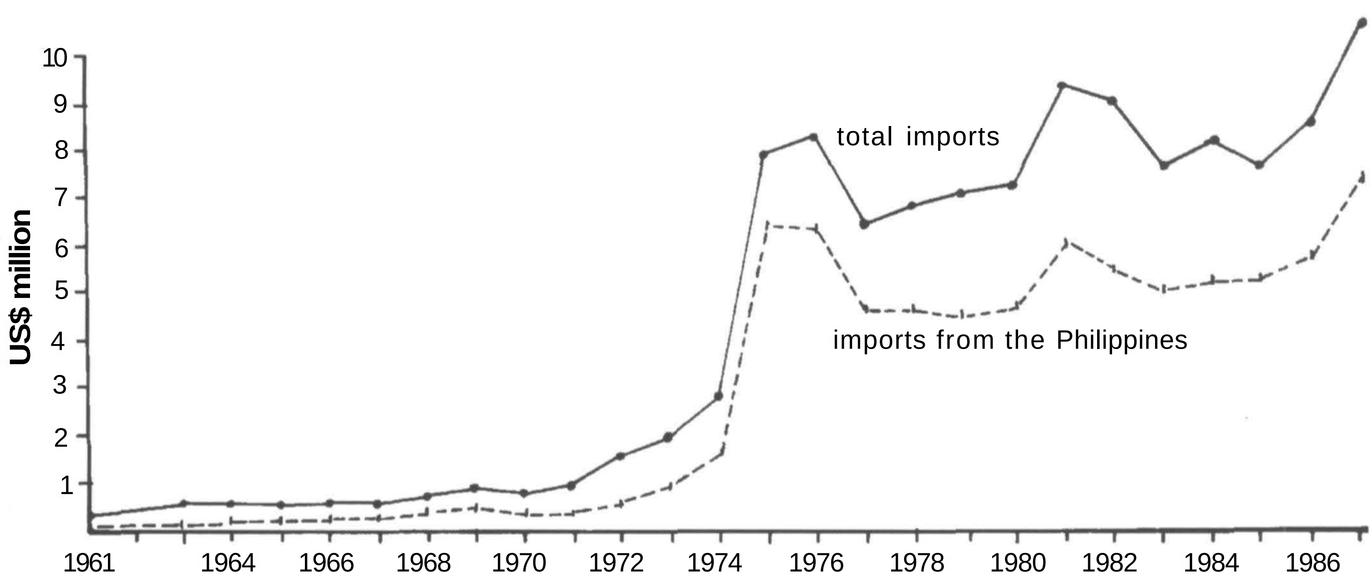


Table 4.6 Major exporters of unworked mother of pearl shells for 1978 and 1985. (Tonnes)		
COUNTRY	**1978**	**1985**
Indonesia	2249	2375[1]
Solomon Islands	297	[552][2]
Papua New Guinea	160	[514][2]
Philippines	594	251[3]
Fiji	104	235[4]
Marshall, Mariana, Caroline Islands	243	[139][5]
Cook Islands	12	[132][5]
New Caledonia	852	[115][2]
India	62	[89][6]
Australia	318	[79][2]
French Oceanic Territories	214	[63][5]
Vanuatu	191	35[7]
TOTAL	**5296**	**4579**

Notes

[1]Indonesiaexports
[2]importstatistics of Japan and Korea
[3]Philippineexports
[4]Tijiexports
[5]importstatistics of Japan
[6]importstatistics of Korea
[7]estimate based on 1984 figure

Table 4.7 Major importers of unworked mother of pearl shell 1985.	
COUNTRY	**TONNES**
Japan	3276[1]
South Korea*	2130[2]
Singapore*	777[3]
Europe*	175[3]
Taiwan*	97[4]
Hong Kong	64[5]

*estimate for 1985 using 1984 export figures for Indonesia
[1]import statistics
[2]export statistics from Indonesia and Philippines
[3]exportstatistics from Indonesia
[4]export statistics from Fiji, Indonesia and Philippines
[5]exportstatistics from Fiji and Indonesia

Table 4.8 Exports of worked shell products from Japan, 1983-1985			
SHELL TYPE	**1983***	**1984***	**1985***
Pearl buttons	83	113	134
Worked mother of pearl	43	89	40
* Tonnes			

Shellcraft

Southeast Asia is the centre of this industry, particularly the Philippines, where shellcraft is promoted by the government as a source of employment (Wells 1982). Japan, Taiwan and South Korea are also involved. In India over 2000 people rely directly on the shellcraft industry for their livelihood, and annual exports are in the region of 500 tons (Shenoy, 1984). Many species of gastropod are involved, including chanks (*Turbinella*), which are mostly collected in Tamil Nadu and sent to West Bengal where they are carved and manufactured into bangles and other jewellery (Heppell 1987). Similar items are made in Bangladesh, with chanks imported from Sri Lanka.

Shellcraft production has increased dramatically over the last two decades. In the 1960s annual imports of shellcraft into the United States were worth less than US$ 1 million, by 1981 US$ 9 million, and by 1986 over US$ 10 million. About 75% of these imports come from the Philippines (Figure 4.4). Exports of articles of worked shells from the Philippines have increased from less than 1000 tonnes in 1976 to more than 4000 tonnes in 1985. It appears that there has been a major shift in the Philippines from exporting raw ornamental shells, to the processing of them within the country and the exportation of shellcraft. The window-pane oyster, *Placuna,* is of particular value. The only major commercial fishery of the window-pane oyster (capiz) is in the Philippines where nearly 3.5 million worked capiz shells articles were exported in 1979 (import value over US$ 2 million) and just over 2 million in 1985 (import value over US$ 1 million).

Philippine shellcraft is exported to many countries around the world, with large quantities going in particular to the United States, Japan, France, United Kingdom, Germany, Italy and Australia (Tables 4.9 and 4.10).

Industrial shell

The shells of giant clams are used in the manufacture of pottery glazes and floor tiles, but details of the amounts involved are largely unknown, although in 1982 up to 660 tons of *Tridacna gigas* shells per month were being brought into Jakarta, Indonesia for that purpose (Usher 1984). Other shells and waste of shells are probally used in the construction industry but, again, little is known about this trade. The export of hundreds of tonnes of powder and waste of shells from Malaysia to Singapore has already been mentioned. India also exports large quantities of 'other shells including powder and waste' (1066 tonnes in 1985), mostly to Middle Eastern countries (Kuwait, Saudi Arabia and United Arab Emirates). Again, this may be for industrial uses. In 1985, Japan imported 1203 tonnes of 'shells and their powder and wastes, not elsewhere specified', mostly from the Philippines, Taiwan and the Marshall, Mariana and Caroline islands.

Conservation issues

Levels of exploitation

Information on population (stock) sizes and levels of exploitation is too poor to determine whether or not particular species are being seriously over-exploited. Data on the life history, abundance, productivity and rates of exploitation from specific localities are required for virtually every species involved in the shell trade.

Table 4.9 Major importers of shellcraft from the Philippines, 1985. Data from Philippines external trade statistics.			
	SHELLCRAFT - Gross weight in tonnes		
DESTINATION	**Light fittings***	**Other items**	**Total**
United States	129	1044	1173
Japan	197	396	593
France	117	243	360
United Kingdom	182	170	352
Germany	210	130	340
Italy	259	81	340
Australia	66	134	200
Hawaii	14	165	179
Canada	30	53	83
Spain	11	69	80
Greece	7	64	71
Finland	4	29	33
Sweden	14	17	31
Netherlands	1	27	28
Portugal	1	24	25

*includes lampshades, chimneys, globes etc.

However anecdotal evidence suggests that conservation problems are on the increase and makes it possible to predict which areas and species are most vulnerable.

Areas vulnerable to stock depletion

Depletion of mollusc populations appears to be occurring on a local basis in some countries. Populations of molluscs in accessible areas and close to tourist centres are clearly more vulnerable to over-collection than those in remote areas. There are several reports of over-collecting in Kenya in areas where collectors concentrate their efforts in order to meet tourist demand (Evans et al. 1977; Kendall 1985) and commercial collectors are now going further afield for shells. There are also reports of over-collecting in Florida (Abbott 1980), Jeddah (UNEP/IUCN 1988), Singapore (Chou 1985), Guam (Hedlund 1977), the Solomon Islands (Craven 1986), the Philippines (Anonuevo et al. 1982), Reunion (Roberts 1977) and the Seychelles (Salm 1978). With the exception of the Philippines, these countries supply shells to the international market in relatively small amounts according to trade statistics and these reports of scarcity emphasize the danger of assuming that apparently minor exporters are free of conservation problems.

Vulnerability of marine molluscs

Most marine molluscs produce numerous planktonic larvae with great dispersal capacity and, potentially, these species should be able to withstand high levels of harvesting. In some instances, however, collecting pressure may be so heavy that even these species can be over-exploited. Species with less 'opportunistic' life histories are clearly more vulnerable.

Geographically widespread species heavily exploited throughout their range

Several edible and 'commercial' species fall into this category, and demonstrate how heavy demand and intensive fishing can have a considerable impact on populations as a whole, even though the species themselves are not at risk of extinction. A detailed resume of the problems associated with these species is beyond the scope of this paper, but some examples are given below, together with references to more complete reports.

The queen conch, *Strombus gigas,* is heavily exploited in the Caribbean: an estimated six million animals are exported to the United States annually, and another six million are consumed locally. Populations are now seriously overfished and declining (Berg and Olsen 1988).

Commercial shells have been over-collected in many localities since the beginning of this century. Reports of declining populations and/or unavailability of large specimens come from French Polynesia (Salvat 1980), Papua New Guinea (Glucksman and Lindholm 1982), the Andaman and Nicobar Islands (Rao 1937), New Caledonia (Bouchet and Bour 1980), Indonesia (Usher 1984), Palau (Heslinga and Hillman 1981), Yap, Truk (McGowan 1958), Vanuatu (Devambez 1959) and Western Australia (Sarti 1983). In Madagascar, the black-lip pearl oyster, *Pinctada margaritifera,* has been so heavily exploited that it is now extinct in certain localities where previously it was numerous (Rabesandratana 1985).

Populations of the larger species of giant clams (Tridacnidae) have declined dramatically in many parts of the Indo-Pacific, as a result of over-collecting both for the shell and meat. The vulnerability of giant clams is due largely to their late reproductive maturity, comparatively short larval life span, poor recruitment to the adult population, and the ease with which they can be collected

Table 4.10 Major importers of worked capiz (*Placuna* spp.) shell articles from the Philippines, 1985. Data from Philippines external trade statistics. Only those countries importing more than 10,000 articles are included.

DESTINATION	NUMBER OF CAPIZ SHELL ARTICLES
West Germany	625,657
Switzerland	433,624
United Kingdom	256,191
Japan	130,479
United States	124,727
Paraguay	121,303
France	91,983
Hawaii	71,292
Hong Kong	64,275
Italy	63,512
Belgium	51,202
Guam	38,027
Sweden	22,130
Canada	20,595
Australia	11,115

from their shallow reef habitat. Stocks of *Tridacna gigas* and *T. derasa* in particular are in danger of extinction in many parts of their range (Munro 1988). Illegal collection by foreign (mainly Taiwanese) fishermen is a problem in many areas.

At present relatively few of the widely distributed 'ornamental' species are known to be similarly affected. The giant triton, *Charonia tritonis,* which occurs naturally at low densities (Wells et al. 1981), seems to have become rare through over-collection, for example in the Philippines (Wells 1981) and Guam (Hedlund 1977). The golden cowrie, *Cypraea aurantium,* now considered a fairly widespread species, but once highly prized because of its apparent rarity, is vulnerable to over-collection because of heavy demand yet relatively low populations. Large numbers of this cowrie entered the market from 1970 to 1975, collected mainly from eastern coastlines of the Philippines, but there has since been a 'radical nosedive' in yield (Anonuevo et al. 1982), suggesting that the gastropod has been over-exploited.

Species with restricted distribution

Many species of 'ornamental' and 'specimen' marine molluscs have a restricted geographical range and are therefore vulnerable to over-collection, particularly if they occur in shallow water. The likelihood of populations being adversely affected is also increased if the species concerned has a naturally low population density and/or low reproductive potential.

One of the few species which has been studied is the leafy-winged murex *Pterynotus phyllopterus,* an uncommon shell endemic to Guadeloupe and Martinique in the Lesser Antilles. It is presently being over-collected (Lamy 1986), although it is not thought to be seriously threatened. There have been anecdotal reports of over-collection of several cowrie species such as the endemic *Cypraea mauiensis* in the Hawaiian Islands (Beals 1976); *C. cribellum, C. esontropia* and *C. broderipi* of Mauritius (Whatmore 1982); and *C. venusta, C. friendii* (= *C. thersites)* and others in south-western Australia (Anon 1985).

Volutes endemic to specific islands or island groups are also known to have become rare, for example, *Lyria deliciosa* and *Cymbiola rossiniana* from New Caledonia (Bouchet 1979). Other shells reported to have been over-collected include the imperial harp, *Harpa costata,* and the violet spider conch, *Lambis violacea,* both endemic to Mauritian waters (Whatmore 1982).

'Rare' species

There are a number of species that are in considerable demand because they are rarely found and collected. In some cases rarity may be a genuine reflection of population densities in the wild. ln other cases, a species may be rare in trade simply because the bulk of the population is inaccessible, for example in deep water. Several deep-water species fetch high prices on the 'specimen shell' markets. New collecting techniques permit collection of comparatively large numbers, and incidental catches by fishermen on trawlers provide a further source.

Other ecological problems

Habitat damage

Various activities connected with shell collecting can alter or degrade habitats. Common types of disturbance include trampling and rock removal. Corals are also deliberately or inadvertently broken in order to remove shells.

Many shell collectors around Cebu in the Philippines, use a fine-mesh 'dredge' which they push across sand and rubble areas where molluscs live, but the practice has evidently declined to some extent, partly because the habitat was altered so drastically that 'even fishes were found to have been affected' (Anonuevo et al. 1982). The collectors have also been forced to collect from more remote areas because of declines in yield in the vicinity of Cebu.

Disruption of ecological balance

Little attention has been paid to the consequences of selective removal of shells on the ecosystem as a whole, but problems can arise. It has been suggested, for example, that over-collection of the giant triton, *Charonia tritonis,* which preys on large starfish, has contributed to population explosions of the crown of thorns starfish, *Acanthaster planci* (Endean and Cameron 1985). Plagues of the starfish have caused extensive damage to coral reefs in many parts of the Indo-Pacific. However the cause of these population explosions is still a matter of considerable controversy. A comparable sequence of events may be responsible for upsurges in numbers of sea-urchins, which graze the surface of corals and, in doing so, cause structural damage to reefs. Along parts of the Kenya coast, populations of the sea urchin *Echinometra mathaei* have increased, perhaps as the result of the selective removal of large numbers of predators such as the bullmouth helmet, *Cypraecassis rufa* (Kendall 1985; Muthiga and McClanahan 1988).

Conservation measures

There are several courses of action that can be taken to control trade in shells, and thus avoid over-exploitation and habitat damage. Conservation problems should not exist if the fisheries are properly managed on an ecologically sound, sustainable yield basis. Producer countries can implement management programmes and control exports, and importing countries can control imports. The problems would also be lessened if demand for ornamental shells declined. A greater 'public' awareness of the conservation issues could help in this respect.

Regulation of 'catches'

One way of controlling exploitation of marine shells is to place limits on the total number or weight that can be collected or exported. The disadvantage of this system is that, unless a quota is set for individual species, there is a temptation to collect the most valuable (and probably the rarest) shells. It is preferable to regulate collection of certain (or all) species by setting limits on number, weight and size of each species that can be taken at a time, and the localities from which they can be collected (see Protected Areas below). Commercial collectors should be licensed, and answerable to a fisheries or wildlife authority. Some examples of fishery management in existence are given in Table 4.11.

There are a number of practical difficulties in controlling exploitation of shells through management of the fishery. A primary difficulty concerns the enormous number of species involved. The lack of basic knowledge about life history, distribution and population dynamics of most of these species means that it is difficult at present to determine appropriate quotas or restrictions.

One of the species most thoroughly investigated is *Trochus niloticus.* Research on its biology and distribution in New Caledonia, the Cook Islands and Palau has enabled the calculation of sustainable yields for certain areas and development of appropriate management strategies. A variety of controls have been introduced in the past (see Table 4.11) and these new data should permit a more rational application of such techniques (Bour and Hoffschir 1985; Heslinga *et al.* 1984; Sims 1985). Potential management techniques include estimation of population density by using high resolution satellite imagery which pinpoints *Trochus* habitat, as is currently under investigation in New Caledonia (Bour *et al.* 1985).

Another difficulty results from the patchy distribution and abundance of some species, caused in part by habitat requirements. Sustainable yields may vary from one area to another, and a management policy devised for a certain species at a particular locality is not necessarily applicable to other areas. Detailed survey and monitoring work is needed in all major collecting areas to determine the type of management required, and to ascertain the success of such programmes.

Enforcement of regulations on quotas and other aspects of collecting is notoriously difficult in areas where large numbers of collectors are involved, especially when they work over a wide area and around remote islands as in the Philippines and in much of the Pacific. In these cases, control of the fishery by export regulations may be a more feasible approach. However, enforcement is a problem even in Australia where cowries are collected at night to avoid fisheries officers and export controls are circumvented by using the mail (Anon. 1985).

The considerable knowledge many collectors themselves have about the distribution and biology of exploited species could be put to use, and they could be encouraged to build on existing traditional techniques of management. Measures taken to ensure conservation of species or habitats are much more likely to succeed if people who are affected by management decisions are involved in their formulation.

Protection in country of origin

In some cases it may be necessary for countries to prohibit the collection of certain shells, such as endemic or rare species. Some examples of countries which have already introduced such legislation are listed in Table 4.11.

Protected areas

Another management technique is that of establishing protected areas where collection of shells is prohibited or restricted to certain zones. These areas can act as reservoirs from which adult molluscs and particularly larvae can spread to neighbouring areas. Most countries now have marine protected areas of some form in which collection of marine organisms is prohibited (among other regulations) (Wells 1988; UNEP/IUCN 1988). However, these sites have rarely been selected with management of mollusc populations in mind, and mollusc populations are generally not monitored. The success of this type of management strategy therefore has yet to be demonstrated. The system of *Trochus* sanctuaries in Palau has been studied and recommendations made for their improvement, including the redesignation of fewer, larger areas which are accessible for periodic surveillance (Heslinga et al. 1984). The four shell reserves established in the Seychelles (Table 4.11) are similarly poorly controlled and have not been monitored to determine whether they are beneficial to shell populations (Wells 1988; UNEP/IUCN 1988).

Improved collecting methods

Given the problems of implementing and enforcing appropriate management strategies, it is particularly important that collectors understand the importance of conserving stocks, and using collecting methods which do not damage the habitat. Guidelines or instructions could be produced for both commercial collectors and tourists. In Papua New Guinea collectors have been issued with a booklet on how to avoid wastage, habitat damage and over-exploitation (Anon. undated) but this programme has never been followed up. A similar booklet is now in preparation for Fiji, following a survey of the feasibility of setting up the shell trade (Parkinson 1982). Several malacological and conchological societies, such as the Hawaiian Malacological Society, issue 'Codes of Conduct' and instructions to collectors. The main principles, as outlined in Wells and Alcala (1987) are:

1) Eggs, juveniles and breeding groups should not be taken.
2) Shells with defects should not be taken (these are in any case generally unsaleable as 'specimen' shells).
3) The habitat should be disturbed as little as possible.
4) Living, attached corals should not be touched.
5) If stones, loose coral or boulders are moved, they should be returned to their original positions.

The United Kingdom-based Marine Conservation Society, in conjunction with the World Wide Fund For Nature (UK), is planning to publish leaflets and posters about the marine curio trade, and ways in which the ecological impact of collecting can be minimised. There is a need for such information to be made available much more widely than it is at present, for shell buyers are often unaware that conservation problems exist.

Controls on exports and imports

A number of producing countries are now introducing legislation to control exports of shells (Table 4.11). Exports may be controlled through a permit system, prohibition of the export of particular species, of unworked shells, etc. The Seychelles in particular has introduced such comprehensive legislation, and recently shells were included under the Wildlife Protection Act of 1984, thus prohibiting the export of native species. Legislation prohibiting the export of unworked shells is beneficial to the country concerned because it encourages the shellcraft industry which is labour intensive and increases the export value of the shells. Shellcraft industries are being promoted in countries such as India (Shenoy 1984) and the Philippines (Wells 1981), and evidence of their success is shown in the trends visible in trade statistics (see Figure 4.1).

Few countries have considered controlling imports of shells. In the United States, the Lacey Act is an effective piece of legislation because it prohibits import of illegally collected or exported wildlife, but at present molluscs are not included on its schedules. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) provides a means of controlling international trade in species considered to be seriously threatened. At present, the only marine molluscs listed are the giant clams (family Tridacnidae). These are listed in Appendix II, which means that a valid export licence is required from the country of origin before the shells, meat or live animals can be traded between parties to the Convention. This provides a useful means of monitoring trade, particularly as custom and fishery statistics tend to be so poor for molluscs. However, the success of CITES depends on the extent to which party states can implement the necessary legislation. Furthermore, the Convention was drawn up specifically for species known to be threatened, and strict criteria must be fulfilled for the listing of species.

Mariculture

One way of relieving pressure on stocks of 'wild' shells is to use cultivated molluscs instead. Although mariculture programmes have been developed for many edible molluscs, they have only recently been attempted with species used in the shell trade: *Strombus gigas, Trochus niloticus, Pinctada margaritifera,* and giant clams.

Considerable success has been achieved with several of these species, larvae and juveniles being reared in hatcheries, and the adults kept in tanks for production of spawn and ultimately for harvesting. The possibility of culturing the leafy-winged murex, *Pterynotus phyllopterus,* has been investigated, but a full-scale project has not been put into operation (Lamy 1986).

It is also possible to use hatchery bred shells to re-seed depleted areas. This management technique is being developed in the Philippines for capiz (details in Wells 1988).

Mariculture clearly has potential and positive benefits, although a considerable amount of research is required before any scheme can be put into operation.

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Table 4.11 Examples of legislation controlling exploitation of marine molluscs. The Table is not exhaustive.

INDIAN OCEAN/RED SEA/GULF	
Djibouti	Shell collecting prohibited under 1980 decree.
Egypt	Collection of shells prohibited in parts of the Sinai and Gulf of Agaba.
India	Chank Fisheries Act: export of unworked chanks prohibited. Pearl Fisheries Ordinance.
Israel	Permits required for collecting; collecting permitted only for scientific purposes (Fainzilber *in litt.* 1987).
Kenya	Permit required for commercial collecting; maximum 5kg ornamental shells collected per day. Visitors with licence may buy and export 5kg.
Madagascar	Collection of mother of pearl controlled since 1929.
Maldives	No official legislation but collection of marine organisms around resort islands prohibited by dive and tourist operators.
Mauritius	Fisheries Act 1980; permit required for import or export of shells. Collection of *Harpa costata* prohibited. In 1984, additional species given total protection: visitors can take up to six shells provided an export permit is obtained. A proposal also made to add a provision to the Act to prohibit commercial collecting.
Oman	Collection of living molluscs prohibited under regulations decreed by the Minister of Agriculture and Fisheries.

Table 4.11 (cont). Examples of legislation controlling exploitation of marine molluscs. The table is not exhaustive.	
Reunion	Collection of living molluscs prohibited under Arrêté 2862 of 21.7.76
Seychelles	Conservation of Marine Shells Act 1981 established 4 shell reserves (2 on Mahé, 1 on La Digue, 1 on Praslin), banned collection from reserves except dead shells on foreshore and collection anywhere of protected species (*Charonia tritonis* the only listed species at present). For other species there is a limit of 20kg per day. Sale and purchase of protected species prohibited; shells may only be exported for personal and non-commercial purposes. This Act repeals Protection of Shells Ordinance 1965, but is poorly enforced.
INDIAN OCEAN/RED SEA/GULF	
South Africa	Permits required for collecting; no collecting permitted in marine reserves (Fainzilber *in litt.* 1987)
Sudan	1975 Amendment of Marine Fisheries Regulations of 1937 prohibits collection of shells. Local order by Commissioner of Red Sea Province bans trade in shells.
CENTRAL INDO-PACIFIC REGION	
Australia	Wildlife (Regulation of Exports and Imports) Act (1982) prohibits unauthorised export of native species of molluscs; permit needed for private collecting, commercial sale and export. Closed season for *Cypraea thersites* (Coleman 1972); collection of *Charonia tritonis* banned.
Fiji	Collection of *Charonia tritonis* banned.
Guam	*Trochus* collection controlled. Collection of *Charonia tritonis* banned.
Hawaii	Collection banned in natural area reserves (Cape Kinau, Maui) and in protected zones on alternating two year basis (Diamond Head Beach Park, Oahu); collection of pearl oyster *Pinctada margaritifera* banned; size regulations on octopus and limpets (*Cellana* spp.)
New Caledonia	*Trochus* fishery controlled
Palau	*Trochus* fishery controlled
Vanuatu	*Trochus* fishery controlled. Minimum size limit of 20cm for collection of *Charonia tritonis.*
WESTERN ATLANTIC	
Bahamas	Fisheries Resources (Jurisdiction and Conservation) Regulations 1986. Collection and export of any marine products by non-Bahamians is prohibited. Management of conch fishery.
Belize	Legislation for management of conch fishery.
Bermuda	Fisheries (Protected Species) Order 1978 protects a number of species (*Stombus gigas, S. costatus, Conus bermudensis, Oliva reticularis, Pecten ziczac, Argopecten gibbus, Pinctada imbricata,* all Cassididae). Scuba divers may not collect; sale of marine animals taken within territorial waters permitted only if for human or animal consumption.
Cayman Is.	Marine Conservation Law (1978): controls on conch fishing; permit required for shell collecting.
Cuba	Legislation for management of conch fishery.
Netherlands Antilles	Marine Environment Ordinance (Bonaire) 1985; licence required for export of reef products.
St Lucia	Legislation for management of conch fishery.
Turks and Caicos	Legislation for management of conch fishery.
United States	Recreational shell collecting controlled by State legislation. Moratorium on commercial conch fishing in Florida; bag limit 10 specimens per recreational collector per day. Collection of live shells in California requires a permit and *bona fide* membership of an approved malacological organisation.
Venezuela	Legislation for management of conch fishery.

References

ABBOTT, R.T., 1980. *The Shell and Coral Trade in Florida.* Special Report 3, TRAFFIC (USA), Washington, D.C.

ADAMS, 1985. *In lift.* 7.2.85.

ANON., 1985. Cowrie shells endangered. *Traffic Bulletin* VI (5).

ANON., 1986. *Yearbook Of Fishery Statistics. Catches And Landings.* Vol. 60. FAO, Rome.

ANON., undated. *Sea Shells as Business.* Department of Business Development, Port Moresby, Papua New Guinea.

ANONUEVO, M.V., CABRERA, J., AND HIZON, M.Y. 1982. *A market study and catalogue of commercially viable seashells.* Final Report, December 1982. University of the Philippines.

BEALS, M., 1976. *Cypraea mauienis* — an endangered species? *Hawaiian Shell News* 24 (1): 10.

BERG, C.J. AND OLSEN, D.A. 1988. Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. In: Caddy, J.F. (Ed.), *Scientific Approaches to Management of Shellfish Resources.* John Wiley and Sons, New York.

BOUCHET, P., 1979. Coquillages de collection et protection des recifs. Report to ORSTOM, Centre de Noumea, New Caledonia.

BOUCHET, P. AND BOUR, W. 1980. The Trochus fishery in New Caledonia. The South Pacific Commission Fisheries Newsletter 20:9-12.

BOUR, W. AND HOFFSCHIR, C, 1985. Evaluation et gestion de la resource en Trocas de Nouvelle Caledonie. Rapport final de Convention ORSTOM/Territoire de Nouvelle Caledonie et dependence, ORSTOM, Noumea.

BOUR, W., LOUBERSAC, L. AND RUAL, P. 1985. Reef thematic maps viewed through simulated data from the future SPOT Satellite. Application to the biotope of topshell (*Trochus niloticus*) on the Tetembia reef (New Caledonia). *Proceedings of the 5th International Coral Reef Congress, Tahiti* 4: 225-230.

CHOU, L.M. 1985. The coral reef environment of Singapore. In: *Proceedings of a conference on the biophysical environment of Singapore and neighbouring countries.* Singapore 3-5 May 1985.

CRAVEN, A., 1986. *In litt.*

DEVAMBEZ, L.C. 1959. Survey of *Trochus* reefs in the central and southern groups of the New Hebrides. South Pacific Commission. 7 pp.

ENDEAN, R. AND CAMERON. A.M. 1985. Ecocatastrophe on the Great Barrier Reef. *Proceedings of the 5th International Coral Reef Congress, Tahiti* 5: 309-314.

EVANS, S., KNOWLES, G., PYE-SMITH, C, AND SCOTT, R. 1977. Conserving shells in Kenya. *Oryx* XIII (5): 480-485.

GLUCKSMAN, J. AND LINDHOLM, R., 1982. A study of the commercial shell industry in Papua New Guinea since World War Two, with particular reference to village production of trochus (*Trochus niloticus*) and green snail (*Turbo marmoratus*). *Science New Guinea* 9: 1-10.

HEDLUND, S.E., 1977. The extent of coral, shell and algal harvesting in Guam waters. *University of Guam Marine Laboratory Technical Report* 37. 34 pp.

HEPPELL, D. 1987. *In litt.*

HESLINGA, G.A. AND HILLMAN, A. 1981. Hatchery culture of the commercial top shell *Trochus niloticus* in Palau, Caroline Islands. *Aquaculture* 22: 35-43.

HESLINGA, G.A., ORAK, O., AND NGIRAMENGIOR, M. 1984. Coral reef sanctuaries for Trochus shells. *Mar. Fish. Rev.* 46(4): 73-80.

KENDALL, B., 1985. The shell trade. *Swara* 8 (1).

LAMY, D. 1986. *Pterynotus phylloptems* (Lamarck, 1822). Mollusque Muricidae des Antilles Franҫhises. Biologie, Ecologie et Elevage. These. Laboratoire de Biologie Marine et de Malacologie.

MCGOWAN, J.A., 1958. The *Trochus* fishery of the Trust Territory of the Pacific Islands. Report to the High Commissioner, U.S. Trust Territory of the Pacific Islands. Saipan, 46 pp.

MUNRO, J.L. 1988. Fisheries for giant clams (Tridacnidae: Bivalvia) and prospects for stock enhancement. In: Caddy, J.F. (Ed.). *Scientific approaches to management of shellfish resources.* John Wiley and Sons, New York.

MUNRO, J.L. AND HESLINGA, G.A. 1983. Prospects for the commercial cultivation of giant clams (Bivalvia: Tridacnidae). *Proceedings of the Gulf and Caribbean Fisheries Institute* 35:122-134.

MUTHIGA, N.A. AND MCCLANAHAN, T.R., 1988. Population changes of a sea urchin (*Echinometra mathaei*) on an exploited fringing reef. *Afr. J. Ecol.* 24 pp.

PARKINSON, B.J. 1982. *The specimen shell resources of Fiji.* South Pacific Commission. 53 pp.

RABESANDRATANA, 1985. *In litt.*

RAO, H.S. 1937. On the habitat and habits of *Trochus niloticus* Linn, in the Andaman Sea. *Records of the Indian Museum Calcutta* 3 9: 47-82.

ROBERTS, R. 1977. Pêche et aquaculture a la Reunion. Collection 'des Travaux de Centre Universitaire de la Reunion.

SALM, R.V. 1978. Conservation of marine resources in Seychelles. Report for IUCN. 41 pp.

SALVAT, B., 1980. The living marine resources of the South Pacific past, present and future. In: UNESCO Population environment relations in tropical islands: the case of eastern Fiji. MAB Technical Notes 13:131-148.

SARTI, N., 1983. Report to the Chief Fisheries Officer on a visit to Ashmore Reef. February 1983. Western Australian Department of Fisheries and Wildlife. Unpublished Report.

SHENOY, A., 1984. Non-edible marine products - a growing cottage industry in India. *Infofish Marketing Digest* 5: 35.

SIMS, N., 1985. The abundance, distribution and exploitation of *Trochus niloticus* L. in the Cook Islands. *Proceedings of the 5th International-Coral Reef Congress,* Tahiti. 5 539-544.

UNEP/IUCN. 1988. *Coral Reefs of the World.* Volume 1: *Atlantic and Eastern Pacific.* Volume 2: *Indian Ocean, Red Sea, and Gulf.* UNEP Regional Seas Directories and Bibliographies. IUCN, Gland, Switzerland and Cambridge, U.K./UNEP, Nairobi.

USHER, G.F. 1984. Coral reef invertebrates in Indonesia: their exploitation and conservation needs. IUCN/WWF Report, Project 1688.100 pp.

WELLS, S.M. 1981. *International trade in ornamental shells.* IUCN Conservation Monitoring Centre, Cambridge, U.K. 22 pp.

WELLS, S.M. 1982. Marine conservation in the Philippines and Papua New Guinea with special emphasis on the ornamental coral and shell trade. Unpublished Report to Winston Churchill Memorial Trust, London. 74 pp.

WELLS, S.M. 1988. Impacts of the precious shell harvest and trade: conservation of rare or fragile resources. In: Caddy, J. (Ed.) Scientific Approaches to Management of Shellfish Resources. John Wiley and Sons, N.Y.

WELLS, S.M. AND ALCALA, A.C. 1987. Collecting of shells and corals. In: Salvat, B. (Ed.) *Human Impacts on Coral Reefs: Facts and Recommendations.* Antenne Museum

WELLS, S.M., PYLE, R.M. AND COLLINS, N.M. 1983. The IUCN Invertebrate Red Data Book. IUCN Conservation Monitoring Centre, Cambridge.

WHATMORE, L., 1982. Mauritius is great but shelling's poor. *Hawaiian Shell News.* Feb. 1982:8.

Chapter 5: Hug a slug - save a snail: a status report on molluscan diversity and a framework for action

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Preview

In the following account, I have attempted to provide additional information on the dramatic loss of animal and plant species worldwide which issue from governmental reports, IUCN and other conservation agencies by summarizing what we know about the status of one phylum, the Mollusca, around the world. Following an introduction which sets the stage with a discussion of interactions between humans and molluscs, the focus turns to the diversity of molluscs: the land snails of continents and islands, the molluscs of freshwaters, and the molluscs of coral reefs. The focus then changes to a discussion of molluscs as economic resources: mollusc fisheries, molluscs as alien species and molluscs as model systems. For each of these subjects I have tried to provide some history and some information on their present status, with the hope that they will provide background for actions that might be taken to ameliorate declining diversity. The required actions form the conclusion of this report.

Introduction

Molluscs and man

"No man is an island" wrote John Donne of human society; his words are equally descriptive of the web of animals and plants that is life on earth. That all forms of life are mutually dependent on each other is axiomatic. We also know that some organisms are more equal than others: plants because of our ultimate dependence on them, insects because there are so many of them, and vertebrates perhaps more because we too are vertebrates and we can relate to the soaring condor and the appealing panda.

Who among us counts the snail and its relatives as significant threads in the web of life and in human society? A reading of both history and science tells us that the Mollusca of the biologist — slugs, clams, pearl oysters, squid, coat-of-mail shells, tusk shells, and nautilus — play more roles in human life than does any other animal group of equivalent rank. From time immemorial molluscs have served as food, tools, currency, medicine, and sources of calcium carbonate. In addition to these practical roles, they also figure in legend and history, and as objects of art and worship, as items of adornment and decoration, and as musical instruments.

The shell middens of antiquity attest to the importance of molluscs as food throughout the world. The first tools, well before even a stone was chipped, were shells used as drills and scrapers. In the early years of the industrial age, when iron wheels became recalcitrant, someone discovered that the mucus of slugs was a satisfactory grease. Conchiolin, ground up bivalve shells, serves as the building blocks of houses in western Australia; in Louisiana it is the foundation for bayou roads. Cloaks woven from the byssus of the bivalve *Pinna* may have been the original golden fleece; tyrolian purple, the dye from a gastropod, was the symbol of royal rank. The sick have browsed through pharmacies in Hong Kong and Beijing for centuries in search of remedies derived from marine snails. Goods and brides were purchased for shells, the money cowrie in China, India, and Africa and the tusk shell on the west coast of the Americas. In China, money cowries were in use from about 1000 BC and the modern character for "precious" or "money" today incorporates the symbol for the money cowrie.

Botticelli's Venus, rising from the sea, was borne landward on a scallop shell; some Pacific islanders attribute the birth of their islands to the giant clam *Tridacna.* Whether history or legend, pearls from freshwater mussels are thought to have led the Romans to invade Britain in the 5th century BC. History also tells us that it was a mollusc which stimulated the initiation of products liability laws when a thirsty shopkeeper drank from a bottle of ginger beer only to find the decomposed remains of a snail therein (K. Brown 1980). Other molluscs have stopped trains and planes (helicid snails in North Africa) and sunk ships (the shipworm *Teredo).*

Molluscs retain many of their traditional roles in human life today. They have also gained new ones, among them recognition as useful animals for experimental studies of the nervous system and in behavior, as tools for the geneticist, and as sources of drugs, tranquilizers and antispasmodics for a variety of ills. Their most significant role may be only now emerging: the ability of bivalves to concentrate small particles and accumulate toxins and other pollutants is being utilized in programmes such as the 'Mussel Watch' (Anonymous 1980) to monitor changes in ocean water quality. Molluscs may well be the model group with which to develop and assess protocols which will tell us about the health of ecosystems in which occur vast numbers of invertebrates, if not vertebrates.

What is a mollusc?

What are these animals which play so many roles in human life? Their name, from the Greek, "mollos" means soft-bodied. That soft body, with a characteristic foot, head, and internal organs, has evolved into a myriad of shapes and forms that inhabit virtually every imaginable ecological niche on earth: in the ocean, on land, and in the freshwaters of lakes, rivers and wetlands.

The "snails" of land and sea are gastropods, meaning "stomach footed," because there is usually a coiled shell containing the viscera which is carried above a slug-like foot. Some gastropods, the "slugs," have either reduced shells or no shells. Clams, mussels and pearl oysters are termed the Bivalvia for the two shells which enclose the body. Bivalves lack a head as we know it in other animals and they feed as water containing food particles flows over their gills. They are found in both freshwater and the ocean. Five groups of molluscs are found only in the sea: the tusk shells or Scaphopoda burrow in soft sediments; the coat-of-mail shells or chitons (Polyplacophora) have a covering of eight interlocking shelly plates, reminiscent of medieval armor, and the Cephalopoda include the shelled pearly nautilus as well as squid and octopus which have no visible shell. The name, meaning "head foot," derives from the fact that they move by tentacles which form part of their heads. Two lesser known groups include fairly small animals (5 - 10 mm) which live at depths of more than 50m, the Monoplacophora and the Aplacophora.

Why save a snail?

Molluscs play essential roles in almost every known ecosystem on land and in the sea. Many molluscs are links in food chains, the pathways between green plants and the animals that are food for humans and other animals. On coral reefs in the Pacific, more than 20% of reef fishes feed on molluscs (Parrish, *et al.* 1985; Hiatt and Strasburg 1960); in turn, 70% of the meat diet of some Pacific islanders consists of reef fish (Marine Resources Management Division, Yap 1989). In all oceans, squid and octopus are the animals on which fishes, whales, dolphins, and sea birds feed. On European coastlines, the minute snail *Hydrobia ulvae* and the mussel *Mytilus edulis* are preyed on by shorebirds and estuarine fish such as flounders and gobies (Green 1968), and, during winter, the oyster catcher *Haematopus ostralegus* feeds on as many as 315 cockles (*Cardium*) a day (Thorson 1971). In South Africa, two species of the snake *Duberria* are so specialized they feed only on snails (van Bruggen 1978). There is also evidence that bivalves may be important to critical stages in the life history of certain food fishes, as the bivalve *Tellina* is to the juvenile plaice in Scottish inshore waters (Boyle 1981).

It has been suggested that the Pulmonata (land snails) alone bring the molluscs "into third place ... in bioenergetic terms of animal turnover in terrestrial ecosystems" (Russell-Hunter 1983). That turnover results from the activities of land snails as they break down dead vegetation, produce soil and increase its fertility, and cycle nutrients. In Israel two species of lichen-eating snails that live on limestone rocks contribute significantly to weathering and soil formation in the rocky desert (Shachak, *et al.* 1987). Movement of the horn shell *Rhinoclavis* on reef flats in the Pacific alters bacterial and chlorophyll concentrations in the sand (Hansen and Skilleter 1988). Mussel beds of hundreds of thousands of individuals packed tightly together stabilize the river bottom and cleanse the river as the bivalves pump water through their bodies in the rivers of North America (Davis 1977).

In some circumstances, molluscs also outweigh both invertebrates and vertebrates in ecosystems: the polygyrid land snail *Mesodon thyroidus* with a density of 63,330 snails per hectare on a floodplain in Illinois and a standing tissue biomass of 26 kg per hectare, exceeded maximal fish biomass in the most productive river in the state (Emberton 1991); the biomass of the giant clam *Tridacna* and the pearl oyster *Pinctada* are more important than the corals in the lagoon at Reao in the Tuamotus (Salvat 1970); and in England in the River Thames at Reading, 80% of the biomass of benthic invertebrates is comprised of unionid mussels (Berrie and Boize 1992).

There is general agreement that the numbers of animal and plant species worldwide are declining at rates which far surpass those which have occurred in geological time. No one knows how many species now exist, but it is estimated that at current rates of extinction, 15-25% of the world's species could become extinct by the middle of the next century (Western and Pearl 1991). If that prediction is valid, the result can only lead to the disruption of major ecosystems worldwide, to widespread human suffering, and to alterations in the course of evolution. The preservation of species is critical to human welfare.

Not least among those animal species undergoing decline are molluscs. Of the perhaps 120,000 species of molluscs worldwide, a number second only to that of the arthropods in terms of species diversity, more than a thousand mollusc species can be found on local, national and international lists as recently extinct, rare, threatened, and endangered species (Kay, this volume). Fifteen percent of the more than 2,000 animals on the 1990 IUCN *Red List of Threatened Animals* are molluscs; 45% of the 272 invertebrate species in the IUCN *Invertebrate Red Data Book* (Wells *et al.* 1983) are molluscs; and more than 80 mollusc species are listed in CITES appendices I and II (CITES, 1990).

The following facts confer both urgency and direction to priorities in planning and implementation of a variety of measures designed to ameliorate rates of loss of molluscan diversity.

1) Although molluscs in all ecosystems appear on the lists of recently extinct, threatened and endangered species, terrestrial and freshwater mollusc species are particularly vulnerable to habitat destruction, over-collection, predation by alien species, and the spread of non-native vegetation into high elevation forests. All five species of an endemic subfamily (Neoplanorbinae) of ancylid pulmonate limpets and two genera of freshwater gastropods, *Tulatoma* (Viviperidae) and *Apella* (Pleuroceridae), have disappeared from the rivers of the United States in historic time (Basch 1962; Davis 1977), and more than 50% of the once exuberant molluscan fauna of North American rivers is now either extinct or endangered (Davis 1977). Virtually all of the land snails of St. Helena were extinct when Darwin visited the island in 1876; more than half of the 41 species of pulmonate tree snail *Achatinella* on the island of Oahu in Hawaii have become extinct since 1911 (Kondo 1970; Hadfield 1986a), and all seven endemic species of *Partula* on the island of Moorea in the Society Islands were extinguished between 1977 and 1987 (Murray *et al.* 1988).

Terrestrial and freshwater molluscs which are threatened account for 92% of the molluscs in the *IUCN Invertebrate Red Data Book* (Wells *et al.* 1983), 96% of the molluscs listed in the *IUCN Red List of Threatened Animals* (1990), and 95% of a world list of endangered mollusc species compiled by Kay (this volume).

These figures represent significant fractions of families and genera: 35% of the North American species in the freshwater mussel family Unionidae (United States Fish and Wildlife Service 1991), the remaining achatinelline snails on Oahu (United States Department of Interior 1986), and 15% of the land molluscs and 50% of the freshwater molluscs of central Europe (Ant 1976).

2) In contrast to the many historical terrestrial and freshwater mollusc extinctions, there is only one recorded extinction in history of a marine mollusc: a small Atlantic limpet (*Lottia alveus*), once abundant on eelgrass on the east coast of North America, is now extinct in the North Atlantic Ocean (Carlton *et al.* 1991). This may be the only historical extinction that is not apparently attributable to human agency (Vermeij 1989). Rather, the limpet was a victim of its own physiology (Gould 1991): its eelgrass host was subject to a massive die-off in the 1920's and 1930's, and, while remnants of the eelgrass populations survived in low salinity waters, the limpet, lacking the flexibility to survive reduced salinities or to move to another host plant, gradually died out.

Nor are the numbers of marine molluscs reported as threatened or endangered as great as those of terrestrial and freshwater molluscs, although marine molluscs are not immune to declining diversity. All seven species of the giant clams (family Tridacnidae) are listed in the *IUCN Red List of Threatened Animals* (Wells *et al.* 1983) as a result of over-exploitation in parts of their range (Yamaguchi 1977), and local extinctions have been recorded throughout the Pacific (Wells *et al.* 1983; Heslinga, *et al.* 1984; Munro 1989). The fishery figures for other marine molluscs which are intensively fished, although uncertain, relate to abalone, *Haliotis* worldwide (Shepherd *et al.* 1992); trochus, *Trochus niloticus* (Heslinga *et al.* 1985), and the green snail, *Turbo marmoratus,* in the Pacific (Yamaguchi and Kikutani 1989); the queen conch, *Strombus gigas,* in the Caribbean (Berg and Olsen 1989); and the loco (*Concholepas concholepas*) on Peruvian and Chilean coastlines (Castilla and Jerez 1986).

Mollusc diversity around the world

The land snails of continents

Every continent has its own land snails: *Bothriembryon* of Australia and the giant African snail *Achatina* of Africa are as typical of those countries as are the kangaroo and the lion. Land snail families and genera, however, may be represented on more than one continent because distribution is a reflection of geological history during which land masses have drifted and mountains have been uplifted. Continental molluscan faunas are, therefore, composed of elements representing different geographies and different histories.

The faunas of most islands are relatively well known; the faunas of continents, partly because of size and complexity, but partly also because we are dependent on 19th century records for much of what we do know, are not so well known. Thus we know very little for large parts of Africa and most of Asia and South America. Even relatively well known regions however, are sources of surprise: 1976-1977 field work in Western and Central Australia increased the number of valid camaenid species from about 40 to 125 (Solem 1979). In Europe and North America new species descriptions and reports of major range extensions are commonplace in each issue of malacological journals. The following account is disparate, but certain themes are repeated with that of destruction of habitat perhaps the most pervasive.

Africa

The fauna

The African continent south of the Sahara is part of the Ethiopian biogeographical region, with an estimated 6,000 land snail species (van Bruggen 1977).

The African land snails reflect the extraordinary geography and history of the continent and include both one of the smallest and the largest land snails in the world (the shell of *Punctum pallidum* measures 0.4 x 1.2 mm, that of *Achatina reticulata* measures 208 mm but with a giant 270 mm specimen of *Achatina achatina* recorded (Groh and Griffiths 1987)), a large number of carnivorous snails, and six endemic families. Two families, the giant African snails in the Achatinidae and the Urocyclidae may have evolved in an ancient equatorial forest belt and then spread south almost to the Cape of Good Hope (van Bruggen 1977). Both families show remarkable radiations: the Achatinidae are adapted to the extremes of desert and alpine conditions, the Urocyclidae include every type of gastropod from typical slugs to snails with large helicoid shells. Of the remaining four endemic families, two families are found in southern Africa, the carnivorous slugs in the Aperidae and the large-shelled (about 40 mm in length) Dorcasiidae which live in desert conditions and which are allied to the South American Strophocheilidae, and two families, the Thyrophorellidae and the Aillyidae, are restricted to West Africa (van Bruggen 1977).

In southern Africa, with perhaps 650 species, van Bruggen (1978) estimates there are about 20 species per 100,000 sq km. Six families account for more than 75% of the species (van Bruggen 1975): the Streptaxidae (>135 species), the Charopidae (>110 species), and the Subulinidae, Urocyclidae, Achatinidae and Enidae (each >100 species); and 90% of the species are endemic (van Bruggen 1978). Five families (Aperidae, Dorcasiidae, Corillidae, Charopidae, and Rhytididae), found only in southern Africa on the African continent, are sometimes called the Southern Relict Fauna because of their relationships with land snails in South America and Australia which suggest that they may have had their roots in Gondwanaland (van Bruggen 1980b).

Although only 0.2% of southern Africa is forested (van Bruggen 1978), most of the southern African land snails are forest dwellers, found on low vegetation and, especially, in litter; a few such as the operculate *Tropidophora* live on tree trunks. The shells of the forest snails are usually dark in colour and decorated with hairy protuberances. Savanna and deserts with low rainfall, high temperatures, and little food and shelter cover large parts of southern Africa and harbour fewer species (perhaps less than 150) than do the forests, but these desert snails are highly endemic and may appear in enormous numbers after rainfall.

The rich land snail fauna of east Africa (Kenya, Tanzania, and Uganda) of about 1,000 species (Verdcourt 1982), dates from at least the Miocene (Verdcourt 1984), and is about 75% endemic today. More than 70% of these land snails are forest dwellers, 13% occur in bushland, thicket and arid areas, and the remaining 5% are found at altitudes of more than 3,000 m (Verdcourt 1972). The dominant families are the Streptaxidae and Urocyclidae (Rodgers and Homewood 1982, Verdcourt 1972).

Status

Given the size of the continent, its extraordinary topography, the fact that it has the longest history of land use in the world, and its political complexity, a summary of the conservation status of the terrestrial molluscs is not possible. The taxonomy and distribution of the land snails of large areas of the continent remain inadequate. In Gabon, West Africa, for example, 75% of the species found in a study of rainforest litter are potentially undescribed (de Winter 1992).

Only one African land snail, the streptaxid *Gulella plantii,* is listed in the *IUCN Red List,* but there are indications of declining diversity. Van Bruggen (1969) notes, for example, that in Zululand "the flora and fauna have suffered less [in game reserves] than elsewhere." Unique habitats such as the fnbos of southern Cape Province with a mediterranean type of climate and about half of its 60 species of land snails endemic, is subject to veld fires that affect the molluscs (van Bruggen 1978). In the montane forest islands of the East Usambaras, the West Usambaras, and Kilimanjaro where there are unique assemblages of land snails known only from 19th century lists which indicate a rich endemic fauna, agricultural encroachment and timber operations have severely reduced forest area, and continuing encroachment puts the land snail fauna at risk (Rodgers and Homewood 1982; Wells *et al.* 1983).

There are ambitious programmes for national and state parks and refuges in Africa, and World Natural Heritage Sites and Biosphere Reserves have been recognized, but continuing incursions into tropical and montane forests by loggers, agricultural encroachment, soil erosion, mining, and the like continue to take a toll.

Asia: India

The fauna

Solem (1984) noted in the introduction to a recent volume on biogeographical studies on non-marine molluscs that "The absence of publications . . . on the Oriental Region .. . reflect the absence of current study." Biogeographers define the region as including all of Asia, that is, India, Sri Lanka, Burma, Thailand, the Malay peninsula, China with Hainan and Formosa, Japan, the Philippines and the Indo-Malayan archipelago to the Celebes and the Moluccas. But apart from the reviews of Solem himself (1959, 1961) on the New Hebrides and New Caledonia, and the 19th-mid-20th century compilations of such authors as van Bentham Jutting (1948, 1950, 1952) on the Indo-Malayan Archipelago (see under Islands below) and Gassies (1863-1880), Crosse (1894) and Franc (1957) on New Caledonia, there are no summaries of the non-marine molluscan faunas of the Oriental Region. On the Indian subcontinent, however, 19th and early 20th century British administrators, soldiers and surveyors such as Blanford, Godwin-Austen and Gude devoted years to the collection, dissection and study of Indian molluscs. Blanford and Godwin-Austin (1908) and Gude (1914, 1921) recorded about 1100 species of pulmonate and operculate land snails; a more recent figure of 1475 species, 525 operculates and 950 pulmonates (Winckworth 1950), has been reported.

The oldest elements in the Indian fauna are considered relicts of the Gondwanaland fauna (Mani 1974a) and are found in Peninsular India, considered by Indian biogeographers as *India vera* (Mani 1974b). Among the molluscs are a bivalve, the freshwater mussel *Mulleria* which is congeneric with a South American species, the streptaxids *Streptaxis* and *Ennea* which are shared with Madagascar and South Africa, and *Glessula* (Ferrusaciidae) which also occurs in South Africa.

Peninsular India also spawned some remarkable species radiations following the breakup of Gondwanaland, among them radiations in the pulmonate Helicarionidae listed with 39 genera and 427 species (Blanford and Godwin-Austin 1908); more recent malacologists recognize 25 genera and 200 species (Parkinson and Groh 1987). In the operculate family Cyclophoridae Gude (1921) lists 24 genera and 432 species.

The Indian land snails appear to be mostly ground-living forms with small ranges and with some very odd shells. In the family Succineidae, usually distinguished by thin, ovate shells, the shell is limpet-like in *Camptonyx* and absent in *Hyalimax.* The largest of the Indian land snails, the imperial snail of India, *Hemiplecta basiliens*, is endemic to the teak forests of the Western Ghats (Jairajpuri 1991). Most Indian land snails are very small, however, 1-2 mm in greatest dimension, and curiously shaped. In the operculate cyclophorids *Cyclotus* and *Pterocyclus* the aperture is twisted and upturned like a tube, a condition apparently occurring where there are strong seasonal fluctuations associated with monsoons, with the tubular aperture accommodating aestivation; in *Opisthostoma nilgirica,* the shell is shaped like a barrel, sculptured with fine axial ribs, and the aperture is like a miniature tuba. Hirsute "spines" and apertural armament are also common.

Status

The work of the early British conchologists can never be repeated as much of India no longer appears to support native terrestrial molluscan faunas. Centuries of habitation associated with massive deforestation have resulted in the disappearance of virtually all natural habitats. Mani (1974a) notes that the characteristic fauna of peninsular India has been virtually eliminated except for small but rapidly dwindling pockets; and there are virtually no land snails at all on the Indo-Gangetic plain, the most densely populated part of India. There is, however, a network of national parks, wildlife sanctuaries and multiple use management areas (Singh 1985) which may encompass tracts of native vegetation where native land molluscs still survive. The National Wildlife Action Plan adopted in 1983 provides for continuing creation of protected areas.

Australia

The fauna

The Australian land snail fauna is estimated at about 500 species (Smith 1984), but with Solem's (1988) report of "perhaps the greatest concentration of short range restricted endemic species found anywhere in the world" in the Ningbing Ranges and Jeremiah Hills of western Australia, earlier figures may be underestimates.

The several different elements in the land snail fauna reflect the complexities of the evolution of Australia itself from part of the continent of Gondwanaland to an island - continent moving north where it meets the islands of Indonesia. Several families are found worldwide (Succineidae, Pupillidae, and Vertiginidae); two families, the operculate Helicinidae and the Achatinellidae, are an old circum-Pacific element; the Camaenidae and Pupinidae are shared with the Indo-Malayan archipelago and Asia; and four families, the Rhytididae, Bulimulidae, Charopidae and the endemic family Caryodidae may be derivatives of the Gondwanaland fauna.

Australia is the flattest and driest of the continents: its highest mountain rises only 2,200 m, and more than half of the continent receives less than 25 cm of rain a year. The southwestern corner, one of the continent's major arid areas, is home to one of Australia's most remarkable land snails, *Bothriembryon,* an endemic genus related to the South American Bulimulidae. There are about 30 species which make up about half the taxa in the area (Smith 1984). They are well adapted to conditions where there is infrequent moisture: some of the snails secrete a mucous plug or epiphragm which enables them to survive for weeks to years until moisture recurs; others, with white shells, "glue" themselves to the trunks of trees or the substrate during drought conditions (Bishop 1981).

If one land snail family can be said to dominate the Australian fauna, it is the highly diversified Camaenidae with species which are adapted to desert conditions in the arid and semi-arid central portion of the continent and in Western Australia and to tropical rainforests in northeastern Queensland. Solem's analyses (1988 and references therein) of the post-Miocene speciation in these snails in the Kimberley district of Western Australia is a masterly account of an exuberant radiation which must represent only a fraction of what remains elsewhere in unexplored areas of the continent.

While deserts occupy a large proportion of Australia, the climate of Queensland and northern New South Wales is tropical to warm temperate and the accompanying rainforests and other vegetation support a molluscan fauna more like that of New Guinea and the Indo-Malayan archipelago than that of the rest of Australia. The fauna is dominated by camaenids such as *Sphaerospira*, *Xanthomelon* and *Meridolum.* Others of the land snails include the operculate prosobranchs such as the Helicinidae and Cyclophoridae. Among the endemics in Queensland are the camaeid *Hadra,* some with shells 60 mm in length, and the rainforest slugs Athoracophoridae and Rathouisiidae.

In temperate southeastern Australia and Tasmania 69% and 30% of the molluscan fauna respectively is endemic; many of these endemics are obligate inhabitants of the rainforest (Smith 1979, 1984). The Charopidae and Punctidae, with a host of species with minute shells and small distribution ranges, comprise 62% of the taxa in southeastern Australia.

Status

There are few areas in Australia that have not been affected by human activity. In New South Wales, more than two thirds of its forest cover has been removed since the time of first European settlement, nearly two thirds of the land in Victoria is privately owned with most cleared for agriculture, and there are estimates that the vegetation in 55% of the arid zone is degraded (Feller *et al.* 1979). Most Australian land snails are ground living snails and vulnerable to habitat alteration by fire and hoofed animals, while the land snails associated with temperate and tropical forests are susceptible to logging and other types of habitat disruption. Despite the apparent disruptions to habitat and other effects, only one Australian land snail is listed in the *IUCN Red List, Anoglypta launcestonensis,* an acavid from Tasmania. Thirty-four species from Australia and Tasmania, and another 90 species from the offshore islands, Lord Howe Island and Norfolk Island are listed as threatened or endangered (B.J. Smith pers. comm.,1987). Australia has in place a programme for the establishment of wildlife habitats, protected areas and reserves, and stringent regulations on introductions. There is provision for wilderness areas in national and state parks in the New South Wales National Parks and Wildlife Act of 1967 and the Victorian National Parks Act of 1975.

Europe

The fauna

Europe, extending north and east to Asia and south to the Mediterranean, and Africa north of the Sahara, is part of the biogeographical region termed the Palearctic. Waldén (1963) suggests a fauna of about 1500 species and 229 genera of which 124 are exclusively European. Numbers of species follow the north-south temperature gradient from the tropical southern Mediterranean-northern African sector with perhaps 800 species to northern taigas and tundra near the Arctic circle where there may be only 20 species (Likharev and Rammel'meier 1952). There are an estimated 16 species per 100,000 sq km (van Bruggen 1978).

The Helicidae is perhaps the most successful family in Europe in terms of numbers of species. It includes the edible snails *Helix* and *Otala,* other commonly occurring and often abundant snails such as the garden snail *Cepaea* and the sandhill snail *Theba pisana,* and a suite of lesser known species with restricted ranges. Other typical European families represented by generic and species radiations are the slugs, Arionidae and Limacidae; the grass snails Valloniidae, the whorl snails Vertiginidae, and the door snails, Clausiliidae.

No families of land molluscs are endemic to the European continent, but there is generic and specific endemism (Peake 1978). The speciation pattern reflects a complex geological history of the continent involving glaciation and changes in climate. In the northern lowlands which were repeatedly glaciated during the Pleistocene there are virtually no endemic species and most of the species are widely distributed, descended from immigrants from the south (Kerney and Cameron 1979). The mountainous south with different substrates and topographical relief has higher species diversity and large numbers of narrowly endemic species in the Alps, Carpathians, Albania, and northern Greece. In the Iberian Peninsula, the bridge between Europe and Africa, more than half of its land snail species are endemic (Puente and Prieto 1992); and in the Caucasus of eastern Europe more than 75% of the species of clausilids, limacids and helicids are endemic (Likharev and Rammel'meier 1952).

Status

Central European landscapes today are very different from the landscapes of pre-human times when vast areas of forests covered the land. Instead there are islands of woods and unwooded areas essentially controlled by human activity. In northern Europe, draining fens, forestry (in Sweden), farming practices dominated by monoculture, road construction, tourist facilities, and the effects of pollution and acid rain have changed the landscape and in so doing impact the molluscan faunas (Waldén this volume). In southern Europe major disruptions of habitat are due to forest fires, agriculture, and tourist development which destroys sensitive areas (that is, those areas with some forest cover) is also occurring at an alarming rate (Bouchet *in litt.)*

Documentation of mollusc distribution and conservation status in northern Europe has accelerated over the last decade with the development of mapping projects and publication of national Red Data books. The data indicate that there is an overall decline in diversity (Collins and Wells 1987) and that more than 200 non-marine molluscs endemic to single countries are now considered threatened in Europe (Wells and Chatfield 1992). The West German and Austrian Red Data books between them list well over 100 threatened and potentially threatened species (Blab *et al.* 1984; Gepp 1983); in Austria over 50% of the non-marine mollusc fauna is considered threatened; in Switzerland, 67% (Turner and Wuthrich 1985) and in the United Kingdom, about 13% (Kerney 1982; Foster 1983) of the terrestrial molluscs are of concern. In Belgium, ranges of some 50 species have declined since 1950 (van Goethem, *et al.* 1987). In France, Bouchet (1990) suggests that of the 53 endemic terrestrial molluscs occurring on French territory, most are restricted to small areas of the Maritime Alps, Corsica and Basque Country, 21 require immediate protection, and one slug species is reported as extinct.

Molluscs were added to the Berne Convention — the Convention on the Conservation of European Wildlife and Natural Habitats — in 1988; 23 species of molluscs are now listed among the more than 80 listed invertebrates. A recently issued Council of Europe directive specifically lists threatened species and habitats.

North America

The fauna

The estimated 750 species of land snails in North America (Solem 1984), which works out to about 5 species per 100,000 sq km (van Bruggen 1978), represents a relatively small fauna compared with that of other continents. There are two reasons for the depauperate fauna. One is geography: large areas of desert, taiga and tundra, short grass prairies and coniferous forest harbour relatively few species. The second reason is a matter of history: much of North America was glaciated in the Pleistocene, and, while this recently glaciated land has been re-colonized by land snails, there is little evidence for much speciation in these areas. About 80% of the indigenous species are therefore concentrated in two areas of the continent which were isolated by a major marine incursion during the Late Cretaceous and early Tertiary: (1) in the east from the plains bordering the eastern limit of the Rocky Mountains to the Atlantic, and (2) in the west from the Rocky Mountains and the Sierra Nevada to the Pacific. The eastern and western faunas merge in the north and south. In the north, where temperature limits distribution, a boreal area is inhabited mainly by circumpolar species; in the south, where a fringe of Texas and Florida borders the Caribbean, there are elements of a much larger Middle American fauna which also inhabits the West Indies, Bermuda, Central America and most of Mexico (Pilsbry 1948; Waldén 1963).

The eastern land snail fauna is dominated by the endemic family Polygyridae (Solem 1984; Walden 1963) with approximately 260 species (Emberton 1991) which are conspicuous in the invertebrate faunas of leaf-litter and floodplain habitats. In Florida, the tree snails *Liguus, Orthalicus* and *Drymaeus* are endemic, and other eastern endemics include genera in the Charopidae, Zonitidae and Pupillidae. Except for the Florida tree snails, the eastern land snails are ground-dwellers, in habitats from the Everglades to high altitude forests in the mountain states. The Florida Everglades harbour not only tree snails but endemic Pupillidae and Cerionidae and the operculate Helicinidae; a Cumberland province in the Blue Ridge and Cumberland Plateau is distinguished by several endemic genera of Zonitidae (Pilsbry 1948; Burch 1962); and the Driftless Area, a small area of southwestern Wisconsin harbours a relict Pleistocene fauna with the rare *Hendersonia occulta rubella* (Morrison 1929).

Western land snails are found from the high altitude forests of the northwest and the Rocky Mountains to the deserts of Colorado and the Mojave. Three families, the Helminthoglyptidae, Ammonitellidae and Oreohelicidae, and two subfamilies Thysanophorinae and Holospirinae (Solem 1984), are endemic to the region. In the northwest in Oregon, Washington, and Idaho, and in California, slugs such as *Ariolimax* and helminthoglyptids *Monadenia* and *Helminthoglytpa,* and the oreohelicid *Ammonitella* are characteristic. In the Rocky Mountains the predominant land snail is *Oreohelix* (Oreohelicidae) with perhaps 35 species (Pilsbry 1948). The southwest with its arid deserts is characterized by a number of distinctive genera in the Helminthoglyptidae: *Sonorella, Chaenaxis* and *Humboldtiana* with the largest of the southwest land snails, and, in the Polygyridae, *Ashmunella* with some 32 species (Bequaert and Miller 1973).

Many of the endemic polygyrids and helminthoglyptids are found in very small, restricted areas: *Helminthoglypta allynsmithi* is known only from a few rock slides in the canyon of the Merced River (Roth 1972). Speciation in the deserts of the southwest, where 68% of the species in Arizona alone are endemic, is also remarkable (Bequaert and Miller 1973), and parallels that in the deserts of southern Africa and in Australia.

Status

The major threats to land snail diversity in North America are habitat loss resulting from land clearing, logging, strip mining, fires, and continuing encroachment of urban centers into native ecosystems.

The centerpiece for the conservation of biodiversity in the United States is the Endangered Species Act of 1973 which authorized an official federal list of endangered and threatened wildlife which is not limited to the United States. Under the Act, species are proposed for listing. Recovery plans, which include habitat conservation and establishment of management and monitoring plans, are subsequently developed. Fifty-eight taxa of molluscs are presently on the federal list, 13 North American land snails and *Papuina pulcherrimus* from Manus Island, and 44 bivalves, 42 from North America and two from elsewhere.

Among the benefits to a listed species is protection from adverse effects of Federal activities, restrictions on take and trafficking, and authorization for the government to seek land purchases or exchanges for important habitat. Various federal agencies have responded to the Act by establishing research programmes, and many of the states have undertaken activities promoting the preservation of endangered biotas.

There is also an elaborate programme of national, state and local parks which provide habitats for some endangered species. The national park, refuge and reserve system includes 186 parks and nature reserves containing 2.2% of the continent (IUCN 1982).

South America

The fauna

The biotic resources of South America, which with Central America and the islands of the West Indies comprise the biogeographical region recognized as the neotropics, are among the richest in the world with 19% of the world's mammal species and one-third of the flowering plant species (Mares 1986). Jaeckel (1969) estimates 10,000 taxa (species, subspecies, races) of non-marine molluscs in South America; Parodiz (1957,1980) lists just over 200 species of land molluscs (5 prosobranch families, 22 pulmonate families) in a catalogue of species from Argentina and bordering areas.

Charles Darwin, travelling from the coast of Chile to the Cordillera through "an uninhabited desert" in 1835 wrote that he " . . . saw traces of only one living animal in abundance, namely the shell of a small Bulimus [*Strophocheilus chilensis* (Sowerby)], which were collected together in extraordinary numbers on the driest spots. In the spring one humble little plant sends out a few leaves and on these the snails feed. As they are seen only very early in the morning, when the ground is slightly damp with dew, the Indians believe that they bred from it" (Darwin 1906). The small "Bulimus" is related to one of the few land shells which is considered a rarity (Dance 1972). *Sultana labeo,* the blubber-lip Bulimus, was discovered in a farmhouse at about 8,000 feet near Chachapoyas, Peru, in 1827; two other specimens were found alive but roasted and eaten by the finder's muleteer. The single shell was deposited in the museum of the Zoological Society of London but subsequently stolen and it was not until 1947 that someone revisiting the area procured additional specimens.

Darwin's small "Bulimus" also represents one of the oldest elements among the South American terrestrial molluscs for it is in the family Strophocheilidae, endemic to the continent but related to the Gondwanaland family Dorcasiidae in Africa. The carnivorous Streptaxidae and veronicellid slugs (Veronicellidae) are found both in South America and Africa. A third Gondwanaland family, the Bulimulidae which is the most widely distributed family in South America (Parodiz 1980), also occurs in Australia.

The continent can be divided into a northern tropical zone (Hylaea and the North) and a temperate Chaco-Pampean area which becomes much cooler in the south (Patagonia) (Parodiz 1980). The two areas have different geological histories, as indicated by both the recent and fossil freshwater mollusc faunas, and the land snail faunas appear to have different origins. In addition to the ancient stocks of South American molluscs, several families appear to have come from the north, among them the Pupillidae and Zonitidae. At least four families would appear to have arrived in South America via Middle America: the Helicidae, Urocoptidae, Oleacinidae and Cerionidae (Pilsbry 1896-1899; Parodiz 1980).

Status

Good data on the landsnails of South and Central America do not exist, and no South American species is listed in the IUCN Red Book. Pain (1981) noted that because of large-scale destruction of forests in certain areas of Brazil, some species of *Strophocheilus* have become scarce or possibly even extinct. The pampas, forests and mountains of South America have suffered fires, logging, erosion and extensive agriculture for centuries. There is an extensive system of parks and reserves: 218 parks and reserves include 2.7% of the continental land area (IUCN 1982), and there are systems of complex environmental laws that provide for the protection of habitats, plants and animals (Mares 1986). The Galapagos Islands, now a national park with conservation efforts supported by an international consortium, are a focal point for the conservation of molluscan biodiversity in South America (additional references under islands).

The land snails of islands

Island faunas

Charles Darwin first called attention to the importance of insular land shells in evolution: "Almost all oceanic islands, even the most isolated and smallest, are inhabited by land-shells, generally by endemic species . . . " (Darwin 1900). Solem (1984), analyzing land snail diversity worldwide, suggests that insular land snails represent " a significant, but unknown, portion of the world diversity of land snails . . . "

The terrestrial biotas of islands are indeed legendary among biologists for the diversity and novelty of their evolutionary products. Among the land shells, that diversity and novelty is represented by the peculiar acavids, 99 endemic species in five genera (Emberton 1990), some of them the size of tennis balls and with eggs 3 cm long from Madagascar; the earthworm-feeding *Paryphanta* from New Zealand; the large, green snail, *Papuina pulcherrima*, from Manus Island; the jewel-like tree snails *Achatinella* from Oahu in Hawaii; the multitudinous *Cerion* from islands in the West Indies; and the elongate, sinistral achatinid *Columna* from a tiny island in the Gulf of Guinea. Island land snails are remarkable not only for species, but for entire families and subfamilies: three families and two subfamilies are endemic to the high islands of the Pacific alone, each taxonomic group with several genera and more species, each island with as many as 100 species of which 90% may be endemic.

The Malay Archipelago and the Philippines

The Malay archipelago was recognized by Alfred Russel Wallace (1872) as one of the world's great centers of animal and plant diversity. Many molluscan elements on islands in the archipelago reflect the fauna of India and Southeast Asia, among them cyclophorid operculates with their extraordinary apertures and protuberances, large helicarionid snails, rathouisiid slugs, and carnivorous streptaxids which reach their southern limits near the Celebes. The large, colourful, arboreal camaenid *Amphidromus* is also prominent on the islands in the archipelago.

The Philippines which are particularly rich in land snails are sometimes considered a separate province within the Indo-Malayan realm. Some of the most handsome land snails in the world are found on these islands, among them the endemic subfamily Helicostylinae (family Bradybaeindae) with nearly 300 species of large, colourful tree snails. The Camaenidae with many endemic species in *Obba* and the Helicarionidae with endemic genera *Lepidotrichia* and *Rhyssota* are also characteristic.

The West Indies

The biota of Middle America and the West Indies is usually included with that of South America in "Neotropica." Simpson (1894) described the land snails of the West Indies as so "astonishingly rich and diversified," that "no other area of the globe of equal extent can be compared with it." He counted 1600 species of land snails in 65 genera, "a number almost as great as that found on the mainland of the entire continent of America." Pilsbry (1948) agreed: "the Middle American fauna is fully equal in numbers of endemic families and genera... and equally entitled to stand as a primary region." In numbers of species, most of the major islands count species in the hundreds: Cuba 600, Jamaica over 500, Haiti 250, Puerto Rico 120. Not only do species numbers run high, but endemism is also high: 40 and 50% of the species are endemic to each island. The islands of the West Indies are also distinguished by the composition of the land snail fauna: there are perhaps 600 species of operculate prosobranchs (Helicinidae, Neocylidae, Annulariidae), a higher proportion than anywhere else. Six pulmonate families are also primary components of these remarkable species radiations. The Sagdidae, Cepoliinae (Helminthoglyptidae), and Cerionidae are endemic to the region. Specimens of *Cerion*, the only genus in the Cerionidae, are often so abundant as to completely cover the vegetation. There are also large numbers of species in the Urocoptidae, the carnivorous Oelacinidae and the orthalicine tree snails (Bulimulidae).

Status of island faunas

Island ecosystems are fragile, and island biotas are among the most vulnerable of all biotas to changing environmental conditions: island species, especially endemics, are virtually defenceless in the face of introduced alien species and manifest a rate of extinction far in excess of that of continental species (Atkinson 1989; Diamond 1984).

Islands have experienced profound changes in landscape since prehistoric time. In the Caribbean, land snail extinctions on Jamaica are attributed to habitat disturbance by humans during the last millennium (Goodfriend and Mitterer 1988). In the Pacific, on Tikopia in the Solomon Islands there are indications of severe human-induced soil erosion perhaps 3000 years ago (Kirch and Yen 1982); on Easter Island, there is evidence of extensive deforestation more than a thousand years ago (McCoy 1976); in Hawaii, extinctions of native land snails with settlements on Oahu began about 1500 BC (Christensen and Kirch 1986).

Change increased in pace in the 18th and 19th centuries as western voyagers explored the oceans. European explorers and settlers introduced hoofed mammals, rats and exotic plants. Darwin, describing St. Helena in 1836, noted that goats had been introduced by the Portuguese in the 16th century, and that a century afterwards "the evil was complete, . . . There can be little doubt that this great change in the vegetation affected ... the land-shells, causing eight species to become extinct ... " (Darwin 1906; and see Cronk 1989; Crowley and Pain 1977). Forests on Pacific islands were similarly destroyed and nearly the entire fauna of the family Endodontidae, a radiation of several hundred species, disappeared between 1900 and 1960 (Solem 1983). In New Zealand, introduced pigs and rats prey on the large endemic ground snails (*Paryphanta, Powelliphanta,* and *Placostylus*) and threaten their existence (Jeffs 1982, Lockley 1980, Ogle 1979, Meads *etal.* 1984). Many of the large, colourful tree snails in the endemic subfamily Helicostylinae in the Philippines are apparently extinct because of the destruction of their forest habitat (Abbott 1989).

Change continues today at an even greater rate as human populations on islands increase in numbers; urbanization affects land from the mountains to the sea; forest habitats are disrupted by encroaching agriculture, logging, roads and runways; tourism takes a toll on islands in the Mediterranean, Atlantic and Caribbean; sand for concrete and cement is removed from the strandline habitat of *Cerion* in the Caribbean; and introduced species decimate populations of indigenous land snails.

Several programmes for the management of protected areas on islands now exist: The Nature Conservancy (United States) purchased and manages large areas of native ecosystems in the Caribbean and Pacific. One of these areas in the Pacific serves as a study site for populations of native snails (Hadfield and Miller 1989). Plans for two national parks on Haiti include protected areas for endemic and potentially threatened land snails (Thompson 1986).

The status of land snails on several islands and island groups is listed in Table 5.1.

Freshwater molluscs

The fauna

There are perhaps 6000 species of gastropods and bivalves (Taylor 1988) which live in the freshwaters of lakes, rivers, hot springs, seeps, and seasonal ponds, habitats which are found on all the continents except Antarctica, in the Arctic, at high elevations, and on remote islands.

The freshwater mussels are perhaps the best known of freshwater molluscs, and, indeed, the pearl mussels *Margaritifera* in Europe may have been the first of the freshwater molluscs to have captured attention: enormous Neolithic shell mounds are evidence of their use as food throughout Europe, and their pearls were in demand for jewels. In the United States early naturalists were astonished at the diversity and abundance of the mussels: Rafinesque described 68 species in 12 genera in 1820 when all of the rivers of Europe had only 12 species (Stansbery 1971). More than 250 species in 47 genera are now recognized. Two families occur respectively in India, South America, Africa and Australia and are thought to represent relicts of the Gondwanaland fauna.

Freshwater mussels are also known for their long lives: some of them live more than 100 years and they are both abundant and speciose. More than 1,000 named species of snails and mussels are known from the Ohio, Tennessee-Cumberland and Coosa-Alabama-Cahaba Rivers of eastern North America alone (Davis 1977). In the Mekong River Valley there is a highly diverse pomatiopsid snail fauna of three tribes, 13 genera and more than 100 species, only recently recognized (Davis 1979) as a major freshwater snail radiation of considerable evolutionary significance. The vast number of endemics in Lake Ohrid in the Balkans comprises half the freshwater molluscan fauna of Europe (Boss 1979; Radoman 1964), and an estimated 73% of the species of freshwater molluscs in Japan are found in Lake Biwa, of which 43% are endemic (Mori 1984). The snail faunas of other lakes such as Baikal in central Asia, Tanganyika in Africa, and Titicaca in South America are equally spectacular (see Boss 1979 for references).

Spring-fed aquatic environments also support remarkable radiations of freshwater molluscs, among them minute hydrobioid snails. In the "four marshes" of Cuatro Cienegas, Mexico, five genera and nine species of hydrobiids are endemic to the basin (Hershler 1985); a radiation of more than 30 species of hydrobioids has been described from springs and wetlands in Florida (Thompson 1968); and more than 40 species of hydrobioids are recognized in the Great Artesian Basin in Australia (Ponder and Clarke 1990; Ponder, this volume).

In contrast to riverine, deep lake, and spring-fed environments, seasonal ponds and wetlands support widely distributed snails: species of *Lymnaea, Physa* and *Ancylus* are found around the world.

Status

Rivers, lakes, and springs are like islands in their isolation and vulnerability to habitat destruction. Rivers have also been exploited for their faunas, and polluted. Indeed it has been asserted that every river system in the world today has been affected in some way by humans (Davies and Walker 1986). Ortmann described the impact in western Pennsylvania as early as 1909: "pollution by .. . sewage . . . coal mines ... oil wells . . . chemical factories . . . [and]... finally damming up certain rivers." The impact of human activities is reflected in the faunas: five species of an endemic subfamily (Neoplanorbinae) of ancylid pulmonate limpets (Basch 1962), two genera of freshwater gastropods, *Tulatoma* (Viviparidae) and *Apella* (Pleuroceridae) (Davis 1977) and 35% of 297 taxa of freshwater mussels are listed as extinct, endangered or candidates for listing as endangered in the United States (United States Fish and Wildlife Service 1991). Populations of the pearl mussels (*Unio crassus* and *Margaritifera margaritifera*) *are* also seriously declining, and are locally extinct in Europe and the United Kingdom (Jungbluth this volume; Bauer 1988; Woodward 1990), and there is but one remaining population of *Margaratifera auricaria* (Altaba 1990).

Lake Baikal, isolated in central Asia, with a unique fauna not only of molluscs but of crustaceans, fish, and seals (Khozov 1963), is threatened by logging of neighboring forests andl effluent from pulp mills. Nearly 4% of Lake Biwa has been filled to create rice fields and recreation areas in the last 50 years and water quality continues to deteriorate (Okuda 1984). De-watering of springs destroys essential habitat of dozens of unique snails. More than half these habitats have disappeared in Florida (Thompson 1968); others are disappearing in Europe as springs dry up and there is physical disruption of the landscape. The immediate danger to Cuatro Cienegas in Mexico is from the effects of canals which drain marshes and lower water level in the springs (Taylor and Minckley 1966). Protection for the mound springs of the Great Artesian Basin is now being discussed (Ponder this volume).

The molluscs of coral reefs

The fauna

Coral reefs, although restricted to the tropics between 30°N and 30°S of the equator and to ocean depths of less than about 30m, cover about 0.1% of the surface of the earth. Thirty percent lie in the area of the Indo-Malayan Archipelago, bounded by Indonesia on the west, northern Australia on the south, the Philippines in the east, and mainland Asia in the north; another 30% occur in the Indian Ocean and Red Sea; 13% are found in the south Pacific; 12% occur in the western Pacific; 14% occur in the Caribbean and north Atlantic; and 1% is found in the south Atlantic (Smith 1978).

The molluscs of coral reefs have long been celebrated for their beauty, diversity, and utility. Among the famous shells of coral reefs are the golden cowrie, *Lyncina aurantium,* and a host of other cowries, cone shells and miters. The giant clams *Tridacna,* pearl oysters *Pinctada,* pearl button shell *Trochus niloticus* and turbinid *Turbo marmoratus* were utilized throughout the pre-western Pacific and form well known fisheries today. Still others of coral reef molluscs, among them the strombids *(Strombus)* and clams such as *Anadara,* remain central to subsistence diets in the Pacific and Indian oceans, and in the Caribbean.

Molluscs also play important roles in coral reefs. As reef builders, bivalves such as the giant clam (*Tridacna*), *Spondylus* and *Chama* and the gastropod wormshells (family Vermetidae) contribute to the framework of the reef and to sediments; and boring bivalves such as the mytilid "stone eater" *Lithophaga* and grazing gastropods, littorines, nerites and chitons remove quantities of limestone (see for example, Taylor and Way 1976) and are key elements in the bioerosion of the reef framework. Molluscs also play essential roles in community structure in food chains and as deposit feeders. The numbers and biomass of molluscs associated with reefs attest to their importance: in the Tuamotus in French Polynesia, molluscs are more important than staghorn coral (*Acropora*) and other corals in the biomass of lagoons (Salvat 1970).

Status

Reefs, which in the past supported human populations because their products were used only for subsistence while waste products were returned to nutrient cycles, are today increasingly degraded by human activity: shells and corals are collected for export, and fishing with poison and dynamite rather than net or spear destroys reefs, as do dredging and blasting channels through the reef to provide for small marinas.

The impact of reef destruction on molluscs is clearly visible: the molluscs of reefs which are destroyed by dynamite or sediment disappear as quickly as do the corals (personal observation). The impact of exploitation is poorly documented (Pointer and Catterall 1988) and is not so clear. While fisheries such as those for *Tridacna, Pinctada, Trochus,* and *Turbo marmoratus* show fluctuating or declining stocks (see below), the strombid *Strombus luhuanus* which is central to subsistence food resources in the Pacific, and the money cowrie *Monetaria moneta* of which millions were exchanged in the 19th century, continue to occur in very large numbers on reef flats through the Pacific. Pointer and Catterall(1988) provide both explanation and model: *Strombus luhuanus* is apparently resilient to gathering practices by traditional methods because of its size-dependent burying habit and partly subtidal distribution which provides refugia from human predation. At Bootless Islet near Port Moresby, Papua-New Guinea, where it has been continuously exploited for more than 500 years (Allen 1977), and at Yule Island in the Gulf of Papua, Papua-New Guinea, where as many as 5 million strombs may be collected in a year (Hinton 1982) there is no evidence of declining stocks. In the Caribbean, however, another strombid species, *S. gigas,* with similar habits, is now being exploited with new fishing technologies such as SCUBA and dredging, and the stock is being overfished (May 1984).

Marine sanctuaries or protected areas are now widespread, the largest is the 200,000 sq. km sanctuary established in 1975 on the Great Barrier Reef in Australia. In the United States there are some 14 sanctuaries off the coasts of nine states and American Samoa. Other protected marine areas include Sandy Bay Marine Preserve in Honduras, Shimomi Marine Park in Kenya, Pemba Island off the coast of Tanzania in East Africa, Tunku Abdul Rahman National Park in Malaysia, and Tubbatataba Reef in the Philippines.

Molluscs as economic resources

Mollusc fisheries

Facts and Figures. Molluscs comprised 8.2% of the world's fisheries catch in 1990 (FAO 1990), exclusive of local subsistence collection. More than 95% of the mollusc fisheries are from marine waters, and more than half of world production is from the north Pacific. Bivalves, primarily oysters, mussels, and scallops, make up 51% of the mollusc fishery, cephalopods 35% and gastropods less than 2% of the catch. Abalone (*Haliotis*) comprises the major gastropod fishery. Nearly all the freshwater catch of molluscs is in Asia (Japan, Korea, Philippines and Indonesia), and is composed largely of freshwater clams (*Corbicula* spp.) (FAO 1990).

Artisanal and recreational fisheries are also sources of molluscs for consumption. Indeed, these fisheries in the Pacific provide native populations with the major portion of their protein for subsistence (Chapman 1987, Cook 1976). Evidence from anthropological and sociological studies indicates that substantial amounts of molluscs are involved: 10-30% of the weight of animal flesh and 6% to 17% of the calories of some Aborigines in Arnhem Land (Meehan 1977).

Declining stocks

That increasing consumer demand for shellfish and squid coupled with limited standing stocks leads to precipitous declines in wild stocks was recognized as early as 1850. In Britain one of the most highly productive oyster fisheries in the 18th century was in the Firth of Forth but annual harvests of more than 20 millions failed before the end of the century (Fullerton 1960). A fishery for the green snail (*Turbo marrnoratus*) initiated in the Ryukyu islands in the early 1880's collapsed in less than 20 years because of overfishing (Yamaguchi and Kikutani 1989). More recent records of declines include those of abalone world-wide (Shepherd *et al.* 1992); mussel landings world-wide (Lutz 1985); wild stocks of the soft-shell clam (*Mya arenaria*) (Beal 1990) and bay quahogs (*Mercenaria mercenaria*) (Bourne 1989) in the United States; and the oceanic squid fishery for *Todaropsis* in Japanese waters in the 1970's (Okutani 1977). The loco (*Concholepas concholepas*) from the coastlines of Chile and Peru, which made up more than 25% of the gastropod catch in the 1980's with a high of 21,236 mt in 1987 was not listed in the FAO fisheries statistics in 1989, and reported at only 227 mt in 1990 (FAO 1990).

The data indicate that many mollusc fisheries populations tend to fluctuate, but, as Roper and Rathjen (1991) suggest for cephalopod fisheries, there remain many unknowns, " . . . stocks can be significantly affected by normal annual or cyclical environmental fluctuations, [and] analyses of population statistics by several national fishery agencies are inadequate to provide dependable assessments of predictable harvestable stocks . . . ". Artisanal fisheries also suffer from declining yields. Consumption of shellfish in the intertidal zones on the Transkei coast of South Africa (Branch 1975; Hockey and Bosman 1986), in the Canaries and Azores (Bouchet in litt.), in Costa Rica (Ortega 1987), and in Hawaii (Kay *et al.* 1982) has affected populations of limpets resulting in smaller mean sizes.

The cropping of marine production entails competition with bottom feeding fishes such as cod and halibut and with whales and pelagic fishes which feed on squid and octopus, as well as causing disruption of bottom communities by dredges and trawls. These detrimental effects along with declining and unpredictable fisheries stocks have provided much of the stimulus for the development of mariculture which is more and more recognized as a viable means of providing for direct production, of generating income, of re-seeding through hatcheries, and of avoiding overharvest and depletion of wild stocks. Mollusc culture accounts for 72% of shelled molluscs marketed and 53% of all marketed molluscs (John Bardach pers. comm., 1991). Culture of abalone in Japan, the United States, Mexico, and New Zealand has now reached a point where Shepherd *et al.* (1992) predict that "the culture of abalone will expand to production levels that will eventually rival or exceed production from wild stocks."

There remains, however, need for the establishment of production-oriented hatcheries around the world to meet expanding regional demands for seedstock. Hatcheries for production and re-seeding can be successful. In the tropical Pacific, hatcheries for the giant clam (*Tridacna*) provide for local conservation, subsistence food production, and large-scale commercial enterprises which generate employment opportunities and export revenue (Heslinga and Fitt 1987). There is a substantial market demand in Taiwan, Hong Kong, Singapore and Japan, and the clams continue to be a subsistence food in the Pacific. Hatcheries in Palau now have the capacity to produce 22,000-55,000 of one of the giant clams (*Tridacna derasa*) on a five-month cycle (Heslinga and Watson 1985). Other commercially important molluscs for which there are also hatcheries in the Pacific include trochus (*Trochus niloticus*) (Heslinga and Hillmann 1981), the green mussel (*Perna viridis*) (Heslinga *et al.* 1985), and the cockle (*Anadara granosa*) (Broome 1985).

The shell trade

The shell trade — collectors items, commercial shell, jewelry, mother-of-pearl, the ornamental trade, shellcraft, and the like — involves thousands of tonnes of shells annually (Wood and Wells this volume). Except for the freshwater pearl mussel, the shells of which are harvested for seed pearls, the bulk of the shell trade involves marine molluscs, primarily pearl oysters (*Pinctada* spp.), trochus, (*Trochus niloticus*), the chank (*Turbinella*), and the green snail (*Turbo marmoratus*).

Marine mollusc fisheries

Pearl oyster beds in the Red Sea were the source of pearls in early Egyptian times and by the beginning of the Christian era pearl fishing was an established industry in the Persian Gulf and the Indian Ocean. Other famous pearl beds occur in the Gulf of Manar, off Trincomalee (Sri Lanka), in north-western Australia, and in the Caribbean. Pearls from French Polynesia were first exported to Valparaiso in 1810, and more than 100,000 tonnes of the pearl oyster (*Pinctada*) have been exported from atolls in the Tuamotus since then (Salvat 1981). The first local extinction of a pearl oyster bed was noted in the Tuamotus in 1827 (Cuming 1827-1828); by the 1850s there was a general depletion of the pearl oyster beds in the Tuamotus (Salvat 1981) and in the Indian Ocean (Thomas

1884). Japanese culture of pearls beginning in 1898 relieved some of the pressures on pearl oyster beds, but between 1900 and 1960 the pearl oyster beds of seven atolls in the Tuamotus had been exhausted, and pearl oysters had disappeared in the Hawaiian Islands (Galtsoff 1933), in Madagascar (Wood and Wells this volume), and in parts of the Indian Ocean.

Ironically it was the decline of pearl oyster populations that led to the exploitation of another marine mollusc in the 20th century. The soft parts of trochus (*Trochus niloticus*) were used by Pacific islanders for food, and the shell cut as bracelets and fish hooks (Hedley 1917). Elsewhere trochus was known only to malacologists until about 1910 when former supplies of pearl shell were depleted and a search began for new sources of mother-of-pearl. The thick, nacreous shell of trochus was ideal for button making and was soon exploited by manufacturers. Vessels formerly engaged in gathering pearl shell were diverted to the work of collecting trochus shell on the Great Barrier Reef from Torres Strait to Port Mackay (Hedley 1917), in the Philippines (Seale 1916), and in New Guinea, the Solomon Islands and Fiji (Hedley 1917). Concerns about over-fishing were almost immediately expressed. Fishery companies licensed in 1926 to fish trochus in the Andaman and Nicobar Islands in the Indian Ocean gathered 500 tonnes of shells in three months, but after three seasons of fishing, quantities of shell fished per season were reduced to less than 40 tonnes, and the rate of collection per diver per hour fell from more than 20 in 1933 to 2-3 in 1935 (Rao 1937). The trend has continued, and local stocks have been fished to near economic extinction in Palau, Yap, Truk, Helen's Reef, New Caledonia, New Hebrides, the Philippines, etc. (Heslinga and Hillmann 1981).

Conventional regulatory methods have not been particularly effective on Pacific islands because there is little capability of enforcement. In these areas, reseeding of selected reefs with hatchery cultured trochus juveniles may be an appropriate means of conserving the resource, and hatcheries are now set up in Palau, Pohnpei, and New Caledonia (Heslinga and Hillmann 1981).

Freshwater mollusc fisheries

The freshwater mussels, the Unionidae in the United States and the Margaritiferidae in Europe and the United Kingdom, have been over-exploited for the pearl button and pearl industry since the turn of the century (Woodward 1990), and continue to be subject to over-exploitation as they are harvested for pearls and for use in the cultured pearl industry. Unionids from the United States currently provide the sole seed material for the world's cultured pearl industry and 5,000 to 6,000 tonnes of raw shell are exported each year, primarily to Japan (Brautigam 1990).

Land snail utilization

Land snails are also utilized for food: *Achatina* in Africa and *Bulimulus* in South America have been eaten for generations, as has the edible snail *Helix pomatia* in Europe. The Romans introduced "escogartiers" to western Europe, snail gardens in which snails were fed on aromatic herbs such as thyme and marjoram (Boyle 1981). The practice of raising land snails for food continues today in France, the United Kingdom, Australia, Taiwan, etc. (Mead 1979, Simpson 1992). Land shells, sewn into necklaces, bracelets and hat bands, also serve as economic resources, often for the tourist industry.

Molluscs as alien species

Alien species have travelled with humans since prehistoric time, and are often so common that they are not recognized for what they are. Virtually every slug found on a garden plant in eastern North America was accidentally imported from Europe (Solem 1974), and the most familiar snails in southern Australia, the common garden snail, *Helix aspersa* and the conical snail *Otala lactea,* were also introduced from Europe (Smith 1981).

The tale of two snails

It has long been recognized that animal and plant introductions into new habitats result in disrupted ecosystems, exterminations of native species and create major environmental and resource management problems. Two snails, the giant African snail, *Achatina fulica,* and the carnivorous *Euglandina rosea* from Florida, provide classic examples of what happens when alien species invade new territories and when biological control goes astray.

The giant African snail's journey from its African homeland through the Indian Ocean, into Asia, and across the Pacific to Hawaii, with occasional forays onto the North American continent, has been chronicled by Mead (1961, 1979). The snail was introduced from South Africa to Mauritius about 1800, and subsequently to Reunion and the Seychelles. It was purposefully carried to Calcutta, India in 1847; by 1900 it was in Ceylon; in 1931 it was in China; during the 1930's the Japanese introduced it to several islands in the western Pacific; and it arrived in Hawaii in 1936. In each new location there was a population explosion within a few months of its arrival and it quickly became an agricultural pest. In the Pacific the giant African snail not only decimates domestic gardens, but is a carrier of the parasite for eosinophilic meningitis (Wallace and Rosen 1969). No effective methods of control have been found, and attempts at biological control have caused more problems than they have solved (Hadfield and Kay 1989).

A carnivorous tree snail from Florida, *Euglandina rosea,* was introduced in Hawaii in 1952 in an attempt to control the giant African snail. There is no evidence that *Euglandina* successfully controls *Achatina* (Hadfield and Kay 1981; Tillier and Clarke 1983); there is incontrovertible evidence that it has caused the extinction of a population of an endemic tree snail (*Achatinella mustelina*) in Hawaii (Hadfield and Mountain 1981; Hadfield 1986a; Hadfield and Miller 1992). *E. rosea* has now been introduced at more than 20 sites on oceanic islands in the Pacific and Indian Oceans and in the Caribbean in attempts to control the giant African snail. On Moorea in French Polynesia it is responsible for the extinction of seven species of the endemic land snail, *Partula* (Murray, *et al.* 1988).

Freshwater introductions

During the last ten years, newspaper headlines have heralded the unwanted arrival of several freshwater molluscs in such distant locations as Southeast Asia, Hawaii, and North America. The apple snails, the ampullarids *Pila* from Asia and *Pomacea* from tropical and subtropical America and the Caribbean, and the viviparid *Cipangopaludina* from Asia, are the most recent of the introductions, found now in rice paddies in Southeast Asia (Mochida 1991) and taro patches in Hawaii (Cowie 1992b). In 1990 the headlines heralded the zebra mussel *(Dreissena* *polymorpha*) which had arrived in the Great Lakes from Europe (Hebert et al. 1989; Haurwitz 1990). In 1980 the Asian clam *(Corbicula)* invaded an Arkansas power plant (Pool and McCullough 1979).

These molluscs have much in common: each accidentally arrived from a point of origin thousands of miles from its present location; in each of the new environments massive populations built up in very short periods of time; and in each of the new environments the snails are disrupting native ecosystems or long-domesticated agricultural systems and wreaking massive economic damage.

The zebra mussel has the longest history of the molluscs as an introduced species. It came originally from the basins of the Black and Caspian Seas, spreading in the late 18th century across Europe and reacihing British waters in 1824 (Kew 1893). It occurs in very large numbers, blocking pipes and channels of domestic and industrial water supply systems (Morton 1969). It probably arrived in the Great Lakes of North America about 1986, and began to build up massive populations with densities of 700,000 per square meter (Roberts 1990). The mussels affect the ecosystems both by disrupting native mussels and other fisheries because of their settlement habit, and, because they are filter feeders, taking in quantities of water and phytoplankton which will eventually disrupt the lower food web with effects reverberating up the food chain (Roberts 1990). The zebra mussel is now moving south through the rivers of the eastern United States.

Another bivalve, *Corbicula fluminea,* was introduced to North America at the end of the 19th century from Asia and was first reported alive from the mouth of the Columbia River between Washington and Oregon in 1938 (McMahon 1982). It moved south through the waterways of California in the 1940's, and then between 1950 and late 1980 was recorded in the waterways of 14 eastern states, from Texas to New York and Florida. Like the zebra mussel, it outcompetes native unionid and sphaeriid bivalves, damages water systems, and clogs irrigation scheme pipelines (McMahon 1982, Clarke 1986).

The mystery snails and apple snails are represented by at least five species of Ampullariidae which were deliberately introduced from their native habitats in the tropics of the Americas and the Caribbean. They were taken to Southeast Asia for culture as food (Mochida 1991), and to Hawaii for culture and as aquarium snails. In Southeast Asia these snails cause serious damage to rice paddies; in Hawaii they damage the taro crop (Cowie pers. comm., 1992)

Other recent freshwater introductions include *Biomphalaria* from South America which, with its parasites, is now found in China and Hong Kong (Dudgeon and Yipp 1983), and the Chinese mussel *Anodonta woodiana* which is now in France and Hungary (Kiss and Petro 1992).

Marine introductions

The introduction of alien marine molluscs along world coastlines is less well documented than are introductions on land and in waterways. The earliest marine introductions were most probably molluscs and barnacles accidentally carried on the wooden hulls of sailing ships. There is increasing evidence that marine species transported deliberately or accidentally by humans to areas where those species did not previously occur are negatively affecting the ecology of marine communities (Carlton 1987, 1989; Carlton, *et al.* 1990).

Nearly forty years ago, Charles Elton (1958) remarked that oysters presented an ever-increasing means for the dispersal of fouling organisms. That observation has been confirmed (Carlton 1987, 1989; Brown 1991). One of the most effective agencies in the transport of alien marine molluscs has been the Japanese oyster (*Crassostrea gigas*), preferentially cultivated because it grows faster and is thus marketable sooner. As a result of transport of this species, the Pacific coast of the United States now supports some 40 non-native molluscan species (Brown 1991), among them the Japanese oyster drill (*Ocenebra japonica*) which feeds on both native and foreign oysters (Hanna 1966).

Ship fouling and ballast also provide transport for marine organisms from one port to another. In the United States, the Asian clam (*Potamocorbula amurensis*) may have been introduced into San Francisco Bay by ballast water about 1986. The bivalve has spread dramatically and is now dominant in some areas (Carlton *et al.* 1990, Nichols *et al.* 1990). Carlton *et al.* (1990) predict it will cause major alterations in the San Francisco Bay ecosystem. A nudibranch introduced into New Zealand waters probably by one of these modes is an opportunist, preempting food and space and is inimical to local faunas (Willan 1987).

Controlling alien species

Control methods for alien terrestrial and freshwater molluscs include chemical (chlorine) and thermal agents (for the control of *Corbicula* in the United States and of the viviparids and apple snails) (Cheng 1989), biological control (for the control of the garden pest *Helix aspersa* in California by the decollate snail *Rumina decollatd*) (Anonymous 1989) (but see the discussion of *Euglandina* as an agent of biological control), and construction of fences around areas to keep out alien predators in areas of suitable habitat (for populations of *Powelliphanta* in New Zealand (Jeffs 1982)). Surveillance and import/export regulations are widely used in the Pacific and in Europe. In the Pacific, governmental agricultural agencies have recently increased surveillance on all islands to prevent the further spread of the giant African snail (*Achatina fulica*). As most marine molluscs have planktonic larvae, there is no way of preventing the spread of these invaders to adjacent areas along a coastline, although species with non-planktonic larval forms may not be so liable to dispersal.

Molluscs as model systems

Mendel's pea plants and Morgan's *Drosophila* are legendary for their roles as model systems from which have stemmed the science of genetics. Molluscs also rank high as particularly useful models from which insights into basic biological principles have emerged. Second only to arthropods in diversity of species, molluscs may be second to none in terms of their distribution in space and time and their versatility in field and laboratory: most molluscs are small enough that they are amenable to experiment; their shells can be marked and are traceable in the field; they can be cultured in terraria and aquaria; many of them are extraordinarily fecund and have short generation times permitting statistical and genetic analyses; and various of their organ systems are easily dissectable.

The molluscan shell

Historians read and interpret history from documents. The molluscan shell is similarly an historical document, on which are recorded time and events. Charles Lyell used them to date the Tertiary because their fossils were particularly numerous and distinct in Tertiary strata. Others have interpreted features of the shell such as coiling (Trueman 1922) and sculpture (Williamson 1981) in attempts to demonstrate lineages of evolving fossils, the coils of the former representing an unbroken lineage, the sculpture of the latter providing the gross differences required by punctuated evolution. Stephen J. Gould (1969), interested in the evolution of form, uses the extraordinarily variable shells of *Cerion* to focus on the question of how the varying shapes of an individual's growth can serve as a source of evolutionary change.

The title of Darwin's *The Origin of Species* included the phrase "by means of Natural Selection;" but the modern view of species formation holds that there are actually two processes, first, geographic isolation of a subpopulation, and subsequently the process of selection. The genesis of the concept of isolation as a mechanism in species formation also lies with mollusc shells but in this case with the colours and colour patterns of shells which can be used in distinguishing species. John Thomas Gulick (1832-1923), a missionary's son in Hawaii, amassed a large collection of the colourful tree shells *Achatinella* on Oahu, and, about 1870, began to question the role of natural selection in the formation of species: "The conditions under which they live are so completely similar . .. The vegetation is much the same; the bird and insect enemies, so far as they have any, are the same, . ." (Gulick 1872). His view (see Gulick 1905 for references), that geographical isolation is an essential in the process has come to prevail (Carson 1987).

Natural selection is, however, a critical factor in preserving variability, especially in cases of balanced polymorphism such as is known in the English garden snail *Cepaea.* These snails exhibit a wide range of colours and banding patterns. The most common colours are yellow and pink, and shells of either colour may be unbanded or may have as many as five bands differing in intensity. The maintenance of different frequencies of the various polymorphic forms is largely due to selective predation by thrushes: banded snails on mottled backgrounds are less visible than unbanded snails and preyed on less frequently; unbanded snails have a survival advantage where the background is fairly uniform. The now classic studies of Cain and Shepperd (see White 1978 for a review) are among the best analyzed in ecological genetics and have set the stage for continuing work utilizing molecular markers.

In the early years of the 20th century when Darwinian theory was under intense scrutiny, one of the first questions asked was that of the relative values of congenital and "environmental" factors of organic structure, the "nature versus nurture" question. Henry Crampton (1925) writes of his interest in the subject as early as 1906 and of his search for "a series of related forms" with which to try to answer the question. He decided on *Partula,* a genus of Pacific island land snails, on which he would employ "the methods of biometry and genetics." Crampton's classic studies laid the foundation for a research programme which today addresses questions of the genetics of speciation, of shell colours and banding, the matter of gene frequencies in the wild, the genetics of coiling, the possibilities of character displacement, and which allows the possibility of molecular analysis of DNA (Murray and Clarke 1980; Johnson, *et al.* 1990; Murray, *et al.* 1991; Cowie 1992a).

Molluscs in communities

Tropical coral reefs are well known for the enormous numbers of species which are associated with them. At the same time, a fundamental starting point in the quest for an understanding of the structure of communities is the principle of competitive exclusion: in equilibrium communities no two species occupy the same niche. This concept was modified by Evelyn Hutchinson who suggested that large numbers of closely related species that appeared to occur in a restricted environment might be explained by resource partitioning. Kohn (1959) in a now classic paper demonstrated that indeed the adult ecological niche of each of some 12 to 14 species of the gastropod *Conns* on solution benches in Hawaii differ significantly with respect to at least two characteristics: the nature of the food, the nature of and relations to the substratum, and their distribution with respect to the ocean. This work has served as the foundation for a host of studies focusing on questions about the historical - geographic, ecologic and evolutionary patterns which account for the high species richness of tropical coral reefs.

The quick and the slow

Except for the cephalopods, some of which have speeds of up to 20 knots, molluscs are usually thought of as slow-moving and rather unexciting. Both the quick and the slow of the molluscs, however, are among the chief players in research in neurobiology.

Squid are known for their active swimming in the surface waters of the open ocean. The stellate nerves contain the giant axons which were used in all the early studies of the nerve impulse. The giant axons innervate muscles in the wall of the mantle. Powerful contractions of those muscles result in the rapid expulsion of water from the mantle cavity and the squid escapes potential predators by jet propulsion. The giant axons, some 650 m in diameter, accommodate microelectrodes from which are recorded the electrophysiological activities associated with a nerve impulse. From these studies have come our understanding of the electrical properties of nerve fibers and those of the cell membrane itself, and a series of discoveries of very wide significance in biology and medicine.

The octopus is different in form from the sleek-bodied squid. It is a visual and tactile animal like ourselves, and, indeed has a nervous system that does many of the things are own does, including learning. It has provided much insight into the structure and function of the brain (Wells 1962) because the octopus brain is far less complicated than that of vertebrates.

As informative as cephalopods are, the slow-moving sea hare, *Aplysia,* may be neurobiology's most celebrated invertebrate today. The sea hare has the advantage of simplicity: there are perhaps a trillion neurons in the human brain and most nerve cell bodies measure only 10-20 m in diameter. *Aplysia* possesses the largest nerve cells in the animal kingdom, cells which can be easily located and identified, cells into which microelectrodes can be inserted allowing both chemical manipulation and electrophysiological measurement (see Audeskirk and Audeskirk 1985 for a review), and cells which are now known to control complex orientation responses, feeding movements and activity rhythms by precisely known motor pathways and networks.

Kandel *et al.* (1983) have traced the neural circuitry involved in behavior involving three forms of learning, habituation, sensitization and classical conditioning. Another opisthobranch, the nudibranch *Hermissenda,* has been trained by classical conditioning and the molecular basis of learning in that animal is being explored (Alkon *et al.* 1985).

Marine gastropods play yet another role for the neurobiologist. Natural toxins from dinoflagellates and venomous snakes have been used in the study of ion channels, the channels through which ions pass into and out of nerve and muscle cells, for many years. The discovery that each species of the marine genus *Conus* has its own small toxic peptides, some of which block the flow of sodium, potassium and calcium ions across membranes, others specific inhibitors of acetylcholine receptors (Olivera *et al.* 1990), has been called "the biggest recent gold mine," in the field in recent years (Barinaga 1990).

A question of age

There are many aspects of life about which we can be uncertain. There is one which is invariant: all animals, including most vertebrates with determinate life histories, age and die. All that is, except for a mollusc in which the developmental programme can be suspended. Gerontologists have traditionally relied on laboratory mice and rats to study the ageing process. The sea slug *Phestilla sibogae* may change all that. *Phestilla,* which is found on coral reefs in the Pacific, lives, feeds and reproduces on a specific coral. It normally spends about three days as a free-swimming larva after hatching, then settles on to the coral and metamorphoses into an adult slug. For the next 60 days it eats the coral and produces eggs; then it dies (Miller and Hadfield 1990). If, however, the slugs are kept swimming in a water column without the coral on which they normally occur, they can live an additional 30 days in a state of almost suspended animation. When they are given their usual coral home, they metamorphose and live their full reproductive span of time.

There are other features of metamorphosis in *Phestilla* which are providing insight into fundamental biological processes. The field of cellular embryology was pioneered by E.G. Conklin's work on another marine gastropod, *Crepidula,* in which he attempted to trace the origin of the organs of the embryo and larva to specific cells in the dividing egg. What perhaps Conklin did not realize was that there is a process which provides in one organism in a brief time span nearly all of the developmental processes which occur in embryology from molecular through tissue transformation (Hadfield pers. comm., 1992). In *Phestilla* in which large numbers of larvae are produced and easily reared, metamorphosis is externally controlled, triggered by a chemical from its prey coral. These features and others provide means for the exploration of a host of the phenomena involved in metamorphosis (Hadfield 1986b, unpublished): the nature of the chemical that induces metamorphosis; the internally signalling pathway of the morphagen; the role of neurotransmitters in metamorphosis; and the occurrence of genes coding for a known family of transmembrane chemoreceptors.

Mussel watch

As canaries once warned miners of "bad air" so are molluscs indicators of "bad water". More than 80 years ago Ortmann (1909) realized that streams in North America without freshwater mussels had something wrong with them, and pointed out the effects of pollutants and river degradation on mussel beds. Bivalves are well known to concentrate small particles and accumulate a variety of toxins. Marine gastropods show the effects of toxins such as mercury by dwarfed and twisted shells, and various physiological abnormalities. In 1976, the Mussel Watch (Goldberg *et al.* 1978), a scheme calling for coordinated and standardized measurement of pollutants in four species of bivalve, including two species of *Mytilus, Crassostrea virginica* and *Ostrea equestris,* was set up at more than 100 sample sites on the coast of North America. The bivalves are analyzed for heavy metals, radionuclides, halogenated hydrocarbons, and petroleum hydrocarbons. The scheme has produced useful data on baseline levels of these substances, and may well be the model with which to develop and assess protocols which tell us about the health of ecosystems worldwide.

Actions required for the conservation of molluscan diversity

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I. Acquire and manage threatened habitats on islands, in aquatic ecosystems, on continents and on coral reefs for the conservation and protection of the native molluscan biota.

Implementation:

1) Identify suitable areas where there are significantly diverse molluscan populations for protected status and establish such areas as refuges, sanctuaries and the like.

Islands

Despite the immensity of habitat destruction on islands, there remain fragments of lowland forest and relatively untouched highland areas where remnants of native biota survive. Some of these may still host viable populations of invertebrates. There are also entire islands, for example, Henderson Island in the Pacific and Aldabra in the Indian Ocean, on which there remain virtually untouched biotas. Programmes for the management of protected areas on islands are feasible, and, indeed, entire islands and groups of islands such as the Northwestern Hawaiian Islands, which are administered as the Hawaiian Islands National Wildlife Refuge by the United States Fish and Wildlife Service, and the Galapagos Islands which are a National Park, have been afforded protection. An initiative for protection of entire islands would recognize the precarious position and the significance of insular biotas.

Continents

The molluscan faunas of Asia, South America, and parts of Africa are not well known, but assuming that greatest diversity of these faunas is associated with forests, as it is in parts of Africa and in Europe and North America, and, given the enormous rate of destruction of forests worldwide, identification of areas where there are significantly diverse molluscan populations for protected status and establishment of such areas as refuges is of highest priority. Molluscs with wide distributional ranges will often fall under the protective custody of national and state parks; species with restricted ranges, known perhaps from a single locality, are highly vulnerable to extinction and would appropriately be identified in a quest for more protected areas.

Freshwater ecosystems

The rate of destruction and disruption of aquatic ecosystems rivals that of the destruction of forests. Identification of, recommendations and support for, and establishment of, protected areas for rivers with significant naiad and freshwater pearl mussel populations, and lakes and springs with diverse radiations of other aquatic molluscs is a priority.

The management of coral reefs

Coral reefs are increasingly impacted by nutrient enrichment (sewage, agriculture), exploitation (overfishing, coral mining), and sedimentation and turbidity. Reef management, however, must operate on a large scale, involve both interaction with fisheries and protected area management teams, and involve regulation of both areas and species. Marine parks and sanctuaries are examples of area regulation; they are designed as reservoirs from which larvae can recruit to damaged and over-exploited reef areas. Randall (1982) estimates that if only five percent of a reef environment is protected, the larvae of marine organisms in the preserves are sufficient to seed adjacent protected areas. Species regulation takes the form of legislation now enacted by many countries to conserve their marine resources, and, indeed, more than 50 species of molluscs are now regulated by individual countries.

II. Develop the data base necessary for knowledge of molluscan diversity.

Implementation

1. Establish biological monitoring programs at the local level to aid in the assessment of the current status of regional molluscan diversity. Monitoring programmed are multipurpose management tools which will provide for:
   1) data on the biotic and abiotic characteristics of the environment which identify regions of greatest molluscan diversity;
   2) immediate warning of non-acceptable impacts of human activities and their waste products on the environment;
   3) a longterm data base to evaluate and forecast natural changes and impacts of human activities;
   4) identification of endangered habitats and species;
   5) identification of stocks of molluscs of potential use in fisheries, the shell trade, and biomedical research.
2. Establish baselines from distributional information now available in systematic works and unpublished information in museum collections to produce base maps of species distributions. Computerize museum records for species/localities through time and establish mechanisms to effect cooperation and networking internationally.
3. Establish priorities for taxa to be added to the database by coordinated action groups for land snails, unionids, marine gastropods, marine bivalves, insular biotas, and freshwater

gastropods; maintain a central data base at a satellite database center to record level of progress.

4. Update and evaluate a world list of extinct (human-caused extinction) and threatened molluscan species. A world list of threatened and recently extinct molluscs serves as a resource for summarizing conservation problems with respect to molluscs, and for material which can be used for purposes of education and publicity. Lists of molluscs for the IUCN Red List, the Invertebrate Red Data Book, CITES, and the Berne Convention have been developed from a data base at the World Conservation Monitoring Centre (WCMC), Cambridge, and a world list has been compiled at the University of Hawaii, Honolulu, Hawaii. However the databases are far from complete, need critical analysis, and require maintenance.

5. Ensure sources of funding for systematics, life history and demographic studies of molluscs, especially those in fragmented and disturbed habitats, threatened and endangered species and those which provide major stocks for mollusc fisheries and the shell trade by supporting molluscan systematics and taxonomy in university programs, museums and conservation management programs.

Are molluscan systematists an endangered species?

No matter how much public education is undertaken, no matter how much legal habitat protection is put in place, and no matter how many alien species are removed, there is no substitute for comprehensive biological knowledge of a fauna. The skills of systematists and taxonomists are pivotal for reliable species identifications, knowledge of life history, and demographics. These are all essential for conservation biology and to agricultural, health, environmental, customs and other agencies which must respond to accidental introductions of pest species, health problems caused by moiluscan-borne diseases or the ingestion of molluscs, declining populations, and importations of shells and shell products. Unfortunately, a recent newspaper headline, "Scientists who study endangered species are themselves in danger of extinction" (Connor 1992) summarizes a widely recognized trend: the numbers of expert systematists and taxonomists in all fields are declining (Oliver 1988, Wilson 1985), and financial and organizational support for systematics, the study of biological diversity, has declined at alarming rates in universities and museums worldwide (Wilson 1985).

What we need to know

Much of the necessary data on biology, life history, demographics, and systematics are lacking for the molluscs which are of most concern. More than 300 names for the renowned, jewel-like achatinelline tree snails of Hawaii have been proposed, but the first data on growth rates, size and age at maturity, and fecundity did not appear until 1981, and even now there are data on only two species (Hadfield and Mountain 1981; Hadfield and Miller 1989). There are few published data on the endangered New Zealand flax snail (*Placostylus*), none on the Manus green snail (*Papuina*). Nor is there a strong data base on age at maturity and fecundity of common alien and pest species such as the giant African snail or the carnivorous Florida snail. Worldwide there are an estimated 20,000 undescribed species of mollusc, and problems in identifying sibling and cryptic species. Demographic, biological and life history studies are essentials in captive breeding programs, and, indeed, the success of the program for captive breeding of *Partula* depends on an intimate knowledge of the life style parameters of those snails (Bloxam and Tonge 1986), while a small scale captive breeding program for Hawaiian achatinelline snails in Hawaii results from the detailed life history studies which served as the basis for designing the program, the successful culture of the fungus on which the snails feed, and the availability of substrate from the native habitat (Hadfield pers. comm., 1990). All exploitation is intimately bound up with fundamental population ecology and reports on virtually every shell fishery note the lack of information on life history, population dynamics, recruitment processes and the like [see for example Harrison 1986 on the Australian abalone; Roper and Rathjen 1991 on cephalopod fisheries; Castilla and Jerez 1986 on the loco (*Concholepas*)].

Hard data are necessary to effect policy and develop funded programs. The results provide knowledge of localities and areas of high species diversity and immediately show what is rare, potentially endangered, and potentially extinct. Decision makers are thereby provided with the information necessary to evaluate issues, and priorities can be established to determine the courses of action needed, that is, whether protection by habitat, cessation of fishing pressure, control of predators, etc.

6. Educate national and governmental agencies such as park services, natural resource conservation agencies, and fisheries on the values of identifying diversity; establish a coordinating committee to provide leadership to stimulate funding internationally.

III. Prevent the introduction of alien species that have negative impacts on native mollusc species and control and eradicate these exotic species where such introductions have already occurred.

Implementation

1. Prohibit worldwide the introduction of alien species without appropriate research into long-range effects of these organisms on native ecosystems. Establish and implement stringent quarantine regulations at all ports of entry.

2. Control and eradicate exotic species such as *Euglandina rosea* where such introductions have already occurred. Circulate among government agencies the strongly worded IUCN position statement "Translocation of Living Organisms" (IUCN 1987b) which cautions against the introduction of species to natural habitats and islands; support and cooperate with government quarantine, agriculture and health departments in monitoring and identifying possible noxious species that arrive accidentally.

IV. Establish self-sustaining captive populations of endangered mollusc species and support their eventual re-introduction into their native habitats.

Implementation

"Habitat protection alone is not sufficient to achieve the goal of the World Conservation Strategy, if the maintenance of biotic diversity, is to be achieved. Establishment of self-sustaining captive populations and other supportive intervention will be needed to avoid the loss of many species, especially those at high risk in greatly reduced, highly fragmented and disturbed habitats. Captive breeding programs need to be established before species are reduced to critically low numbers, and thereafter need to be coordinated internationally according to sound biological principles, with a view to the maintenance or re-establishment of viable populations in the wild" (IUCN 1987a).

Captive breeding programs should not detract from the immediate concern of protecting molluscan faunas in the wild, but they are a cost-effective way of dealing with rare species (Wilson 1987; Wells this volume), and the publicity generated by a few carefully selected projects can enhance public awareness of mollusc conservation issues. Laboratory reared populations provide information on species which can be applied to their conservation in nature, for example by providing estimates of genetic diversity in small populations and of the numbers needed to sustain viable populations.

A captive breeding program involving the Pacific land snail *Partula* has been underway for several years (see, for example, Bloxam and Tonge 1986), and six species of *Partula* from Moorea survive today only in the laboratory and in zoos. The program demonstrates that genetic stocks can survive, even though, as in this case, all seven Moorean species of *Partula* in the wild are apparently extinct (Murray *et al.* 1988). Other threatened non-marine molluscs currently bred in captivity include *Powelliphanta* in New Zealand, *Geomalacus maculosus* in Europe, and *Partulina* in Hawaii.

V. Promote public awareness and concern for molluscan conservation programmed.

Implementation:

1. Create and develop public awareness through education programmed of the importance of molluscs to humans in culture, agriculture and ecosystems and as part of the natural heritage as natural resources.

Molluscs neither soar like the condor, nor are they cuddly like the panda. Pleas to "save a snail" or "hug a slug" rarely convince the shell collector to leave a shell behind or attract funds for research from the conservation community or the public. Indeed, in the western world, snails and slugs are seemingly more often seen as pests and carriers of disease than recognized for their utility. Some molluscs do cause damage to agricultural crops and ornamental gardens; some molluscs are intermediate hosts for diseases such as those caused by the human blood fluke, cattle liver fluke and the rat lungworm. For the most part, however, molluscs are agricultural pests where they are alien intruders in ecosystems (Godan 1983). In India, with more than 1500 species of native land snails, seven mollusc species (<1%) are known to cause some damage to agricultural and horticultural gardens, but only one, the giant African snail (*Achatina fulica*), an introduced species, is considered serious. The spread of disease by snails can also be attributed in many instances to human-induced changes in ecosystems: the high incidence of blood fluke in Egypt has been associated with the introduction of perennial irrigation (van der Schalie 1973).

2. Establish training workshops in molluscan taxonomy and systematics for field workers. At the local "field" level, particularly where there are mollusc fisheries and mariculture and in shell importing and exporting countries, taxonomic skills are essential for identification purposes and necessary for the implementation of management techniques and for conservation in general. Workshops involving teams of experts in molluscan systematics and taxonomy could provide the expertise to workers in the field, giving them needed knowledge and confidence.

3. Adopt and encourage the utilization of the deep knowledge of marine life possessed by traditionally trained "master fishermen" on Pacific islands by establishing cooperative work units of western-trained conservation officers to better manage insular biotas and reefs.

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Table 1

The status of terrestrial molluscs on islands for which data are available.

Atlantic and Mediterranean

Aegean Islands

14 families, 60 genera, 40-50% species endemic. Human influence since the 3rd century: agriculture, goat raising, fire, urbanization. Local extinctions in historic time caused by human activity. Reference: Mylonas 1984.

Azores

67 land snail species, 41.8% endemic. Zonitidae show most radiation. References: Walden 1983, 1984.

Canary Islands

157 land snail species. 78% endemic, 49% of endemic taxa in *Hemicycla* and *Napaeus.* References: Walden: 1983, 1984.

Cape Verde Islands

21 land snail species, 43% endemic. References: Waldén 1983, 1984.

Madeira

261 land snail species, 74% endemic, more than half endemics in helicid subfamily Geobirinae. 17 species extinct or near extinction, 22 rare and endangered, 19 rare. References: Cook, *et al.* 1972; Walden 1983, 1984, 1986.

St. Helena

Ca. 100 species associated with forests; virtually all presumed extinct. Goats introduced by the Portuguese in 1513; original vegetation replaced as a result of browsing, grazing, erosion, cutting for timber and fuel, introduction of alien plants, clearing for cultivation, plantations, pasture. References: Crowley and Paine 1977; Cronk 1989; Solem 1977; Woodward 1991.

Sao Tome and Principe

Several unusual taxa endemic to these islands: monotypic achatinid *Atopolcochlis, Lignus alabaster,* sinistral *Columna;* and in the monotypic Thyrophorellidae, the sinistral *T. thomensis.* References: Groh and Griffiths 1987; Naggs 1992.

Caribbean

Puerto Rico

Ca. 85 species. Natural vegetation drastically altered with arrival of European colonists 500 years ago: by 1912 >80% of island deforested by clearing for agriculture, grazing, timber; introduction of goats and cattle. <1% remained pristine. Reference: Densmore 1986.

West Indies: Jamaica

500 land snail species, more than 50% operculates; generic and species endemism. Radiations of Sagdidae and Urocoptidae. Local extinctions from habitat destruction before European arrival; continuing destruction of forests; north coast almost completely denuded. References: Goodfriend and Mitterer 1988; Groh and Parkinson 1987; Simpson 1894.

Indian Ocean

Madagascar

400 land snail species, 98% endemism. The Gondwanaland family Acavidae with 99 nominal species dominant; *Trophidophora* with 50 species. *Achatina fulica* and *Euglandina rosea* introduced. Threats: virtual complete deforestation with severe soil erosion. References: van Bruggen 1980a; Emberton 1990; Groh and Griffiths 1987; Solem 1984.

Mauritius

130 land snail species, 64% endemic. The carnivorous Streptaxidae dominant; speciation also in *Tropidophora* and Helicarionidae. *Achatina fulica and Euglandina rosea* introduced. Extinct: the streptaxid *Gibbus lyonetianus,* other streptaxids and most operculates. Threats: *Euglandina* implicated in extinction of native species; extensive deforestation with ebony forest replaced by sugar cane. References: Griffiths *et al* 1993; Groh and Griffiths 1987; Walden 1984.

Reunion

48 land snail species, 42% endemic. *Achatina fulica* and *Euglandina rosea* introduced. Extensive deforestation. Reference: Walden 1984.

Seychelles

41 land shell species, 15 freshwater species, 41% endemic. Land shells probably disappeared prior to 1869 with the nearly complete destruction by fire and timber cutting of the original flora; most of granitic island species now found only in summit relict forests where "they barely survive." Recent extinctions: three species not traced recently; on St. Anne 30 endemic species at risk. *Achatina fulica, Euglandina rosea, Gonaxis quadrilateris* introduced. Aldabra, an elevated reef, with virtually undisturbed land snails. References: Gerlach 1987; Griffiths et al. 1993; Lionnet 1984; Nevill 1869.

Pacific Ocean

American Samoa. Tutuila and Manua Islands

>50 species, many single island endemics. *Achatina fulica, Euglandina rosea,* and *Gonaxis kibweziensis* introduced. Endangered: *Samoana conica, S. abbreviata, Trocomorpha aria, Eua zebrina.* Recent extinctions: Ofu - 1 endodontoid; Ta'u - 3 Charopidae, 1 endodontoid presumed extinct; Tutuila - 2 Charopidae, 1 Helicarionidae. Threats: introduced *Euglandina* and *Gonaxis,* upper elevation forest lost to agriculture and hurricanes, rat predation. References: Clench 1949; Miller, *et al.* 1993; Solem 1975, 1983.

Austral Islands: Rapa

100 species listed; estimated 200 species; 98% endemic. Tornatellinidae and Endodontidae dominant, with several radiations. 50% extinct 1934-1960; small fossil locality distant from remaining patches of native forest with large numbers of zonitids, partulids, endodontoids today restricted to the remaining forest. One-fifth of native forest remains of the once entirely forested island. Introduced feral cattle and goats causing extensive destruction by uprooting and extensive erosion. References: Cooke 1935; Paulay 1985; Solem 1976,1983,1984.

Fyi: Viti Levu

15 families, 58 species, including 2 endemic charopid genera, one endemic genus in Cyclophoridae. *Lau Archipelago.* 39 species from three islands, 27 endemic, 9 introduced by Polynesian voyagers and European commercial activities; endemic taxa and introduced species not competing. References: Garrett 1887a; Germain 1932; Solem 1978,1983,1990.

Galapagos Islands

90 land snail species, most single island endemics; fauna dominated by *Bulimulus.* Endangered: 30 bulimulid species. Local extinctions from habitat destruction before arrival of Europeans. Recent extinctions: *B. nux* once abundant on San Cristobal and Floreana (two subspecies remain). Threats: introduced fire ants and black rat; destruction of native vegetation by clearing, grazing, exotic plants. References: Chambers and Steadman 1986; Coppois 1984, 1986; Coppois and Glowacki 1983; Coppois and Wells 1987; Dall 1896; A. Smith 1966.

Hawaiian Islands

Ca. 1,000 land snail species, >90% endemic, most single island endemics. Spectacular radiations in tree snails *Achatinella* on Oahu, and in ground-living Amastridae *Carelia* on Kauai. Local extinctions from habitat destruction before arrival of Europeans; overcollection of tree snails in the 19th century. Recent extinctions: 20 species of Achatinellines; *Carelia* and other ground-living amastrids. *Achatinella* registered as an endangered genus under Endangered Species Act. *Achatina fulica* and *Euglandina rosea* introduced. Threats: habitat loss caused by agriculture, deforestation, urban development and the introduction of hoofed mammals; predation by the introduced *Euglandina rosea*, triclad *Platydemus manokwari.* References: Christensen and Kirch 1986; Hadfield 1986a; Hadfield and Miller 1989; Hadfield and Mountain 1981; Kondo 1970.

Lord Howe Island and Norfolk Island

Lord Howe: >50 endemic species. Several extinctions recorded among them the freshwater snail *Posticobia norfolkensis* for Norfolk Island. Threats: clearing of native vegetation; land degraded by introduced species. References: Ponder 1981, personal communication; Solem 1983; Turner, *et al.* 1968

Mangareva

33 species including 3 endemic genera of Endodontidae. In 1934 nearly all the islands had been continuously burned over, ridges were bare of trees, and the endemic forest had disappeared. A fossil bed produced several endodontid species. All but one or two native species presumed extinct. References: Cooke 1935; Solem 1976, 1990.

Mariana Islands. Guam:

5 species *Partula;* 6 species Charopidae. *Achatina fulica, Euglandina rosea, Gonaxis kibweziensis, G. quadrilateralis* introduced. *Euglandina* possibly contributed to decline of 3 endemic species of *Partula* and extinction of one species. Terrestrial triclad *Platydemus manokwari* effective in control of giant African snail but contributes to decline *of Partula.* Threats: habitat destruction and fragmentation; effects of *Euglandina.* References: Griffiths et al. 1993; Mead 1979; Smith and Hopper 1992.

Marquesas Islands

88 land snail species, about 50% of potential fauna; 78% endemic, mostly single island endemics. Speciation in Zonitidae (28 spp.), Endodontidae (12 spp.), Pupillidae (6 spp.) Partulidae (18 spp.) Tornatellinidae (11 spp.) Succineidae (2 spp.), Helicinidae (8 spp.). Extinct: lowland species collected by Garrett in 1880's. Threats: flora below 608 m profoundly altered by humans, native vegetation destroyed by introduced grazing animals and grass *Paspalum;* goats have destroyed flora of steep slopes; continuing burning. References: Adamson 1935, 1936; Garrett 1887b; Solem 1976.

New Caledonia

300-400 endemic land snail species, most restricted to small areas of the island; 10% derive from Indo-Malayan archipelago, others show Gondwanaland affinities; 80% represent a monophyletic radiation of the Charopidae, 10% a radiation of the Rhytididae which prey on the Charopidae. *Achatina fulica* and *Euglandina rosea* introduced. Threats: habitat destruction with all endemic species at risk, especially the Charopidae in Mt. Koghi hills. References: Griffith *et al.* 1993; Mead 1979; Solem 1961, 1984; Tillier and Clarke 1983.

New Hebrides

73 land snail species, 57 endemic, 10 widespread Pacific species, 5 species are "tropical tramps." Most of the endemic species are in the Charopidae (9), Bulimulidae (9), Rhytididae (5) and Partulidae (5). Threats: continuing deforestation and habitat disruption. Reference: Solem 1959.

New Zealand

About 1000 species of land snails, 99.5% endemic. Distinguishing elements include the leaf-veined slugs Athoracophoridae; large, earthworm eating snails in the Rhytididae; minute snails in the Charopidae; and the Bulimulidae. North Island snails display the highest sympatric diversity in the world. Endangered: Rhytididae, small scattered populations of Bulimulidae, Placostylus, Paryphanta. Threats: introduced mammals such as rats; habitat disruption. References: Climo, et al. 1986; Jeffs 1982; Lockley 1980; Powell 1979; Solem 1984; Solem et al. 1981.

Papua New Guinea and Irian Jaya

Numbers of land snail species vary from 198 (Iredale) to >500 for Irian Jaya (van Bentham Jutting). Dominants include the Camaenidae (*Papuina*), Helicarionidae, Cyclophoridae. *Papustyla pulcherrima* from Manus Island listed in *Red Data Book* and under U.S. Endangered Species Act. References: van Bentham Jutting 1965; Iredale 1941.

Philippines

Estimates of 1100-3000 species; extraordinarily high diversity. Extinct: many endemic species assumed extinct or seriously endangered. Threats: deforestation. References: Parkinson, *et al.* 1987; van Bruggen 1989, personal communication.

Pitcairn Islands: Henderson Island

14 land snail species (Christensen), 8 with 100% endemicity (Paulay). Evidence of Polynesian habitation but the island is relatively undisturbed; in 1934 the fauna lacked most of the exotics introduced to other Pacific islands. *Pitcairn Island:* limited areas of vegetation remaining. References: Christensen 1983; Cooke and Kondo 1960; Paulay 1991.

Society Islands: Tahiti

80 land snail species. *Achatina fulica* and *Euglandina rosea* introduced. 9 species *Partula* extinct. References: Clarke *et al.* 1984; Crampton 1916, 1932; Garrett 1884; Kondo 1970; Mead 1979; Murray and Clarke 1980; Solem 1984, 1990; Tillier and Clarke 1983.

References

ABBOTT, R.T. 1989. *Compendium of landshells.* Burlington: American Malacologists.

ADAMSON, A.M. 1935. Marquesan insects. M.S. thesis, Univ. of Hawaii.

ADAMSON, A.M. 1936. Marquesan insects: environment. *Bernice P. Bishop Museum Bull.* 139.

ALKON, D., M. SAKAKIBARA, R. FORMAN, J. HARRIGAN, I.LDERHENDLER, J. FARLEY. 1985. Reduction of two voltage dependent K^+ currents mediates retention of a learned association. *Behav. Neural Biol.* 44: 278.

ALLEN, J. 1977. Fishing for wallabies: trade as a mechanism for social interaction, integration and elaboration on the Central Papuan coast. In: Friedman, J. and M.J. Rowlands, eds. *The evolution of social systems.* London: Duckworth Publications, pp. 419-456.

ALTABA, C.R. 1990. The last known population of the freshwater mussel *Margaritifera auricularia* (Bivalvia, Unionida): a conservation priority. *Biol. Conserv.* 52: 271-286.

ANONYMOUS. 1980. *The International Mussel Watch.* National Academy of Sciences, Washington, D.C.

ANONYMOUS, 1989. *Sunset Magazine.* Oct.: 28.

ANT, A. 1976. Areal vesandenungen und gegenwaragei stand der Gefahrdung mitteleuropaische Land und Susswassermollusken. *Schrift. fur vegetationsk.* 10: 309-339.

ATKINSON, I. 1989. Introduced animals and extinctions. In: D. Western and M.C. Pearl, eds. *Conservation for the 21st century.* New York: Oxford University Press, pp. 54-75.

AUDESKIRK, T. AND G. AUDESKIRK 1985. Behavior of gastropod mollusks. In: Willow, A.O.D., ed. *The Mollusca* Vol. 8 *Neuro-biology and Behavior* Part 1. New York: Academic Pres.

BARINAGA, M. 1990. Science digests the secrets of voracious killer snails. *Science* 249: 250-251.

BASCH, P.F. 1962. Radulae of North American ancylid snails. II. Subfamily Planorbinae. *The Nautilus* 75: 145-149.

BAUER. G. 1988. Threats to the freshwater pearl mussel *Margaritifera margaritifera* L. in central Europe. *Biol. Cons.* 45: 239-253.

BEAL, B. 1990. NCRI sponsors soft-shell clam (*Mya arenaria*) hatchery/management program. *NCRI News* (National Coastal Research and Development Institute 5 (1): 1,3.

van BENTHAM JUTTING, T. 1948. Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. I. Critical revision of the Javanese operculate land-shells of the families Hydrocenidae, Helicinidae, Cyclophoridae, Pupinidae and Cochlostomatidae. *Treubia* 19: 539-604.

van BENTHAM JUTTING, T. 1950. Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. II. Critical revision of the Javanese pulmonate land-shells of the families Helicarionidae, Pleurodontidae, Fruticicolidae and Streptaxidae. *Treubia* 20: 381-505.

van BENTHAM JUTTING, T. 1952. Systematic studies of the non-marine Mollusca of the Indo-Australia Archipelago. III. Critical revision of the Javanese pulmonate land-shells of the families Ellobiidae to Limacidae, with an appendix on Helicarionidae. *Treubia* 21: 19-73.

van BENTHAM JUTTING, W.S.S. 1965. Non-marine Mollusca of west New Guinea. Part 4, Pulmonata, 2. *Nova Guinea* (Zool.) 32: 205-304.

BEQUAERT, J.C. AND W.B. MILLER. 1973. *The mollusks of the arid southwest.* Tucson: The University of Arizona Press.

BERG, C.J. and D.A. OLSEN. 1989. Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. In: Caddy, J.F. (Ed.). *Marine invertebrate fisheries: their assessment and management.* New York: John Wiley & Sons.

BERRIE, A.D. and B.J. BOIZE. 1992. Host utilization by glochidia of *Anodonta anatina* and *Pseudanodonta complanata* in the River Thames, England. In: F. Giusti and G. Manganelli, eds. Abstracts 11th International Malacological Congress, Siena: 13.

BISHOP, M.J. 1981. The biogeography and evolution of Australian land snails. In: Keast, A., ed. *Ecological biogeography of Australia.* The Hague: Junk.

BLAB, J., E. NOWAK, W. TRAUTMANN, and H. SUKOPP. 1984. *Rote Liste der gefahrdeten Tiere und Pflanzen in der Budesrepublik Deutschland.* Naturschutz Aktuell Nr. 1.

BLANFORD, W.T. and H.H. GODWIN-AUSTEN. 1908. *The fauna of British India.* Mollusca. Testacellidae and Zonitidae. London: Taylor and Francis.

BLOXAM, Q.M.C. and S. TONGE. 1986. Breeding programmes for reptiles and snails at Jersey Zoo — an appraisal. *Int. Zoo Yb.* 24/25: 49-56.

BOSS, K.J. 1979. On the evolution of gastroods in ancient lakes. In: V. Fretter and J. Peake (eds.), *Pulmonates* Vol. 2A, pp. 385-428. London: Academic Press.

BOUCHET, P. 1990a. La malacofaune Francaise: endemisme, patrimoine naturel et protection. *Rev. Ecol. (Terre Vie)* 45: 259- 283.

BOUCHET, P. 1990b. *In lift.*

BOURNE, N. 1989. Clam fisheries and culture in Canada. In: J.J. Manzi and M. Castagna, eds. *Clam mariculture in North America.* New York: Elsevier.

BOYLE, P.R. 1981. *Molluscs and man.* Institute of Biology Studies in Biology No. 134. London: Edward Arnold.

BRANCH, G.M. 1975. Notes on the ecology of *Patella concolor* and and *Cellana capensis,* and the effects of human consumption on limpet populations. *Zoologica Africana* 10: 75-85.

BRAUTIGAM, A. 1990. Trade in Unionids from the United States for the cultured pearl industry. *Tentacle* 2: 1-2.

BROOME, M.J. 1985. The biology and culture of marine bivalve molluscs of the genus *Anadara.* ICLARM, Manila, Philippines.

BROWN, A.C. 1991. Introduced species. In: Talbot, F.H. and R.E. Stevenson, eds. *The Encyclopedia of the earth. Oceans and Islands.* New York: Smithmark. pp. 218-220.

BROWN, K. 1980. The snail that changed the law. Strandloper No. 204: 2.

BRUGGEN, A.C. VAN. 1969. Notes on the distribution of terrestrial molluscs in southern Africa. *Malacologia* 9: 256-258.

BRUGGEN, A.C. VAN. 1975. Studies on the land molluscs of Zululand. *Zool. Verhandl.* 103: 1-116.

BRUGGEN, A.C. VAN. 1977. A preliminary analysis of African non-marine Gastropoda. Euthyneura Families. *Malacologia* 16:75-80.

BRUGGEN, A.C. VAN. 1978. Land molluscs. In: M.J.A. Werger, ed. *Biogeography and ecology of southern Africa.* Monographiae Biologicae. The Hague: Junk. pp. 877-923.

BRUGGEN, A.C. VAN. 1980a. A preliminary checklist of the terrestrial molluscs of Madagascar. *Achatina* 8: 147-164.

BRUGGEN, A.C. VAN. 1980b. Gondwanaland connections in the terrestrial molluscs of Africa and Australia. *Malac. Soc. Australia.* 4: 215-222.

BRUGGEN, A.C. VAN. 1989. Personal communication.

BURCH, J.B. 1962. *How to know the eastern land snails.* Dubuque: Wm. C. Brown Company.

CARLTON, J. 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean. *Bull. Mar. Sci.* 41: 452-465.

CARLTON, J. 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., J.K. THOMPSON, L.E. SCHEMEL, and F.H. NICHOLS. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis.* I. Introduction and dispersal. *Mar. Ecol. Prog. Ser.* 66: 81-94.

CARLTON, J., G.J. VERMEU, D.R. LINDBERG and E.C. DUDLEY. 1991. The first historical extinction of a marine invertebrate in an ocean basin. *Biol. Bull.* 180: 72-80.

CARSON, H.L. 1987. The process whereby species originate. *Bioscience* 37: 715-720.

CASTILLA, J.C. and G. JEREZ. 1986. Artisanal fishery and development of a data base for managing the loco, *Concholepas concholepas* resource in Chile. In: G.S. Jamieson and N. Bourne, eds. *North Pacific Workshop on Stock Assessment and Management of Invertebrates. Can. Spec. Publ. Fish. andAquatic Sci.* 92: 57-74.

CHAMBERS, S.M. and D.W. STEADMAN. 1986. Holocene terrestrial gastropod faunas from Isla Santa Cruz and Isla Floreana, Galapagos: evidence for late Holocene declines. *Trans. San Diego Soc. Nat. Hist.* 21: 89-110.

CHAPMAN, M.D. 1987. Women's fishing in Oceania. *Human Ecol.* 15:267-288.

CHENG, E.Y. 1989. Control strategy for the introduced snail, *Pomacea lineata.* on rice paddy. *British Crop Protection Council Monograph* 41: 69-75.

CHRISTENSEN, C.C. 1983. *In lift.*

CHRISTENSEN, C.C. and P.V. KIRCH. 1986. Nonmarine mollusks and ecological change at Barbers Point, O'ahu, Hawai'i. *Bishop Mus. Occ. Pap.* 26: 52-80.

CITES. 1990. Appendices I, II. Convention on International Trade in Endangered Species of Wild Fauna and Flora. IUCN.

CLARKE, A. 1986. Competitive exclusion of *Canthyria* (Unionidae) by *Corbicula fluminea* (Muller). *Malacology Data Net* (Ecosearch Ser.) 1: 58-65.

CLARKE, B.C., J. MURRAY, and M.S. JOHNSON. 1984. The extinction of endemic species by a program of biological control. *Pacif. Sci.* 38: 97-104.

CLENCH, W.J. 1949. Cyclophoridae and Pupinidae of Caroline, Fijian, and Samoan Islands. *B.P. Bishop Mus. Bull.* 196:1-52.

CLIMO, F.M., D.J. ROSCOE, and K.J. WALKER. 1986. Research on land snails in New Zealand. Wildlife Research Liaison Group, Wellington, New Zealand.

COLLINS, N.M. and S.M. WELLS. 1987. Invertebrates in special need of protection in Europe. Nature and Environment Series No. 35, Council of Europe, Strasbourg. 170 pp.

CONNOR, S. 1992. Research on rare species 'may soon become extinct.' *Independent* Jan. 1992.

COOK, J.M. 1976. Farmers and fishermen of Tubuai: changing subsistence patterns in French Polynesia. PhD. thesis University of Kansas.

COOK, L.M., T. JACK, and C.W.A. PETTITT. 1972. The distribution of land molluscs in the Madeiran archipelago. *Bol. Mus. Mun. Funchal* 26: 5-30.

COOKE, CM. Jr. 1935. In: H.E. Gregory, Report of the Director. *B.P. Bishop Mus. Bull.* 133: 36-55.

COOKE, CM. Jr. and Y. KONDO. 1960. Revision of Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). *B.P. Bishop Mus. Bull.* 221.

COPPOIS, G. 1984. Distribution of bulimulid land snails on the north slope of Santa Cruz Island, Galapagos. *Biol. Journ. Linn. Soc.* 21: 217-227.

COPPOIS, G. 1986. Threatened Galapagos bulimulid land snails:an update. Abstracts. Ninth International Malacological Congress Edinburgh, Scotland: 18.

COPPOIS, G. and C. GLOWACKI. 1983. Bulimulid land snails from the Galapagos. 1. Factor analysis of Santa Cruz Island species. *Malacologia* 23: 209-219.

COPPOIS, G. and S. Wells. 1987. Threatened Galapagos snails. *Oryx* 21: 236-241.

COWIE, R.H. 1992a. Evolution and extinction of Partulidae, endemic Pacific island land snails. *Phil. Trans. R. Soc.Lond. B.* 335: 167-191.

COWIE, R.H. 1992b. Introduced ampullariid and viviparid snails in Hawaii. *Pacif. Sci.* 46: 397.

CRAMPTON, H.E. 1916. Studies on the variation, distribution, and , evolution of the genus *Partula.* The species inhabiting Tahiti. *Carnegie Instn. Wash. Publ.* 228: 1-313.

CRAMPTON, H.E. 1925. Contemporaneous organic differentiation in the species of *Partula* living in Moorea, Society Islands.yl/n. *Nat.* 59:5-35.

CRAMPTON, H.E. 1932. Studies on the variation, distribution, and evolution of the genus *Partula.* The species inhabiting Moorea. *Carnegie Inst. Wash. Publ.* 410: 1-335.

CRONK, Q.C.B. 1989. The past and present vegetation of St. Helena. *Journ. Biogeogr.* 16: 47-64.

CROSSE, H. 1894. Faune malacologique terrestre et fluviatile de la Nouvelle-Caledonie et ses dependences. *Jour, de Conchy.* 42:161-473.

CROWLEY, T.E. and T. PAIN. 1977. Le faune terrestre del'ile de Sainte-Helene. *Ann. Mus. Roy. de L 'Afrique Centrale,* Ser. 8 Sciences Zoologiques 220: 534-575.

CUMING, H. 1827-1828. Journal of a voyage from Valparaiso to the Society and the adjacent islands performed in the schooner *Discoverer* Samuel Grimwood Master in the years 1827 and 1828. Manuscript. Mitchell Library, Sydney.

DALL, W.H. 1896. Insular land shell faunas, especially as illustrated by the data obtained by D.G. Baur in the Galapagos Islands. *Proc. Acad. Nat. Sci. Philadelphia,* 1896: 395-459.

DANCE, S.P. 1972. *Shells and shell collecting.* London: Hamlyn.

DARWIN, C.R. 1900. *Me origin of species.* 6th edition. London: John Murray.

DARWIN, C.R. 1906. *Journal ofresearches into the geology and natural history of the various countries visited during the voyage of H.M.S. Beagle.* London: J.M. Dent & Co.

DA VIES, B.R. and K.F. WALKER. 1986. The ecology of river systems. In: Davies, B.R. and K.F. Walker, eds. *River systems as ecological units. An introduction to the ecology ofriver systems.* Dordecht: Dr. W. Junk.

DAVIS, G.M. 1977. Rare and endangered species: a dilemma. *Frontiers* 41: 12-14.

DAVIS, G.M. 1979. The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. *Acad. of Nat. Sci. Philadelphia Monogr.* 20.120 p.

DENSMORE, D. 1986. Endangered plants of our Caribbean islands: a unique flora faces unique problems. *Endangered Species Techn. Bull.* 11: 3-4.

DIAMOND, J.M. 1984. Historic extinctions. A Rosetta stone for understanding prehistoric extinctions. In: P.S. Martin and R.G. Klein, eds. *Quaternary Extinctions, a Prehistoric Revolution.* Tucson: University of Arizona Press, pp. 824-862.

DUDGEON, D. and M.Y. YIPP. 1983. A report on the gastropod fauna of aquarium fish farms in Hong Kong, with special reference to an introduced human schistosome host species: *Biomphalaria straminea* (Pulmonata: Planorbidae). *Malac. Rev.* 16: 93-94.

ELTON, C.S. 1958. *The ecology ofinvasions.* London: Chapman and Hall.

EMBERTON, K.C. 1990. Acavid land snails of Madagascar subgeneric revision based on published data (Gastropoda: Pulmonata: Stylommatophora). *Proc. Acad. Nat. Sci. Philadelphia* 142: 101-117.

EMBERTON, K.C. 1991. The genitalic, allozymic and conchologica evolution of the tribe Mesodontini (Pulmonata: Stylommatophora: Polygyridae). *Malacologia* 33: 71-178.

FAO. 1990. Yearbook. Fishery statistics. Catches and landings. Vol. 71, Food and Agriculture Organization of the United Nations, Rome.

FELLER, M., D. HOOKER, T. DREHER, I. EAST, and R. JUNG. 1979. Wilderness in Victoria: an inventory. Monash Publications in Geography No. 21.

FOSTER, A. 1983. National review of non-marine Mollusca. Invertebrate Site Register Report 4. N.C.C., Chief Scientist Team.

FRANC, A. 1957. Mollusques terrestres et fluviatiles de 1'Archipel Neo-Caledonien. *Mem. Mus. Hist. Nat. Paris,* n.s., ser. A, Zool., 13, 200 pp.

FULLERTON, J.H. 1960. In: CM. Yonge, *Oysters.* Collins: London.

GALTSOFF, P.S. 1933. Pearl and Hermes Reef, Hawaii, hydrological and biological observations. *B.P. Bishop Mus. Bull.* 107.

GARRETT, A. 1884. The terrestrial Mollusca inhabiting the Society Islands. *Journ. Acad. Nat. Sci. Philadelphia* (2) 9: 17-114.

GARRETT, A. 1887a. On the terrestrial mollusks of the Viti Islands, Part I. *Proc. Zool. Soc. London:* 164-189.

GARRETT, A. 1887b. Mollusques terrestres des lies Marquises (Polynesie). *Bull Soc. Malac. France* 4: 1-48.

GASSIES, J.b. 1863-1880. Faune conchyliologique terrestre et fluvio-lacustre de la Nouvelle-Caledonie.Ac?. *Soc. Linn.* Bordeaux, 24: 211-330 (Part 1), 28: 1-212 (Part 2), 34: 1-107 (part 3).

GEPP, J. 1983. *Rote Listen Gefahrdeter Tiers Osterreichs.* Bundesministeriums fur Gesundheit und Umweltschutz. Vienna. 242 pp.

GERLACH, J. 1987. *The land snails of the Seychelles.* Northhamptonshire: Gerlach.

GERMAIN, LOUIS. 1932. La faune malacologique des iles Fidji. *Ann. Inst. Oceanogr.* n.s. 12: 39-63.

GODAN, D. 1983. *Pest slugs and snails.* Berlin: Springer.

GOETHEM, J.L. van, R. MARQUET, and J.J. de WILDE. 1987. Quelques conclusions au sujet de l'Atlas Provisoire des Gasteropodes Terrestres de la Belgique. *Apex* 2: 85-97.

GOLDBERG, E.E., V.T. BOWEN, J.W. FARRINGTON, G. HARVEY, J.H. MARTIN, P.L. PARKER, R.W. RISEBROUGH, W. ROBERTSON, E. SCHNEIDER, E. GAMBLE. 1978. The mussel watch. *Envir. Conserv.* 5: 101-126.

GOODFRIEND, G.A. and R.M. MITTERER. 1988. Late Quaternary land snails from the north coast of Jamaica: local extinctions and climatic change. *Palaeogeogr., Palaeoclimat., andPalaeont.* 63: 293-311.

GOULD, S.J. 1969. An evolutionary microcosm: Pleistocene and recent history of the land snail *P.* (*Poecilozonites*) in Bermuda. *Bull. Mus. Comp. Zool.* Harvard 138: 406-531.

GOULD, S.J. 1991. On the loss of a limpet. *Natural History* June: 22-27.

GREEN, J. 1968. *The biology ofestuarine animals.* London: Sidgwick and Jackson.

GRIFFITHS, O., A. Cook and S.M. Wells. 1993. The diet of the introduced carnivorous snail *Euglandina rosea* in Mauritius and its implications for threatened island gastropod faunas. *J. Zool., Lond.* 229: 79-89.

GROH, K. and O. GRIFFITHS. 1987. Africa and adjacent islands. In: Parkinson, B., with J. Hemmen and K. Groh. *Tropical Landshells of the world.* Wiesbaden: Verlag Christa Hemmen.

GROH, K. and B. PARKINSON. 1987. Florida-Caribbean. In: Parkinson B., with J. Hemmen and K. Groh. *Tropical Landshells of the world.* Wiesbaden: Verlag Christa Hemmen.

GUDE, G.K. 1914. *The fauna of British India. Mollusca II. Trochomorphidae and Janellidae.* London: Taylor and Francis.

GUDE, G.K. 1921. *The fauna of British India. Mollusca-III. Land Operculates.* London: Taylor and Francis.

GULICK, J.T. 1872. On the variation of species as related to their geographical distribution, illustrated by the Achatinellinae. *Nature* 6: 222-224.

GULICK, J.T. 1905. *Evolution, Racial and Habitudinal.* Washington, D.C.: Carnegie Institution.

HADFIELD, M.G. 1986a. Extinction in Hawaiian achatinelline snails. *Malacologia* 27: 67-81.

HADFIELD, M.G. 1986b. Settlement and recruitment of marine invertebrates: a perspective and some proposals. *Bull. Mar. Sci.* 39: 418-425.

HADFIELD, M.G. and E.A. KAY. 1981. The multiple villainies of *Euglandina rosea. Hawaiian Shell News* 29 (4): 5.

HADFIELD, M.G. and S.E. MILLER. 1989. Demographic studies of *Partulina proximo. Pacif. Sci.* 43: 1-16.

HADFIELD, M.G. and S.E. MILLER. 1992. Alien predators and decimation of endemic Hawaiian tree snails. *Pacif. Sci.* 46: 395.

HADFIELD, M.G. and B.S. MOUNTAIN. 1981 [for 1980]. A field study of a vanishing species, *Achatinella mustelina* (Gastropoda, Pulmonata), in the Waianae mountains of Oahu. *Pacif. Sci.* 34: 345-358.

HANNA, G.D. 1966. Introduced mollusks of western North America. *Occ. Pap. Calif. Acad. Sci.* 48: 1-108.

HANSEN, J.A. and G.M. SKILLETER. 1988. Effects of deposit feeding by the gastropod *Rhinoclavis aspera,* on microbial abundance and production in coral reef sediments. *Abstracts. 8th Internatl. CoralReef Symp.* Aug. 1988. Townsville, Australia. No. 161.

HARRISON, A.J. 1986. Gastropod fisheries in the Pacific with particular reference to Australian abalone. *Can. Spec. Publ. Fish. Aquat. Sci.* 92: 14-22.

HAURWITZ, R. 1990. Marauding mussels may migrate here from Lake Erie. *The Pittsburg Press.* Sunday Oct. 25 1989. In: *AMU News* 21:11.

HEBERT, P.D.N., B.W. Muncaster, and G.L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. *Can. J. Fish.* Aquat. Sci. 46: 1587-1591.

HEDLEY, C. 1917. The economics of *Trochus niloticus. Austr. Zool.* 1: 69-73.

HERSHLER, R. 1985. Systematic revision of the Hydrobiidae (Gastropoda: Rissoacea) of the Cuatro Cienegas Basin, Coahuila, Mexico. *Malacologia* 26: 31-123.

HESLINGA, G.A. and W.K. FITT. 1987. The domestication of reef-dwelling clams. *Bioscience* 37: 332-339.

HESLINGA, G.A. and A. HILLMANN. 1981. Hatchery culture of the commercial top snail *Trochus niloticus* in Palau, Caroline Islands. *Aquaculture* 22: 35-43.

HESLINGA, G.A. and T.C. WATSON. 1985. Recent advances in giant clam culture. *Proc. 5th Int. Coral ReefSymp.* 5: 531-538.

HESLINGA, G., O. ORAK, and M. NGIRAMENGIOR. 1985. Coral reef sanctuaries for *Trochus* shells. *South Pacific Comm. Fish.* Newsletter No. 35: 17-20.

HESLINGA, G.A., F.E. PERRON and O. ORAK.1984. Mass culture of giant clams (f. Tridacnidae) in Palau. *Aquaculture* 39: 197-215.

HIATT, R.W. and D.E. STRASBURG. 1960. Ecological relationships of the fish fauna on coral reefs in the Marshall Islands. *Ecol. Monogr.* 30: 65-127.

HINTON, A. 1982. Conservation in perspective. *Keppel Bay Tidings.* Oct.-Nov.

HOCKEY, P.A.R. and A.L. BOSMAN. 1986. Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. *Oikos* 46: 3-14.

IREDALE, T. 1941. Abasiclist of the land Mollusca of Papua. *Austr. Zool.* 10: 51-94.

IUCN. 1982. Directory of neotropical protected areas. Dublin: Tycooly International Publications.

IUCN. 1987a. The IUCN Policy Statement on Captive Breeding. SSC Captive Breeding Specialist Group. IUCN. 3 pp.

IUCN. 1987b. The IUCN Position Statement on Translocation of Living Organisms. Species Survival Commission. IUCN. 20 pp.

IUCN. 1990. *Red List of Threatened Animals.* International Union for Conservation of Nature and Natural Resources. 105

JAECKEL, S.G.A., JR. 1969. Die Mollusken Sudamerikas. In: E. J. Fittkau, J. lilies, H. Klinge, G.H. Schwabe, H. Sioli, eds. *Biogeography and ecology in South America,* vol. 2. Monographie Biologica vol. 19. Junk: The Hague, pp. 794-827.

JAIRAJPURI, M.S. 1991. *Animal resources of India Protozoa to Mammalia.* Zoological Survey of India.

JEFFS, A. 1982. Endemic snail species close to extinction. *Forest and Bird* 14:9.

JOHNSON, M.S., MURRAY, J. and B. CLARKE. 1990. The coil polymorphism in *Partula suturata* does not favour sympatric speciation. *Evolution AA:* 459-464.

KANDEL, E., T. ABRAMS, L. BERNIER, T. CAREW, R. HAWKINS, J. SCHWARTZ. 1983. Classical conditioning and sensitization share aspects of the same molecular cascade *in Aplysia. Cold Spring Harbor Symp. Quant. Biol.* 47: 821-830.

KAY, E.A., CORPUZ, G. and W. MAGRUDER. 1982. Opihi. Their biology and culture. Aquaculture Development Program. State of Hawaii Dept. of Land and Natural Resources.

KERNEY, M.P. 1982. The mapping of non-marine Mollusca. *Malacologia* 22: 403-407.

KERNEY, M.P. and R.D. CAMERON. 1979. *A field guide to the land snails ofBritain and Northwest Europe.* London: Collins.

KEW, H.W. 1893. *The dispersal of shells.* International Science Series 75.

KHOZOV, M. 1963. *Lake Baikal and its life.* Monographie Biologicae. The Hague: Junk.

KIRCH, P.V. and D.E. YEN. 1982. Tikopia: the prehistory and ecology of a Polynesian outlier. Honolulu: *B.P. Bishop Mus. Bull.* 238.

KISS, A. and E. PETRO. 1992. Distribution and biomass of some Chinese mussel *Anodonta woodiana* Lea, 1834 Bivalvia: Unionacea) Population in Hungary. In: Giusti, F. and G. Manganelli, eds. *Abstr. 11th Intern. Malacol. Congr. Siena* 1992: 31-33.

KOHN, A.J. 1959. The ecology of *Conus* in Hawaii. *Ecol. Monogr.* 29: 47-90.

KONDO, Y. 1970. Extinct land molluscan species. Colloquium on Endangered Species of Hawaii. Mimeo. B.P. Bishop Museum, Honolulu, Hawaii.

LIKHAREV, I.M. and (1952). Terrestrial mollusks of the U.S.S.R. 1962 translation. Israel Program for Scientific Translation, Jerusalem.

LIONNET, G. 1984. Terrestrial testaceous molluscs of the Seychelles. In: Stoddart, D.R., ed. *Biogeography and ecology ofthe Seychelles Islands.* Monographiae Biologicae. The Hague: Junk.

LOCKLEY, R.M. 1980. *New Zealand endangered species.* New Zealand: Cassell.

LUTZ, R.A. 1985. Mussel aquaculture in the United States. In: Huner, J.V. and E.E. Brown, Eds. *Crustacean and mollusk aquaculture in the United States.* Cincinnati: Avi Publishing Co.

MANI, M.S. 1974a. Biogeography of the Peninsula. In: Mani, M.S., ed. *Biogeography of India.* Monographiae Biologicae. The Hague: W. Junk. pp. 614-647.

MANI, M.S. 1974b. Biogeography of the eastern borderlands. In: Mani, M.S., ed. *Biogeography of India.* Monographiae Biologicae. The Hague: W. Junk. pp. 648-663.

MARES, M.A. 1986. Conservation in South America: problems, consequences, and solutions. *Science* 233: 734-739.

MARINE RESOURCES MANAGEMENT DIVISION. 1987. FY-1987 Annual Re- port. Yap State Dept. of Resources and Development, Colonia, Yap.

MAY, R.M. 1984. Introduction. In: May, R.M., ed. *Exploitation ofmarine communities.* Kahlem Konferenzen 1984. New York: Springer Verlag. pp. 1-10.

MCCOY, P. 1976. *Easter Island settlement patterns in the late prehistoric and protohistoric periods.* New York: Easter Island Committee, International Fund for Monuments.

MCMAHON, R.F. 1982. Ecology of an invasive pest bivalve, *Corbicula.* In: Russell-Hunter, W.D., Ed. *The Mollusca.* Vol 6. Ecology. San Diego: Academic Press, pp. 505-561.

MEAD, A.R. 1961. *The giant African snail. A problem in economic malacology.* Chicago: University of Chicago Press. 257 pp.

MEAD, A.R. 1979. *Pulmonates* 2B. *Economic malacology with particular reference to Achatina fulica.* In: Fretter, V. and J. Peake. New York: Academic Press.

MEADS, M.J., K.J. WALKER, G.P. ELLIOTT. 1984. Status, conservation, and management of the land snails of the genus *Powelliphanta* (Mollusca: Pulmonata). *New Zealand Journ. of Zool.* 11: 277-307.

MEEHAN, B. 1977. Man does not live by calories alone: the role of shellfish in a coastal cuisine. In: Allen, J., J. Golson and R. Jones, eds. *Sunda andSahul. Prehistoric studies in* Southeast Asia, Melanesia and Australia. New York: Academic Press.

MILLER, S.E. and M.G. HADFIELD. 1990. Developmental arrrest during larval life and life-span extension in a marine mollusk. *Science* 248: 356-358.

MILLER, S.E., R. COWIE, B. SMITH and N. ROJEK. 1993. The decline of partulid snail populations in American Samoa. *Species* 20: 65.

MOCHIDA, O. 1991. Spread of freshwater *Pomacea* snails (Pilidae, Mollusca) from Argentina to Asia. *Micronesica Suppl.* 3:51-62.

MORI, S. 1984. Molluscs. In: S. Horie, ed. *Lake Biwa.* Monographiae Biologicae. Vol. 54. The Hague: Junk, pp.331-337.

MORRISON, J.P.E. 1929. On the occurrence of *Hendersonia* in Crawford County, Wisconsin. *Nautilus* 43: 41-45.E.

MORTON, B.S. 1969. Studies on the biology of *Dreissena polymorpha* Pall. 4. Habits, habitats, distribution and control. *Water Treatment and Examination* 18: 233-240.

MUNRO, J.L. 1989. Fisheries for giant clams (Tridacnidae: Bivalvia) and prospects for stock enhancement. In: Caddy, J.F. (Ed.). *Marine invertebrate fisheries: their assessment and management.* New York: John Wiley & Sons.

MURRAY, J. and B. CLARKE. 1980. The genus *Partula* on Moorea: speciation in progress. *Proc. R. Soc. Lond.* B. 211: 83-117.

MURRAY, J., E. MURRAY, M.S. JOHNSON, and B. CLARKE. 1988. The extinction of *Partula* on Moorea. *Pacif. Sci.* 42: 150-153.

MURRAY, J., STINE, O.C., and M.S. JOHNSON. 1991. The evolution of mitochondrial DNA in *Partula. Heredity, Lond.* 66: 93-104.

MYLONAS, M. 1984. The influence of man: a special problem in the study of zoogeography of terrestrial molluscs on the Aegean Islands, Greece. In: Solem, A. and A.C. van Bruggen, eds. *World-wide snails,* pp. 249-259. Leiden: E.J. Brill.

NEVILL, G. 1869. Additional notes on land-shells of the Seychelles Islands. *Proc. Zool. Soc. London:* 61-62.

NICHOLS, F.H., J.K. THOMPSON, and L.E. SCHEMEL. 1990. Remarkable invasion of San Francisco Bay (California, U.S.A.) by the Asian clam *Potamocorbula amurensis.* Displacement of a former community. *Mar. Ecol. Progr. Ser.* 66: 95-101.

OGLE, C.C. 1979. Critical status of *Placostylus* and *Paryphanta* land snails in the far north. Fauna Survey Unit report 14. New Zealand Wildlife Service.

OKUDA, S. 1984. The influence of human activities on Lake Biwa. In: S. Horie, *ed. Lake Biwa.* Monographie Biologicae. The Hague: Junk. pp. 635-641.

OKUTANI, T. 1977. Stock assessment of cephalopod resources fished by Japan. FAO Fisheries Technical Paper No. 173.

OLIVER, J.H., JR. 1988. Crisis in biosystematics of arthropods. *Science* 240: 967.

OLIVERA, B.M., J. RIVIER, C. CLARK, C.A. RAMILO, G.P. CORPUZ, FE C. ABOGADIE, E.E. MENA, S.R. WOODWARD, D.R. HILLYARD, L.J. CRUZ. 1990. Diversity of *Conus* neuropeptides. *Science* 249: 257-263.

ORTEGA, S. 1987. The effect of human predation on the size distribution of *Siphonaria gigas* (Mollusca: Pulmonata) on the Pacific coast of Costa Rica. *Veliger* 29: 251-255.

ORTMANN, A.E. 1909. The destruction of the fresh-water fauna in western Pennsylvania. *Proc. Amer. Philosph. Soc.* 48: 90-110.

PAIN, T. 1981. Meet the Strophocheilidae. *Hawaiian Shell News* 29 (8): 1,6.

PARKINSON, B. and K. GROH. 1987. Tropical Asia. In: Parkinson, B., J. Hemmen and K. Groh. *Tropical landshells of the world.* Wiesbaden: Christa Hemmen.

PARODIZ, J.J. 1957. Catalogue of the land Mollusca of Argentina. *Nautilus* 70: 122-135; 71: 22-30, 63-67.

PARODIZ, J.J. 1980. Distribution and origin of the continental South American malacofauna. *Malacologia* 22: 421-425.

PARRISH, J.D., M.W. CALLAHAN and J.E. NORRIS. 1985. Fish trophic relationships that structure reef communities. *Proc. Fifth Internatl. Coral Reef Congress, Tahiti,* vol. 4: 73-78.

PAULAY, G. 1985. Adaptive radiation on an isolated oceanic island: the Cryptorhynchinae (Curculionidae) of Rapa revisited. *Biol. Journ. Linn. Soc.* 26: 95-187.

PAULAY, G. 1991. Henderson Island: biogeography and evolution at the edge of the Pacific Plate. In: Dudley, E.C., ed. *The Unity of Evolutionary Biology. The Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology.* Vol. 1: 304-313. Portland: Dioscoroides Press.

PEAKE, J. 1978. Distribution and ecology of the Stylommatophora. In: V. Fretter and J. Peake, eds. *Pulmonates* Vol. 2A. New York: Academic Press, pp. 429.-526.

PILSBRY, H.A. 1896-1899. Non-Marine Mollusca of Patagonia. *Rep. Princeton Univ. Exped. Patagonia* 3 (Zoology) (5): 513-633.

PILSBRY, H.A. 1948. Land Mollusca of North America (North of Mexico). *Acad. Nat. Sci. Philadelphia,* Monograph No. 3, Vol. 2, Pt. 2: i-xlvii +521-1113.

POINER, I.R. and C.P. CATTERALL. 1988. The effects of traditional gathering on populations of the marine gastropod *Strombus luhuanus* Linne 1758, in southern Papua, New Guinea. *Oecologia* 76: 191-199.

PONDER, W.F. and G.A. CLARKE. 1990. A radiation of hydrobiid snails in threatened artesian springs in western Queensland. *Rec. Australian Mus.* 42: 301-363.

POOL, D. and J.D. MCCULLOUGH 1979. The Asiatic clam *Corbicula manilensis* from two reservoirs in eastern Texas. *The Nautilus* 93: 37.

POWELL, A.W.B. 1979. *New Zealand Mollusca.* Auckland: Collins.

PUENTE, A.I. AND C.E. PRIETO. 1992. Endemic Helicoidea species of the Iberian peninsula (Pulmonata). In: Giusti, F. and G. Magnelli, eds. *Abstr. 11th Intern. Malacol. Congr. Siena:* 94-95.

RADOMAN, P. 1964. Nove Ohridske Hidrobide (III). *Arh. Biol. Nauka* 15: 101-119.

RANDALL, J.E. 1982. Tropical marine sanctuaries and their significance in reef fisheries research. In: G.R. Huntsman, W.R. Nicholson, and W.W. Fox, Jr. *The Biological Bases for Reef Fishery Management.* NOAA Technical Memorandum NMFS-SEFC-80. pp. 167-178.

RAO, H.S. 1937. On the habitat and habits of *Trochus niloticus* Linn, in the Andaman Seas. *Rec. Ind. Mus.* 39: 47-82.

ROBERTS, L. 1990. Zebra mussel invasion threatens U.S. waters. *Science* 265: 1370-1372.

RODGERS, W.A. and K.M. HOMEWOOD. 1982. Species richness and endemism in the Usambara mountain forests, Tanzania. *Biol. J. Linn. Soc.* 18: 197-242.

ROPER, C.F.E. and W. RATHJEN. 1991. World-wide squid fisheries: a summary of landings and capture techniques. *Journ. Cephalopod Biol.* 2: 51-63.

ROTH, B. 1972. Native mollusks — little known and little loved. *Sierra Club Bull.* 57 (6): 5-7.

RUSSELL-HUNTER, W.D. 1983. Overview: Planetary distribution of and ecological constraints upon the Mollusca. In: Russell-Hunter, W.D., ed. *The Mollusca* Vol. 6. New York: Academic Press, pp. 1-27.

SAL VAT, B. 1970. II. Importance Biologique et sedimentologique de la faune malacologique dans les atolls Polynesiens. *Cah. Pacif.* 14: 8-53.

SAL VAT, B. 1981. Preservation of coral reefs: scientific whim or economic necessity? Past, present and future. *Proc. Fourth Int. Coral Reef Symp. Manila* 1: 225-229.

SHACHAK, M., C.G. JONES and Y. GRANOT. 1987. Herbivory in rocks and the weathering of a desert. *Science* 236: 1098-1099.

van *dei SCHALIE, H. 1973. Damn(n) large rivers* — then what? *The Biologist* 55:29-35. Seale, A. 1916. Sea products of Mindanao and Sulu II: pearls, pearl shells, and button shells. *Phil. J. Sci.* D. 11: 245-264.

SHEPHERD, S.A., M. J. TEGNER, and S.A.G. DEL PROO. 1992. *Abalone of the world.* Oxford: Fishing News Books.

SIMPSON, C.T. 1894. Distribution of the land and freshwater mollusks of the West Indian Region, and their evidence with regard to past changes of land and sea. *Proc. U.S. Natl. Mus.* 17: 423-429.

SIMPSON, R.D. 1992. The status of the market and production of edible snails in Australia. F. Giusti and G. Manganelli, eds. *Abstr. 11th Intern. Malacol.* Congr., Siena.

SINGH, S. 1985. Protected areas in India. In: Conserving Asia's Natural Heritage. In: J.W. Thorsell, ed. Proc. 25th Working Session of IUCN's Commission on National Parks and Protected Areas, pp. 11-18.

SMITH, A.G. 1966. Land snails of the Galapagos. In: Bowman, R.I.,ed. *The Galapagos.* Berkeley: University of California Press.

SMITH, B. and D. HOPPER. 1992. The status of tree snails (Gastropoda: Partulidae) on Guam, with a resurvey of sites studied by H.E. Crampton in 1920. *Pacif. Sci.* 46: 77-85.

SMITH, B.J. 1979. Survey of non-marine molluscs of south-eastern Australia. *Malacologia* 18: 103-105.

SMITH, B.J. 1981. Introduced non-marine molluscs in Australia. *Victorian Nat.* 98: 24-26.

SMITH, B.J. 1984. Regional endemism of the south-eastern Australian land mollusc fauna (Gastropoda: Pulmonata). In: A. Solem and A.C. van Bruggen, eds. *World-wide snails.* Leiden: E.J. Brill/W. Backhuys.

SMITH, S.V. 1978. Coral reef area and contributions of reefs to processes and resources of the world's oceans. *Nature* 273 (5659): 225-226.

SOLEM, A. 1959. Systematics and zoogeography of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana: Zool.* 43:1-359.

SOLEM, A. 1961. New Caledonian land and fresh-water snails. *Fieldiana: Zoology.* 41: 413-501.

SOLEM, A. 1974. *The Shell Makers. Introducing Mollusks.* New York: Wiley Interscience.

SOLEM, A. 1975. Final Report. OES 14-16—0008-873. Upolu. Office of Endangered Species, Washington D.C.

SOLEM, A. 1976. *Endodontoid land snails from Pacific islands. (Mollusca: Pulmonata: Sigmurethra). Part I. Family Endodontidae.* Illinois: Field Museum of Natural History, Chicago. 508 pp.

SOLEM, A. 1977. Fam. Charopidae. La faune terrestre de l'ile de Sainte-Helene. 4th Pt. *Ann. Mus. Roy. de l'Afrique Centrale.* 220: 521-533.

SOLEM, A. 1978. Land snails from Mothe, Lakemba, and Karoni Islands, Lau Archipelago, Fiji. *Pacif. Sci.* 32: 39-45.

SOLEM, A. 1979. A theory of land snail biogeographic patterns through time. In: Van der Spoel, S., A.C. van Bruggen, and J. Lever, eds. *Pathways in Malacology.* Utrecht: Bohn, Scheltema and Holkema. pp. 225-249.

SOLEM, A. 1983. *Endodontoid land snails from Pacific islands.* (*Mollusca: Pulmonata: Sigmurethra*). *Part II. Families Punctidae and Charopidae, Zoogeography.* Illinois: Field Museum of Natural History, Chicago. 336 pp.

SOLEM, A. 1984. A world model of land snail diversity and abundance. In: Solem, A. and A.C. van Bruggen (Eds). *World-wide snails.* Leiden: E.J. Brill/W. Backhuys.

SOLEM, A. 1988. Maximum in the minimum: biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, northern Kimberley, Western Australia. *J. Malac. Soc. Aust.* 9: 59-113.

SOLEM, A. 1990. Limitations *of equilibrium theory* in *relation to* land snails. *Atti dei ConvengniLincei* 85: 97-116.

SOLEM, A., F.M. CLIMO, and E.J. ROSCOE. 1981. Sympatric species diversity of New Zealand land snails. *N.Z. J. Zool.* 8: 453-485.

STANSBERY, D.H. 1971. Rare and endangered mollusks in the eastern United States. In: Jorgensen, S.E. and R.W. Sharp, eds. *Proc. Symp. rare and endangered mollusks (naiads) of the United States.* Unted States Fish and Wildlife Service.

TAYLOR, D.W. 1988. Aspects of freshwater mollusc ecological biogeography. *Palaeogeogr., Palaeoclimatoi, Palaeoecol.* 62: 511-576.

TAYLOR, D.W. and W.L. MINCKLEY, 1966. New world for biologists. *Pacific Discovery* 19: 18-22.

TAYLOR, J.D. and K. WAY. 1976. Erosive activities of chitons at Aldabra Atoll. *Journ. Sedim. Petrol.* 46: 974-977.

THOMAS, H.S. 1884. A report on pearl fisheries and chank fisheries, 1884. Madras: The Government Press.

THOMPSON, F.G. 1968. *The aquatic snails of the family Hydrobiidae of Peninsular Florida.* Gainesville: University of Florida Press.

THOMPSON, F.G. 1986. Land mollusks of the proposed National Parks of Haiti. Report.

THORSON, G. 1971. *Life in the sea.* New York: McGraw Hill.

TILLIER, S. and B.C. CLARKE. 1983. Lutte biologique et destruction du patrimonine genetique: le cas des mollusques gasteropodes pulmones dans les territoires francais du Pacifique. *Genet. Set. Evol.* 15:559-566.

TRUEMAN, A.E. 1922. On the use of *Gryphaea* in the correlation of the Lower Lias. *Geol. Mag.* 59: 256-268.

TURNER, H. and M. WUTHRICH. 1985. *Systematic catalogue of Swiss Mollusca.* Swiss Federal Institute of Forestry Research, Birmensdorf, Switzerland. 2nd edition.

TURNER, J.S., C.N. SMITHERS, and R.D. HOOGLAND. 1968. The conservation of Norfolk Island. *Austr. Conserv. Found., Spec. Publ.* 1, 41pp.

UNITED STATES DEPARTMENT OF THE INTERIOR. 1986. Endangered and threatened wildlife and plants. January 1, 1986. 50 CFR 17.11 and 17.12.

UNITED STATES FISH AND WILDLIFE SERVICE. 1991. Endangered and threatened wildlife and plants. 50 CFR 17.11 and 17.12. July 15.

VERDCOURT, B. 1972. The zoogeography of non-marine Mollusca of East Africa. *Journ. of Conch.* 27: 291-307.

VERDCOURT, B. 1982. In: W.A. Rodgers and KM. Homewood, Species richness and endemism in the Usambara mountain forests, Tanzania. *Biol. J. Linn. Soc.* 18: 197-242.

VERDCOURT, B. 1984. Discontinuities in the distribution of some East African land snails. In: Solem, A. and A.C. va Bruggen, eds. *World-wide snails.* Leiden: E.J. Brill/W. Backhuys.

VERMEIJ, G.J. 1989. Saving the sea: what we know and what we need to know. *Conserv. Biol.* 3: 240-241.

WALDEN, H.W. 1963. Historical and taxonomical aspects of the land Gastropoda in the North Atlantic region. In: A. Love and D. Love, Eds. *North Atlantic Biota and their History.* New York: Pergamon Press. pp. 153-171.

WALDEN, H.W. 1983. Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. With an annotated check- list. *Ann. Zool. Fennici* 20: 255-275.

WALDEN, H.W. 1984. On the origin, affinities, and evolution of the land Mollusca of the mid-Atlantic islands, with special reference to Madeira. *Bol. Mus. Mun. Funchal* 36: 51-82. Walden, H.W. 1986. Endangered land mollusc species in Sweden and on Madeira. In: *Abstracts Ninth International Malacol. Congr. Edinburgh Scotland.*

WALLACE, A.R. 1872. *The Malay Archipelago.* London: MacMillan and Co.

WALLACE, G.D. and L. ROSEN. 1969. Studies on eosinophilic meningitis. V. Molluscan hosts of *Angiostrongylus cantonensis* on Pacific islands. *Am. J. Trop. Med. Hyg.* 18: 206-216.

WELLS, M.J. 1962. *Brain and behaviour in cephalopods.* London: Heinemann.

WELLS, S.M. and J.E. CHATFIELD. 1992. Conservation priorities for European non-marine molluscs. In: Giusti, F. and G. Magnelli, eds. *Abstr. 11th Intern. Malacol. Congr. Siena:* 203-204.

WELLS, S.M., R.M. PYLE and N.M. COLLINS. 1983. *The IUCN Invertebrate Red Data Book.* Cambridge, UK: IUCN

WESTERN, D. and M.C. PEARL, eds. 1991. *Conservation in the 21st century.* New York: Oxford University Press.

WHITE, M.J.D. 1978. *Modes of speciation.* San Francisco: Freeman.

WILLAN, R.C. 1987. The mussel *Musculista senhousia* in Australasia; another aggressive alien highlights the need for quarantine at ports. *Bull, of Mar. Sci.* 41: 475-489.

WILLIAMSON, P.G. 1981. Palaeontological documentation of speciation in Cenozoic molluscs from Turkana Basin. *Nature* 293: 699-702.

WILSON, E.O. 1985. Time to revive systematics. *Science* 230: 1227.

WILSON, E.O. 1987. The little things that run the world. (The importance and conservation of invertebrates). *Conserv Biol.* 1: 344-346.

WINCKWORTH, R. 1950. In: Jairapjpuri, M.S. 1991 *Animal resources of India Protozoa to Mammalia.* Zoological Survey of India,

de WINTER, A.J. 1992. Gastropod diversity in a rain forest in Gabon, West Africa. In: Giust, F. and G. Magnelli, eds. *Abstr. 11th Intern. Malacol. Congr. Siena:* 172-173.

WOODWARD, F.R. 1990. *Margaritifera margaritifera.* European Invertebrate Survey.

WOODWARD, F.R. 1991. Dr. William B. Lorrain and St. Helena's endemic land shells. *Hawaiian Shell News* 39 (11): 1,4.

YAMAGUCHI, M. 1977. Conservation and cultivation of giant clams in the tropical Pacific. *Biol. Conserv.* 11: 13-20.

YAMAGUCHI, M. and K.-I. KIKUTANI. 1989. Feasibility study of green snail transplantation to the Federated States of Micronesia. South Pacific Aquaculture Development Project, Food and Agriculture Organization of the United Nations. Suva, Fiji. 25 pp.

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Polar Bears: Proceedings of the Tenth Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 1991, £10.00, US$20.00.

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