A Hierarchical Ecological Approach to Conserving Marine Biodiversity

MARK A. ZACHARIAS* AND JOHN C. ROFF†

*Land Use Coordination Office, Province of British Columbia, PO Box 9426 Stn Prov Govt, Victoria, British Columbia V8W 9V1, Canada, email mark.zacharias@gems6.gov.bc.ca
†Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada

Abstract: *A number of ecological models have been developed to provide an understanding of the various biotic and abiotic components required to conserve biodiversity and to reconcile objectives and methods between those interested in the conservation of species (e.g., population management) and those advocating the conservation of spaces (e.g., protected areas). One of the better known efforts—pioneered in the Pacific Northwest of the United States—is a hierarchical ecological framework that separates biodiversity into compositional, structural, and functional attributes at the genetic, population, community-ecosystem, and landscape levels of organization. We present an adaptation of this terrestrial framework consistent with the ecological function of marine environments. Our adaptation differs in its treatment of the community and ecosystem levels of organization. In our marine framework, the community level denotes predominantly the biotic community components of biodiversity, and the ecosystem level—consistent with marine terminology—denotes predominantly physical and chemical components. The community and ecosystem levels are further separated into those attributes based on ecological structures such as depth or species richness and those based on ecological processes such as water motion or succession. The distinction between the biotic (genetic, population, and community) and abiotic (ecosystem) is required because the biological components of biodiversity such as competition or predation are often more difficult to observe than the abiotic components such as upwellings, substratum, or temperature. As a result, efforts to conserve marine biodiversity are often dependent on the observable abiotic (ecosystem) components, which can be used as surrogates for the identification and monitoring of biotic (community) components. We used our hierarchical framework to identify and suggest how conservation strategies could be implemented in marine environments depending on whether existing data are to be used or new data are to be collected.*

Estrategia Ecológica por Jerarquías para Conservar la Biodiversidad Marina

Resumen: *Se ha desarrollado una gran cantidad de modelos ecológicos para entender los diversos componentes bióticos y abióticos requeridos para conservar la biodiversidad y reconciliar objetivos y métodos entre aquellas personas interesadas en la conservación de especies (por ejemplo, manejo poblacional) y aquellas que abogan por la conservación de espacios (por ejemplo, áreas protegidas). Uno de los esfuerzos más conocidos—iniciado en el océano Pacífico del noroeste de los Estados Unidos—es un marco ecológico y jerárquico que separa la biodiversidad en atributos estructurales, funcionales y de composición a niveles de organización genética, de población, de comunidad/ecosistema y de paisaje. Presentamos una adaptación de este marco de trabajo terrestre, consistente con la función ecológica de ambientes marinos. Nuestra adaptación difiere en el tratamiento de los niveles de organización de comunidad y ecosistema. En nuestro marco marino, el nivel de comunidad denota predominantemente los componentes bióticos comunitarios de la biodiversidad, y el nivel de ecosistema—consistente con la terminología marina—denota predominantemente los componentes f¡sicos y químicos. Los niveles de comunidad y ecosistema son separados aún más en aquellos atributos basados en estructuras ecológicas tales como la profundidad y la riqueza de especies y aquéllos basados en procesos ecológicos tales como el movimiento del agua y la sucesión. La distinción entre lo biótico (genético, población y comunidad) y lo abiótico (ecosistema) se requiere puesto que los componentes biológicos de la biodiversidad, tales como la competencia o la depredación son a menudo más*

Paper submitted April 13, 1999; revised manuscript accepted January 5, 2000.

difíciles de observar que los componentes abióticos tales como las corrientes de ascendencia, el substrato o la temperatura. Como resultado, los esfuerzos para conservar la biodiversidad marina dependen frecuentemente de los componentes abióticos observables (ecosistema), los cuales pueden ser usados como substitutos para la identificación y el monitoreo de componentes bióticos (comunidad). Utilizamos un marco conceptual jerárquico para identificar y sugerir la manera en que las estrategias de conservación podrían ser implementadas en ambientes marinos dependiendo de la existencia de datos a utilizar, o de la necesidad de colectar nuevos datos.

Introduction

Most efforts at protecting marine environments have focused on the conservation of species (e.g., fisheries, whales), whereas in the past 20 years there has been a shift to the conservation of spaces (e.g., marine reserves; National Research Council 1995). Considerable literature exists on how conservation objectives can be met by these two approaches, but there have been recent arguments that neither approach has been applied successfully toward the conservation of biodiversity in the marine environment (National Research Council 1995; Allison et al. 1998; Simberloff 1998).

Difficulties with the management and conservation of single species (populations) are well known and have been thoroughly addressed by Launer and Murphy (1994), Weaver (1995), Niemi et al. (1997), and Simberloff (1998). In marine environments, these difficulties are often exacerbated by a poor understanding of trophic structures and the tendency to conserve one population by shifting anthropogenic pressures onto another perceived to be in "better shape." Conversely, there is an increasing awareness that conserving spaces often fails to encompass the ecological conditions and processes necessary to protect marine biodiversity. Most criticism of efforts to conserve marine spaces is directed toward the insufficient size of marine reserves and the failure to address external threats transported into an area as a result of the three-dimensional nature of marine environments (Allison et al. 1998).

A primary limitation of both the species and spaces approaches is the connectivity of marine environments, where threats such as habitat loss, climate change, pollution, and introduced species operate on what Ricklefs (1987) terms ". . .processes beyond the normal scale of consideration" that cannot be mitigated by means of traditional marine conservation measures. Although there is a growing realization that efforts to conserve marine biodiversity are often inadequate, few studies have examined what measures are required to properly address the major conservation issues in marine environments. The inability to progress beyond species or spaces approaches to marine conservation can be attributed in part to a lack of understanding of the mechanisms structuring marine biodiversity. An example of the fundamental gaps in our knowledge of how marine environments operate is demonstrated in the debate surrounding the degree to which biological or physical processes structure various types of marine communities (May 1992; National Research Council 1995). The conservation implications of this debate are clear: how can an environment be conserved when the components that support it are undefined?

This difficulty is not unique to marine environments; it has been addressed in terrestrial conservation in part through the development of ecological models of biodiversity. The purpose of these models is to provide an understanding of the various components required to conserve biodiversity and to reconcile objectives and methods between those interested in the conservation of species and those advocating the conservation of spaces. These models are also used to outline the structure and function of various habitats and communities and the scales at which they operate. One of the better-known models—developed in the Pacific Northwest of the United States—is a framework that conceptualizes biodiversity into compositional, structural, and functional attributes at genetic, population, community-ecosystem, and landscape levels (Franklin et al. 1981; Norse et al. 1986; Office of Technology Assessment 1987; Noss 1990). Compositional components include the genetic composition of a population, the composition of a community or ecosystem, and the spatial and temporal distribution of these communities throughout a landscape. Structural attributes are composed of biotic and abiotic features that contribute to biodiversity by providing various habitats and patchiness at different levels of organization. Functional attributes include the processes required to sustain biodiversity, which include climatic, geologic, hydrologic, ecological, and evolutionary processes (Noss 1990; Huston 1994; Table 1).

Using work by Noss (1990) and others as a basis, we present a hierarchical framework consistent with the ecological composition, structure, and function of marine environments. This framework will be used to address a number of outstanding marine conservation issues (Table 2) and to provide guidance for those responsible for the implementation of marine conservation strategies.

Framework for Marine Environments

Work by Noss (1990) and others, although designed for terrestrial environments, has some relevance to marine

Table 1. Compositional, structural, and functional attributes of biodiversity proposed by Noss (1990), contrasted with our proposed framework for marine environments.

Compositional		*Structural*		*Functional*	
Noss	*our framework*	*Noss*	*our framework*	*Noss*	*our framework*
Genes	genes	genetic structure	genetic structure	genetic processes	genetic processes
Species, populations	species, populations	population structure	population structure	demographic processes, life histories	demographic processes, life histories
Communities, ecosystems	communities	physiognomy, habitat structure	community composition	interspecific interactions, ecosystem processes	organism-habitat relationships
Landscape types	ecosystems	landscape patterns	ecosystem structure	landscape processes and disturbances, land-use trends	physical and chemical processes

environments (Franklin et al. 1981; Norse et al. 1986; Office of Technology Assessment 1987). The separation of structural and functional attributes and the division of biological organization into four hierarchical levels is consistent with the function of marine environments (Mann & Lazier 1996; Nybakken 1997). Where this work needs to be adapted for application to the conservation of marine biodiversity is in the translation of communities, ecosystems, and landscape types into meaningful marine equivalents.

Table 2. Objectives for the development of a hierarchical ecological framework for the conservation of marine biodiversity.

Objectives	*Description*
Standardize terminology	Identify common terminology, clarify ambiguous language, and attempt to equate terrestrial terminology with marine equivalents.
Clarify objectives	Identify the components (e.g., habitat vs. community) of a marine environment requiring protection. Develop marine equivalents to the population, community, ecosystem, and landscape levels of organization.
Relate scales	Relate spatial and temporal scales of community and ecosystem organization to those of conservation efforts.
Identify gaps in knowledge and data	Determine information and knowledge required to properly implement conservation strategies.
Organize existing research	Identify whether research has been based on biotic or abiotic approaches and at what scale(s) the research has been applied.
Identify conservation methodologies	Identify possible techniques or approaches to conserve marine environments.
Direct the collection of new data	Direct the collection of new information in a manner that facilitates conservation efforts.

In the marine environment, the genetic and species-population levels of organization can be utilized in the same manner as in terrestrial environments, but communities and ecosystems have different connotations. In marine environments, communities are generally perceived as biological entities and ecosystems as physically and chemically defined systems (May 1992). Given the importance of abiotic (ecosystem) components for marine biodiversity, and the fact that the term *ecosystem* is already used to denote abiotic processes, our framework separates the community (biotic) from the ecosystem (abiotic) levels.

We adapted to marine environments the terrestrial framework proposed by Noss (1990) (Table 1). It is fundamentally similar to the terrestrial framework with the following exceptions: subdivision of the community and ecosystem levels; changes to the structural and functional attributes to reflect the biotic and abiotic nature of these two respective levels; and elimination of the landscape level, which has no acknowledged counterpart in the marine environment and is subsumed into our ecosystem level.

We used compositional attributes to allocate structural (static) and functional (process-dynamic) attributes within the ecological hierarchy (Table 3). Community attributes are based on biological structure and process, whereas ecosystem attributes are based primarily on physical and biophysical process. The genetic level of the hierarchy is not included in Table 3 because it does not differ from the terrestrial framework (Noss 1990). Spatial and temporal scales do not dictate the levels of organization to the same extent as in the terrestrial framework. For example, an inland sea or continental shelf could be considered either a set of communities or an ecosystem, and migratory populations often span entire oceans. The biological processes identified under the community approach, however, generally operate at much smaller spatial and temporal scales than do ecosystem processes. There are some exceptions, however, including succession (temporal) and migration (spatial).

Separating attributes at their population, community, and ecosystem levels in the marine environment is important because there are conservation implications at each level of the hierarchy. Attributes at the population and ecosystem levels such as migration or water movement tend to be easier to observe than community attributes such as competition. Of all the levels, ecosystem attributes such as depth tend to be the easiest to observe. In addition to the relative ease of monitoring population and ecosystem attributes, abiotic attributes such as water movement and temperature tend to be easier to observe and predict than biotic attributes such as disease. Ecosystem processes such as productivity, however, involve both biotic and abiotic components and therefore have different implications for conservation than strictly abiotic attributes. Water motion for example, is an ecosystem process driven by forces that (with the possible exception of global climate change) are generally immutable from human activities. Other ecosystem processes such as biogeochemical cycles, events, and productivity may be more sensitive to human activities than many community processes such as predation and competition.

It is relatively easy to monitor ecosystem and population process and structure (Table 3) where structural and process attributes are identified based on whether they can be observed, measured or modeled or have been applied to the conservation of biodiversity. It is evident that observing structure is easier than observing process and that structural attributes can be both observable features, such as depth, or ecological concepts used to infer process, such as metapopulations. We also suggest that structure is the result of the operation of process, and therefore that observing structure can be used as a surrogate for inferring process, which is often unobservable (Table 3).

We evaluated a representative sample of marine research against the framework to identify at what compositional level these studies were undertaken (Table 4). We identified those research efforts that utilized a combination of community and ecosystem levels as a fourth level of organization. All four approaches have been implemented during the past 50 years at various scales and with different terminology, suggesting that there are no standard conservation approaches for different types of environments.

Applying the Framework to the Conservation of Marine Environments

Our framework establishes the conservation approaches that can be applied to the marine environment under

Table 3. The marine ecological framework.[a]

Population		*Community*		*Ecosystem*	
structure (static)	*process (function)*	*structure (static)*	*process (function)*	*structure (static)*	*process (function)*
Population structure[b,c]	migration[b,c]	transition areas[b]	succession[b,c]	water properties [b,c,d]	biogeochemical cycles[b,c,d]
Distribution[b,c]	recruitment[b]	functional groups [b,c]	predation[b]	bottom topography[b,c,d]	productivity[b,c,d]
Dispersion[b]	reproduction[b]	meta populations[b,c]	competition[b]	boundaries[b,c,d]	water motion[b,c,d]
Keystone species[b]	retention[b]	heterogeneity[b]	parasitism[b]	wave exposure[b,c,d]	events/ disturbance[b,c,d]
Indicator species[b,c,d]	evolution[b]	endemism[b]	mutualism[b]	substrate type[b,c,d]	anomalies[b,c,d]
Umbrella species[b]		diversity[b,c]	disease[b]	depth[b,c,d]	coupling[b,c,d]
Charismatic species[b]		alternate stable states[b]	commensalism[b]	illumination[b,c,d]	retention[b,c]
Vulnerable species[b,c]		species richness[b,c,d]		stratification[b,c,d]	entrainment[b,c]
Economic species[b]		species evenness[b,c,d]		patchiness[b,c,d]	desiccation[b,c]
		species abundance[b,c,d]		dissolved gasses[b,c]	
		representative and distinct areas[b,c,d]		representative and distinct areas[b,c,d]	
		biomass[b,c,d]			

[a] *Attributes of structure (statics) and process (function or dynamics) are arranged under the population, community, and ecosystem levels of organization (compositional attributes). Structural attributes in this framework can be a measurable attribute or a theory. An indicator species, for example, may be used to indicate the presence of a community, but its application toward conserving biodiversity falls under the population approach.*
[b] *Observable phenomenon.*
[c] *Observable phenomenon that has been measured, quantified, or modeled, leading to an understanding of its influence on biodiversity.*
[d] *Observable phenomenon that has been applied to the monitoring of biodiversity.*

Table 4. A representative sample of marine literature assessed as to whether it falls under population, community, or ecosystem approaches as we defined them.

Approach	*Studies*	*Environment or species studied*	*Key terminology*	*Scale*
Population (biotic)	Paine 1966	rocky intertidal shorelines (*Pisaster* spp.)	keystone species	meters
	Estes & Palmisano 1974	rocky subtidal pelagic (*Enhydra lutris*)	umbrella species	meters
Community (biotic)	Augier 1982	benthic communities in the Mediterranean	biocoenoses	continental
	Thorsen 1957	global inventory of benthic communities	iso-parallel communities	oceanic
	Peres & Picard 1964	Mediterranean	facies	100s km
	Ekman 1953	global distribution of fauna	faunistic regions	oceanic
	Glemarec 1973	European North Atlantic	etages	continental
Community-ecosystem (biotic and abiotic)	Connor 1997	intertidal environments	biotopes	100s km
	Dauvin et al. 1994	French coastlines	biocoenoses	100s km
	Pielou 1979	zoogeographic communities	biotic provinces	oceanic
	Menge 1992	rocky intertidal shorelines	bottom-up influences	meters
	Cowardin et al. 1979; Dethier 1992	intertidal and shallow subtidal environments	habitat types	meters
	Metaxas & Scheibling 1996	rocky-shore tide pools		meters
	Briggs 1974	global faunal assemblages	realms	oceanic
Ecosystem (abiotic)	Hayden et al. 1984	hierarchial abiotic classification	provinces	oceanic
	Dolan et al. 1972	coastal classification		continental
	Hesse et al. 1951	delineation of water masses	domains	oceanic
	Sherman et al. 1980	global coastal	large marine ecosystems	oceanic
	Caddy & Bakun 1994	regional studies of nutrient enrichment	marine catchment basins	oceanic

the population, community, and ecosystem levels of spatial, temporal, taxonomic, and functional organization (Table 3). These techniques can and have been applied to enact conservation measures, and we provide examples of how this framework could be applied.

The first level of the framework encompasses population-level techniques, which have been used extensively in marine environments primarily under the guise of fisheries management. There have also been other applications of population-level approaches to the study and conservation of marine environments, including the use of sea otters (*Enhydra lutris*) as an umbrella species, starfish (*Pisaster* spp.) as a keystone species, and eelgrass (*Zostera* spp.) as an indicator species (Paine 1966; Estes & Palmisano 1974; Table 4).

The second level in the ecological framework is the community. Although conservation at the community-level may require more knowledge of structure and process than at the population level, community level approaches are considered more robust because the conservation of an environment does not rest on a few key species (Simberloff 1998). Community-level approaches to conservation have been applied in all marine environments, but predominantly to the benthos (Thorsen 1957; Augier 1982; Table 4).

Many studies have combined ecosystem structure and process with community and/or population approaches to build a biophysical framework of a community and its abiotic environment. Ecosystem structure and process are integral parts of this type of analysis to determine which biotic or abiotic variables or combinations of variables can be used to conserve biodiversity. Included in this community-ecosystem approach are studies that relate community composition to what is often termed habitat. For the purposes of this framework, habitat is the combination of ecosystem structures and processes listed in Table 3 which supports a recognizable community. This combined approach has been used extensively in the intertidal zone, where community and ecosystem data have been used to develop "biotopes" or "habitat types" (Menge 1992; Connor 1997; Table 4).

The third and final level in the ecological framework is the sole use of ecosystem structure and process to achieve conservation ends. The advantages of this approach are that ecosystem structure and process are relatively easy to observe and monitor, often indicate the presence of large areas of productivity or diversity (e.g., upwellings or anomalies), and often can be correlated with biological communities. This approach has been advocated by Hayden et al. (1984) to classify coastal environments and by Caddy and Bakun (1994) to classify marine catchment basins (Table 4).

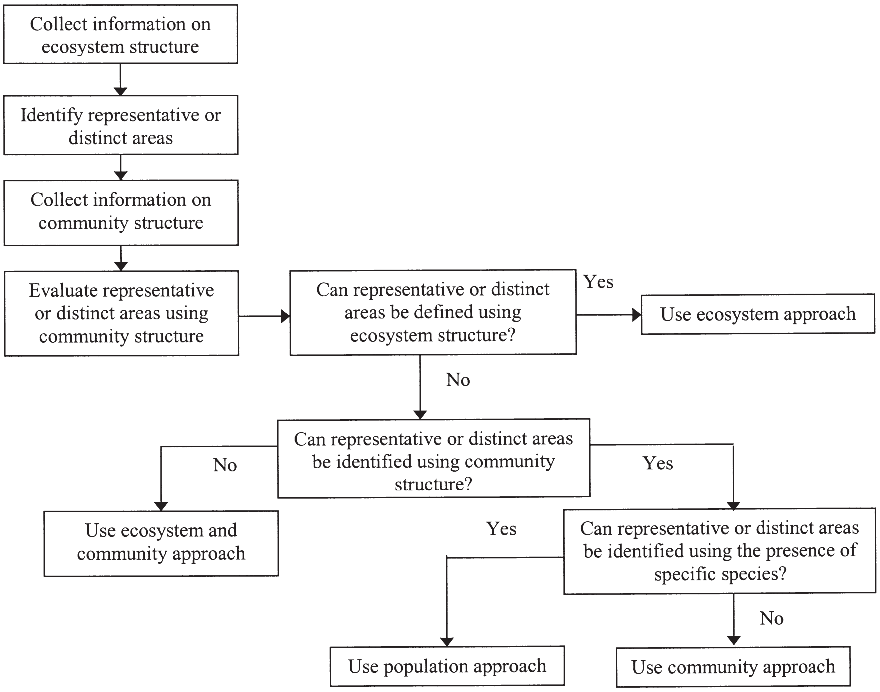

Figure 1. An approach to decision making in marine conservation if new information is to be collected. The approach could also be applied in areas with existing comprehensive abiotic and biotic datasets.

Although marine conservation efforts vary depending on the objectives and environments under consideration, one possible opportunity to apply the framework for conserving biodiversity is when new data are to be collected (Fig. 1). A second approach applies the framework using existing data (Fig. 2).

If a new study is planned and new data are to be collected, ecosystem data are often the easiest to obtain (Fig. 1). Because many conservation strategies are based on the identification of representative and/or distinct areas, ecosystem structure can be used to initially identify these areas (Fig. 1). To assess the validity of the representative and distinct areas generated from the ecosystem data, data on community structure can be collected to compare community-defined boundaries with ecosystem-defined boundaries. If ecosystem structure can be used to identify ecologically relevant representative and distinct areas, then ecosystem structure alone can be used to direct conservation efforts. If defining representative and distinct areas cannot be achieved using ecosystem structure, then community structure may be used to define representative or distinct areas. If community structure can be used to identify representative or distinct areas, then population approaches could be used because the collection of data on certain species requires less effort than the collection of data for the entire community. If neither community nor ecosystem structure is applicable, then a combination of the two approaches could be applied. For example, representative and distinct ecosystem structures, in the form of substrate, depth, and relief can be sensed remotely by acoustic methods. If for some reason, such as excessive

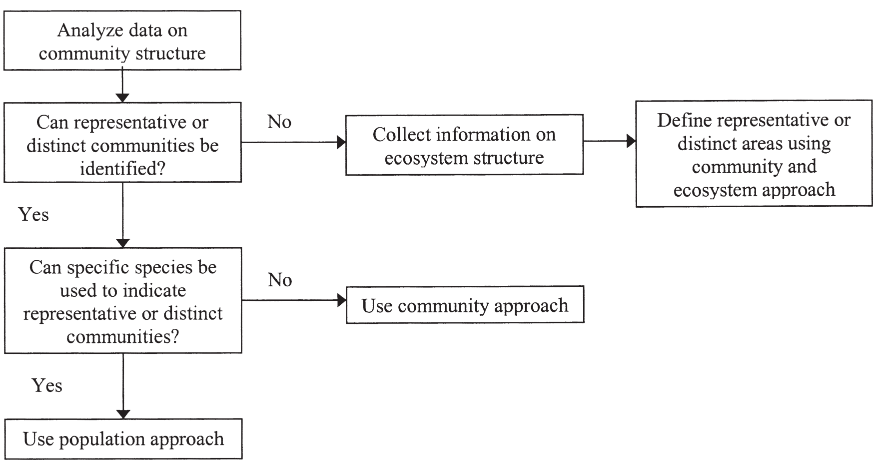

Figure 2. An approach to decision making in marine conservation if existing information is to be used. This approach assumes that the majority of existing data are biological in nature (e.g., catch statistics or trawl data).

depth or spatial heterogeneity, these ecosystem data cannot identify representative and or distinct areas, then data on community types could be collected by a variety of means, including grab sampling, diving, or remote video. These community data could also be used to identify representative and distinct areas, although the level of effort required to obtain this information is generally higher than ecosystem efforts. An analysis of the community data may suggest that the identification of only a few key species is required to identify representative and distinct areas, so a population-level approach can be utilized. Finally, both ecosystem and community data may be needed to address deficiencies in each method and properly identify representative or distinct areas.

If existing data are to be used, most efforts will begin at the community level (Fig. 2). Because most marine data have been collected at the community level (e.g., fishery catch statistics or trawl surveys), conservation efforts using existing data are often forced to begin here. One of the first objectives is to analyze existing data on community structure to determine whether representative or distinct communities can be identified. If this is possible, then population-level techniques could be applied to determine whether single species approaches (indicator, keystone, umbrella species) could be applied. If representative or distinct areas cannot be identified by means of community structure, then data on ecosystem structure need to be collected and both community and ecosystem structure used to identify these areas.

Conclusions

The hierarchical framework we present is a useful tool in understanding the relationships between structure and process and how these relationships change among the population, community, and ecosystem levels of organization. This knowledge can then be used to assess the various conservation options for marine environments and to assess how a conservation program might be structured given the type of marine environment under study. This framework can also be used to provide options regarding which components of marine biodiversity can be observed, measured, or applied to the modeling, inventory, or monitoring of marine environments. Now that an overall codification of approaches to marine conservation has been proposed, in future communications we will explore the advantages of the various possible approaches at the population, community, and ecosystem levels.

Literature Cited

Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications **8** (supplement 1): 79–92.

Augier, H. 1982. Inventory and classification of marine benthic biocoenoses of the Mediterranean. Nature and environment series 25. Council of Europe, Strasbourg, France.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill, New York.

Caddy, J. F., and A. Bakun. 1994. A tentative classification of coastal marine ecosystems based on dominant processes in nutrient supply. Ocean and Coastal Management **23:**201–211.

Connor, D. W. 1997. Marine biotope classification for Britain and Ireland. Joint Nature Conservation Review, Peterborough, United Kingdom.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. FWS/OBS-79/31. U.S. Fish and Wildlife Service, Washington, D.C.

Dauvin, J. C., G. Bellan, D. Bellan-Santini, A. Castric, J. Comolet-Tirman, P. Francour, F. Gentil, A. Girard, S. Gofas, C. Mahe, P. Noel, and B. de Reviers. 1994. Typologie des ZNIEFF-Mer. Liste des parameters et des biocoenoses des cotes francaises metroplitaines. Collection patrimoines naturels. Volume 12. Secretariat Faune-Flore Museum National d'Histoire Naturelle, Paris.

Dethier, M. N. 1992. Classifying marine and estuarine natural communities: an alternative to the Cowardin system. Natural Areas Journal **12(2):**90–99.

Dolan, R., B. P. Hayden, G. Hornberger, J. Zieman, and M. Vincent. 1972. Classification of the coastal environments of the world. The Americas. Technical report 1. Office of Naval Research, Geography Programs, University of Virginia, Charlottesville.

Ekman, S. 1953. Zoogeography of the sea. Sidgwick & Jackson, London.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role and structuring nearshore communities. Science **185:**1058–1060.

Franklin, J. F., K. Cromack, W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas fir forests. General technical report PNW-118. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Glemarec, M. 1973. The benthic communities of the European north Atlantic continental shelf. Oceanography and Marine Biology Annual Review **11:**263–289.

Hayden, B. P., G. C. Ray, and R. Dolan. 1984. Classification of coastal and marine environments. Environmental Conservation **11(3):** 199–207.

Hesse, R., W. C. Allee, and K. P. Schmidt. 1951. Ecological animal geography. Wiley, New York.

Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, New York.

Launer, A. E., and D. D. Murphy. 1994. Umbrella species and the conservation of habitat fragments: a case of threatened butterfly and a vanishing grassland ecosystem. Biological Conservation **69:** 145–153.

Mann, K. H., and J. R. N. Lazier. 1996. Dynamics of marine ecosystems: biological-physical interactions in the oceans. Blackwell Science, London.

May, R. M. 1992. Biodiversity: bottoms up for the oceans. Nature **357:** 278–279.

Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores. Ecology **73:**755–765.

Metaxas, A., and R. E. Scheibling. 1996. Top-down and bottom-up regulations of phytoplankton assemblages in tidepools. Marine Ecology Progress Series **145:**161–177.

National Research Council. 1995. Understanding marine biodiversity. Washington, National Academy Press, Washington, D.C.

Niemi, G. A., J. M. Hanowski, A. R. Lima, T. Nichols, and N. Weiland. 1997. A critical analysis on the use of indicator species in management. Journal of Wildlife Management **61:**1240–1251.

Norse, E. A., K. L. Rosenbaum, D. S. Wilcove, B. A. Wilcox, W. H. Romme, D. W. Johnston, and M. L. Stout. 1986. Conserving biological diversity in our national forests. The Wilderness Society, Washington, D.C.

Noss, R. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology **4:**355–364.

Nybakken, J. 1997. Marine biology: an ecological approach. Addison Wesley Longman, New York.

Office of Technology Assessment. 1987. Technologies to maintain biodiversity. U.S. Government Printing Office, Washington, D.C.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100:**65–75.

Peres, J. M., and J. Picard. 1964. Nouveau manel de bionomie de la mer Mediterranee. Recl. Trav. Stn mar. Endoume, Bull. **31(47):**1–147.

Pielou, E. C. 1979. Biogeography. Wiley-Interscience, New York.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science **235:**167–171.

Sherman, K. L., M. Alexander, and B. D. Gold, editors 1980. Large marine ecosystems: patterns, processes, and yields. American Association for the Advancement of Science, Washington, D.C.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biological Conservation **83:**247–257.

Thorsen, G. 1957. Bottom communities (sublittoral or shallow shelf). Memorandum of the Geographical Society of America **67:**461–534.

Weaver, J. C. 1995. Indicator species and scale of observation. Conservation Biology **9:**939–942.