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Quantifying Coral Reef Ecosystem Services

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Chapter 6

1
Coral Reefs: Introduction and Overview

1.1 Quantifying coral reef ecosystem services

Coral reefs have been declining during the last four decades as a result of both local and global anthropogenic stresses (MEA 2005). In response, governments, nongovernmental organizations (NGOs), and academia initiated numerous research efforts to elucidate the nature, causes, magnitude, and potential remedies for the decline. This work has led to the widely-held belief that the recovery of coral reefs is unlikely if public and private sector decisions that affect coral reefs continue to ignore the economic value of the goods and services provided by these ecosystems (MEA 2005). If this perception is correct, successful conservation will, in most instances, require that environmental benefits (or, ecosystem services) are routinely included in economic and social decisions (Pearce & Turner 1990; Pearce & Moran 1994; Daily et al. 1997; Turner et al. 2003; Chee 2004; Boyd & Banzhaf 2007; Turner 2010). However, this approach presupposes knowledge of what the ecosystem services are, what their magnitudes and values are, what ecosystem characteristics provide them, how those characteristics are affected by human activities, and how human activities may affect the future provision of ecosystem services. With this knowledge, decisionmakers could have access to a more complete characterization of the consequences of different policy options.

Table 1-1. Economic benefits provided by coral reefs

A. Direct extractive uses	B. Direct nonextractive uses
1. Commercial fishing	1. Scuba diving
2. Subsistence fishing	2. Snorkeling
3. Aquarium fish	3. Boating
4. Sport fishing	4. Pharmaceutical chemicals
5. Coral jewelry	5. Nonpharmaceutical natural products
6. Pharmaceutical harvesting	
7. Nonpharmaceutical harvesting	
C. Indirect uses	**D. Nonuse values**
1. Fish habitat	1. Existence value
2. Nutrients	2. Cultural value
3. Reduced flooding	3. Option value
4. Less storm damage	4. Quasi-option value
5. Fewer deaths from storms & flooding	5. Bequest value
6. Reduced erosion from storms & flooding	6. Instrumental value
7. Mangrove & seagrass protection	7. Intrinsic value
8. Sealife nursery protection	8. Scientific value
9. Global life support	9. Scarcity value

Source: Beaumont *et al.* 2008; Burke *et al.* 2008; Cesar 2002; Cesar & Chong 2005; David *et al.* 2007; Ghermandi *et al.* 2009; Moberg & Folke 1999; Naber *et al.* 2008; Nunes *et al.* 2009; Remoundou *et al.* 2009; Spurgeon 1992.

The ecosystem services in Table 1-1 are organized in categories normally used for valuation purposes. The services can also be organized according to their ecological role, an approach used in the Millennium Ecosystem Assessment (MEA 2005). The MEA used four categories: provisioning, regulating, cultural, and supporting. Coral reefs, with high species diversity and topographically complex habitat, are valued in all categories (McKinney 1998). *Provisioning services* include food (fish and invertebrates), materials for construction (sand and coral blocks), pharmaceutical and cosmetic compounds (bio-mining), jewelry, curios, and ornamental fish. *Regulating services* include land accretion and shoreline protection from waves and currents (which allows growth of seagrass and mangrove communities), and carbon sequestration. Major *cultural services* include recreation and tourism; in addition, coral reefs provide coastal communities an inherent sense of place. Sometimes less obvious are the *supporting services* of coral reefs, such as sand for beach formation, biological primary and secondary production, and biological diversity.

The economic value of some of these services (*e.g.*, commercial fishing) are established in markets, while others have nonmarket values for local, state/regional, and national/international segments of the population (Table 1-2).

Table 1-2. Market and nonmarket value estimates for selected ecosystem services at local, state/regional, and national/international levels [small (+), moderate (++), or high (+++)]

Ecosystem Service*	Sector	Local	State	National
Tourism	Market	+++	+	+
	Nonmarket	+	+++	+++
Recreation	Market	+	+	+
	Nonmarket	++	—	—
Commercial Fisheries	Market	+	++	++
	Nonmarket	—	—	—
Shoreline Protection	Market	—	—	—
	Nonmarket	++	++	++
Non-Use Existence Value	Market	—	—	—
	Nonmarket	++	++	++
Biodiversity	Market	++	+	+
	Nonmarket	+	+++	+++

* Tourism and recreation include snorkeling, diving, fishing, and viewing in reef areas; commercial fisheries include spiny lobsters, shrimp, finfish, and aquarium fish; shoreline protection is based on damage avoided from storms; nonuse existence value is based on what people are willing to pay to conserve coral reefs; biodiversity has both market value (*e.g.,* potential pharmaceutical products) and nonmarket value (existence value).

Source: EPA (2009)

An estimated 173,488 km^2 of coral reefs exist in U.S. jurisdictions widely distributed across the Pacific Ocean, western Atlantic Ocean, Caribbean Sea and Gulf of Mexico (Figure 1-1, Table 1-3) (Rohmann *et al.* 2005; Waddell 2005, p. 8). This is roughly the areal extent of the State of Florida. Nearly 12 million people in these jurisdictions directly benefit from shoreline protection, recreation, subsistence fishing, and sense of place provided by reefs. Some of them owe their livelihood to the services provided by coral reefs. Others worldwide benefit from tourism, commercial fishery harvests, pharmaceutical products, jewelry, and non-use services such as natural beauty and biodiversity. Many of these beneficiaries contribute to the success of non-governmental organizations (*e.g.,* The Nature Conservancy (TNC), Coral Reef Alliance, Reef Relief, Reef Environmental Education Foundation (REEF), and the World Wildlife Fund (WWF)) in raising money for protection of coral reefs, and in supporting actions by the U.S. Government to establish and fund the interagency Coral Reef Task Force, National Marine Sanctuaries, National Parks, local action strategies, and legislation (*e.g.,* Coral Reef Conservation Act) for protection of coral reefs.

There is an urgent need to manage coral reefs and coastal zones differently. Over the past two decades, there have been precipitous declines in coral reefs (Waddell & Clark 2008), despite their widely held status as highly valued and highly important ecosystems. An estimated 19% of the world's reefs have been lost in the last 30 years, 15% are threatened with loss by 2030, and another 20% with loss by 2050 (Wilkinson 2008). Many of the causes of this decline are well known. Stony corals (*Scleractinia* spp.), which provide the calcareous reef infrastructure, are suffering worldwide from massive bleaching (resulting from the loss of symbiotic algæ) and higher than normal mortality. The most common trigger for bleaching events is elevated sea surface temperatures. Also at the global level, increasing seawater acidity from elevated atmospheric CO_2 is slowing the calcification processes responsible for coral growth and repair. At local scales (Figure 1-2), corals are under chronic assault from fishing and land use practices that release sediments, nutrients, toxic contaminants, and potentially pathogenic microorganisms into the reef environment.

The loss or impairment of coral reefs directly results in the reduction or loss of ecosystem services provided by the reefs to humans. When reef-building stony corals die, they become covered in algæ and other organisms that eventually erode the remnant skeletons. Unfortunately, coral reefs are among the few marine environments to exhibit disturbance-induced phase shifts (akin to "tipping points") in which lush, complex coral communities dominated by reef-building stony corals are transformed relatively quickly into "biologically impoverished wastelands overgrown with algæ" (Bellwood *et al.* 2004; Work *et al.* 2008). As coral skeletons erode and crumble, reefs lose the highly complex ecological and physical architectures that provide shelter and resources for the uniquely abundant and diverse reef biota. The loss of the reefs' physical structure (such as that currently being experienced in the Caribbean) is referred to as "flattening" (*i.e.,* losing topographic complexity) (Alvarez-

Filipi *et al.* 2009). This term would also be appropriate to describe the loss of ecological structure and biodiversity that make these ecosystems so valuable to humans. Inevitably, these losses will adversely affect human well-being.

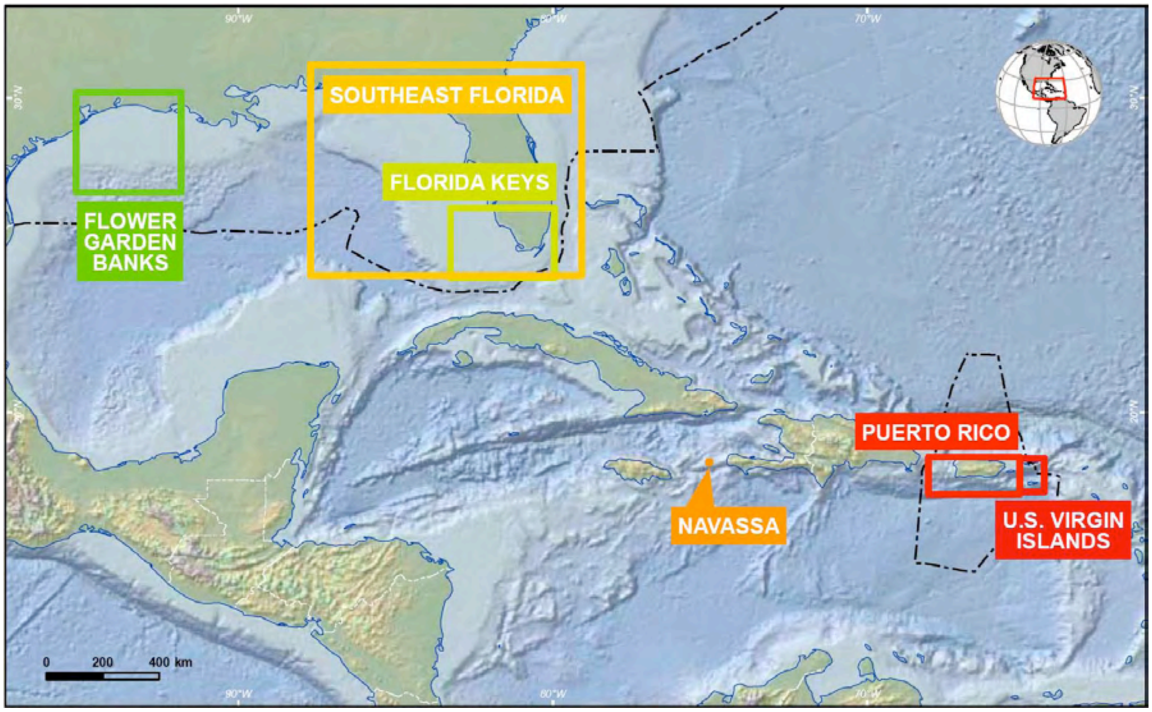

Figure 1-1a. **U.S. jurisdictions with coral reefs. The Atlantic Ocean, the Caribbean Sea, and the Gulf of Mexico.** (figure from Waddell & Clarke 2008, p. 10)

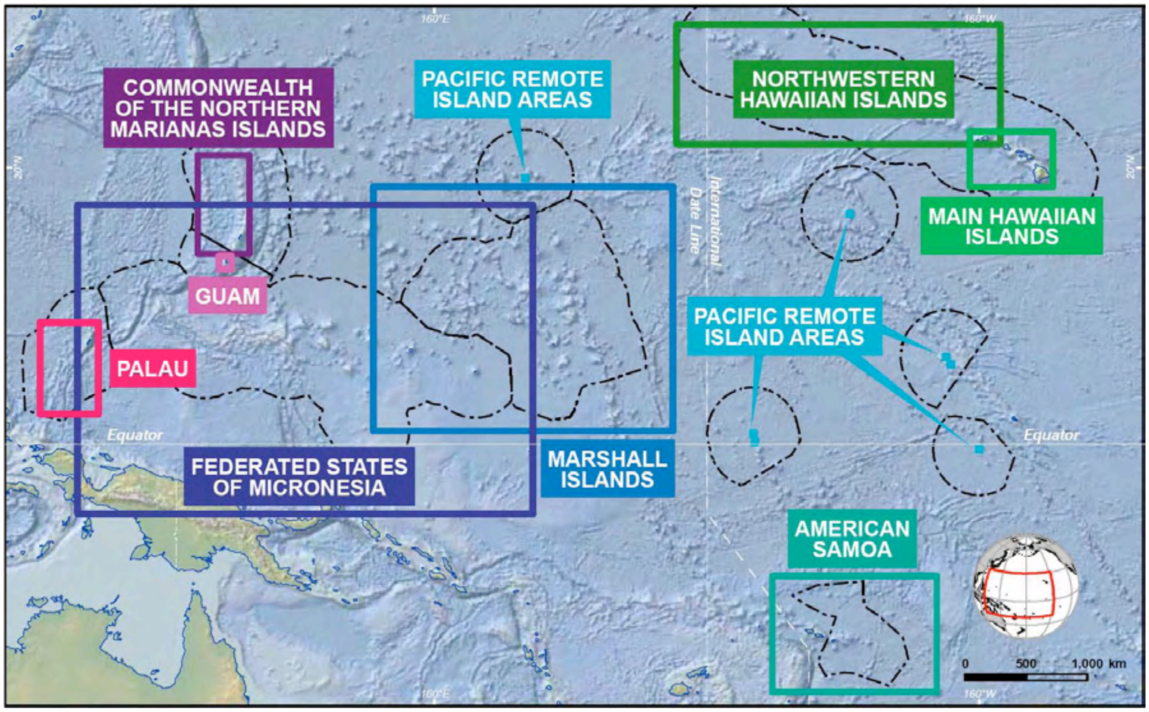

Figure 1-1b. U.S. jurisdictions with coral reefs. The Pacific Ocean. (Waddell & Clarke 2008, p. 12)

Table 1-3. Areal extent estimates for potential shallow water coral reefs inside 10 fathom (18 m) and 100 fathom (183 m) depths and local populations that benefit from coral reefs

U.S. Jurisdiction	Reef Area (km^2)		Population
	<10 fathoms[a]	<100 fathoms[a]	
Florida[b]	30,801	113,092	5,213,884[c]
Puerto Rico[d]	2,302	5,501	3,971,020[e]
U.S. Virgin Islands[f]	344	2,126	109,825[e]
Navassa Island	3	14	0
Flower Gardens NMS[g]	0	164	0
Main Hawaiian Islands[h]	1,231	6,666	1,283,388[i]
Northwestern Hawaiian Islands (NWHI)[j]	1,595	13,771	0
American Samoa[k]	55	464	65,628[e]
Pacific Remote Islands[l]	252	436	100[e]
Northern Mariana Islands (CNMI)[m]	124	476	86,616[e]
Guam	108	276	178,430[e]
Marshall Islands	13,456[n]	13,456[n]	64,522[e]
Federated States of Micronesia	14,517[n]	14,517[n]	107,434[e]
Palau	2,529[n]	2,529[n]	20,796[e]
Total	**67,317**	**173,488**	**11,774,315**

a Areas estimated from NOAA nautical charts except for the Marshall Islands, the Federated States of Micronesia, and the Republic of Palau, which were estimated from Landsat satellite imagery of shallow waters (<15 m).

b Florida corals extend along the Atlantic Ocean coast of Florida to Jupiter Inlet, Florida and along the Gulf of Mexico coast of Florida to Tarpon Springs, Florida.

c 2007 estimate for five coastal counties: St. Lucie, Martin, Palm Beach, Broward, Miami-Dade and Monroe counties. Total population of Florida is 18,251,243 (Census Bureau 2010).

d Puerto Rico includes the islands of Puerto Rico, Desecheo, Culebra, Vieques, and Mona.

e Projected 2009 population (CIA 2010)

f The U.S. Virgin Islands includes the islands of St Thomas, St John, and St Croix.

g The NOAA nautical chart depicts only the 100 fathom depth curve for this location.

h The Main Hawaiian Islands includes the islands of Hawaii, Maui, Molokai, Lanai, Kahoolawe, Oahu, Kauai, and Niihau.

i 2007 estimate (Census Bureau 2010)

j The NWHI includes the islands and atolls of Nihoa, Necker, French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan, Lisianski, Pearl and Hermes, Midway, and Kure. Numerous shallow-water seamounts, such as St. Rogatein Bank or Raita Bank, also are located in the NWHI.

k American Samoa includes the islands of Tutuila, Ofu, Olosega, Tau, Swains, and Rose Atoll.

l The Pacific Remote Islands include Howland, Baker, and Jarvis Islands, Palmyra, Johnston, and Wake Atolls, and Kingman Reef.

m The CNMI includes the islands of Rota, Aguijan, Tinian, Saipan, Farallon de Medinilla, Anatahan, Sarigan, Guguan, Alamagan, Pagan, Agrihan, Asuncion, Maug, and Farallon de Pajaros.

n Unpublished estimates of potential coral ecosystem area visible in Landsat satellite imagery. Area estimates generally include seafloor features visible in water 18–27 m (10–15 fathoms) deep. NOAA does not produce nautical charts of these locations.

Source: Rohmann *et al.* (2005); Waddell (2005, p. 8).

The Ecosystem Research Program (ESRP) is a concerted research effort within the U.S. Environmental Protection Agency (EPA) Office of Research and Development (ORD) to better incorporate consideration of ecosystem services in decision processes. The overall goal of the ESRP is to provide decision-makers information on the nature and magnitude of environmental benefits provided by ecosystems and the means to understand how policy or management choices will affect the provision of those benefits (*i.e.*, the nature and magnitude of the economic benefits [see Table 1-1 for a list of benefits and Table 1-2 for their relative magnitudes]).

Completion of research in the Coral Reef Project (CRP) is expected to advance the understanding of coral reef ecosystem services, how they are affected by human activities, and how management and policy decisions influence their delivery. If this information is incorporated into public and private decision-making and the policy analyses that precede it, the resulting decisions will undoubtedly have a firmer scientific basis and a more inclusive consideration of the benefits provided by coral reef ecosystems. This report provides a review of previous studies of ecosystem services and economic benefits provided by coral reefs and how those ecosystem services are linked to characteristics (attributes) of the reef.

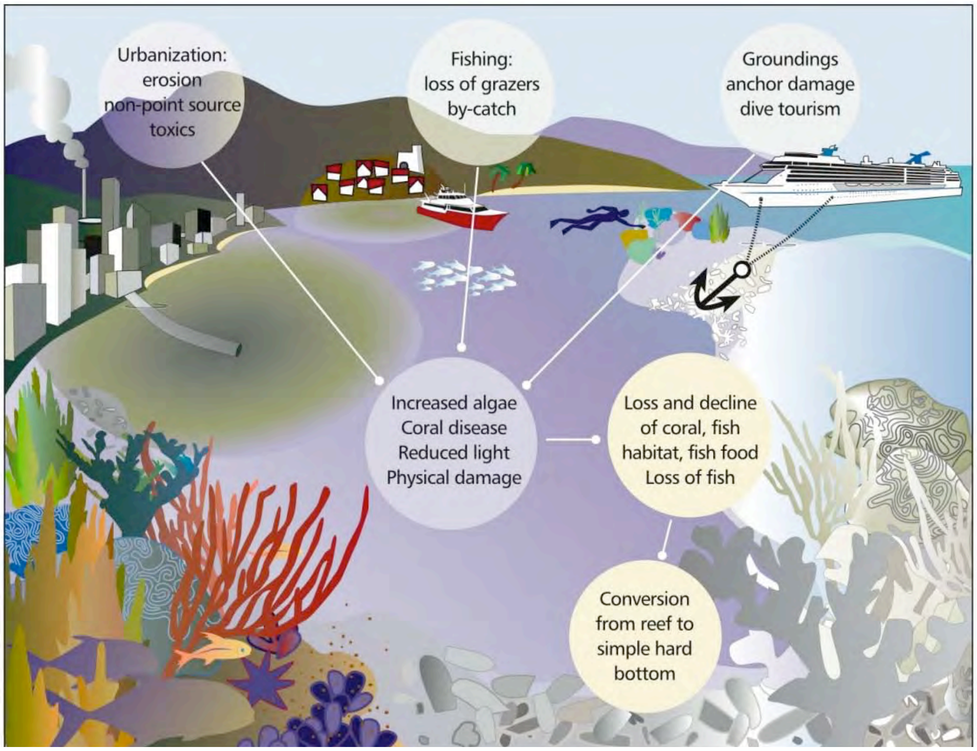

Figure 1-2. **Conceptual model of a coral reef ecosystem illustrating local effects of driving forces (urban development, industrial production, fishing, tourism), pressures (industrial effluent, sedimentation and erosion, over fishing, groundings), state (healthy coral reef on the left and degraded coral reef on the right), and impacts (loss of fish and coral species, conversion of reef habitat to rubble). Adverse impacts reduce the natural benefits and value of coral reefs unless steps are taken to reduce pressures.** (figure and caption from Bradley *et al*. 2010)

1.2 Purpose and organization

The purpose of this report is to provide an overview of the published literature with respect to three aspects of ecosystem services provided by coral reefs: (1) which services have been identified; (2) what, if any, methods were used to quantify the services; and, (3) what connections were identified between the services and the attributes of the reef. The goal is to lay the foundation for selecting research questions that, if answered, would fill gaps in our current understanding of the links between coral reef attributes and the delivery of services by the coral reef ecosystem. Ultimately, the goal is to identify coral reef indicators that can be used to estimate the quantity of ecosystem services being delivered by coral reef ecosystems and to predict the extent to which the current quantities are likely to change in the future.

1.3 Ecosystem services and economic benefits

There exists a certain imprecision prevalent in the current use of the term “ecosystem services”. Many authors tend to conflate “ecosystem services” and “economic benefits”, thereby creating a confusing logical muddle. In this report, ecosystem services are viewed as an ecological construct that creates wholly, or partially, the economic construct of economic benefits, which is the core of policymaking. Ecosystem services can always be quantified in physical terms (*e.g.*, kg of fish, board feet of lumber), but they are always linked to economic benefits, which are usually valued in monetary terms (*e.g.*, market value of fish catch or lumber). In the case of shoreline protection provided by coral reefs, the presence of the reef attenuates the energy contained in waves reaching the shoreline, and that attenuation reduces the wave-induced erosion of the shoreline and, during storms, the extent of near-shore flooding, damage to buildings and property, and danger to humans and livestock. The shoreline protection ecosystem service could be characterized as the amount of wave energy attenuation attributable to the presence of the reef, or in the case of a foregone ecosystem service, the increase in wave energy attributable to a diminishment of the reef’s size. The economic benefits from shoreline protection would be the value of the property, lives, and well-being preserved by the attenuation of the wave energy, or the value lost due to the increase in wave energy. However, the value of the economic benefit is a function of how much erosion is prevented, how much property is protected, and how many human and livestock lives are saved. Transforming energy attenuation into a physical quantification of economic benefits should be a joint exercise for scientists and economists, with the former leading the conversion modeling and the latter leading the identification of the economic benefits to be quantified, but the subsequent valuation of the benefits would be the bailiwick of economists. To determine which ecosystem services are the most important for policymaking requires working backward from the economic benefits to identify the services that created those benefits (Figure 1-3).

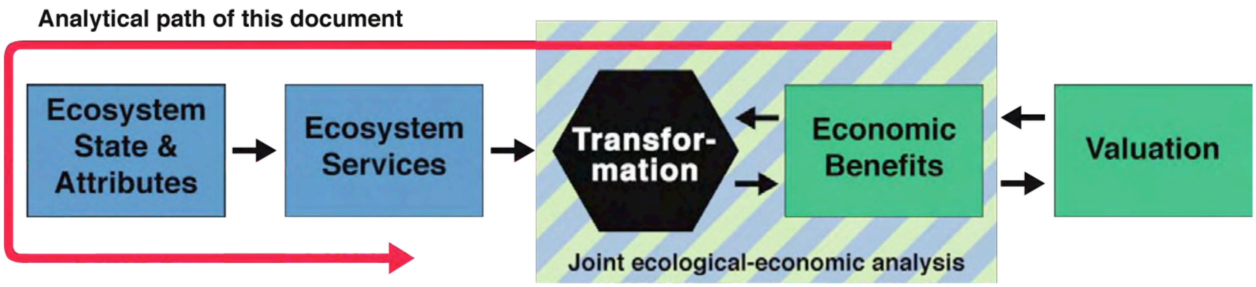

Figure 1-3. Ecosystems provide services that, in turn, provide economic benefits. Some services have a direct, one-to-one correspondence to benefits, but more commonly services have to be transformed, disaggregated, or combined to yield benefits. Services and many benefits can be quantified in physical terms; the value of benefits is usually estimated in monetary terms; services are not valued *per se*, but their importance can be inferred from the value of the benefits they create.

The journey traversed in creating this report, then, began by identifying the most valuable economic benefits arising from coral reefs, followed by an assessment of which ecosystem services contribute to those benefits. Subsequently, the literature was reviewed to find examples where these ecosystem services had been wholly or partially quantified and where the links between these services and coral reef attributes were investigated.

Identification and quantification of coral reef ecosystem services began in the 1980s (Hodgson & Dixon 1988; Mattson & DeFoor 1985; McAllister 1988; Munro & Williams 1985), followed in the early 1990s by the first unified estimates of the value of the economic benefits generated by those services. Numerous studies have estimated quantities and values for specific services and the derived benefits received from coral reefs, but fewer have done so for the whole range of coral reef services and benefits (see Pendleton [2008] and Conservation International [2008] for reviews; also see Table 1-1 references). In most cases, reefs are valued to determine or demonstrate the economic impact of a planned or implemented decision. The decision under consideration plays a role in what is quantified and how the services are valued. For example, one early coral reef study focused on the economic value of biodiversity, because the study area was an existing marine reserve established to protect biodiversity (Bakus 1983); another study approached valuation more broadly because it was intended to reinforce the creation of a Marine Protected Area in exchange for international debt reductions (David *et al.* 2007). The services valued can vary from study to study (Table 1-4), depending on the decision, the availability of information, and the expertise or insight of the authors.

Despite the wide variety of services that have been measured and valued, there are certain services that are almost always considered, because they make very significant contributions to the total economic value (TEV includes all direct and indirect use values plus all nonuse values). The values can be calculated at a global, regional, or local scale (Table 1-5).

The values reported in Table 1-5 suggest that the four most valuable economic benefits are: fisheries, natural products, shoreline protection, and tourism and recreation. This report examines each of these in a separate chapter.

Table 1-4. Examples of the variety of ecosystem services valued by previous coral reef studies

Study	Direct Use	Indirect Use	Nonuse
Spurgeon 1992	Fisheries, aquarium and curio trade, pharmaceutical, construction, tourism, research, education, social value	Biological support, physical protection, global life support, social services	Existence value, option value, intrinsic value
Berg *et al.* 1998	Tourism, mining, fishing	Coastal protection	Food security, biodiversity
Pet-Soede *et al.* 1999	Blast fishing, nondestructive fishing, tourism	Coastal protection	—
Burke *et al.* 2002	Tourism, recreation, fishing, blast fishing, poison fishing, mining	Coastal protection	Aesthetic, biodiversity
Cesar 2002	Live reef fish, mariculture, aquarium trade, pharmaceutical, tourism, recreation, research, education, aesthetic	Biological support (habitat), physical protection, carbon store	Future uses, new information, bequest value, existence value
Burke & Maidens 2004	Tourism, recreation, fishing	Coastal protection	—
MEA 2005	Food, medicines, cultural and amenity, aesthetic, recreational	Biodiversity, biological regulation, nutrient cycling, climate regulation, disease control, waste processing, flood protection, erosion control	—
Spurgeon 2006	Fisheries, tourism, recreation, mining,	Biodiversity, coastal protection, carbon storage	Intergenerational equity, existence value
Burke *et al.* 2008	Tourism, recreation, fishing	Coastal protection	—
Hicks *et al.* 2009	Fishery, cultural, research, aesthetic, recreational	Biological control, habitat/refuge, waste regulation, coastal protection	Bequest, option, and existence values

Table 1-5. Estimated annual economic impact from coral reef ecosystem services at global, regional, national, and local levels

Scale/Location	Tourism	Fisheries	Coastal Protection	Biodiversity	Carbon Storage	Ref.
Global	$9.6 billion	$5.7 billion	$9.0 billion	$5.5 billion	—	1
Caribbean	$2.1 billion	$0.3 billion	$1.5 billion	—	—	2
Indonesia	$103m	$1.221 billion	$314m	$9m	—	7
Philippines	$108m	$620m	$326m	$10m	—	7
St. Lucia	$160m–$194m	$0.5m–$0.8m	$28m–$50m	—	—	6
Tobago	$101m–$130m	$0.8m–$1.3m	$18m–$33m	—	—	6
Turks & Caicos Islands	$18.2m	$3.7m	$16.9m	$4.7m	—	8
Jamaica Portland Bight	$11m	$19m	$0.4m	$18m	$4m	3
Jamaica Montego Bay	$315m	$1.3m	$65m	$19.6m	—	4
Jamaica Montego Bay	$400m	$4m	$65m	—	—	5

References:
1: Cesar *et al.* (2003) 2: Burke & Maidens (2004) 3: Cesar *et al.* (2000) 4: Ruitenbeek & Cartier (1999)
5: Gustavson (1998) 6: Burke *et al.* (2008) 7: Burke *et al.* (2002) 8: Carleton & Lawrence (2005)

Source: Partially adapted from Conservation International (2008).

1.4 Ecological integrity, ecological resilience, and biodiversity

Ecological integrity, resilience, and biodiversity are all concepts that portray slightly different aspects of ecosystem condition but convey the same sense that the attributes, processes, and functions of an ecosystem are all integral to the ecosystem itself and necessary for sustaining it as well as its continued provision of services. These concepts represent the “glue” (Pearce & Moran 1994, p. 22; Turner *et al.* 2000) of the properly functioning ecosystem, supporting the growth of reef-building corals for shoreline protection, the presence of unique and diverse species to attract tourists, the creation of potentially useful natural products, and the maintenance of habitat and nurseries for harvestable fish stocks. Assessing the extent to which an ecosystem possesses any of these concepts provides insight into the many elements and processes that we do not know, understand, and cannot otherwise measure. The development of concise, rigorous definitions and unambiguous metrics for these three attributes continues but remains unfinished.

In choosing which topics to cover in this report, considerable thought was given to the role of ecological integrity, ecological resilience, and biodiversity. Are these economic benefits, ecosystem services, or something else? How, or should, they be included in our analysis? In the end, we decided that they were natural features rather than ecosystem services or economic benefits (see the Definitions section at the bottom of Table 6-1, page 153), and consequently should not be included in this report.

1.4.1 Ecological integrity

The Millennium Ecosystem Assessment (MEA 2005) describes supporting services as “those that are necessary for the production of all other ecosystem services”, including soil formation, photosynthesis, primary production, and nutrient cycling, among others. Some have called these “biotic services” (Moberg & Folke 1999) or “fundamental services” (Holmlund & Hammer 1999). Although called services, these could otherwise be characterized as functions of the ecosystem that ensure ecosystem persistence and resilience, which are required for the sustainable delivery of services. The same characteristics of the reef ecosystem have also been called “regulation functions” (de Groot 1992) and “primary” or “glue” value of the ecosystem (Pearce & Moran 1994, p. 22; Turner *et al.* 2000). In many respects, these are all descriptions of ecological integrity, a concept that has evolved from the stated objective of the Clean Water Act (CWA): “The objective of this Act is to restore and maintain the chemical, physical, and biological integrity of the Nation’s waters.” (CWA 1972).

Although often debated, a generally accepted definition of ecosystem integrity is:

> the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region (Frey 1975; Karr & Dudley 1981; Karr *et al.* 1986; Angermeier & Karr 1994).

Ecological integrity thus encompasses a variety of scales (genetic, taxonomic, ecological), elements (genes, species, populations, landscapes), processes (colonizations, mutations, extinctions), and a dynamic biology in terms of evolution and biogeography. Intended or not, the concept of ecological integrity appears to encompass the natural functions of an ecosystem that provide services. Ecological integrity is generally decomposed into the components described by the CWA—represented as the overlap of physical, chemical, and biological integrity (Figure 1-4). Yoder (1995) argues that the three components are not equal and that physical and chemical integrity are components of biological integrity. Regardless, many authors (*e.g.*, Turner *et al.* 2000) suggest that ecological integrity is a component that should be valued as an ecosystem service.

Healthy reefs maintain their structure and function and provide the supporting services that allow for the fulfillment of reasonable human needs through more direct provisioning of ecosystem services, such as shoreline protection, fisheries production, and recreational opportunities (McField & Richards Kramer 2007). A number of indicators have been proposed and monitored for assessing reef health (van Beukering & Cesar 2004; Healthy Reefs Initiative 2010).

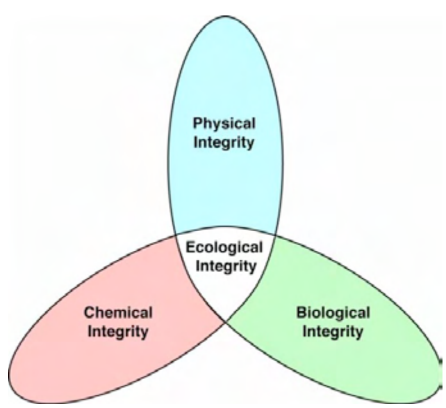

Figure 1-4. Ecological integrity as the overlap of physical, chemical, and biological integrity.

1.4.2 Ecological resilience

Ecological integrity is often equated with ecological health and ecological resilience. Although "health" is an anthropocentric concept, it implies that a stressed ecosystem is similar to a diseased individual. While use of the term is sometimes neither accurate nor precise (Ehrenfeld 1992), carefully structured definitions have been proposed using Energy Systems models (Campbell 2000). Ecological resilience—"the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks" (Walker *et al.* 2004; Folke 2006)—is a more potent concept. Moberg and Folke (1999) conclude that managing resilience is the key to maintaining delivery of ecosystem services. Clearly related to ecological integrity, resilience emphasizes the ecosystem's capacity to buffer stress and reduce rates of system change. Hollings (1973) states that ecological resilience "determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist". Ecosystem integrity and resilience are thus closely linked, but provide a few distinctions. Ecosystem integrity emphasizes a natural condition with implied stability, whereas resilience emphasizes stability with an implied natural condition.

In the case of resilience, more than one stable state can exist. When considering a single stable state, resilience is measured by the amount of time (after disturbance) required to return to the stable state (referred to as engineering resilience). When considering multiple stable states, resilience is measured by the amount of disturbance needed to shift the system to an alternative stable state (referred to as ecological resilience). This approach allows that an ecosystem can slide into a highly stable, but less desirable state—in fact, less desirable states are often extremely resilient and difficult to revert to desired conditions (Scheffer *et al.* 2000; Gunderson & Holling 2002; Walker *et al.* 2004). Reversion to a desired state is the goal of ecosystem restoration. Although ecosystem resilience is not usually considered an ecosystem service, it is similar to low ecosystem integrity in that a less desirable state is expected to provide fewer ecosystem services.

1.4.3 Biodiversity

Biodiversity is frequently cited as an ecosystem service (*e.g.*, Cesar 2002; CI 2008). Taken literally, biodiversity is simply taxa richness, which is not an ecosystem service but is an ecosystem attribute that can contribute to a variety of reef services. High biodiversity may contribute to ecological integrity, but there are many examples of natural systems with high integrity that do not exhibit high biodiversity. Biodiversity more likely plays a contributory role in ecological resilience—high species richness usually provides functional redundancy in the ecosystem, which increases resilience. If a keystone species is lost, another functionally redundant species may take its place, and the ecosystem persists in its original state.

1.4.4 Insurance value

While the preponderant view seems to be that ecological integrity, resilience, and biodiversity are not ecosystem services, a recent proposal by The Ecology and Economics of Biodiversity (TEEB) initiative combines the three concepts under the rubric of "insurance value", which is defined as "the value of ensuring that there is no regime shift in the ecosystem with irreversible negative consequences for human wellbeing" (Pascual *et al.* 2010). A similar notion put forward by Balmford *et al.* (2008) is "infrastructure value", which is the capacity of an ecosystem to maintain its provision of ecosystem services despite variability and disturbance.

The concept that ecosystem biodiversity and resilience provide insurance against a variety of uncertainties has been generally accepted for some time in the environmental economics literature. While this literature's view of insurance value has been evolving over the past 20 to 30 years, the notion that insurance value is a distinct economic nonuse benefit that can be valued is not generally accepted, because of the difficulties described below. Generally speaking, the insurance value of ecosystems is considered part of option value and quasi-option value (Pearce & Moran 1994, pp. 19-21; Pearce 2001; Weikard 2001), but our limited understanding of ecological processes precludes our being able to be sufficiently certain of ecological outcomes to move from uninsurable uncertainty to insurable risk (Pearce & Pearce 2001; Turner *et al.* 2003; Barbier 2006; Turner 2010; Abson & Termansen 2011).

In the 1990s, Pearce and Moran (1994), Perrings (1995a; 1995b; 1998), Swanson *et al.* (1994), Turner (1992), and others began describing how biodiversity and resilience might have an insurance value analogous to crop insurance, and included it as an element of option value. They took care to distinguish between the insurable risk (the probability that a known adverse outcome might occur) and the uninsurable uncertainty (wherein neither the outcome nor the probability are known) (Perrings 1995b). That biodiversity and ecological resilience provided insurance in a more general sense was recognized, but the tangled complexity of the relationship between that insurance and those "natural features" was viewed as an almost insurmountable hurdle to its proper characterization (Pearce 2004). In the past five years, Baumgärtner and colleagues have developed a more generalized and rigorous definition of insurance value (Baumgärtner 2007; Baumgärtner & Quaas 2006; Quaas & Baumgärtner 2008; Baumgärtner & Strunz 2010), but the means to measure it as a distinct value not embedded in whole or in part within other use and nonuse benefits (specifically, option value and quasi-option value) remains to be defined. The importance of viewing insurance value (or the value of any ecosystem service) in terms of the value of a marginal change rather than a lump sum value is regularly emphasized (Pearce 1998; Toman 1998; Heal 2000; Pearce & Pearce 2001), and to properly assess the value of marginal changes, ecological models must be able to predict the effect of small state changes (an ability that remains beyond our reach).

Even though our incomplete understanding of ecological functions and processes and our resulting inability to predict ecological outcomes prevent us from moving from uninsurable uncertainty to insurable risk, it may be that the inherent instability of ecosystems near thresholds (or, tipping points) may preclude a quantification of the insurance value. Though these limitations suggest that insurance value may be best characterized in qualitative terms (Fromm 2000), insurance value remains a powerful and tangible concept that should be included in any ecological assessment.

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2
Coral Reefs: Tourism and Recreation

Tourism is one of the most important economic sectors worldwide and few environments are more important for tourism and recreation than coastal zones.
(Moreno & Amelung 2009)

2.1 Describing the service

2.1.1 Definitions

It is important to understand the terms "tourism" and "recreation", particularly in the context of ecological economics.

Webster defines recreation as "refreshment of strength or spirits after work; also: a means of refreshment or diversion" (Merriam-Webster 2010). Recreational activities are enjoyed by both tourists and residents of a given geographic location. However, the common practice of economists is to differentiate between tourism and recreation based upon the source of demand.

Tourists: people who "travel to and stay in places outside their usual environment for more than twenty-four (24) hours and not more than one consecutive year for leisure, business and other purposes not related to the exercise of an activity remunerated from within the place visited" (UNWTO 1995).

Residents: people who live at a particular place for a prolonged period (Leeworthy 2002; Princeton WorldNet Glossary 2010a).

2.1.2 Tourism and the economy

Tourism is a significant sector of the global economy. According to the UN World Tourism Organization, tourism has become one of the largest and fastest growing economic sectors in the world—as much as 30% of the world's exports of commercial services and 6% of overall exports of goods and services are due to tourism. Globally, tourism ranks fourth after fuels, chemicals, and automotive products in exports. For many developing countries, it is a main income source and the number one export category (UNWTO 2009).

According to Goeldner and Ritchie (2009), global travel and tourism in 2011 is expected to account for:

- $7.0 trillion of economic activity
- 260 million jobs

The travel and tourism industry accounts for 24% of all U.S. service exports and 8% of total U.S. exports. Tourism is our nation's third largest retail industry and the nation's largest service export. There are currently more than 7m Americans employed directly in the travel industry, 9 million indirectly, for a total of over 16m jobs. In 29 states, tourism is the first, second, or third largest employer (Goeldner & Ritchie 2009; Table 2-1).

Congress passed "The Travel Promotion Act of 2009", which highlights the importance of travel and tourism to our national economy. The act creates a public-private partnership—the Corporation for Travel Promotion—to help bring more international visitors to the United States (Sánchez 2010).

Table 2-1. Economic impact of travel and tourism (2009 preliminary data)

Travel expenditures*	$704.4 billion
Travel-generated payroll	$186.3 billion
Travel-generated tax revenue	$113.0 billion
Travel trade surplus	$22.0 billion
Travel-generated employment (direct)	7.4m jobs
Travel-generated employment (indirect)	9m jobs

* includes spending by domestic and international travelers in the U.S. on travel related expenses (*i.e.*, transportation, lodging, meals, entertainment & recreation, and incidental items)

Source: Goeldner & Ritchie (2009); U.S. Travel Association (2010)

Tourism demand is strongly dependent on the economic conditions in major generating markets. Discretionary income is particularly dependent upon economic conditions. Tourism tends to account for a relatively large part of discretionary income, particularly in emerging economies. And most significantly, "the growth of international tourism arrivals significantly outpaces growth of economic output as measured in Gross Domestic Product (GDP)" (UNWTO 2010).

Marine tourism is the industry sector relevant to coral reef ecosystems. Orams (1999) provides a working definition for marine tourism: "Marine tourism includes those recreational activities that involve travel away from one's place of residence and that have as their host or focus the marine environment (where the marine environment is defined as those waters that are saline and tide-affected)." This definition excludes business or work-related activities such as commercial fishing, shipping, oil exploration, and scientific research.

The definition includes activities that have as their focus the marine environment such as shore-based fishing, land-based whale-watching, or reef walking (Orams 1999). It also includes marine tourism development (accommodation, restaurants, food industry, and second homes) and the infrastructure supporting marine development (*e.g.*, retail businesses, marinas, and activity suppliers) (Hall 2001).

2.1.3 Tourism and recreation activities related to coral reefs

Coral-reef based tourism and recreation is a subset of marine tourism. Leeworthy and Wiley (2001) provide estimates for a comprehensive list of coastal and marine recreational uses. Recreational activities on or associated with coral reefs include:

- Scuba diving
- Underwater photography
- Viewing nature and wildlife
- Surfing
- Snorkeling
- Recreational (sport) fishing
- Beach sunbathing
- Collecting objects (*e.g.*, dead shells, fragments of corals, driftwood)

2.1.3.1 Recreational (scuba) diving

Scuba diving is a type of diving that uses Self-Contained Underwater Breathing Apparatus (SCUBA) equipment for the purpose of leisure and enjoyment.

The first documented underwater diving took place in 500 BC, when Scyllis demonstrated the practical use of breath-hold diving by performing military exploits for the King of Persia. In the 1600s, dive bells were invented, with air being pumped in from the surface. In the 19th century, Bert and Haldane researched the effects of water pressure on the body, and began to define safe limits for compressed air diving. Also in the 19th century, improvements in technology (*e.g.*, compressed air pumps, carbon dioxide scrubbers, regulators, etc.) made it possible for people to stay under water for long periods, although still using surface air (Martin 1997).

But it was not until the 20th century, with the invention of SCUBA, that recreational diving was really possible. Further developments in technology have reduced the cost of training and equipment. Swim fins, masks, dive computers and other scuba gear are available and affordable (Freeland 2010). Today, scuba diving is well regulated, with internationally governed training programs and a code of conduct (Basiron 1997).

Scuba diving has become a popular leisure activity and globally, there are many locations that derive significant income from scuba diving tourists. Recreational diving is an industry that is dependent upon the condition of the underwater resources. Certain types of features make an interesting dive, and most of these are found on coral reefs including:

- Wildlife at the site (e.g., coral, sponges, fish, rays, mollusks, cetaceans, sharks and crustaceans).
- Complex topography of the site (e.g., coral reefs, drop offs).
- Historical or cultural items at the site (e.g., ship wrecks, aircraft) provide both historical value and form artificial habitats for marine fauna.
- Good underwater visibility. Poor visibility is caused by particles in the water, such as mud, sand and sewage.
- Temperature. Warm water diving is comfortable and convenient.

The growth in recreational scuba diving can be measured by analyzing the increase in Professional Association of Dive Instructors (PADI) diver certifications (Figure 2-1).

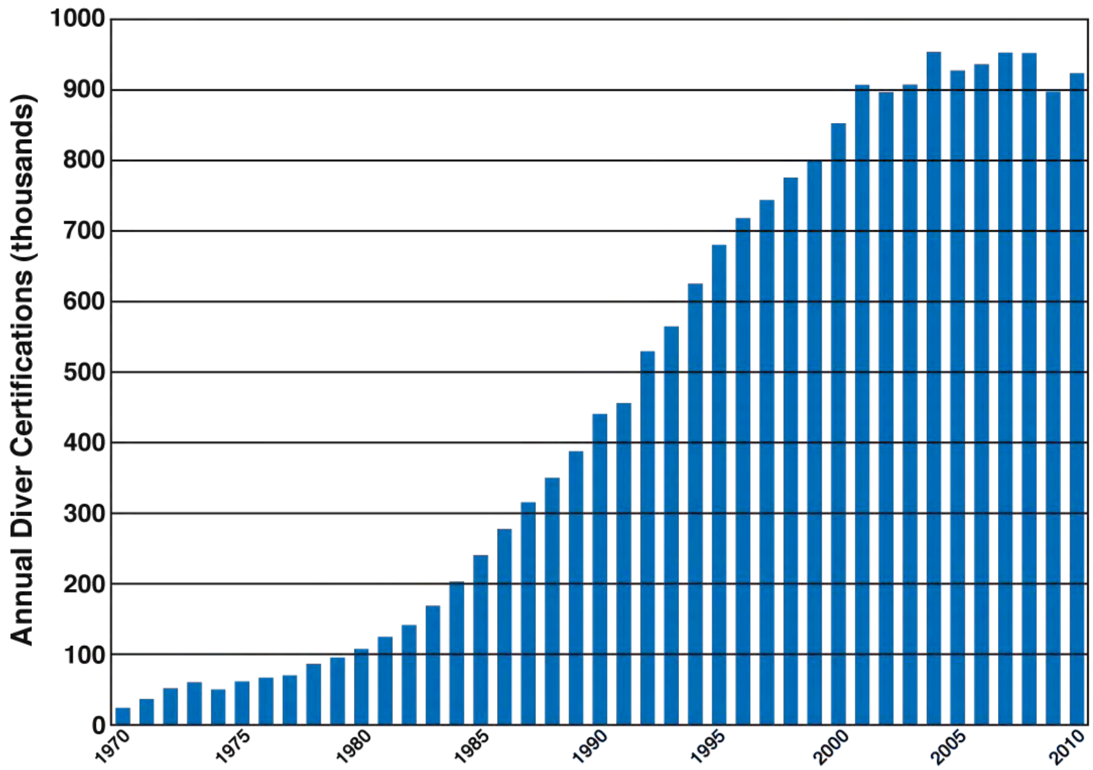

Figure 2-1. Annual diver certifications by the Professional Association of Dive Instructors (PADI).
Source: PADI 2011

2.1.3.2 Snorkeling

Snorkeling is the practice of swimming while equipped with a diving mask, a shaped tube called a snorkel, and fins. A wetsuit may also be worn in colder waters. Snorkel equipment allows the snorkeler to observe underwater attractions for extended periods of time with relatively little effort and minimal cost.

The earliest documented snorkeling dates back to 3000 BC, when sponge farmers in Crete used hollow reeds to allow them to breathe while diving under water (Snorkeling 2010). Leonardo da Vinci is credited with inventing the first modern snorkel, a hollow breathing tube attached to a leather diver's helmet. Advancements in plastic and rubber in the 20th century greatly improved the construction of snorkels, masks and fins.

While snorkeling is possible in almost any body of water, snorkelers prefer locations where there are minimal waves, warm water, and something particularly interesting to see near the surface. Coral reefs are particularly attractive to snorkelers because they:

- occur in calm, warm waters;
- are populated with visually attractive biota (e.g., corals, sponges, brilliantly colored fish, turtles);
- have clear waters providing high visibility;
- often have sunken ships and other historical artifacts nearby; and,
- may have designated snorkeling areas (reducing conflicts with boats and fishers).

2.1.3.3 Underwater photography

Underwater photography is the process of taking photographs while scuba diving, snorkeling, or swimming. The first documented underwater color photograph was taken off the Florida Keys in 1926 by Dr. William Longley and *National Geographic* staff photographer Charles Martin. Their equipment included cameras encased in waterproof housing and pounds of highly explosive magnesium flash powder for underwater illumination (*National Geographic* 2010).

Since then, underwater photography has evolved considerably. Today there are options that fit almost any budget, ranging from simple point-and-shoot disposable cameras to sophisticated single lens reflex (SLR) cameras (Gilbert & Alary 2010). Digital technology has further accelerated the evolution of underwater photography, eliminating the constraints associated with film (*e.g.*, waiting to get film developed and toxic chemicals used in developing film). Today most underwater photographers are able to capture images digitally that would have been considered "ground breaking" in the film era (Yonover 2010).

The goal of underwater photography is to bring back an image that will inform, entertain or educate. Attributes that contribute to good underwater photographs include:

- Clear water. If the water is not clear, underwater pictures will not be either.
- Colorful fish, corals and other biota.

2.1.3.4 Recreational (sport) fishing.

Recreational fishing, fishing for pleasure or competition, is included as a component of tourism and recreation. Commercial fishing (*i.e.*, fishing for profit) and subsistence fishing (*i.e.*, fishing for survival) are covered in the following chapter on fishing.

Many common salt water game fish spend some portion of their lives in coral reef ecosystems including tarpon, shark, bonefish, permit, sailfish, marlin, bonito, pompano and mackerel. Historically, sport fishers, even if they did not eat their catch, almost always killed them to bring them to shore to be weighed or for preservation as trophies. To protect recreational fisheries, sport fishermen now often catch and release or tag and release, which involves fitting the fish with identity tags, recording vital statistics, and sending a record to a government agency.

Recreational fishing is governed by a variety of conventions, rules, licensing restrictions and laws that typically restrict sportfishing to hook, line, rod and reel rather than with nets or other aids.

Recreational fishing is big business, generating more than $125 billion in economic output and more than one million American jobs. At nearly 40 million, more Americans fish than play golf (24.4 million) and tennis (10.4 million) combined. If fishing were ranked as a corporation, it would be 47 on the 2007 Fortune 500 list of America's largest companies based on total sales (Allen & Southwick 2008).

The recreational fishing industry consists of enterprises such as the manufacture and retailing of fishing tackle, the design and building of recreational fishing boats, and the provision of fishing boats for charter and guided fishing trips. The American Sportfishing Association (ASA) is the sportfishing industry's trade association, committed to looking out for the interests of the entire sportfishing community (ASA 2010).

While recreational fishing is possible in almost any body of water, sport fishermen prefer locations where there are minimal waves (calm water). Coral reefs are particularly attractive to recreational fishers because they:

- occur in calm waters;
- are found where the weather is generally hot and sunny; and,
- are populated with a wide diversity of fish species, including large, hard-fighting fish (tarpon, sailfish, sharks, mahi mahi).

2.1.3.5 Viewing nature and wildlife.

Nature and wildlife watching is the practice of observing nature and wildlife (*e.g.*, birds, dolphins, fish, manatees, turtles, whales) in their natural habitat. Viewing is performed with the naked eye or through a visual enhancement device like binoculars. The wildlife found in coral reefs and the adjacent seagrasses and mangroves are diverse and fascinating creatures. They range from the charming and intelligent dolphin to the gentle, slow-moving manatee.

Guidelines for responsible wildlife viewing have been developed by federal and state agencies and NGOs. These agencies support responsible wildlife viewing as a positive way to promote conservation and respect for the animals and the marine environment.

Wildlife viewing is a significant commercial activity. For example:

- Whale-watching is estimated to be worth up to $2.1 billion per annum worldwide to whale watching operations, employing around 13,000 workers (Cisneros-Montemayor et al. 2010).
- Bird-watchers contributed $36 billion per annum in the U.S. alone, and a fifth (20%) of all Americans identify themselves as birdwatchers (U.S. Fish & Wildlife Service 2006).

Wildlife viewing can be done on an individual basis or through organized tours with knowledgeable marine naturalists. Guided bird tours have become a major business with at least 127 companies offering tours worldwide (Wikipedia 2010a). Guided kayak nature tours are a popular way to view birds, manatees, fish, and other wildlife in mangroves adjacent to reefs.

Recreational wildlife viewing is an industry that is dependent upon the condition of the supporting habitat. Coral reefs and the adjoining mangroves and seagrasses are particularly attractive to wildlife viewers because they:

- occur in calm waters;
- are found where the weather is generally hot and sunny; and,
- are populated with a wide diversity of species, including birds, dolphins, fish, manatees, turtles, and whales.

2.1.3.6 Beach sunbathing and swimming.

Sunbathing on wide sandy beaches is a popular recreational activity. Sandy beaches are an important part of the attraction for major tropical and subtropical destinations, and many tourists spend at least some time at the beach. White, soft sandy beaches composed of coral and shell particles are a favorite. The contrast between white sand beaches and the emerald, light blue, and sparkling azure colors of tropical and subtropical sea waters is especially beautiful.

Coral reefs and mangroves play an important role in building and maintaining white sand beaches. Coral reefs serve as a sand source. The sand is made of limestone of recent biological origin (*e.g.,* corals, foraminifera, calcareous algæ, mollusks, and crustaceans) (UNEP/GPA 2003). Production of sand results from two processes: wave erosion of the coral reefs and fish feeding on the coral and excreting coral sand (*e.g.,* parrot fish, butterfly fish, and trigger fish).

However, not all beaches are made up of coral sand. Many Caribbean beaches are composed of sand derived from weathered rock, and others consist of a mixture of coral and terrigenous sands.

Reefs also reduce wave energy creating calm waters desirable for swimming. Many sunbathers spend some portion of their time swimming or wading in the water.

Attributes that contribute to good sunbathing beaches include:

- White coralline sands;
- Generally hot, sunny weather; and,
- Calm, warm waters

2.1.3.7 Collecting objects (beachcombing).

Beachcombing is the recreational activity of searching the beach and the intertidal zone for items that have washed in with the tide (*e.g.,* corals, seashells, sponges, sea fans, fossils, pottery shards, artifacts, sea beans, sea glass, and driftwood). Beachcombing provides the opportunity to achieve better emotional, physical and spiritual health at little or no financial cost (Ritterbush 2008, 2010).

Many beachcombers use knowledge of storms, geography, ocean currents, and seasonal events to determine the arrival and exposure of rare finds (LaMotte 2004; Robinson & Robinson 1995; McRee 2009). Beachcombers tend to focus on the area from just above the high tide line, usually marked by a row of seaweed and debris (wrack), down to the water's edge (McRee 2009)**.**

Beachcombing equipment can be as simple as a bag or bucket to put the shells in and a shell identification guide. Many beachcombers also use a metal detector, which aids in locating jewelry, coins and artifacts buried in the sand. Beachcombers tend to be environmentally conscious and serve as stewards of the seashore (Ritterbush 2008).

Currently recognized beachcombing experts include: oceanographer Dr. Curtis Ebbemeyer (*Flotsamterics and the Floating World*); eco-educator Dr. Deacon Ritterbush (*A Beachcomber's Odyssey*); sea glass experts Richard LaMotte (*Pure Sea Glass*) and C.S. Lambert (*Sea Glass Chronicles*); geologist Margaret Carruthers (*Beach Stones*); shell specialists Chuck and Debbie Robinson (*The Art of Shelling*); and, zoologists Dr. Blair Witherington and Dawn Witherington, (*Florida's Living Beaches: A Guide for the Curious Beachcomber*) (Wikipedia 2010b).

Beaches adjacent to coral reefs are particularly attractive to beachcombers because they:

- provide unique, beautiful shells, corals, and sponges;
- often have wide sandy beaches;
- generally have hot and sunny weather; and,
- experience occasional tropical storms that bring in treasures.

2.1.3.8 Surfing.

Surfing is the sport of riding a surfboard toward the shore on the crest of a wave (Princeton WorldNet Glossary 2010b). Ancient Polynesians (*e.g.,* Hawaiians**,** Samoans, Tongans, Tahitians, and Māori) integrated surfing into their culture and considered surfing an art. Hawaiians referred to this art as *he'e nalu*, which translates into English as "wave sliding". Samoans call surfing *fa'ase'e* or *se'egalu* (Krämer 1994). The most skilled surfers were often members of the upper class, which included chiefs and warriors, who had access to the best waves (Young 1983).

In 1779, Lieutenant James King, the newly promoted captain of the HMS Discovery (following Captain James Cook's demise), devoted two full pages of the ship's log to a description of surfboard riding, as practiced by the locals at Kealakekua Bay on the Kona coast of the Big Island. His entry is the earliest written account of surfing (Marcus 2010). The sport was also recorded in print by Augustin Krämer, a 19th century German ethnologist, author, collector, and expert on Polynesian and Samoan culture.

European missionaries forbade or discouraged many Polynesian traditions including surfing. By the 20th century surfing had almost disappeared. Only a few Hawaiians continued to practice surfing and the art of crafting surfboards. In 1905, Duke

Kahanamoku and his friends created a surf club in the Waikiki area of Hawaii. Duke and his friends are credited for bringing surfing back to Hawaii and exposing the world to surfing. In 1907, Jack London went to Hawaii and was introduced to surfing by Alexander Hume Ford, an eccentric journalist and wanderer. London subsequently wrote *A Royal Sport: Surfing in Waikiki*, which included descriptions of Waikiki and Alexander Hume Ford. His story was published in the October 1907 edition of *The Lady's Home Companion* and again in 1911 as part of *The Cruise of the Snark*. In 1907, another member of the Waikiki surf club, George Freeth, introduced surfing to California. Duke Kahanamoku introduced surfing to Australia in 1915.

Until the 1960s only a small number of people were involved in surfing, mainly in Hawaii, Australia and California. The release of the movie *Gidget* moved surfing from an underground culture to a national fad. Since then, films about surfing have continued to play a part in the evolution of surfing.

Globally, there are over 10 million surfers. In the Indo-Pacific, the commercial surf tourism industry is strongly linked to the clothing, fashion, and entertainment industries, and marketed through specialist surfing magazines and surfing media (Buckley 2002).

Coral reefs and other shallow water formations (*e.g.*, rocks, sandbars, etc.) allow waves to break, thereby forming a surfable wave. Collectively, these breaks are known as surf breaks (Silmalis 2007). A reef break is a wave that breaks over a coral reef. When a coral reef is exposed to open ocean, there is potential for a fast and hollow wave. As the wave swell approaches from deep water, it hits the shallower reef, escalating in height before pitching and curling over the reef. The waves at Pipeline in O'ahu, Cloudbreak in Fiji, and Jaws in Maui are among the most famous and photographed reef-break waves. Experienced surfers are rewarded with a fast tubing ride on a ramp-like wave. Most surfing competitions take place on reef breaks (The Surfing Site 2010).

According to Baker (2007), the Caribbean has fewer surf breaks than the Pacific, but offers great surfing during winter and spring. The waves provide short powerful rides, sometimes sweeping over the coral reefs, creating demanding tubes. The best surfing conditions occur when Atlantic storms push through the Caribbean in late May through early September (hurricane season) and December through March (when Atlantic storms push through the Caribbean). When coral reefs are destroyed, waves may diminish, so preserving coral reefs is critical to preserve the sport of surfing (NOAA 1997).

2.1.4 Tourism and recreation: businesses

A diverse range of businesses forms the coral reef tourism industry. Those directly associated with coral reef tourism include small businesses such as charter fishing boat operators, sea kayak tours, and scuba diving instructors, etc. They also include moderate-sized private companies like coral reef dive-boat operators and large corporations such as those that manufacture and retail fishing tackle and recreational fishing boats. An even greater number of businesses are indirectly associated with coral reef tourism (*e.g.*, boat maintenance shops, coastal resorts, island ferry services, and artists). Government agencies monitor and manage coral reef tourism (*e.g*., park authorities, fisheries control agencies, tourism marketing and promotion bodies, law enforcement agencies, and marine safety organizations). Nonprofit groups also form an important component of the industry (*e.g.*, clubs for scuba diving and fishing) (Orams 1999).

2.2 Necessary conditions for providing the service

Coral reefs are the most biologically diverse marine ecosystems on earth, rivaled only by tropical rainforests (Sebens 1994; Odum 1997). Coral reefs cover less than 0.1% of the ocean's surface (an area about half the size of France) but support about 25% of all marine species (Wilkinson 2004; Mulhall 2007).

Coral reefs occur in seas with very specific environmental and climatic conditions.

- Mainly in tropical and subtropical seas—between 30°N and 30°S latitudes.
- Warm ocean temperatures (68–82°F, or 20–28°C). Warm water flows along the eastern shores of major land masses.
- Generally at depths of less than 150 ft (46 m), where sunlight penetrates. Because reef- building corals have a symbiotic relationship with zooxanthellæ, a type of microscopic algæ, sunlight is necessary for these corals to thrive and grow.
- High salinity, low CO2 concentration, and low acidity, facilitating precipitation of calcium from the water necessary to form a coral polyp's skeleton.
- Strong wave action. Waves carry food, nutrients, and oxygen to the reef, distribute coral larvæ, and prevent sediment from settling on the coral reef.
- Most corals grow on a hard substrate.

Coral reefs depend on the interaction of many species, including hard and soft corals, fish, sponges, crustaceans (including shrimp, lobsters, and crabs), echinoderms (including starfish, sea urchins, and sea cucumbers), sea turtles, and cetaceans. Hard and soft corals provide the structural habitat that supports this high abundance and diversity. Bryozoans encrust coral skeletons and reefs debris, cementing the reef structure. Fish, crabs, and lobsters find shelter in the reef structure and play a vital role in the reef's food web.

2.2.1 Linkages among reef condition, reef structures, and reef functions with respect to delivery of the service

The complex three-dimensional coral reef structure provides habitat for the high numbers and diversity of marine organisms that support tourism and recreation (Bradley *et al.* 2008; Fisher *et al.* 2007; Courtney *et al.* 2007; Cesar 2002; Wilkinson 2002; Done *et al.* 1996; Hoegh-Guldberg 1999; Muscatine 1980, 1990; Reaka-Kudla 1996; Sebens 1994; Sale 1991; Crossland *et al.* 1991; Sutton 1983; Loya 1972). Stony corals are the basic building blocks of the coral reef (Human & DeLoach 2002). Massive species (*e.g.*, *Montastrea* spp., *Diploria* spp.) and branching corals (*e.g.*, *Acropora* spp.) provide significant three-dimensional surface area that functions as essential habitat for fish and other reef-dwelling animals (Mumby & Steneck 2008; McField & Richards Kramer 2007; Moberg & Folke 1999). Tourism and recreation are, therefore, directly or indirectly dependent upon the reef-building corals (Moberg & Folke 1999).

Most reef-building corals have photosynthetic algæ (zooxanthellæ) that live in the coral tissue. The coral provides the zooxanthellæ with a protected environment and compounds they need for photosynthesis. The zooxanthellæ provide glucose, glycerol, and amino acids (the products of photosynthesis) that the coral uses to make proteins, fats, and carbohydrates, and produce calcium carbonate (Barnes 1987; Barnes & Hughes, 1999; Lalli & Parsons 1995; Levinton 1995; Sumich 1996). Zooxanthellæ also give stony corals their beautiful, bright coloration.

When stony corals become physically stressed, they expel their zooxanthellæ and the coral colony bleaches (Barnes & Hughes 1999; Lalli & Parsons 1995). This, in turn, results in a reduction of energy (in the form of various photosynthates) being provided to the host (Hoegh-Guldberg & Smith 1989; Brown 1997), and a subsequent loss of tissue biomass (Porter *et al.* 1989; Szmant & Gassman 1990; Fitt *et al.* 1993), coral skeletal deposition (Goreau & MacFarlane 1990), and fecundity (Szmant & Gassman 1990). Extended periods of coral bleaching can result in the coral's death.

Poor coral health may also adversely impact fish production. While overall abundance of reef fishes is correlated mainly with structural complexity of reefs (Jones & Syms 1998; Done 1999), several short-term studies have documented decreases in fish productivity, species richness, fish biomass, and potential yield (reef biocapacity) (Warren-Rhodes *et al.* 2003; Graham *et al.* 2006; Sano 2004) resulting from lost coral structural complexity. Over the long term, however, coral reef structure will reduce in complexity as corals die and bio-erode.

Coral reefs are part of a tropical marine "seascape that functionally links them with the adjacent tropical ecosystems (*i.e.*, mangrove forests and seagrass meadows)" (Mumby & Steneck 2008). This seascape mosaic: (McField & Richards Kramer 2007; Mumby *et al.* 2004)

- provides critical foraging areas, nurseries and refugia;
- provides physical and chemical buffering;
- facilitates energy and material flows; and,
- creates corridors for transient species.

For example, mangroves strongly influence the community structure of fish on neighboring coral reefs (Mumby *et al.* 2004), and also trap sediments, nutrients and pollutants, improving the water quality on nearby reefs (Grimsditch & Salm 2006). Seagrasses contribute nutrients to the coral reefs and produce colored dissolved organic matter (CDOMs), which can protect coral against bleaching by screening harmful solar radiation (Salm & West 2003).

Reef fish respond to this spatial mosaic, many showing pronounced associations with specific habitat types (Sale & Kritzer 2008). Coral reefs provide essential habitat for adult fish. The three-dimensional coral reef structure protects shorelines and creates calm waters necessary for seagrass meadows and mangrove forests to thrive. The rainbow parrotfish, grunts, barracudas, and several snapper species depend on these mangrove forests and seagrass beds for nursery habitat (McField & Richards Kramer 2007).

The tropical marine mosaic also supports "charismatic megafauna", large animal species with widespread popular appeal (*e.g.*, manatees and dugongs, sea turtles, rays, sharks, and dolphins). Some of these species (*e.g.*, manatees and sea turtles) use a variety of habitats during different life stages (McField & Richards Kramer 2007).

Many of the attributes discussed above make coral reefs particularly attractive destinations for tourists. The warm, sunny weather, clear, calm waters, and wonderful species diversity and richness all contribute to this appeal. The desirability of these attributes for tourism and recreation has been well documented in the literature. For example, Pendleton (1994) points out that scuba divers look for high-quality coral reef habitats (as indicated by live coral coverage), coral and fish diversity, and water clarity. Leujack and Ormand (2007) reported that 51% of survey respondents were interested in both fish and corals, whereas 36.5% were only interested in fish and 5.2% only in corals, while another 5.2% stated that besides being interested in corals they also looked for other things on the reef. Uyarra *et al.* (2005) found that divers correctly perceived differences between sites in the condition of biological attributes such as:

- fish species richness;
- total number of fish schools;
- live coral cover;
- coral species richness; and,
- reef structural complexity.

Leeworthy *et al.* (2004) grouped survey respondents' preferences into three categories:

- natural resource attributes (e.g., clear water, amount of living coral, fish/biota diversity, megafauna, and beach quality);
- natural resource facilities (e.g., parks, shoreline access, marina facilities, mooring buoys, boat ramps); and,
- other facilities (parking, roads, rest rooms) and services.

Studies in Israel (Weilgus 2004) and Tobago (Beharry-Borg & Scarpa 2010) have documented the importance of water clarity, coral cover, and fish abundance for divers and snorkelers.

There are other factors that influence the selection of a tourism venue, including the availability of facilities and amenities (*e.g.*, boats, dive shops, fishing guides, hotels and restaurants, etc.), the perceived "healthy" condition of the waters (*e.g.*, lack of pollution, absence of debris), and even perceptions of crowding (Park *et al.* 2002; Beharry-Borg & Scarpa 2010). Inglis *et al.* (1999) and Leujack and Ormand (2007) documented the effect of perceived crowding on snorkelers' enjoyment. Table 2-2, below, summarizes some of the most important attributes that have been identified in the literature.

Table 2-2. Features relevant to the perceived value of coral reefs

<table>
<tr><th colspan="2">Natural Features</th><th rowspan="2">Social Features</th></tr>
<tr><th>Biotic Features</th><th>Abiotic Features</th></tr>
<tr><td>Species richness (coral, fish, sponges, etc.)</td><td>Warm ocean temperatures</td><td>Perceptions of crowding
• # of divers/snorkelers
• # of proximal boats</td></tr>
<tr><td>Variety of species characteristics (coral, fish, sponges, etc.)
• colorful
• large
• rare</td><td>Water clarity</td><td>Lack of pollution</td></tr>
<tr><td>Charismatic megafauna species diversity (birds, marine mammals, turtles)</td><td>Calm waters</td><td>Absence of debris</td></tr>
<tr><td>Coral health</td><td>White coralline sands</td><td></td></tr>
<tr><td>3-dimensional reef structure</td><td>Proximity to deep ocean & waves</td><td></td></tr>
<tr><td>Coral/macroalgæ ratio</td><td>Connectivity with the adjacent tropical ecosystems</td><td></td></tr>
</table>

The coral reef tourism industry depends upon high-quality, pristine or undisturbed assets (Basiron 1997). Coral reef degradation directly impacts delivery of the tourism and recreation services (Cooper *et al.* 2009). For example, recreational fishing is extremely dependent upon the health of coral reefs since many marine game fish species (*e.g.*, tarpon, groupers, snook, barracuda, and dolphin) utilize reef habitats for at least part of their life cycles (Bryant *et al.* 1998).

Recreational diving is especially sensitive to reef condition, and thus particularly vulnerable to degradation (Cooper *et al.* 2009). As an example, dive tourism in Zanzibar decreased by 20%, snorkeling in Sri Lanka declined substantially, and there was an estimated $1.5m annual loss in tourism dollars in the town of El Nido, Philippines, after the mass bleaching and coral mortality of 1998 (Wilkinson *et al.* 1999; Cesar 2000; Bruno 2008). The relative cover of benthic habitats in an area may be indicative of snorkeling or swimming opportunities, with certain types of benthic habitats, such as patch reefs or *Montastrea*-dominated reefs, having greater recreational value than those dominated by seagrass or macroalgæ (Mumby *et al.* 2008).

2.3 Measuring the service

The recreational ecosystem services provided by coral reefs (the opportunity to dive, snorkel, and fish) have not been directly measured. However, there are surrogate measurements related to the natural features that support these ecosystem services that can (and have) been measured. These could potentially serve as, or be combined into, multi-metric indicators of final ecosystem services.

A wide range of biological indicators have been developed and are documented in Jameson *et al.* (1998). Methods for monitoring stony corals, octocorals, fish, benthos, and sponges have been developed and tested by EPA.

2.3.1 Stony corals (scleractinians)

Stony corals (phylum Cnidaria, class Anthozoa, subclass Hexacorallia) build and maintain the physical infrastructure that supports all other organisms in the community (Fisher *et al.* 2007; Fisher *et al.* 2008). Stony corals constitute the basic framework and substrate for many other organisms that penetrate the skeletal mass (sponges, polychætes, sipunculides, bivalves, and gastropods). The complex skeletal structure of stony corals also provides habitat for the high numbers and diversity of marine organisms that support fisheries and tourism (Crossland *et al.* 1991; Done *et al.* 1996; Hoegh-Guldberg 1999; Muscatine 1980, 1990; Reaka-Kudla 1996; Sebens 1994; Wilkinson 2002). Coral structures also protect coastal shorelines from wave and current erosion (Costanza *et al.* 1997; Pernetta 1992).

Because the health, growth, and recruitment of stony corals are crucial to reef sustainability and future benefits, these corals are often considered the primary indicator organisms for reef communities (Loya 1972; Brown 1988; Done 1997). Stony coral colony size is an extremely important attribute, because colony size determines the contribution of each colony and species to community habitat, biomass, photosynthetic activity, metabolism, and calcium carbonate deposition. Colony size is a major determinant of growth, reproduction, population dynamics and community interactions (Fisher 2007).

The stony coral rapid bioassessment protocol (RBP) (Fisher 2007) relies on three observations (colony identification, colony size, and proportion of live tissue), that can be combined in different ways to generate multiple indicators that characterize the value and sustainability of coral reefs. These indicators can be used to assess the capability of reefs to continue providing ecosystem services such as reef-based tourism and recreation (Table 2-3). Unique to the RBP is the ability to generate three-dimensional indicators that help to quantify the complex three-dimensional structure of the reef that is so important to providing the ecosystem services.

2.3.2 Octocorals (gorgonians)

Marine octocorals (phylum Cnidaria, class Anthozoa, subclass Octocorallia [aka Alcyonaria]) (including gorgonians, blue coral, soft corals, and sea pens) are sessile invertebrates that provide substantial spatially varied biogenic habitat for adult and juvenile fish and other invertebrates (Pugliese 1998; Lybolt 2003). Octocoral surface area and topographical heterogeneity are therefore extremely important attributes.

EPA has developed a method that can be performed in conjunction with stony coral monitoring to estimate the total three-dimensional surface area of octocorals on coral reefs. Divers classify marine gorgonians by colony morphology and measure their maximum height and diameter. Morphology-specific equations are used to calculate surface area. These indicators can be used to assess habitat availability for fish and macrobenthos.

The protocol may be supplemented to identify gorgonians by taxonomy and report adverse health conditions (*e.g.*, bleaching, disease, predation, etc.) These additional observations can be used to estimate additional indicators (gorgonian abundance, density, and richness) (Santavy *et al.* in review). These additional indicators could be used to assess features that would be attractive to divers and snorkelers.

2.3.3 Sponges

Marine sponges (phylum Porifera) provide habitat for fish and other invertebrates, cement and reinforce reef structure, contribute to nitrogen and carbon cycling through microbial symbionts, and efficiently filter sediment, algæ, and small organisms from the water column. Three-dimensional sponge area is the critical attribute that supports these services.

EPA has developed a method that can be used to estimate the three-dimensional surface area of marine sponges. Divers classify sponges by colony morphology, then measure height and maximum diameter. Dimensions are converted to surface area using a formula derived for each morphological type. If the necessary expertise is available, additional data collection can include taxonomic identification and adverse physical condition (*e.g.*, bleaching, disease, and predation). Such data will permit estimation of sponge abundance, density, surface area, and, if included in the protocol, taxa richness and physical condition (Santavy *et al.* in review).

2.3.4 Fishes

Reef fish are major components of coral reef ecosystems. The coral reef ecosystem is a very complex environment with many niches. Reef fish fill these niches, helping to sustain the balance of the reef. Reef fish also provide a readily available food source and are an important aspect of tourism and recreation (*e.g.*, sportfishing and diving/snorkeling).

Species diversity and richness are critical attributes that support these services. NOAA has developed and tested fish survey techniques that can be performed in conjunction with stony coral monitoring. Divers assess the species, numbers, and sizes of all reef fishes within an underwater transect. This protocol is a noninvasive, timed, rapid assessment that takes approximately 30 minutes to complete (Menza *et al.* 2006). The fish are classified according to size categories. Visual data are used to estimate abundance, species richness, and biomass for the fish populations and different feeding guilds sampled. Although not yet included in the protocol, the visual data collection could be expanded to include indicators of fish color, which is an attribute of interest to divers and snorkelers.

2.3.5 Mangroves and seagrasses

Remote sensing provides an efficient way to track the change in the areal extent of mangrove forests and seagrass meadows over time. Landsat or other satellite images can be used to measure the extent and spatial patterns of coral reefs, seagrass meadows, and mangrove forests (McField & Richards Kramer 2007). The development of indicators that relate landscape composition and pattern attributes (including hydrology and transitional coastal systems) to coral reef condition is a new research area for EPA.

Table 2-3. Stony coral rapid bioassessment protocol coral condition indicators*

Abundance and Composition	
Abundance	number of colonies
Density	number of colonies per m^2 sea floor
Relative species abundance	abundance of a particular species per total abundance
Species (taxa) richness	number of species occurring in a reef or region
Species frequency	proportion of sites where a species occurs
Species diversity	index of taxa richness and relative abundance
Protected species	richness and abundance of protected coral species
Community composition	relative richness or abundance of a species or groups of species with some discretionary biological or physical attribute (*e.g.*, tolerance)
Physical Status	
Colony surface area (CSA)	3D skeletal surface area of an entire colony (m^2)
Total surface area (TSA)	Σ CSA for all colonies at a transect, station or reef
3D total coral cover (3DTC)	TSA per m^2 sea floor
Average colony surface area (AvCSA)	TSA / # colonies
Population structure	colony size distribution for a species compared to colony number or other attribute
Community structure	colony size distribution for all species compared to colony number or other attribute
Biological Condition	
Percent live tissue (%LT)	proportion of live coral tissue on each colony
Average percent live tissue (Av%LT)	Σ %LT / # colonies
Colony live surface area	live tissue on a colony (m^2) = (CSA × [%LT / 100])
Live surface area (LSA)	Σ colony live surface areas at a transect, station or reef (m^2)
3D live coral cover (3DLC)	LSA per m^2 sea floor
Percent Live Surface Area (%LSA)	comparative ratio of live and total surface area = ([LSA / TSA] × 100)

* Indicators are derived from three core observations (colony identification, colony size, and proportion of live tissue) on stony coral colonies and can represent cumulative or average values for transects, stations, and reefs or for a particular species or group of species.

2.4 Valuing the service

Across the globe, nearly half a billion people are located within 100 km of a coral reef, and therefore, receive some benefit from the ecosystem services provided by coral reefs (Park *et al.* 2002). Local communities depend on coral reefs as an important source of employment, income, and tourism revenues (Ahmed *et al.* 2007). Consequently, tourism (and recreation) is one of the most commonly valued ecosystem services. Tourism (and recreation) is a direct, largely nonconsumptive use of coral reef ecosystems. Sportfishing is largely catch and release, so we consider it to be nonconsumptive even though a portion of sportfishing remains consumptive.

There is a considerable body of literature on valuation of tourism and recreation in coral reef environments. Many different valuation methods have been developed, tested, and applied globally; however, the results are rarely comparable (Burke *et al.* 2008). Values for ecosystem services (UNEP-WCMC 2006) will vary according to:

- the location (e.g., reefs that are major tourist destinations will have a higher value in terms of diving and other reef-related activities than those where tourism has not been developed);
- the length of time being considered and whether a prediction for the future is involved (e.g., all reefs are potentially of value for diving tourism, but some may have no value at present);
- visitor responses to marginal changes in reef quality (e.g., some people are more sensitive to changes and will place a higher value on maintaining reef quality than those less sensitive to such changes); and,
- the method used and the assumptions made.

Table 2-4 below describes commonly used approaches to economic valuation and relates them to particular services. Approaches relevant to tourism and recreation are Travel Cost (TC), Effect on Production (EoP), Financial Analysis (FA), and Contingent Valuation Method (CVM). A brief description of some of these methods is given in the following sections.

Table 2-4. Methods used for valuing goods and services of coral reef ecosystems

Generally Applicable Methods
▶ Using the change in conventional market value of goods and services that results from a change in the environmental resource • Change in Productivity / Effect of Production (EoP) • Change in Stock (houses, infrastructure, land) at Risk (SaR) • Loss of earnings / Human capital approach (HC) • Opportunity cost approach (OC) ▶ Using the value of direct expenditures (cost based) • Preventive expenditures (PE) • Compensation payments (CP) ▶ Using the observed market prices to analyze the current economic activity generated (Financial Analysis)
Potentially Applicable Methods
▶ Using implicit or surrogate market values – indirect approaches • Property-value and other land-value approaches (PV) • Travel-cost approaches (YC) ▶ Using the magnitude of potential expenditures (cost based) • Replacement costs (RP) • Shadow-project costs (SPC)
Survey-Based Methods
▶ Using surveys of individuals to elicit values • Contingent valuation method (CVM) – hypothetical markets and situations (Willingness-to-Pay [WTP] and Willingness-to-Accept [WTA])

Source: Cesar 2000

2.4.1 Effect on production (EoP)

EoP estimates the difference in value of productive output before and after the impact of a threat or a management intervention. The change in net profit (*i.e.*, effect on production) can be calculated and used as a proxy for the loss in tourism value. One challenge with this method is determining and modeling the relationship between the damage to an environmental resource and its corresponding impact on the production of the specified good or service. An example of EoP is the previously cited coral mortality in 1998 and loss of tourism revenues in Zanzibar, Sri Lanka, and the Philippines (Bruno 2008).

2.4.2 Financial analysis (FA)

FA uses observed current financial activities, revenues, costs, and financial flows in the economy from market-based uses of the reef (such as diving and snorkeling) to analyze the economic activity generated by use of an ecosystem good or service.

Data availability and quality vary considerably and have direct bearing on the statistical confidence of the resulting analysis. In addition, this approach will *underestimate* the tourism value of reefs, because it omits consumer surplus (the additional welfare a consumer enjoys beyond what he or she has paid for the service) (Cooper *et al.* 2009).

An example is the World Resources Institute (WRI) economic valuation of coral reefs in Tobago and St. Lucia (Burke *et al.* 2008). Using FA, Burke *et al.* (2008) valued direct and indirect economic impacts from visitor spending in 2006 associated with coral reefs in Tobago to range from $101m to $130m and in St. Lucia from $160m to $194m.

For both EoP and FA, it is important to calculate secondary (*i.e.*, indirect) impacts on the economy from spending by coral reef associated visitors. Economists estimate the magnitude of these *indirect* impacts using a tourism multiplier. A multiplier of 1.6, for example, represents 60 cents of additional impact for every $1 in direct tourist expenditure. The size of the multiplier is influenced by the portion of goods and services used in the tourism sector that are produced domestically, such as linens, beverages, food, dive equipment, and construction materials. (Cooper *et al.* 2009).

2.4.3 Travel costs (TC)

TC uses the travel time or travel costs as a proxy "total entry fee", and therefore, it is a measure of a person's willingness to pay for visiting a particular tourist location. The further away people live from the location, the higher the costs. A demand curve can be developed and the associated consumers' surplus can be determined. This surplus represents an estimate of the value of the environmental good in question (*e.g.*, the coral reefs).

An example of TC is given by Pendleton (1995), who used this method to estimate the economic value of the Bonaire Marine Park. Pendleton used marine park permit data to estimate the number of visitors from each state and county. This number was then divided by the population of the state or county to determine a visitation rate that was then regressed on travel costs, providing the demand curve for coral reef associated vacations to Bonaire. Pendleton was then able to calculate the annual value of Bonaire Marine Park at approximately $19.2m.

2.4.4 Contingent valuation method (CVM)

CVM is used to obtain information on consumers' preferences by asking people what they are willing to pay for a benefit (willingness to pay or WTP), or what they are willing to accept by way of compensation to tolerate a loss (willingness to accept or WTA). Analysts may use either a direct questionnaire/survey or experimental techniques in which subjects respond to different stimuli under controlled conditions. Analysts now use a combination of conjoint analysis (developed in the social psychology field) and multi-attribute utility theory (Adamowicz *et al.* 1998).

An example of a CVM is given by Spash (2000), who surveyed visitors to Montego Bay (Jamaica) and Curacao (Netherlands Antilles) to estimate the benefits of maintaining and improving coral reef biodiversity (a nonuse benefit). Respondents were willing to pay $3.24 per person for Montego Bay and $2.08 per person for Curacao to preserve coral reef biodiversity (Spash 2000). A weakness in applying CVM in this context is whether respondents believe that coral reefs possess inherent rights or that humans have a duty to protect coral reefs. Such preferences could increase WTP by up to a factor of three (Spash 2000).

Economists are now combining various approaches to achieve a more robust valuation. Park *et al.* (2002) developed a TC-CV model of demand for trips to the Florida Keys focusing on willingness to pay to preserve the current water quality and coral reef condition. The integrated model "incorporates key factors for establishing baseline amenity values for tourist dive sites, including perceptions of reef quality and dive conditions" (Park *et al.* 2002).

2.4.5 National scale valuation of tourism

Most countries maintain National Account Systems (NAS), which provide a complete and consistent conceptual framework for measuring the economic activity of a nation. NAS are derived from a wide variety of source data including surveys, administrative and census data, and regulatory data. Most countries have a national statistical office or central bank that compiles, integrates, harmonizes, and publishes the data. NAS include a number of aggregate measures (*e.g.*, gross domestic product [GDP], disposable income, savings and investment) and other information (*e.g.*, input-output tables that show how industries interact with each other in the production process).

In the United States, the Bureau of Economic Analysis (BEA) is responsible for the national account. BEA prepares and publishes a variety of economic statistics on U.S. industries, including the annual industry accounts and the benchmark input-output accounts. U.S. industries are defined according to the North American Industry Classification System (NAICS) (BEA 2010).

The North American Industry Classification System (NAICS) was cooperatively developed by the United States, Canada, and Mexico, and it uses a production-oriented conceptual framework that groups establishments into industries based on the activity in which they are primarily engaged. Corporate entities using similar raw material inputs, similar capital equipment, and similar labor are classified in the same industry. NAICS is based on the product that is being produced (*e.g.*, accommodation services) rather than who is consuming the product (*e.g.*, a tourist or a local resident).

Tourism is not designated as an industry in NAICS. Measuring the economic contributions of tourism presents a twofold challenge:

1. the "Tourism Industry" is actually made up of parts of many industries; and,
2. tourism is traditionally measured and understood from the demand side (*i.e.*, what are visitors spending?), while industries are properly measured from the supply side (*i.e.*, what is being produced?).

To properly value tourism in a manner consistent with the other economic accounts, the World Tourism Organization and the United Nations developed the Tourism Satellite Account (TSA) standard (Sacks 2004). "Satellite accounts provide a framework linked to the central accounts and which enables attention to be focused on a certain field or aspect of economic and social life in the context of national accounts; common examples are satellite accounts for the environment, or tourism, or unpaid household work" (OECD 2010).

The BEA develops the U.S. Travel and Tourism Satellite Accounts (TTSAs), based on the benchmark input-output accounts and consistent with the integrated annual industry accounts. BEA methods used to prepare the TTSAs are consistent with the methods used to estimate GDP, national income, and other national economic measures. The BEA (2010) characterizes the TTSAs in the following way:

> The TTSAs present a detailed picture of travel and tourism activity and its role in the U.S. economy. These accounts present estimates of expenditures by tourists, or visitors, on 24 types of goods and services. The accounts also present estimates of the income generated by travel and tourism and estimates of output and employment generated by travel and tourism-related industries. The accounts are updated annually and have been expanded to provide quarterly estimates of the sales of goods and services to travelers and employment attributable to those tourism sales.

Several states are now developing their own TTSAs (Alaska, Delaware, Hawaii, New Jersey, North Carolina, Rhode Island, South Carolina, and Virginia) (Aydin 2008). There has also been interest in developing a TTSA for Florida (Ayden 2008; Florida Tax Watch News 2007).

2.4.6 National scale valuation of recreational fishing

The Sustainable Fisheries Act of 1996 (PL 104-297) and the Magnuson-Stevens Fishery Conservation and Management Reauthorization Act of 2007 (PL 109-479) both amend the Fishery Conservation and Management Act of 1976 and are incorporated into 16 U.S.C. 1801. Together, they mandate collection of detailed information on marine recreational fishing. Since 1981, the National Marine Fisheries Service (NMFS) has conducted an annual survey of marine recreational fisheries covering all fishing modes (private/rental boat, party/charter boat, and shore) and including estuarine and brackish water. A variety of survey methods are used, including:

- a coastal household telephone survey (CHTS);
- a telephone survey of for-hire fishing vessel operators (FHS); and,
- a field intercept survey of angler fishing trips.

Additional information is also obtained from State or regional logbook programs and is used to supplement survey data to produce more robust catch and effort estimates (NOAA 2009).

An additional source of information on recreational fishing can be obtained from the U.S. Fish and Wildlife Service's National Survey of Fishing and Hunting (NSFH), which collects economic information about recreational saltwater fishing at five-year intervals. The NSFH canvasses the U.S. population by telephone and conducts personal interviews with a subsample to obtain statistically reliable results at the State level.

2.4.7 Noneconomic human dimensions measures

Economic values are contingent on income and wealth and, therefore, cannot capture the full value of ecosystem services. Human values (*e.g.*, social, political, cultural, spiritual) can also be measured. Several key concepts (importance, satisfaction, and expectation) can be measured using survey techniques.

- Importance refers to how a consumer would rate various attributes of the service. Important attributes would presumably figure heavily in choices among alternatives (Alpert 1980).
- Satisfaction is the consumer's fulfillment response received from a service (Myers & Alpert 1968). Satisfaction is influenced by the consumer's perceptions of experienced quality, service quality, price, and other factors (Loomis et al. 2008a).
- Expectation is what the consumer believes is most likely to happen. An expectation may or may not be realistic. Expectations may significantly condition perceptions of experiences or services.

2.4.7.1 *Importance-satisfaction ratings.*

Martilla and James (1977) first described the concept of importance-satisfaction when considering people's demands for goods and services. Importance-satisfaction involves rating certain attributes of the service on their importance to the rater and on satisfaction with the service. Connecting importance-satisfaction ratings to a conceptual model of economic demand and value allows for interpretation of the satisfaction ratings as "indicators" of demand and value for particular ecosystem attributes/ecosystem services. Importance-satisfaction ratings are widely used to assess the demand for outdoor recreation (Guadagnolo 1985; Richardson 1987; Joppe *et al.* 2001; Tonge & Moore 2007) and have recently been used to assess demand for tourism and recreation associated with coral reefs (Johns *et al.* 2003a, 2003b; Leeworthy & Bowker 1997; Leeworthy & Wiley 1996/1997; Leeworthy *et al.* 2004).

2.4.7.2 *Expectancy-discrepancy analysis.*

Expectancy-discrepancy theory suggests that satisfaction is a measure of how closely a consumer's desired experiential outcome is to that consumer's perceived reality once the activity takes place (Vroom 1964; Porter & Lawler 1968). When perceptions meet or exceed expectations, consumers tend to be more satisfied (Manning 1999). Two consumers may receive the same service at the same time and place, but experience very different satisfaction levels due to their expectations. Expectancy-discrepancy analysis was used by Loomis *et al.* (2008a, 2008b, 2008c) in their valuation of recreational fishing, diving, and snorkeling in the Florida Keys.

2.4.7.3 *Norm curves.*

Social norms are the rules of behavior that coordinate interactions within a society or group. Normative theory involves identifying the standards that individuals and groups use to evaluate behavior and social/environmental conditions. Jackson (1965) developed a methodology — return-potential curves — to measure norms. The methodology involves using stakeholder surveys to measure respondent normative evaluations of varying levels of indicators. The personal norms of individuals can then be aggregated to test for the existence of social norms. Social norm curves (Manning *et al.* 1999) can be used to determine the level at which indicator values shift from acceptable to unacceptable conditions.

Normative theory and methods have been used to formulate standards of quality for outdoor recreation, including issues related to crowding (Shelby 1981; Heberlein *et al.* 1986; Whitaker & Shelby 1988; Patterson & Hammitt 1990; Williams *et al.* 1991; Vaske *et al.* 1986; Manning *et al.* 1996; Jacobi & Manning 1999), ecological impacts at campsites (Shelby *et al.* 1988), and wildlife management practices (Vaske & Donnelly 1988). Researchers have begun using photographs and videos to represent levels of impacts (Vaske *et al.* 1996; Manning *et al.* 1999). Visual representations can be used to effectively "tell a story" and resonate well with stakeholders.

2.4.7.4 *Emergy.*

Emergy analysis is another way to quantify ecosystem services. Odum (1996) defined emergy as "the available solar energy used up directly and indirectly to make a service or product". After converting energies of different kinds to the same kind of energy (*i.e.*, solar joules, sej) by multiplying each by the appropriate emergy per unit factor (sej/J), the value of an ecological or economic product or service is determined by summing the inputs. Emergy has units of solar emjoules denoting that it is an accumulation of available energy used in the past. The emergy of an ecosystem product, such as fish, can be converted to a monetary value by dividing by the emergy to dollar ratio of the economy in which the item was sold. The emergy to money ratio is the total emergy flows supporting an economy divided by the dollar flow of the GDP of the economy. Emdollars then redistribute the monetary flow of the system in proportion to the emergy flows, thereby assigning each item the portion of the total buying power in the system attributable to it based on its emergy relative to the emergy of all other products and services in the system's economy including those not counted by economic measures. Emdollar values can be compared to dollar values of the same item to determine the unvalued work of nature that was required for an item compared to the human services required for the same item.

2.5 Reflections

There is considerable variation in the way coral reef based tourism and recreation is defined, measured, and valued. Generally, existing definitions are incomplete and not rigorously developed. Linking the attributes to the ecosystem service should be a step towards standardization. While there are regional differences as to which sectors are operative and at what level, if we develop an appropriate classification framework, that variability should not matter.

We have a fundamental understanding of the factors that affect delivery of the tourism and recreation ecosystem service. We need to improve our understanding of the cumulative and synergistic effects of multiple stressors in both a spatial and temporal context. The application of landscape ecology approaches and metrics to understand coral reef ecosystem functions and to assess the impacts of a variety of management activities (both terrestrial and aquatic) may contribute significantly to our understanding.

We also need to develop, test, and refine indicators that are sufficiently sensitive to distinguish the effects of human disturbance from those of natural variability and that can serve as quantitative estimates of services provided. Ecological models can help to illustrate and quantify relationships among environmental and ecological reef elements and can be used to investigate thresholds for reef persistence and sustainable delivery of services.

Better understanding of consumer preferences vis-à-vis the attributes would be helpful.

- The colloquial literature, including marketing materials, may reflect what people are actually looking for from their tourism experience but does not quantify its value.
- NOAA has done a fairly comprehensive analysis of consumer preferences for the Florida Keys National Marine Sanctuary, although the survey questionnaire could be refined somewhat based upon the attributes work.
- We need the same type of statistically valid information for USVI and Puerto Rico.

From a valuation perspective, the Tourism Satellite Accounts could contribute significantly towards the valuation of coral reef ecosystem services, if refined both from a scale perspective (need to have state or finer scale TSAs), and in a manner that can link them directly to reef-based tourism (need to be able to separate out tourism associated with the coral reef from nonreef-based tourism). If the consumer preference surveys are properly designed, they could help quantify the latter and fill in the gaps with nonmarket values.

Throughout this chapter, we have been using the commonly used term “tourism and recreation” as the ecosystem service. However, more precise terminology is needed to facilitate the interaction between ecological assessment and economic valuation of changes in ecosystem goods and services (Munns personal communication). One approach would be to distinguish between final and intermediate ecosystem services (Boyd & Banzhaf 2007; Daily & Matson 2008). Final ecosystem services are the components of nature, directly enjoyed, consumed, or used to yield human well-being. These are described in units upon which accounting systems and valuation can be based. Intermediate ecosystem services are the components of nature that are not directly enjoyed, consumed or used to yield human well-being, but that are important for the production of final ecosystem services. Final ecosystem services are the units upon which valuation will be based. It is also important to understand intermediate services, because their relationship to final services is of great importance in understanding, assessing, predicting and managing final services and the human well-being provided (Ringold *et al.* 2009). Clearly differentiating between final ecosystem services and intermediate ecosystem services precludes “double counting” (Boyd 2008).

Within “tourism and recreation” there is a suite of final ecosystem services. We are defining these as “opportunities”, since the ecosystem does not actually provide tourism and recreation, but rather provides the opportunity for humans to enjoy recreational experiences. We have identified the following final ecosystem services:

- Recreational fishing opportunity
- Recreational diving/snorkeling opportunity
- Recreational underwater photography opportunity
- Recreational surfing opportunity
- Opportunity to view nature and wildlife
- Opportunity to sunbath and swim at the beach
- Opportunity to collect objects (beachcombing)

Ecosystem production functions describe the relationship between intermediate ecosystem services and final ecosystem services. The intermediate ecosystem services that support tourism and recreation include:

- Production of benthic and aquatic prey for consumption by recreational fish
- Coral reef formation and maintenance
- Maintenance of water quality
- Maintenance of reef breaks
- Maintenance of biological integrity and biodiversity
- Sand production

Table 2-5 illustrates the ecosystem services (final and intermediate), as well as those features that support them. The table serves to help address the following question: *What biophysical metrics directly facilitate the integration of biophysical measurement, analysis, and models with analyses of the social and economic benefits derived from ecosystem goods and services?*

Table 2-5. Final ecosystem services and supporting features for tourism and recreation

Ecosystem Service(s)		Natural Features	Social Values	Complementary Goods & Services	Ecosystem-Derived Benefits	Potential Indicators of Final Ecosystem Service(s)
Final (FES)	Intermediate					
Tourism & Recreation						
Recreational Fishing Opportunity	Production of benthic and aquatic prey for consumption by recreational fish	Fish diversity and abundance	Desirability of fish species and size for rod-and-reel catches	Adequate infrastructure (boats, marinas, etc.)	Revenues from tourism and recreation activities	Abundance of catchable snappers and groupers
Recreational Diving/Snorkeling Opportunity	Coral reef formation & maintenance; maintenance of water clarity; production of benthic and aquatic prey for consumption by recreational fish	Coral diversity, abundance and health; fish diversity and abundance; water clarity	Desirability of coral reef for recreation based on physical appearance (color, visibility, etc.)	Access to reef, safe swimming conditions, adequate infrastructure (hotels, dive boat operators, etc.)	Revenues from tourism and recreation activities	Taxa richness, size and density of reef organisms
Recreational Underwater Photography Opportunity	Coral reef formation & maintenance; maintenance of water clarity; production of benthic and aquatic prey for consumption by recreational fish	Coral diversity, abundance and health; fish diversity and abundance; water clarity	Desirability of coral reef for recreation based on physical appearance (color, visibility, etc.)	Access to reef, safe swimming conditions, adequate infrastructure (hotels, dive boat operators, etc.)	Revenues from tourism and recreation activities	Taxa richness, size and density of reef organisms
Recreational Surfing Opportunity	Reef breaks	3-D reef structure	Desirability based on wave size and speed	Access to reef, adequate infrastructure (hotels, board shops, etc.)	Revenues from tourism and recreation activities	3-D structure and proximity to deep ocean
Opportunity to View Nature and Wildlife	Biological integrity	Biodiversity (birds, marine mammals, turtles)	Desirability of species (rarity, size)	Access to reef and adequate infrastructure (boats, tour guides)	Revenues from tourism and recreation activities	Taxa richness, presence of specific species
Opportunity to Sunbath and Swim at the Beach	Water quality, shoreline protection, sand production	White coralline sands; calm waters	Desirability of coralline sand beach for sunbathing (size, cleanliness, appearance)	Access to beach	Revenues from tourism and recreation activities	Areal extent of beach, color of beach, water temperature, days of sunshine, beach trash
Opportunity to Collect Objects (Beachcombing)	Water quality	Wide sandy beaches, biodiversity, occasional storms	Desirability of walking on beach and of finding beautiful & unusual objects	Access to beach	Revenues from tourism and recreation activities	Areal extent of beach, frequency of storms, proximity of reef, taxa richness of invertebrates

Definitions *(proposed by the Ecosystem Services Research Program and currently under discussion by the Program)*

- **Final Ecosystem Service** – Output of ecological functions or processes that directly contributes to social welfare or has the potential to do so in the future (broadly based on Boyd & Banzhaff [2007]).
- **Intermediate Ecosystem Service** - Output of ecological functions or processes that indirectly contributes to social welfare or has the potential to do so in the future.
- **Natural Features** – The biological, chemical, and physical attributes of an ecosystem or environment.
- **Social Values** – The social attributes that influence economic demand for an ecosystem service.
- **Complementary Goods & Services** - Inputs (usually built infrastructure or location characteristics) that allow a good or service to be used by complementing the ecological condition. For example, complementary goods and services that allow the presence of fishable fish to become an opportunity for recreational fishing will include aspects of site accessibility, such as road access, available parking and the presence of a fishing pier, all of which make fishing at the site possible and enhance enjoyment of the activity.
- **Ecosystem-Derived Benefits** - The contribution to social welfare of ecosystem goods and services. In the ESRP, the term applies specifically to net improvements in social welfare that result from changes in the quantity or quality of ecosystem goods and services attributable to policy or environmental decisions.
- **Indicator of Final Ecosystem Service** – Biophysical feature, quantity, or quality that requires little further translation to make clear its relevance to human well-being (*i.e.*, "public-friendly" measurement)

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Appendix 2-A
Studies quantifying tourism and recreation

The following table lists studies and the endpoint they used to quantify tourism and recreation. Also included are the biological reef attributes and the physical and socioeconomic variables used to estimate that endpoint. The method and location of the studies are also given.

Reef attributes	Physical variables	Socioeconomic variables	Method	Location	Citation
Final Ecosystem Service: Recreational Diving/Snorkeling Opportunity					
Coral cover			Survey questionnaire	Bolinao, Philippines	Ahmed *et al.* (2007)
Coral bleaching; coral cover; fish species composition (preference for more colorful reef fish)			Survey questionnaire	Zanzibar & Mafia	Andersson (2007)
Coral cover, abundance of fish	Coastline development on shoreline, water clarity, plastic debris, risk of contracting ear infection by swimming in polluted water	number of boats, presence of MPA, number of snorkelers, fee	Survey questionnaire	Tobago	Beharry-Borg & Scarpa (2010)
Coral biodiversity, coral cover, fish biodiversity, fish stock, algæ cover			Model	Kihei Coast, Hawaii	van Beukering & Cesar (2004)
"Pristine" coral reef condition; coral diversity; fish diversity and abundance	Water clarity	Swimming restrictions; payment vehicle	Two survey questionnaires – tourist exit survey and tourist operator survey; face-to-face interviews of 400 households for recreational fishing; three focus groups	Bermuda	van Beukering *et al.* (2010)
Fish abundance, coral health	Water clarity		Survey questionnaire and pictures of alternative scenarios	Florida Keys	Bhat (2003)
Coral reef and coral health			Survey questionnaire	Seychelles	Cesar *et al.* (2004)
Coral quality			Survey questionnaire	Phi Phi Islands, Thailand	Christiernsson (2003)
		Perceptions of crowding (social carrying capacity), ease of access	Summary article		Davis & Tisdell (1996)
Coral diversity	Water clarity	Number of divers per site per year	Survey questionnaire & photo analysis	Bonaire	Dixon *et al.* (2000)
Diversity of colorful marine life	Water clarity	Clean and odor-free water; crowd-free experience	Survey questionnaire	Great Barrier Reef, Australia	Hajkowicz (2006)
Amount of live coral, fish and sea life diversity, fish abundance	Water clarity	Access and availability of facilities	Survey questionnaire	Florida Keys	Leeworthy & Wiley (1996)

Reef attributes	Physical variables	Socioeconomic variables	Method	Location	Citation
Final Ecosystem Service: Recreational Diving/Snorkeling Opportunity (con't)					
Amount of live coral, fish and sea life diversity, fish abundance	Water clarity	Access and availability of facilities	Survey questionnaire	Florida Keys	Leeworthy & Wiley (1997)
Amount of live coral, fish and sea life diversity, fish abundance	Water clarity (visibility)	Access and availability of facilities	Survey questionnaire	Florida Keys	Leeworthy *et al.* (2004)
Coral health, fish abundance, large fish, coral cover		Perceptions of crowding (social carrying capacity), knowledge of ecosystem, experience snorkeling	Self-administered questionnaires	South Sinai, Egypt	Leujak & Ormond (2007)
Species richness, density and average size of organisms				Jervis Bay, Australia	Lynch *et al.* (2004)
Health of corals	Current WQ		Survey questionnaire	Florida Keys	Park *et al.* (2002)
Species diversity (fish and corals), percent coral cover	Visibility (water clarity)	Dive tag price	Survey questionnaire	Bonaire National Marine Park	Parsons & Thur (2007)
Percent coral cover			Model	Roatán, Honduras	Pendleton (1994)
Coral reef biodiversity (inferred from other study)			Interviews (survey) of municipal fishers, gleaners, seaweed farmers, and tourism business operators	Bohol Marine Triangle, Philippines	Samonte-Tan *et al.* (2007)
Amount of marine life		number of divers at a site at any one time	Survey questionnaire	Worldwide ?	Sorice *et al.* (2007)
Coral biodiversity			In-person interviews using open-ended elicitation questions	Jamaica & Curacao	Spash (2000)
Coral growth	Access to reef, safe swimming conditions, water quality	Adequate infra-structure (hotels, dive boat operators, etc.)		American Samoa	Spurgeon *et al.* (2004)
Aesthetic beauty of dive site (not defined further)			Survey questionnaire	Similan Islands, Thailand	Tapsuwan & Asafu-Adjaye (2008)
Coral diversity, abundance and health; fish diversity and abundance	Warm temperatures, clear waters, beach characteristics	Low health risks	Survey questionnaire	Bonaire & Barbados	Uyarra *et al.* (2005)
Coral bleaching, "marine life"			Questionnaire; four different surveys, secondary data sources	Indian Ocean (Tanzania/Kenya & Maldives/ Sri Lanka)	Westmacott *et al.* (2000)
Abundance and diversity of corals and fish	Water clarity (visibility)	Entrance fee	Video of alternative diving sites; survey questionnaire	Eilat, Israeli Red Sea	Wielgus *et al.* (2003)

Reef attributes	Physical variables	Socioeconomic variables	Method	Location	Citation
Final Ecosystem Service: Recreational Diving/Snorkeling Opportunity (con't)					
Abundance and variety of fishes, number of "unusual", and number of "large" fish			Interview	Jamaica	Williams & Polunin (2002)
Final Ecosystem Service: Recreational Fishing Opportunity					
Target sportfishing species (bonefish, permit, tarpon)			Survey questionnaire	Belize	Fedler & Hayes (2008)
Target sportfishing species abundance and diversity		Clean and odor-free water; crowd-free experience	Survey questionnaire	Great Barrier Reef, Australia	Hajkowicz (2006)
Target sportfishing species (80 fish and invertebrate species)				Jervis Bay, Australia	Lynch *et al.* (2004)
Final Ecosystem Service: Beach Recreation Opportunity					
Quality of beaches			Survey questionnaire	Florida Keys	Leeworthy & Wiley (1996)
Quality of beaches			Survey questionnaire	Florida Keys	Leeworthy & Wiley (1997)
Quality of beaches			Survey questionnaire	Florida Keys	Leeworthy *et al.* (2004)
Final Ecosystem Service: Wildlife Viewing Opportunity					
Large wildlife (manatees, whales, dolphins, sea turtles)			Survey questionnaire	Florida Keys	Leeworthy & Wiley (1997)

3
Coral Reefs: Fish & Coral for Food, Aquaria, & Ornaments

All oceans are affected by humans to various degrees, with overfishing having the most widespread and dominant direct impact on food provisioning services that will affect future generations
(MEA 2005)

3.1 Describing the service

3.1.1 Definitions

A fishery is an entity engaged in harvesting fish, which is typically defined in terms of the people involved, species or type of fish, area of water or seabed, method of fishing, class of boats, purpose of the activities or a combination of these identifiers (FAO 2010).

Although a fish in the strictest sense is an aquatic vertebrate with fins, the term fisheries is used more broadly, to include mollusks, crustaceans, or any other aquatic animals (and in a few cases, aquatic plants) that are harvested. These include, but are not limited to, oysters, scallops, conch, squid, octopus, lobster, shrimp, and kelp.

Fisheries are most often associated with food production, but harvest of aquatic organisms can be for other purposes, such as for sale as live aquarium fish, bait, or fish meal for agriculture. Other uses include harvest of shells and skeletons for curios and jewelry (Table 3-1).

Food production from coral reefs includes both fish and invertebrate organisms that are harvested on the reef or spend at least a portion of their life cycle on the reef and are harvested elsewhere.

Food products are derived from commercial fishing (for profit), subsistence fishing (for survival), or recreational fishing (for pleasure). Because the benefit of recreational (sport) fishing is pleasure, it is discussed in the Tourism and Recreation section. Artisanal fishing is a term that usually describes traditional harvesting techniques (e.g., rod and tackle, spear, throw-net) that are more likely to represent a small-scale, low-intensity (usually subsistence) fishery. Although coastal fisheries in many parts of the world are mostly artisanal, some dominate the catches of some species or particular year/size classes.

Table 3-1. Benefits or amenities derived from fish production

- Seafood for human consumption (fish & invertebrates)
- Live fish and coral for aquariums (Chan & Sadovy 2000)
- Shells and skeletons for ornamental art and jewelry
- Recreational fishing for pleasure (Brander *et al.* 2007; NOAA 2009)
- Human health and well-being (Olsen *et al.* 1984; WHO 2010)
- Fish meal and oil for livestock and aquaculture feed

3.1.2 Benefits of coral reef fisheries

3.1.2.1 Seafood.

The most commonly described and most highly valued benefit of coral reef fisheries is food for human sustenance. In general, humans are obtaining their protein from fish, both marine and freshwater, in ever-increasing numbers. After the remarkable increase in both marine and inland capture of fish during the 1950s and 1960s, world fisheries production has leveled off since the 1970s. This leveling of the total catch follows the general trend of most of the world’s fishing areas, which have apparently reached their maximum potential for fisheries production, because the majority of stocks have been fully exploited. Therefore, it is very unlikely that substantial increases in total catch will be possible in the future.

The total food fish supply and hence consumption has been growing at a rate of 3.6% per year since 1961, while the world’s population has been expanding at 1.8% per year. The proteins derived from fish, crustaceans, and mollusks account for between 13.8% and 16.5% of the animal protein intake of the human population. The average apparent global per capita consumption increased from about 9 kg per year in the early 1960s to 16 kg per year in 1997, nearly doubling in 40 years (FAO 2002). Currently, two-thirds of the total food fish supply is obtained from capture fisheries in marine and inland waters, while the remaining one-third is derived from aquaculture.

Typically, fish provide about 20–30 kcal per person per day. In a few countries, such as Iceland, Japan, and some small island states, where there are few alternative proteins or the people have a strong preference for fish, fish can contribute up to 180 kcal per person per day. Fish proteins are essential in the diet of some densely populated countries where the total protein intake level is low. Worldwide, about a billion people rely on fish as their main source of animal protein. Dependence on fish is usually higher in coastal than in inland areas. About 20% of the world's population derives at least 20% of its animal protein intake from fish, and some small island states depend almost exclusively on fish. Artisanal coral reef fisheries provide an inexpensive source of protein and employment where few alternatives exist (Burke & Maidens 2004). For example, Seychelles has one of the highest per capita consumption rates of fish in the world (65 kg per year) with 900–1,000 artisanal fishers fishing full-time at 35 landing sites (Cesar et al. 2004).

The current annual global harvest from tropical reef fisheries has been estimated at six million metric tons (Polunin & Roberts 1996). Some scientists have estimated that worldwide coral reefs could produce a sustainable fisheries yield of 20m–35m metric tons per year (Crossland et al. 1991; Hatcher et al. 1987); however, Birkelund (1997) argues that coral reefs cannot or should not sustain such large fisheries yields.

3.1.2.2 Live fish and coral for aquaria.

Another specialized coral reef fishery is the collection of live fish and coral for aquaria (Livengood & Chapman 2007). The United States is the single largest importer of ornamental fish in the world, but the European Union is the largest market for ornamental fish (FAO 1996–2005; Chapman 2000). Estimates of the magnitude and value of the aquaria fishery vary widely. Livengood and Chapman (2007) estimate the value of ornamental fish and invertebrates imported into different countries worldwide at $278m. Chan and Sadovy (2000) conducted a survey of marine aquarium shops in Hong Kong and estimated that close to a million individual coral reef fish enter the aquarium trade annually with an average value of about HK$60 (~$8) per fish. Bruckner (2005) estimated the market to be 14m–30m fish per year, with an import value of $28m–$44m.

3.1.2.3 Ornaments and jewelry.

Species of "precious coral" such as red and pink corals (Family Coralliidæ), black corals (Order Antipatharia) and gold corals (Family Parazoanthidæ) have historically been harvested from many parts of the world for high end jewelry and beads (Hourigan 2008; Grigg 1984, 1989). It has been estimated that precious coral catch reached roughly 450 tons per year in the 1980s and has now declined to roughly 50 tons per year (Oceana 2010). The United States and the European Union proposed thirty-one species of the family Coralliidæ (*Corallium* spp. and *Paracorallium* spp.) for inclusion in the Convention on International Trade in Endangered Species (CITES) Appendix II (Oceana 2010). However, the measure failed to reach the two-thirds majority at the 2010 CITES conference in Doha, Qatar (ENS 2010).

3.2 Providing the service

3.2.1 Linkages among reef condition, reef structures, and reef functions with respect to delivery of fishes for aquaria and food

Almost a third of the world's marine fish species are found on coral reefs (Moberg & Folke 1999). Reefs provide essential habitat for adult fish, and their physical structure creates quiet water areas necessary for seagrass and mangrove nurseries. Valued open water commercial fish such as groupers, snappers, grunts, and barracuda spend critical life stages on the reef and in the reef-seagrass-mangrove system (Mumby *et al.* 2004, 2008; Mumby 2004; Dorenbosch *et al.* 2004). Some reefs in the Pacific and Indian Oceans are extremely rich in species (Tibbetts 2004); for example, Pereira (2000) lists 794 species in 93 families of reef-associated fishes that live in Mozambique waters.

3.2.1.1 Scleractinian corals.

Coral reefs are composed of a physical infrastructure that provides essential fish habitat. The infrastructure is constructed by reef-building scleractinians, or "stony corals". These corals are distinguished by their ability to secrete an extracellular calcium carbonate (aragonite) skeleton, which in most cases forms a solid, relatively permanent reef structure. To form the skeleton, scleractinians rely on symbiotic algæ to produce energy for skeletal growth through photosynthesis. Capturing the energy from sunlight is one reason that stony corals are usually found in shallow, transparent waters. The durability of stony coral skeletons provides an enduring reef habitat that allows the evolution of complex reef communities that include harvestable fish and invertebrates. Dahl (1973, p. 240) stated:

> The production, occupation, and destruction of surface area are, therefore, basic reef processes, and the balance between them is an essential aspect of the reef ecosystem. The efficient production of surface is a primary function of many reef organisms, and the control of surface by secondary occupants is a basic competitive force and a major determinant of reef communities.

Scleractinians provide enormous reef surface area. Although slow-growing by most standards, scleractinian corals can live for hundreds of years, and some species can grow to the size of an automobile (WS Fisher, personal communication).

In the Caribbean, the dominant, large reef-building corals are in the *Montastraea* genus, which includes *M. cavernosa* and three closely related species ((*M. annularis*, *M. faveolata*, and *M. franksii*) that are often referred to as the *Montastraea* complex.

Montastraea colonies are often found on the fore-reef and appear particularly critical to the biodiversity of fish and invertebrates and for maintaining the structure, function, and flow of reef services (Mumby *et al.* 2008; Beets & Friedlander 1998). The Caribbean acroporid species, *Acropora palmata* and *A. cervicornis* are also relatively large and are highly branched, which provides additional surface area and greater reef complexity. Unfortunately, these species are vulnerable to elevated water temperatures that would result from climate warming and white-band disease (Aronson & Precht 2001). Because of enormous losses suffered by acroporids in the last three decades, both of these critical species are listed as threatened. As might be expected, healthy stony corals appear to be critical to productive fisheries. Fish productivity, species richness, fish biomass, and potential yield have all been reported to decrease with a decline in stony coral health (Warren-Rhodes *et al.* 2003).

Mumby *et al.* (2008) used 11 classes of reef habitat as surrogates for species, functions, and ecosystem services and found that one-fourth to one-third of benthic invertebrates and fish occurred in the *Montastraea*-dominated fore-reefs, which consistently had the highest richness, the highest number of processes, and the most services. Yet only 10% of fish species functional classes were unique to any one habitat. Functional classes of fish were an effective surrogate for total fish and benthic species richness, and the representation of species or functional classes ensured inclusion of all processes and services in the design of a reserve network. This research suggests that using the number of fish functional groups as a proxy indicator for benthic richness may be helpful in managing reef functions, services, and biodiversity for maintaining the resilience of reefs.

3.2.1.2 Reef structural complexity.

The physical structure of reef habitat influences the biodiversity and ecosystem functions of a reef community (Alvarez-Filip *et al.* 2009). In general, more complex habitats facilitate species coexistence through niche partitioning and provision of spatially delineated refuge from predators (Beets & Friedlander 1998; Bruno & Bertness 2001). Physical structures influence the spaces that are inhabited by organisms by defining volume, orientation, accessibility, water residence time, and food availability, among other factors (Scheffers *et al.* 2003). The rich diversity of coral reefs rests partly in the provision of habitable surface area and partly in the variability of that surface area.

There has been a widespread decline in the health of coral reefs that has reduced the amount and complexity of the available habitat for fish. A potential consequence of this decline, referred to as “reef flattening” (Alvarez-Filip *et al.* 2009), is the loss of species richness and abundance of reef fishes and invertebrates (Gratwicke & Speight 2005; Idjadi & Edmunds 2006; Wilson *et al.* 2007).

For coral reefs, there appears to be a strong positive correlation of habitat complexity to fish species richness (Walker *et al.* 2009; Pittman *et al.*2007). Rugosity (an indicator of habitat complexity) has, therefore, been used successfully in the Virgin Islands as an index of fish diversity and in data-poor areas may be used to spatially assess where areas of high fish species richness may occur. Studies on the recruitment behavior of epibenthic communities have also shown that substrate irregularity may encourage the diversity of initial substrate colonizers, which may result in higher diversities later in succession (Breitburg 1985). Habitat complexity, especially appropriately-sized holes or cover for a particular species, provide shelter from predators (Hixon & Beets 1993; Roberts & Ormond 1987; Friedlander & Parrish 1998; Aguilar-Perera & Appeldoorn 2008).

3.2.1.3 Seascape connectivity.

Along with coral reefs, seagrass meadows and mangrove forests combine in a complex and dynamic mosaic that provides critical foraging areas, nurseries, and refugia for fish and invertebrates (Christensen *et al.* 2003; Aguilar-Perera & Appeldoorn 2007; McField & Richards Kramer 2007). Some commercially important species and threatened species, such as the rainbow parrot fish, utilize mangroves exclusively as nursery habitat, and the biomass of other fish is significantly increased when mangrove habitat is available (Mumby *et al.* 2004, 2008; Meynecke *et al.* 2008). Functional dependency of some fish on specific habitats, like the mangrove-dependent rainbow parrotfish, can also make them more vulnerable to extinction (Mumby *et al.* 2004). Proximity to seagrass and mangrove nursery habitat and the connectivity of reefs with nursery habitat has been measured using a variety of landscape connectivity metrics (Dorenbosch *et al.* 2004; Meynecke *et al.* 2008; Mumby 2006; Edwards *et al.* 2010).

Recent studies have directly compared the value of seagrass and mangrove habitats with the value of other possible shallow water habitats (Dorenbosch *et al.* 2006). Nagelkerken *et al.* (2000) used a visual survey technique to evaluate the importance of mangroves, coral reefs, and seagrasses as habitat for juvenile fishes in Bonaire. Their study showed that all three habitats were important nursery areas, but for different species. A similar study in the Indo-Pacific (Dorenbosch *et al.* 2006) documented ontogenetic shifts from juvenile habitats (seagrasses and mangroves) towards adult habitats (coral reefs). In a multi-year study in La Parguera, Puerto Rico, Pittman *et al.* (2010) found a high degree of multi-habitat use, with size-dependent ontogenetic habitat shifts. The importance of different habitats for juveniles and adult fishes is shown in Table 3-2.

Table 3-2. Important (×) habitats for juveniles and adults of selected fish species
☒ indicates the most important habitat for juveniles

Species	Juveniles			Adults			Study Location	Ref.
	Seagrass	Mangrove	Coral Reefs	Seagrass	Mangrove	Coral Reefs		
Acanthurus chirurgus (doctorfish)	☒	–	×	–	–	×	Bonaire	N
Chætodon capistratus (foureye butterflyfish)	×	☒	–	–	–	×	Bonaire	N
Cheilinus undulatas (humphead wrasse)	☒	–	–	–	–	×	Indian Ocean	D
Hæmulon flavolineatum	☒	×	×	–	–	×	Bonaire	N
(French grunt)	×	☒	×	–	–	×	Puerto Rico	P
Hæmulon plumierii (white grunt)	☒	×	×	–	–	×	Puerto Rico	P
Hæmulon sciurus	☒	×	–	–	–	×	Bonaire	N
(bluestriped grunt)	×	☒	–	–	×	×	Puerto Rico	P
Lutjanus apodus	×	☒	–	–	×	×	Bonaire	N
(schoolmaster snapper)	×	☒	×	×	×	×	Puerto Rico	P
Lutjanus griseus	×	☒	–	–	×	–	Bonaire	N
(gray snapper)	×	☒	–	–	×	–	Puerto Rico	P
Lutjanus mahogoni (mahogany snapper)	×	☒	×	–	×	×	Puerto Rico	P
Lutjanus synagris (lane snapper)	×	☒	☒	–	–	–	Puerto Rico	P
Ocyurus chrysurus	☒	–	–	–	–	×	Bonaire	N
(yellowtail snapper)	×	–	×	×	–	×	USVI	P
Scarus guacamaia (rainbow parrotfish)	–	☒	–	–	–	×	Indian Ocean	D
Sparisoma radians (bucktooth parrotfish)	×	×	–	×	×	–	Puerto Rico	P
Sparisoma viride (stoplight parrotfish)	☒	–	×	–	–	×	Bonaire	N
Sphyræna barracuda (great barracuda)	×	☒	–	×	×	×	Bonaire	N

References: D: Dorenbosch *et al.* (2006) N: Nagelkerken *et al.* (2000) P: Pittman *et al.* (2010)
Source: Partially adapted from Nagelkerken *et al.* (2000).

3.2.2 Linkages among reef condition, reef structures, and reef functions with respect to provision of stony corals, black corals and precious corals for aquaria stock and jewelry

Corals collected for the aquarium and jewelry industries generally are rare, slow-growing, long-lived species (USFWS 2011). According to the Global Marine Aquarium Database (GMAD), there are 61 species of soft corals and 140 species of stony corals collected for aquaria (Wabnitz *et al.* 2003). Of the approximately 220 species of precious corals (those used in the jewelry industry), only about 16 are commercially important (Hanfee 1997). Precious corals are found in deeper water (250–1600 feet depth) and include red and pink corals, black corals, gold corals and bamboo corals (Tsounis *et al.* 2010).

Coral condition is an important characteristic of corals collected for both the aquarium and jewelry industries. Corals collected for the aquaria trade must be healthy enough to survive collection and transport. Precious corals must be healthy enough that their skeletons can be formed into jewelry. It is not known how structural complexity or seascape connectivity relate to corals for aquaria stock and jewelry.

3.3 Measuring the service

3.3.1 Fish

A number of indicators of fisheries production are directly monitored as attributes of reef condition, including fish abundance, fish size, conch abundance, lobster abundance, and the biomass of commercially important species (McField & Richards Kramer 2007; Healthy Reefs Initiative 2010). Reef fish surveys are one method of measuring the available fish biomass. A variety of standardized methods has been developed and implemented (Bohnsack & Bannerot 1986; McField & Richards Kramer 2007; Schmitt & Sullivan 1996; Pattengill-Semens & Semens 2003). Divers swim along transects, estimating the number and size ranges of fish species. Several metrics that can be used as indicators of stock status can be derived from the data (*e.g.,* species abundance, density, size structure, and frequency-of-occurrence; total fish biomass; commercially significant fish biomass) (Ault *et al.*1998; Paddack *et al.* 2009; McField & Richards Kramer 2007). Paddack *et al.* (2009) conducted a meta-analysis of reef fish density obtained from 48 studies covering 318 reefs across the Caribbean and found that overall reef fish density has been declining significantly for more than a decade, at rates that are consistent across all subregions of the Caribbean basin (6%–22.7% per year and in three of six trophic groups). There appears to be a considerable lag-time between degradation of coral reef habitat and the decline of fish populations; however, a consistent significant decline across several trophic groups and among both fished and nonfished species indicates that Caribbean fishes have begun to respond negatively to habitat degradation (Paddack *et al.* 2009).

Fishery-dependent population estimates can also be developed using catch data (*e.g.*, the National Marine Fisheries Service (NMFS) headboat catch and effort data). The NMFS data provide total numbers of individual fish in the catch as well as total weight in the catch by species by year (Ault *et al.* 1998).

3.3.2 Stony corals

Despite the fact that more stony corals (greater abundance) and larger corals provide greater habitat for fish and invertebrates (Beets & Friedlander 1998), few studies are available that directly measure coral surface area. Most commonly, stony coral studies measure “live coral cover”, which reflects only a 2-dimensional planar area viewed from above the coral. The planar approach is convenient but does not account for colony height, which can vary widely, and cannot be used to estimate colony surface area (quantity of habitat). The concept of 3-dimensional (3D) colony surface area has been explored (Dahl 1973; Szmant-Froelich 1985; Roberts & Ormond 1987; Babcock 1991; Alcala & Vogt 1997; Bak & Meesters 1998), but only recently have 3D colony surface area methods been developed for use in applied field studies (Fisher 2007; Fisher *et al.* 2007; Fisher *et al.* 2008; The Nature Conservancy 2010).

3.3.3 Reef structural complexity

The structural complexity of reefs is determined by size, shape, and juxtaposition. Complexity refers not only to the surface area but also to the size variability of spaces, which provide different habitats for organisms with different sizes and behaviors. A complexity index (Aronson *et al.* 1994) and a similar rugosity index (NOAA 2008) are calculated from comparison of the length of a chain to the distance covered by the chain when draped over a coral reef (Risk 1972; Rogers *et al.* 1982; Connell & Jones 1991). Despite the intention to measure multiple aspects of reef complexity, this approach only measures the cumulative height of coral colonies on a reef, which is only one component of complexity. Since reef height reflects greater surface area, this is a useful measurement for predicting habitat availability. Another component of complexity, however, is variability in spaces, which is created by corals of different sizes and holes or caves in coral structures. In a recent study, Fisher *et al.* (2008) calculated the coefficient of variation of colony size to reflect this component of complexity. Others have developed tools to estimate holes and caves in coral structures (Scheffers *et al.* 2003). While all of these approaches are useful, no truly comprehensive method has yet been presented to indicate reef complexity.

3.3.4 Seascape mapping

Despite the fact that the earliest landscape ecology studies of marine systems had their beginnings in the classic works of Levins (1969) and Levin and Paine (1974), it is only within the last decade or so that we have seen a significant increase in the application of landscape ecology principles to seascapes. Early work concentrated on mapping habitats and understanding reef functions and processes (Dierssen *et al.* 2003; Kvernevik *et al.* 2002). Even though this work continues, there has been recent growth in the availability of spatial data from GIS (geographic information system) and remote sensing technologies, which are necessary to map coral reef habitats (Phinn *et al.* 2008). This, in combination with survey and monitoring data of reef attributes, has led to methods that increase the data resolution needed to make meaningful observations at more local scales (Harbourne *et al.* 2006).

These developments have also inspired work on spatially explicit modeling and mapping of fish distributions and fish production (and service provisioning) on reefs (Pittman *et al.* 2010; Pittman *et al.* 2007; Mumby *et al.* 2008; Purkis *et al.* 2008). Although mapping of services is in its infancy, trade-offs in managing services result in changes in the location or scale of the beneficiaries (*e.g.*, local fisheries or jobs versus global tourists), which we are only beginning to understand (Hodgson & Dixon 2000). The connectivity of coral reef fish habitat and nursery habitat is important to fish production, so methods for mapping these habitats at finer scales and methods to measure the connectivity of habitat used throughout the life cycles of fishes is increasingly important in making land use and other management decisions.

3.3.5 Fisheries modeling

Ecopath is a trophic structure model that simulates ecological processes in complex food webs, while *Ecosim* allows the simulation of scenarios to maximize benefits under different management regimes and allows evaluation of tradeoffs for different decisions. Combined socioeconomic and ecologic process models such as *EwE* (*Ecopath* with *Ecosim*) have been used to evaluate fisheries management alternatives. Examples include managing a resource to optimize biodiversity or habitat for at-risk species, or optimizing social values in terms of fisheries jobs (Cheung & Sumaila 2008). *Ecopath* was used by Pauly *et al.* (2000) to document the structural changes in global fisheries. By looking at all historic data and estimating the trophic level of each species, Pauly *et al.* (2000) estimated that top predators are being lost and that the average catch is lower in the food chain today than in the past. This approach might be useful at a more local level to determine sustainable levels of harvest.

Another program, *Marxan*, is a model used to design marine protected areas (MPAs). The model incorporates an optimization algorithm for finding spatially cohesive sites that meet specified criteria, such as biodiversity (Smith *et al.* 2002).

Jordan *et al.* (2008) demonstrated an approach that links production at the scale of habitat patches to large-scale delivery of the ecosystem service (edible fish). This framework may be used to model habitat effects for use in predicting and managing coral reefs and other coastal habitats, to identify sources of uncertainty and data gaps to improve the precision and accuracy of predictions, and to demonstrate the potential for large-scale effects of multiple small-scale decisions on delivery of ecosystem services.

3.4 Valuing the service

Coral reef associated fisheries encompass both direct and indirect values (van Beukering *et al.* 2010). Most of the research on the value of ecosystem services has focused on direct use values (*e.g.*, consumption for food, marine ornamentals) or indirect use values (*e.g.*, habitat provisioning, cultural and recreational importance).

Fisheries agencies often use the annual ex-vessel value (*i.e.*, the gross value paid to commercial fishermen for their harvest). For example, in 2000 the annual ex-vessel value of commercial fisheries associated with U.S. coral reefs was estimated at over $137.1m (NOAA 2001). The ex-vessel value is an incomplete value of the fishery: it does not include the value added by processors and vendors; it does not reflect the value of future catches; and, it does not reflect the uncertainty surrounding the ability to obtain a comparable income in the future. For more complete fisheries valuation, economists estimate either the present value (PV) or the net present value (NPV) of the fishery (Cheung & Sumaila 2008; Costanza *et al.* 1989). PV represents a series of future cash flows expressed in today's dollars. NPV is a method used in evaluating investments; the NPV of all cash outflows (such as the cost of the investment) and cash inflows (returns) is expressed in today's dollars. Both PV and NPV use a discount rate (*i.e.*, the rate at which society as a whole is willing to trade off present for future benefits) to calculate the value.

Data on the trade of marine ornamentals is, at best, qualitative . Collectors are generally small-scale fishermen working alone or in small groups, using artisanal equipment (Wabnitz *et al.* 2003). CITES covers some marine ornamentals (including all species of stony corals) and provides some trade data. National governments also produce statistics regarding the export or import of marine ornamentals. A few countries report the actual number of specimens exported (*e.g.*, Singapore and the Maldives). More precise data can be obtained by interviewing collectors (Cesar *et al.* 2002), but this has not been done at a global scale.

For indirect use values (habitat provisioning) researchers may have derived a value for the resource by first identifying a management scenario (MPA, No-Take Areas, incentive programs, etc.) from which they determined what the expected increase in fish production and its value would be (opportunity cost methods). The value of fisheries has also included attempts to calculate the Total Economic Value (TEV) of reefs, which includes fish production (Spurgeon 1992; Cesar 2002), but difficulties arise when trying to sum nonuse and use values. Random utility models are most often used in valuation of recreational fishing (Bockstael *et al.* 1989; McConnell *et al.* 1995). Many of these methods, except for determination of the present monetized value of fish for food consumption, use contingent valuation methods to determine what people are willing to pay, accept, or volunteer for the service (Table 3-3).

Cesar (2000), Moberg and Folke (1999), and Spurgeon (1992) provide excellent reviews on problems coral reefs face and on what types of values and valuation methods should be used for valuing different benefits (Table 3-4) . Stressors have been translated into "disservices" for the purposes of valuation. For example, Cesar *et al.* (1997) used a quasi-option value approach to evaluate the costs (potential losses due to the threat) and benefits of overfishing.

Table 3-3. Valuation methods

1. Stated preference
Uses surveys to determine WTP (willingness to pay) or WTA (willingness to accept) or WTV (willingness to volunteer one's services for fundraising, etc.) **a. Discrete or Dichotomous Choice Method** A good or service (or change in a good or service) is presented to samples of individuals. Randomly assigned dollar amounts are presented, and individuals in the sample group choose their preferred amount. This is consistent with how choices are made in markets and helps the analyst to derive estimates of economic value. **b. Choice Methods – Multi-Attribute Utility Theory** This method uses conjoint-type analysis to yield changes in total economic value or changes in preference rankings for changes in attributes.
2. Revealed preference
a. Travel Cost Method Uses the distance one has to go and the cost involved to assess value (*e.g.*, bird watching) **b. The value of time spent traveling, or the opportunity cost of travel time** **c. Opportunity cost** The value of the best alternative to a given choice, or the value of resources in their next best use. In regard to time, the opportunity cost of time spent on one activity is the value of the best alternative activity that the person might engage in at that time. **d. Random utility modeling** A version of the travel cost method that is often used for recreational fishing.
3. Cost/benefit analysis
4. Damage cost avoided, replacement costs, substitutes
5. Hedonic pricing
The hedonic pricing method is used to estimate economic values for ecosystem or environmental services that directly affect market prices. It is most commonly applied to variations in housing prices that reflect the value of local environmental attributes (*e.g.*, housing values of Wisconsin lake front property increases with greater water clarity). It can be used for estimating the economic benefit of environmental quality, including air pollution, water pollution, or noise environmental amenities, such as aesthetic views or proximity to recreational sites.
6. Costless choice method
Dixon & Sherman (1990)
7. Total consumer surplus
Consumer surplus is the difference between the total amount that consumers are *willing and able to pay* for a good or service (indicated by the demand curve) and the total amount that they actually do pay (*i.e.*, the market price for the product). An example might be the cost savings in property tax relief to individuals who place conservation easements on their properties (these are deed restrictions that landowners voluntarily place on their land to protect important resources). The total consumer surplus is simply the sum of all the consumer surpluses for each individual good purchased.
8. Direct cost
For example, research expenditures by the Smithsonian Institution surveying coral reefs in Belize
9. Change in productivity approach
Difference in value of the biologically supported economic activity in situations with and without the reef (can use fish production and yield estimates with and without MPA, or production on degraded versus undegraded reefs)
10. Percentage dependence technique
The value of the supported activity multiplied by an estimate of the percentage dependence of the activity on the reef's presence
11. Replacement cost
For example, cost of installing artificial coastal defenses to replace reef protection function or fish production (*e.g.*, artificial reefs)

12. Option price
Option value (benefit received by retaining the option of using a resource in the future by protection or preserving it today) plus expected consumer surplus (the measure of the *welfare* that people gain from the consumption of goods and services, or a measure of the benefits they derive from the exchange of goods).
13. Bioeconomic models
In this approach, both supply and demand are estimated. Production functions relating natural system attribute inputs along with capital, labor and energy inputs are estimated and cost curves and the supply curve are estimated. Demand curves for the good or service are also estimated. The outputs are changes in consumer's surplus, producer's surplus, and a special part of producer's surplus—economic rent (ER) or the amount of profit over and above a normal return to investment. ER is a measure of welfare for the fisheries where no one pays a price for the fish.
14. Total economic value (TEV)
TEV is an aggregation of consumer's surplus, producer's surplus/economic rent (CS, PS/ER). This includes use and nonuse/passive economic use values (both direct and indirect). These values are used in Benefit-Cost Analysis (BCA), damage assessments and restorations.
15. Value transfer
From meta-analysis of valuation studies (Brander *et al.* 2007)
16. Noneconomic human dimensions measures
(A more extensive discussion of these measures is provided in section 2.4.7 of this report.) **a. Importance-satisfaction ratings** **b. The value of time spent traveling, or the opportunity cost of travel time** **c. Opportunity cost** The value of the best alternative to a given choice, or the value of resources in their next best use. In regard to time, the opportunity cost of time spent on one activity is the value of the best alternative activity that the person might engage in at that time. **d. Random utility modeling** A version of the travel cost method that is often used for recreational fishing.

Source: except where noted, from Spurgeon (1992), Moberg & Folke (1999), and Cesar (2000).

Table 3-4. Categories of values

Direct use value
▶ Extractive value (*e.g.*, fisheries, coral for jewelry) ▶ Nonextractive value (*e.g.*, scuba diving)
Indirect use value
▶ Habitat that supports fish ▶ Nutrients ▶ Shoreline protection ▶ Global life support
Nonuse values
▶ Existence value (*i.e.*, value attributable to the presence of the reef, whether used or not) ▶ Option value (*i.e.*, potential future direct or indirect used, such as bioprospecting) ▶ Bequest value (*i.e.*, value of preserving for future generations) ▶ Intrinsic value (*i.e.*, innate value without reference to humans)

Source: Spurgeon (1992); Cesar (2000).

Income derived from fishing is another important benefit. Surveys conducted by Cinner *et al.* (2008) found that fishers from poorer households would be less likely to exit a severely declining fishery. They suggest that wealth generation and employment opportunities targeted at the poorest fishers would help reduce fishing effort in overfished areas (Cinner *et al.* 2008).

3.5 Reflections

3.5.1 Threats to coral reef fisheries

Global landings of fish have been in serious decline since the mid-1980s (Pauly *et al*. 2005). Overfishing has been identified as one of the major causes of reef ecosystem decline in recent decades, because the loss of harvested fish species changes the structure and functioning of reef systems (Jackson *et al.* 2001; MEA 2005; Pauly *et al*. 2000; Burke & Maidens 2004) and reduces reef resilience to natural disturbances (Hughes *et al.* 2003). While the loss or reduction of specific functional groups (*e.g.*, herbivores) through overfishing may reduce the size of harvestable fish stocks, overfishing of keystone herbivores like parrot fish and surgeon fish completely alter reef dynamics. Their loss substantially increases growth of macroalgæ and can cause a phase shift in the reef system from coral to algal dominance (Hughes *et al.* 2003; Pandolfi *et al.* 2003; Burke & Maidens 2004).

Many tropical fish species (*e.g.*, groupers and snappers) form large spawning aggregations once or twice a year. The fish that come to these aggregations are the oldest and largest individuals in the population (Coleman *et al.* 2000; Domeier & Colin 1997; Beets & Friedlander 1998; Smith 1972). These aggregations are easily targeted by fishermen, and intensive fishing during spawning can quickly deplete a population (Burke & Maidens 2004; Beets & Friedlander 1998). Removing the largest individuals from the population decreases spawning potential and reduces larval recruitment, since larger animals produce more eggs (McField & Richards Kramer 2007; Roberts & Hawkins 2000). There is also evidence that spawning-site fidelity is a learned behavior, and when heavy fishing at aggregation sites removes the experienced fish, new recruits are unable to locate the aggregation site (Coleman *et al*. 2000; Warner 1990; Clark & Tracey 1993; Sadovy & Eklund 1999).

Destructive fishing methods pose another threat to coral reefs and to sustainable fish populations. Cyanide fishing (using cyanide to stun reef fish for collection of live fish for the aquarium trade); blast fishing (using explosives to kill or stun reef fish); muroami netting (nets that are weighted and dropped repeatedly onto coral); and gleaning (digging through reefs with steel tools in search of abalone and invertebrates) have significant impacts on the reef structure, connectivity of the reef with other habitats, and community structure of nontarget species (Pauly *et al.* 2000; Cesar 2002).

3.5.2 Management options

The American Fisheries Society (AFS) supports conservative management of reef fishes to avoid rapid overfishing and stock collapse (Coleman *et al*. 2000). Two management approaches (essential fish habitat and marine protected areas) can be combined to help maintain fish populations at sustainable levels.

3.5.2.1 Essential fish habitat (EFH).

The EFH provision of the 1996 Sustainable Fisheries Act (PL 104-297 1996) amended the habitat provisions of the Magnuson Act (now called the Magnuson-Stevens Act) to require the National Marine Fisheries Service (NMFS), the Fishery Management Councils, and Federal agencies to protect, conserve, and enhance essential fish habitat. Congress defined EFH as “those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity.” Additionally, EFH that is determined to be particularly important to the long-term productivity of populations of one or more managed species, or to be particularly vulnerable to degradation, can be identified as “habitat areas of particular concern” (HAPC) to help provide additional focus for conservation efforts (Duval *et al*. 2004).

EFH can account for spatial and temporal variation in the distribution of life history stage, seasonal and geographic distributions, abundance, and interactions with other species. However, the regulations governing EFH designation do not provide for temporal designation (*i.e.*, a habitat is EFH all year long). Fisheries management plans now include a description and identification of EFH, a description of potential threats (including how different fishing methods affect EFH), and actions to conserve and enhance habitat (EPA 2005).

Spawning aggregations are potential EFH, since they are concentrated production sites and can be predictable in space and time (Lindemann *et al.* 2000). EFH can also be identified by correlating benthic habitat variables with the distribution, abundance, and size of reef fishes (Pattengill-Semmens & Semmens 2003). NOAA’s Biogeography Program has produced benthic habitat maps of most U.S. coral reefs. These data have been used to identify and map structural habitats used by fish species at different life stages (Recksiek *et al.* 2001). The goal is to develop predictive habitat affinity models for selected fish species that will support location of essential fish habitat.

3.5.2.2 Marine protected areas (MPAs).

MPAs or no-take areas (NTAs) may provide the best protection against overfishing (Hughes *et al*. 2003), so it is not unexpected that a large body of literature is focused on optimization of MPA system design and the ecosystem service benefits that they provide (Roberts & Polunin 1993; Trexler & Davis 2000; Cesar 2000; Pendleton 1995; Arias-Gonzalez *et al.* 2004; Roncin *et al.* 2008; Stelzenmüller *et al.* 2008). Protected areas are an effective management tool, because “if well enforced they change human behavior”, and in actuality, it is human behavior and not the resource that is managed (Hughes *et al.* 2003). Reserves in the Mexican Caribbean generally have a greater number of species, higher organism density, and larger-sized herbivores than unprotected reefs (Nuňez-Lara *et al.* 2003; Arias-Gonzalez *et al.* 2004).

But estimates of the no-take area needed to be effective may be economically prohibitive in the short term despite the increasing probability of the future collapse of the industry and the system as a whole. For example, Hughes *et al.* (2003) point out that ecological modeling studies indicate that at least 30% of the world's coral reefs should be NTAs to ensure the sustainability of exploited fish stocks. While this may seem extreme, Moberg and Ronnback (2003) point out that it is most likely more cost effective to try to preserve ecosystem functioning than to restore or replace ecosystems when they have been degraded or lost.

The quantitative associations between fish populations and their habitats is a key issue in determining EFH and establishing MPAs and NTAs that protect fish and the fisheries. These must incorporate concepts of targeted fish species, life history stages, age structure, genetic diversity of the stock, community structure, and physical habitats (Recksiek *et al.* 2001; Roberts *et al.* 1993; Coleman *et al.* 2000; Murray *et al.* 1999). While precise corridors of connectivity between habitats are not yet fully understood, MPAs that encompass areas of connected habitats (*e.g.*, coral reefs, seagrass meadows, mangroves forests) may best protect fisheries (Pittman *et al.* 2010; Mumby *et al.* 2004; Lindemann *et al.* 2000).

MPAs may also address other management concerns, such as how to allocate ecosystem services among user groups. The Florida Keys National Marine Sanctuary (FKNMS) is using no-take areas and other marine zoning methods to resolve conflicts between users.

3.5.3 Conclusions

Fisheries are fairly well defined, but measurements and valuation are incomplete and vary widely. Attributes associated with fishing have been identified, and scientists have begun to link those with fish production. Spatial and temporal analysis of fish populations and their use of various habitats has advanced considerably in recent years.

Linking the attributes to ecosystem services (not just fish production) (Table 3-5) and conducting valuation studies will further advance the science. Fish production is an ecological endpoint, a necessary part of the realization of benefits (amenities, goods, or services) to people. The benefits can be thought of as ecosystem service endpoints for which there are values. Valuation places a monetary or nonmonetary value on these benefits by establishing a relationship between the inputs (physical, biological, socioeconomic factors) and the output (benefit). This relationship may be defined by a model, statistical equation, function, or conceptual model.

Often the methods available to value a service, benefit, amenity, or stock, dictate how the benefits are described. The same benefit may have very different inputs depending on the scale of analysis, the area under investigation, the focus of the research (individual type of fish, what people in a particular area value most highly, the availability of certain tradeoffs, etc.). As we suggest in Chapter 1, it may be helpful to distinguish between ecological services (which are expressed in physical units) and economic benefits (which are expressed in monetary units). Some researchers have derived ways to combine the monetary and nonmonetary benefit values of a system to compare purely economic values with the value of the system as a whole (Odum 1996).

Ecological models can be used to illustrate and quantify relationships among environmental and ecological reef elements and to investigate thresholds for reef persistence and sustainable delivery of services. This information can be applied in the development of EFH and MPAs, with the ultimate goal of a sustainable fishery.

Table 3-5. Final ecosystem services and supporting features for fish production

Ecosystem Service(s)		Natural Features	Social Values	Complementary Goods & Services	Ecosystem-Derived Benefits	Potential Indicators of Final Ecosystem Service(s)
Final (FES)	Intermediate					
Fishing						
Seafood Products (fish, shellfish, algæ harvested)	Biological integrity	Fish diversity and abundance; coral health; seascape connectivity; and structural complexity	Desirability of species based on taste	Adequate infrastructure (boats, marinas, etc.)	Revenue from commercial seafood fisheries	Abundance of commercially desirable fish species
Aquarium Products (live fish & coral taken)	Biological integrity	Coral diversity, abundance and health; fish diversity and abundance; seascape connectivity; and structural complexity	Desirability of species for aquaria based on physical appearance (color, size, etc.), rarity		Revenue from sales of aquarium fish and coral	Species abundance and diversity of target populations
Material Removed for Curios and Jewelry	Biological integrity	Coral diversity, abundance and health; water clarity	Aesthetic values and artistic inspiration	Diving and boating infrastructure	Revenue from sales of curios and jewelry	Species abundance and diversity of target populations

Definitions *(proposed by the Ecosystem Services Research Program and currently under discussion by the Program)*

- **Final Ecosystem Service** – Output of ecological functions or processes that directly contributes to social welfare or has the potential to do so in the future (broadly based on Boyd & Banzhaff [2007]).
- **Intermediate Ecosystem Service** - Output of ecological functions or processes that indirectly contributes to social welfare or has the potential to do so in the future.
- **Natural Features** – The biological, chemical, and physical attributes of an ecosystem or environment.
- **Social Values** – The social attributes that influence economic demand for an ecosystem service.
- **Complementary Goods & Services** - Inputs (usually built infrastructure or location characteristics) that allow a good or service to be used by complementing the ecological condition. For example, complementary goods and services that allow the presence of fishable fish to become an opportunity for recreational fishing will include aspects of site accessibility, such as road access, available parking and the presence of a fishing pier, all of which make fishing at the site possible and enhance enjoyment of the activity.
- **Ecosystem-Derived Benefits** - The contribution to social welfare of ecosystem goods and services. In the ESRP, the term applies specifically to net improvements in social welfare that result from changes in the quantity or quality of ecosystem goods and services attributable to policy or environmental decisions.
- **Indicator of Final Ecosystem Service** – Biophysical feature, quantity, or quality that requires little further translation to make clear its relevance to human well-being (*i.e.*, "public-friendly" measurement)

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4
Coral Reefs: Shoreline Protection

4.1 Defining the service

Coral reefs form natural barriers along the coast, protecting coastlines from erosion, flooding, and storm damage (UNEP-WCMC 2006; WRI 2009). In general, the term "shoreline protection" refers to the ability of reefs to attenuate offshore wave energy, providing sheltered nearshore waters, and protecting coastlines from erosion, flooding, and storm damage. Shoreline protection has been defined in various ways, including intermediate biophysical ecosystem services endpoints that are indirectly relevant to human well-being, final ecosystem services endpoints that are directly relevant to human well-being, or ecosystem-derived benefits that provide social value (Table 4-1; Wainger & Boyd 2009). However, far greater progress has been made in advancing our understanding of wave energy attenuation than in linking that attenuation to the provision of ecosystem services. The key to quantifying shoreline protection is to understand the links between reef attributes, physical processes, and benefits relevant to society.

Table 4-1. Measures that have been used to quantify shoreline protection

Ecological processes
Physical processes
• Reduction in wave energy, velocity, or height
Biological processes and structures
• Damage to coral reefs by hurricanes and storm events
• Presence of seagrasses or mangroves
• Fish density and species composition
Ecosystem services
• Rates of beach or shoreline erosion
• Shoreline geography
• Wave set-up during extreme events
• Coastal inundation during extreme events
Socioeconomic benefits
• Reduced property damage or loss of life during extreme events
• Dollar value of avoided damages during extreme events
• Dollar value to build artificial wave breaks

Categories derived from Wainger & Boyd 2009

The physical properties of wave attenuation have been measured and modeled in studies of numerous locales worldwide, including the Caribbean (Lugo-Fernandez *et al.* 1998), Australia (Hardy & Young 1996), and Hawaii (Gerritsen 1981). Ocean waves traveling over coral reefs experience significant attenuation of energy, height, and velocity (Wolanski 1994; Gourlay & Colleter 2005; Lowe *et al.* 2005). Wave attenuation by coral reefs has biological consequences for the reef itself as well as inshore ecosystems:

- shelter is provided to nearshore coral from damaging effects of hurricanes (Woodley et al. 1981);
- low-energy environments are created that are favorable to the growth of highly valued wetlands, including seagrasses and mangroves (Birkeland 1985); and,
- recruitment and nursery habitats (mangroves and seagrasses) for fish are protected (DeMartini et al. 2009).

Shoreline protection has also been quantified using metrics that are more directly relevant to humans. Wave energy moderation provided by reefs can greatly influence the geography of the coastline (Black & Andrews 2001) and reduce the rate of shoreline erosion (Frihy *et al.* 2004). The value of such ecosystem services is often underappreciated until expensive beach restoration (Riopelle 1995) or artificial breakwaters are needed to protect eroding beaches (Berg *et al.* 1998; Talbot & Wilkinson 2001). Reefs also play an important role in mitigating coastal flooding caused by natural hazards, such as large storms, hurricanes or cyclones, and tsunamis, which can cause immense property damage and loss of human life (Sudmeier-Rieux *et al.* 2006).

Quantifying shoreline protection in terms of hazard mitigation is challenging and often anecdotal. Although hurricanes or cyclones occur worldwide, much of the information on coastal flooding, property damage, and loss of life comes from examining the effects of reefs in mitigating tsunami damage in Asian countries (UNEP-WCMC 2006). Recent extreme events undoubtedly color the interpretations of shoreline protection, as do regional differences in geography, coastal development, and frequency of storm events (WRI 2009).

4.2 Providing the service

4.2.1 *Presence of the reef*

The scientific evidence for shoreline protection by coral reefs is largely anecdotal and observational, quantified by various physical, biological, and social endpoints with and without the presence of reefs (Table 4-1). The presence of coral reefs has long been known to provide wave-sheltering and protection to the coastline, with locals utilizing calm waters for navigation routes, fishing, and recreation (UNEP-WCMC 2006). The presence of reefs is associated with:

- the inshore presence of seagrasses and mangroves (Birkeland 1985; Ogden & Gladfelter 1983; Short et al. 2007);
- a reduction in offshore wave energy reaching the shoreline (Lugo-Fernandez et al. 1998);
- reduced rates of shoreline erosion (Hayden et al. 1978); and,
- reduced property damage and loss of life during extreme events (EJF 2005; UNEP-WCMC 2006).

Furthermore, the presence of certain reef types or species (*e.g.*, patch reef, *Acropora* spp., or *Montastraea* spp.) has also been used to characterize the relative magnitude of wave energy attenuation (Mumby *et al.* 2008).

4.2.2 *Reef attributes*

Beyond the presence or absence of a reef, key attributes such as reef height, width, and topography (see Table 4-2) need to be monitored to provide a more detailed understanding of wave energy attenuation.

The contribution of reef attributes to the hydrodynamic processes governing wave energy attenuation by coral reefs have been extensively modeled and studied with field observations (Monismith 2007). The general idea is that incoming waves break at the face of the reef, causing an initial increase in water level within the surf zone, which pushes waves over the reef flat as they travel to shore (Figure 4-1). Offshore wave height and propagation over the reef will determine the height of waves reaching the shore, typically quantified by the wave set-up (the increase in water level above the still water level) and wave run-up (the height along the beach that water reaches due to incoming waves).

Table 4-2. Reef attributes that contribute to wave attenuation. Definitions are a synthesis of those used in literature (see Appendix 4-A; also Figure 4-1 and Glossary)

Attribute	Definition
Presence of reef	indicates whether or not an offshore reef is present near the coastal area of interest.
Reef continuity	the extent to which the reef is uninterrupted or unfragmented in distribution; namely, the absence of large gaps such as those due to degradation or coral mining.
Reef depth	the distance from the ocean surface to the top of the reef; may be an assumed or fixed value in simulation models, or an average value from field observations for the reef in question.
Reef distance	the distance between the reef crest at the seaward edge of the reef and the edge of the shoreline; essentially, the width of the lagoon; may be an assumed or fixed value in simulation models, or an average value from field observations for the reef in question.
Reef height	the distance from the top of the reef to its base; may be an assumed or fixed value in simulation models, or an average value from field observations for the reef in question.
Reef roughness	the bottom drag coefficient (which characterizes friction); may be approximated in field studies by variability in colony height, or other measures of topography, along the reef flat; may be estimated indirectly by fitting models to data on wave energy attenuation.
Reef slope	the angle, from gradual to steep, of the reef front where offshore waves are first encountered; may be an assumed or fixed value in simulation models, or an average value from field observations for the reef in question.
Reef type	describes the general structure of the reef and its relationship to the shoreline, including fringing reefs that border the shoreline, barrier reefs that are separated from shore by a deep lagoon, atoll reefs that form a circular barrier around an island, and patch reefs that are small, isolated reef outcrops.
Reef width	the length of the reef flat, the flat expanse of reef from where offshore waves first crest over the reef to the edge closest to the shoreline; may be an assumed or fixed value in simulation models, or an average value from field observations for the reef in question.

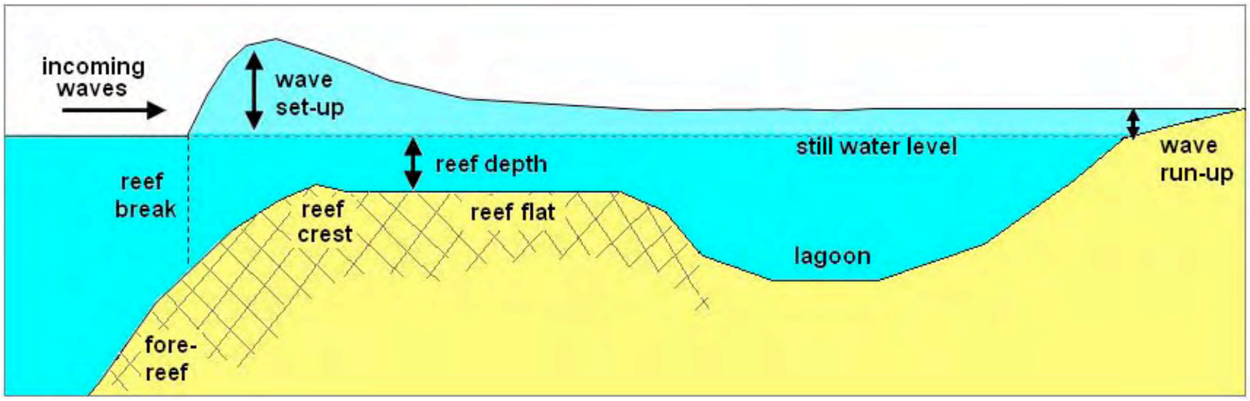

Figure 4-1. Illustration of wave set-up and attenuation over a reef (redrawn from Monismith [2007]).

Coral reefs reduce offshore wave energy primarily in two ways: (1) the steep gradient from deep water to shallow causes the wave to break at the reef crest; and, perhaps more importantly, (2) the increased bottom friction along the reef flat creates drag (Wolanski 1994; Lowe *et al.* 2005). Reef depth is perhaps the simplest single attribute that can be related to wave attenuation (Gourlay 1994; Barbier *et al.* 2008). Reef area, reef slope, and distance from shoreline are additional key attributes derived from field (Young 1989; Hardy & Young 1996; Brander *et al.* 2004) and modeling studies (Tait 1972; Gourlay & Colleter 2005). In general, wave energy attenuation decreases with increasing reef depth across the reef flat, with greater energy being attenuated as reef width increases (Figure 4-2; Kunkel *et al.* 2006), such that broad, shallow reefs provide the greatest attenuation. Tidal variations in water depth and initial offshore wave height can also influence the degree of wave attenuation (Madin *et al.* 2006).

Modeling studies indicate that friction across the reef surface is a strong determinant of the degree of wave energy attenuation, as can be seen in Figure 4-2 (Sheppard *et al.* 2005; Kunkel *et al.* 2006). Drag coefficients used to quantify reef friction in simulation models are often calibrated by comparing model outcomes to field data. These coefficients indicate that coral reefs exert ten times more drag than sandy bottoms (Tait 1972; Roberts *et al.* 1975; Lugo-Fernandez 1998; Reidenbach *et al.* 2006). Measurements of *in situ* reef friction are challenging to obtain. Field estimates of reef roughness based on the standard deviation of reef height have provided values similar to model-calibrated estimates of reef friction(Lowe *et al.* 2005). Other methods for estimating reef roughness have been used, including draping chains over reefs along a transect to generate a linear measure of surface topography. There are as yet no standard methods for deriving wave energy attenuation from field measurements of reef roughness (Monismith 2007).

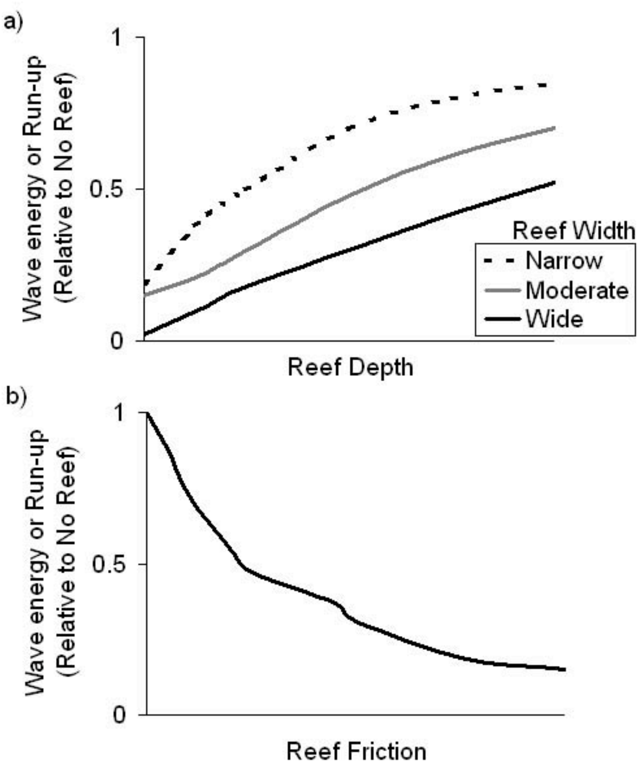

Figure 4-2. Relationship of wave energy with increasing reef depth and width (top) and with increasing reef friction (bottom) (derived from Sheppard *et al.* [2005] and Kunkel *et al.* [2006])

4.2.3 Reef health

The health of a coral reef is an important determinant of wave attenuation. Degraded reefs have diminished roughness, and model simulations indicate the reduction in reef friction reduces the reef's attenuation of wave energy (Figure 4-2; Kunkel *et al.* 2006; Sheppard *et al.* 2005). A reduction in reef friction of approximately 50% could produce a doubling of wave energy reaching the shores behind those reefs. Dead corals on degraded reefs break or disintegrate easily under wave action, resulting in reduced reef height and roughness and, consequently, in reduced attenuation of wave energy. In general, the degree of shoreline protection afforded by reefs during storms reflects a balance between the reef's attenuation of wave energy and the damage inflicted on the reef itself by that storm event (Lacambra *et al.* 2008).

Reef continuity is another important indicator of shoreline protection (WRI 2009). Damage to reefs from coral mining , in which large sections of coral are harvested to provide blocks for construction, can accelerate rates of beach erosion and require expensive beach restoration (Riopelle 1995). Fragmented reefs can allow high energy tsunami waves to reach the shoreline (Nott 1997) and may intensify flooding (Fernando *et al.* 2005; Chatenoux & Peduzzi 2005). Furthermore, sections of degraded reef that have been invaded by macroalgæ may afford less protection than reefs with a high abundance of large stony coral species (Mumby *et al.* 2008).

Shoreline protection may be devalued by as much as 80%–90% when reefs are degraded (Burke & Maidens 2004). For valuation purposes, reefs are assumed to retain their protective capacity until coral cover (living tissue) loss exceeds 25%, after which the value of coastal protection declines linearly with increasing loss of coral (Cesar 1996; Pet-Soede *et al.* 1999). The most extreme degradation leads to loss of reefs, which can have severe consequences for property damage and human life in the case of extreme hazard events (Sudmeier-Rieux *et al.* 2006).

4.3 Measuring the service

Shoreline protection has been quantified in numerous ways that vary in their relevance to human well-being (Table 4-3). Natural features, including reef attributes and physical variables, have been translated into metrics of shoreline protection using anecdotal information, statistical relationships, and mechanistic models. Estimates of coastal protection also depend on socioeconomic variables.

4.3.1 Physical processes

Incoming waves encountering the steep gradient at the reef front causes the waves to break, producing a sudden increase in wave amplitude that diminishes (or attenuates) as the residual wave energy moves toward shore (Figure 4-1). Numerous field, laboratory, and modeling studies have looked at physical endpoints of shoreline protection in terms of reductions in wave energy, wave height, or wave velocity from offshore to the shoreline (reviewed in Gourlay & Colleter [2005], Sheppard *et al.* [2005], and Monismith [2007]; see Table 4-3). Field studies have measured as much as a 68%–95% reduction in wave energy as waves travel over the reef flat (Roberts *et al.* 1975; Gerritsen 1981; Young 1989; Lugo-Fernandez *et al.* 1998; Brander *et al.* 2004). Tidal variations in reef depth will produce variations in the degree of wave energy attenuation. At high tide, waves within the normal range may be reduced only slightly by the reef, whereas at low tide all waves may effectively be blocked (Madin *et al.* 2006). Attenuation of wave energy and height are essential for understanding the height of wave inundation on the shore, referred to as wave run-up, which also has been modeled (Kunkel *et al.* 2006). Wave run-up may be a potential indicator of damage from flooding, and physical models can be used to translate reductions in wave height into flood hazard maps, depending on the slope and porosity of the shoreline (FEMA 2007).

4.3.2 Biological processes

Shoreline protection by coral reefs has also been quantified through the health and survival of highly valued biological components in near-shore areas and along the coast. For example, the presence of outer reefs can shelter nearshore coral from damaging effects of hurricanes (Woodley *et al.* 1981). The protection afforded by coral reefs also creates low-energy environments favorable to the growth of seagrasses or mangroves in coastal wetlands (Ogden & Gladfelter 1983; Birkeland 1985; Short *et al.* 2007; Sheaves 2009). Reefs reduce the vulnerability of wetlands to damage and vegetative loss during hurricane events (Fourqurean & Rutten 2004). Wetlands themselves provide numerous ecosystem services (Mumby *et al.* 2008) and in many regions are more important for coastal protection than the presence of reefs (EJF 2005; Cochard *et al.* 2008). Reefs appear to serve as a first line of defense by diffusing wave energy and protecting coastal wetlands, thereby enhancing the protective value of those wetlands. Whether there exists a synergistic relationship between wave energy attenuation by reefs and shoreline protection by mangrove and seagrass wetlands has not been studied.

Table 4-3. Measures used to quantify shoreline protection, and the major reef attributes, physical parameters, and socioeconomic parameters used to estimate that protection's value (see Appendix 4-A for details)

Measures	Reef Attribute	Physical Variables	Socioeconomic Variables
Physical processes			
Reduction in wave energy, velocity, or height in appropriate units	Reef depth, width, slope, roughness, distance to shore	Offshore wave energy & height; Tidal depth	
Biological processes			
Damage to coral by hurricanes (*e.g.*, prevalence of broken coral)	Presence of outer reef; Reef depth, width, slope	Hurricane path	
Presence of seagrasses or mangroves (*e.g.*, area)	Presence of reef; Gap in reef		
Fish density & species composition	Presence of reef	Water motion; Wind or wave exposure	
Ecosystem services			
Rates of shoreline erosion (*e.g.*, distance or volume lost per year)	Presence of reef; Reef depth	Wave energy; Beach elevation & sediment grain size	
Shoreline geography (*e.g.*, presence of salients & tombolos, change in shoreline position)	Reef width; Distance from shoreline	Wave height and period	
Wave set-up during extreme events	Presence of reef; Reef depth, width, slope, & roughness	Offshore wave energy, height, & amplitude	
Coastal inundation during extreme events (*e.g.*, decrease in area inundated)	Presence or area of reef; Gap in reef;	Distance from hazard event; Slope of coastline;	
Socioeconomic benefits			
Decrease in property damage or loss of life during extreme events	Presence of intact reefs		
Value of avoided damages	Presence of reef; Reef type, continuity, & distance from shore	Coastal geography; Storm height & frequency	Property values
Replaces need for costly artificial breakwaters or beach replenishment	Presence of reef		Breakwater costs; Restoration costs

Reductions in wave energy by reefs may also provide prime wave-sheltered habitat for larval fish and enhance local recruitment. Lower water velocities and reduced wave exposure are associated with high juvenile fish densities (Burgess *et al.* 2007; DeMartini *et al.* 2009). Fish assemblages in wave-sheltered reefs often have different species than exposed habitats, including small fish species whose locomotion and foraging activities may be inhibited in fast-moving water (Fulton & Bellwood 2005). Increased fish abundance would likely increase fishing and tourism services, something that has been discussed anecdotally (UNEP-WCMC 2006) but not linked directly to the physical processes of wave energy attenuation.

4.3.3 Ecosystem service measures

Physical hydrodynamic processes associated with coral reefs affect the geography, appearance, and stability of the shoreline. The strength and pattern of waves reaching the beach determine rates of beach erosion and shapes the contours of the shoreline (Hayden *et al.* 1978). Models have been developed to predict rates and patterns of shoreline changes under a variety of wave conditions (Frihy *et al.* 2004). Assuming the edge of the shoreline may change by an average of 0.4 meters per year in unprotected areas, an example of a quantitative measure of an ecosystem service is given in Berg *et al.* (1998), who estimated that 1 km^2 of reef, protecting 5 km of shoreline along the coast of Sri Lanka could prevent a loss of 2,000 m^2 of land per year. The presence of reefs can also influence the contour of the shoreline through the creation of salients (bell-shaped extensions of the shoreline toward the reef) and tombolos (shoreline extensions connecting to offshore sandbars) (Figure 4-3). The size of these shoreline extensions depends on the width of nearby reefs and reef distance offshore (Black & Andrews 2001). Coral reefs also play a role in replenishing sandy beaches and islands as corals and other calcified organisms break down after death (UNEP-WCMC 2006).

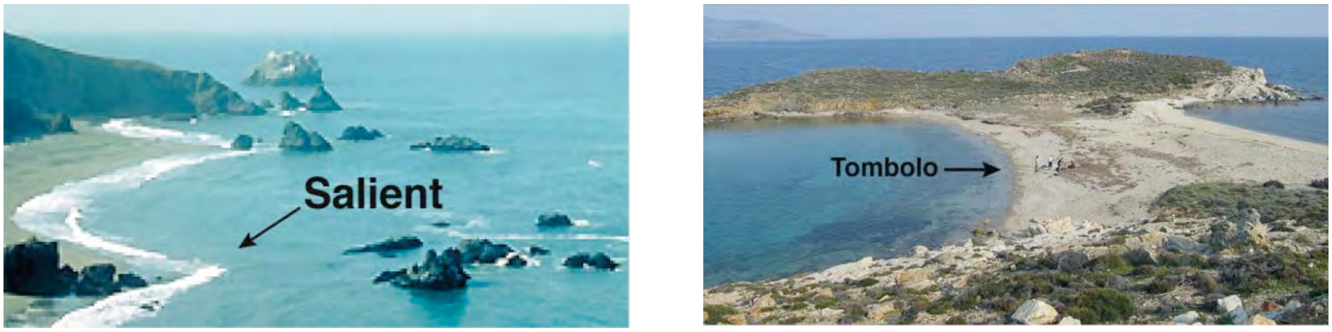

Figure 4-3. Reef influences on shorelines: salient (left) and tombolo (right).
(photo credits: salient – California State Parks [2011]; tombolo – Tim Bekaert [2005])

Reductions in wave energy or wave height by coral reefs have clearer socioeconomic relevance when connected to wave run-up or coastal flooding during storm or extreme hazard events. Numerous studies that have examined wave run-up during tsunami events suggest that, while there is some evidence of reduced flooding in areas behind reefs (Fernando *et al.* 2005), channelized or fragmented reefs may actually accelerate movement of tsunami waves to the coastline (Nott 1997; Chatenoux & Peduzzi 2007). Modeling studies indicate the buffering ability of reefs is largely dependent on the state of reef health (Kunkel *et al.* 2006). In other observational studies, however, reefs appeared to have little protective value, and tsunami inundation was largely determined by wave height and coastal topography (Baird *et al.* 2005). Coral reefs may be more effective at buffering normal wave action or storm events than tsunamis, which have longer wavelengths and larger wave amplitudes (Cochard *et al.* 2008).

4.3.4 Socioeconomic benefits

The value of reefs in shoreline protection is often underappreciated until quantified in terms of human lives, property damage, or economic costs. Anecdotally, the presence of reefs is linked to diminished property damage and loss of life during hurricanes (Whittingham *et al.* 2003) or tsunamis (Liu *et al.* 2005; WI 2005; UNEP 2005; EJF 2005; UNEP-WCMC 2006). In one study of a tsunami's effects, areas protected by reefs experienced wave heights of only 2–3 m with inundation extending only 50 m inland with no loss human life (Fernando *et al.* 2005). In contrast, just 3 km to the north where there was no coral reef to protect the shore, the same tsunami resulted in a 10 m wave that flooded 1.5 km inland and killed 1,700 people. This evidence is largely anecdotal, however, and there is some question as to whether reefs substantially reduce coastal inundation during tsunami events (Baird *et al.* 2005; Cochard *et al.* 2008).

Although shoreline protection can be a significant contributor to the total economic value of coral reefs, it is largely underestimated by decision-makers, except during times of crisis. A few studies (see below) have attempted to place a dollar value on coastal protection by reefs, either in terms of expected damages or beach/shoreline replacement costs due to reef degradation (Chong 2005).

4.4 Valuing the service

There are many coral reef studies estimating costs of reef restoration, fisheries value, or recreational value, but only a few studies have looked at the economic value of shoreline protection (Chong 2005; Table 4-4). One approach to valuing coastal protection is to estimate defensive expenditures required to replace the loss of the reef. When reefs are severely degraded, they may need to be replaced with artificial breakwaters that may cost $10m per linear kilometer to construct (Wells & Edwards 1989; Weber 1993; Berg *et al.* 1998; Talbot & Wilkinson 2001). In other cases, expensive beach and shoreline restoration is needed as a consequence of lost coral reefs (Riopelle 1995).

Another approach to estimating the economic value of coastal protection is to estimate the damages avoided due to the presence of the reef. In a study of Indonesian Reefs, Cesar (1996) estimated the monetary value of damage avoided based on the value of three types of coastal development: (1) the value of agricultural production ($820 per km coastline); (2) the cost of replacing homes and road infrastructure ($50,000 per km coastline); and, (3) hotel expenditures toward maintaining beaches ($1,000,000 per km coastline). These values, or similarly derived values, have been used to value damages avoided due to the presence of reefs in Bermuda (Beukering *et al.* 2010), the Philippines (White *et al.* 2000), throughout the Caribbean (Burke & Maidens 2004), southeast Asia (Burke *et al.* 2002), and worldwide (Cesar *et al.* 2003).

The economic value of coral reefs depends on more than just the presence of the reef. Reliable economic estimates require knowledge of biological, physical, and socioeconomic factors that influence the provision of and need for coastal protection

(WRI 2009). First, the value of shoreline protection will depend on whether the coastal area is vulnerable to erosion or storm damage, namely low-lying lands near the coast. Second, coastal vulnerability is determined by the physical stability of the shoreline (including coastal geomorphology and geology, elevation, and vegetation) and the potential for storm surges (including offshore wave energy and hurricane frequency). Third, reef attributes such as distance from shore, reef continuity, and type of reef determine the protective capability of the reef. Fourth, the amount and value of coastal development will determine the potential value of protection. All of these factors must be considered when estimating the potential economic damages resulting from the loss of reefs. This approach has been used to estimate the value reef coastal protection throughout the world as ranging from $0.3 billion to $2.2 billion (Burke *et al.* 2002; Burke & Maidens 2004). Coastal development, sedimentation, pollution, overfishing, and climate change can severely degrade reefs, reducing their protective ability by an estimated 80–90%, with a potential net loss of benefits associated with shoreline protection on the order of $140m to $420m per year in the Caribbean (Burke & Maidens 2004).

Table 4-4. Estimated values of shoreline protection (modified from Chong 2005)

Location	Total Value	Study
Americas		
Bermuda	$266m	Beukering *et al.* 2010
Caribbean	$720m	Cesar *et al.* 2003
Caribbean	$700m–$2,200m	Burke & Maidens 2004
USA	$172m	Cesar *et al.* 2003
Asia		
Australia	$629m	Cesar *et al.* 2003
Indian Ocean	$1,595m	Cesar *et al.* 2003
Indonesia	$314m	Burke *et al.* 2002
Japan	$268m	Cesar *et al.* 2003
Philippines	$326m	Burke *et al.* 2002
SE Asia	$5,047m	Cesar *et al.* 2003
Pacific	$579m	Cesar *et al.* 2003
Sri Lanka	$30m	Berg *et al.* 1998
World	$9,009m	Cesar *et al.* 2003
Values per kilometer of shoreline		
Caribbean		
Low development	$2,000–$20,000	Burke & Maidens 2004
Medium development	$30,000–$60,000	Burke & Maidens 2004
High development	$100,000–$1,000,000	Burke & Maidens 2004
Indonesia		
Remote areas	$820	Cesar 1996
Some construction	$50,000	Cesar 1996
Major infrastructure	$1,000,000	Cesar 1996
Philippines	$5,000–$25,000	White *et al.* 2000
Maldives	$10,000,000	Talbot & Wilkinson 2001

4.5 Reflections

Final ecosystem services for shoreline protection are summarized in Table 4-5. Natural features, including reef attributes and physical variables, contribute to biophysical processes that provide ecosystem services, such as wave energy attenuation. These natural processes directly benefit humans by reducing shoreline erosion and protecting coastlines from inundation during extreme events. Social values, such as the desirability of coastal housing or the attractiveness of sandy beaches, influence the demand for shoreline protection. Complementary goods and services, such as the availability, intensity, and location of coastal development or the absence of constructed breakwaters, influence the opportunity to take advantage of shoreline protection. The existence of constructed breakwaters, including rubble mounds and artificial reefs, can also diminish the demand for shoreline protection by natural reefs.

4.5.1 Improving current knowledge

Physical models of wave energy attenuation are based on relatively simple physical assumptions, so field validation of mathematical models of wave energy attenuation would improve our ability to characterize the degree of protection provided under different conditions (Monismith 2007). Furthermore, the reef is generally treated as a single object, rather than a living community. Although some models have attempted to connect reef roughness to wave energy attenuation (Sheppard *et al.* 2005; Kunkel *et al.* 2006), there is little understanding of how reef attributes, such as species composition or skeletal calcification rates, contribute to wave attenuation, or how growth, reproduction, and survival contribute to sustainable shoreline protection.

Our understanding of the social benefits of shoreline protection is largely derived from anecdotal evidence, but it could be improved with more quantitative or statistical studies relating property damage or loss of life to reef attributes and physical properties of the coastline. Furthermore, studies of flooding or potential damage during extreme events are largely tied to tsunamis (UNEP-WCMC 2006). Less is known about the extent to which reefs reduce hurricane damage, but the protection provided by reefs may result from buffering wave energy rather than reducing inundation (Cochard *et al.* 2008).

The presence of reefs is associated with providing wave-sheltered environments for mangroves and seagrasses (Birkeland 1985), yet there is little understanding of how subtle changes in reef integrity may impact these neighboring systems. Furthermore, wetlands themselves are important for coastal protection and their protective ability may be enhanced by the presence of reefs as a first line of defense (EJF 2005). However, the potential synergistic relationship between reef shoreline protection and the provision of wetland ecosystem services is not well understood.

Few studies have attempted to quantify or value indirect consequences of shoreline protection by reefs (Chong 2005). Direct consequences of storm events, hurricanes, and tsunamis include loss of lives, housing, and buildings. These direct losses can have long-lasting reverberations as the affected society becomes vulnerable to disease epidemics or economic instability (Cochard *et al*. 2008). The potential value of shoreline protection will depend on the likelihood of such indirect consequences, and the potential for the local economy to rebound from disasters. Historical data on disease outbreaks, economic losses, and time to economic recovery for post-hurricane or post-tsunami economies might suggest which societies are particularly vulnerable to a loss of shoreline protection. The current lack of consideration of indirect consequences is an oversight that may lead decision makers to underestimate the potential value of shoreline protection.

4.5.2 Connecting biophysical processes and ecosystem services to socioeconomic benefits

For biophysical endpoints to be relevant to humans, they must connect to an ecosystem service or social benefit (Wainger & Boyd 2009). Ideally, our ability to quantify shoreline protection in socially relevant endpoints requires that we characterize two relationships in quantitative terms: (1) that between reef attributes and the physical environment; and, (2) that between the physical environment and ecosystem services, including their social benefits (Figure 4-4). Natural features of the environment, including attributes of the reef and physical attributes of offshore waves, affect physical ecosystem processes, such as attenuation of wave height or energy. Attenuation of wave energy by reefs leads to protection from shoreline erosion or flooding, but the degree of protection will depend on physical variables, such as coastal geography, vegetation, and the frequency of storm events. Humans derive benefits from shoreline protection through reductions in property damage or loss of life, but the value of protection will depend on socioeconomic factors, such as the degree of coastal development and property values (WRI 2009). Wave energy attenuation can also indirectly benefit humans by providing wave-sheltered habitats for fish or protecting wetlands, which themselves provide ecosystem services.

The quantitative relationships between reef attributes and shoreline protection and between physical processes and socioeconomic benefits are poorly understood. Models of wave energy attenuation are reasonably adept at accounting for the impacts of reef attributes such as height, width, slope, and roughness (Lowe *et al.* 2005; Sheppard *et al*. 2005; Kunkel *et al.* 2006). However, our understanding of the socioeconomic benefits, such as the prevention of property damage or loss of life, is largely anecdotal, based solely on the presence or absence of a reef (UNEP-WCMC 2006). Further research and modeling efforts are needed to provide useful quantifications of these relationships.

Table 4-5. Final ecosystem services and supporting features for shoreline protection

Ecosystem Service(s)		Natural Features	Social Values	Complementary Goods & Services	Ecosystem-Derived Benefits	Potential Indicators of Final Ecosystem Service(s)
Final (FES)	Intermediate					
Shoreline Protection						
Protection from shoreline erosion	Decreased erosion in kg/ha/y Reduction in wave energy, velocity, or height Presence of reef	Reef height, width, slope, & roughness	Reef continuity Offshore wave energy & wave height Tidal depth	Beach elevation, sediment grain size Attractiveness of sandy beaches	Desirability of housing near water Absence of constructed breakwaters Higher property values	Opportunity to use beaches (see Chapter 2) % reduction in rates of shoreline erosion due to presence of reef
Protection from coastal inundation during extreme events area in hectares protected Reduction in wave set-up, or storm surge Presence of reef	Reef height, width, slope, roughness	Reef continuity Wave energy	Distance from hazard event	Slope of coastline	Frequency & intensity of extreme events Past history of extreme events Absence of constructed breakwaters	Location, intensity, and value of coastal development Lower insurance rates

***Definitions** (proposed by the Ecosystem Services Research Program and currently under discussion by the Program)*

- **Final Ecosystem Service** – Output of ecological functions or processes that directly contributes to social welfare or has the potential to do so in the future (broadly based on Boyd & Banzhaff [2007]).
- **Intermediate Ecosystem Service** - Output of ecological functions or processes that indirectly contributes to social welfare or has the potential to do so in the future.
- **Natural Features** – The biological, chemical, and physical attributes of an ecosystem or environment.
- **Social Values** – The social attributes that influence economic demand for an ecosystem service.
- **Complementary Goods & Services** - Inputs (usually built infrastructure or location characteristics) that allow a good or service to be used by complementing the ecological condition. For example, complementary goods and services that allow the presence of fishable fish to become an opportunity for recreational fishing will include aspects of site accessibility, such as road access, available parking and the presence of a fishing pier, all of which make fishing at the site possible and enhance enjoyment of the activity.
- **Ecosystem-Derived Benefits** - The contribution to social welfare of ecosystem goods and services. In the ESRP, the term applies specifically to net improvements in social welfare that result from changes in the quantity or quality of ecosystem goods and services attributable to policy or environmental decisions.
- **Indicator of Final Ecosystem Service** – Biophysical feature, quantity, or quality that requires little further translation to make clear its relevance to human well-being (*i.e.*, "public-friendly" measurement)

One possible approach for linking reef attributes with socioeconomic benefits of shoreline protection would be to integrate socioeconomic metrics into physical process models. Wave attenuation by reefs has been fairly well characterized in laboratory experiments, field observations, and models (as reviewed in Gourlay & Colleter [2005], Sheppard *et al.* [2005], and Monismith [2007]), and it has been connected to shoreline changes using predictive models (Frihy *et al.* 2004). However, for all intents and purposes, there are no studies connecting changes in wave energy or height to potential loss of life or property damage. The Reefs at Risk shoreline protection index (WRI 2009), which is used to calculate the damage prevention provided by reefs, indirectly accounts for a number of physical processes by considering key reef attributes related to wave attenuation. In addition to reef distance from shore, Reefs at Risk includes reef type as a proxy for reef depth and slope, and reef degradation as a proxy for bottom friction. However, these factors are combined into a single index reflecting shoreline stability and fail to capture more subtle changes in reef topography or species composition that may influence wave energy attenuation.

Bayesian probabilistic networks could be useful for characterizing the complex relationships between reef attributes and probabilistic characterizations of exposure, damage, and cost (Cochard *et al.* 2008). Physical models of wave energy attenuation that permit subtle changes in reef height, slope, width, and friction, combined with the physical properties of the coastline and local climate, could be the basis for developing predictive models for the probability of flooding or shoreline erosion. These could then be tied to socioeconomic factors, such as the degree of coastal development, to predict the probability of property damage, loss of life, or a variety of indirect consequences. Such models could reflect the uncertainty associated with largely anecdotal information and could be updated as probabilistic characterizations of relationships or physical process models are improved.

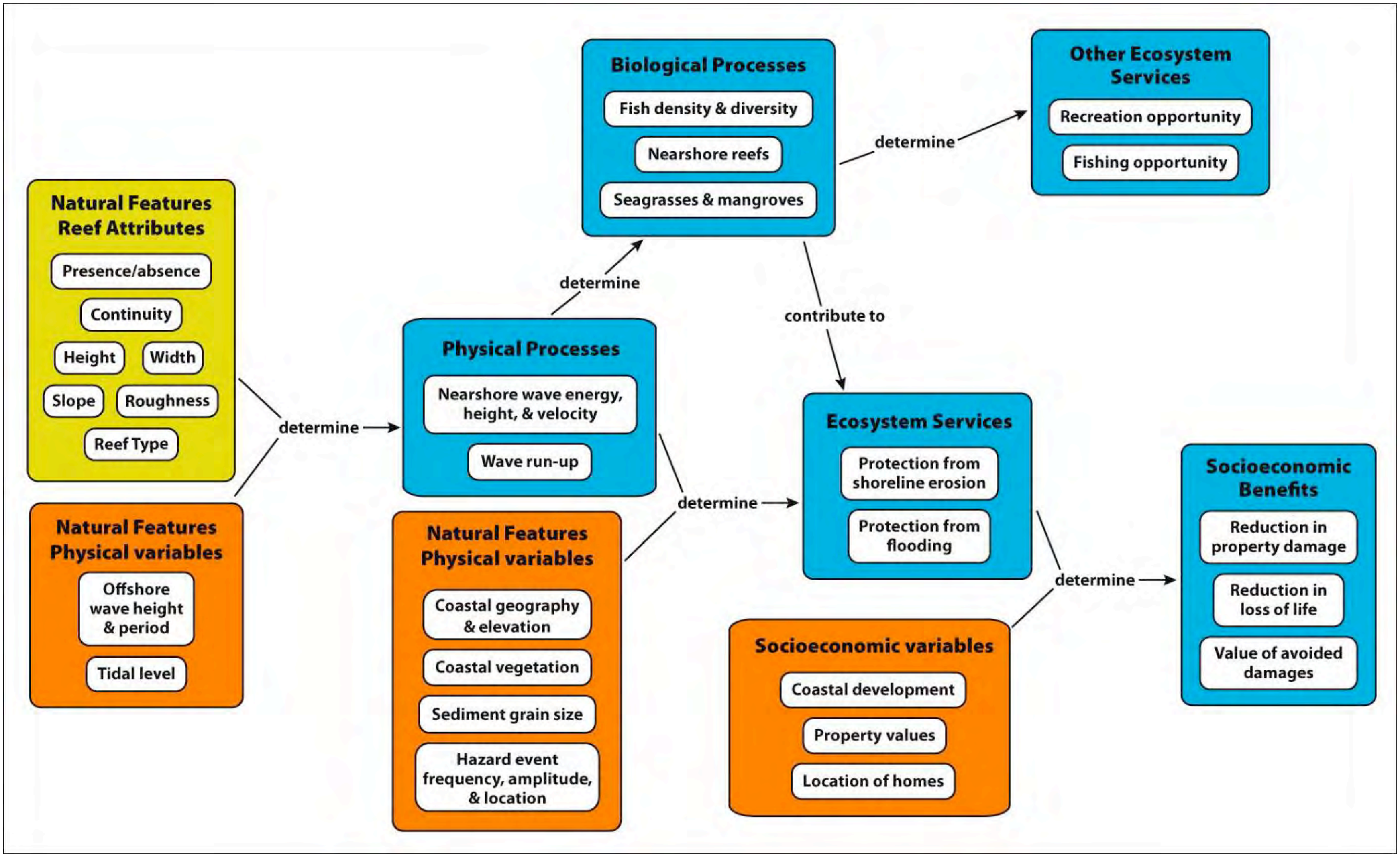

Figure 4-4. **Conceptual diagram showing how reef attributes (yellow), and various physical or socioeconomic variables (orange), can be used to determine various endpoints quantifying shoreline protection (blue).**

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Appendix 4-A

Studies quantifying shoreline protection

The following table lists studies and the endpoints they used to quantify shoreline protection. Also included are the biological reef attributes and the physical and socioeconomic variables used to estimate that endpoint. The method and location of the studies are also given.

Ecosystem Service Endpoint	Reef Attributes	Physical Variables	Socioeconomic Variables	Method	Location	Citation
Physical processes						
wave height	reef top water depth			Statistical analysis	Australia	Barbier *et al.* 2008
% change in wave height	distance to beach; variation in reef topography; reef depth	low or high tide		Field study	Australia	Brander *et al.* 2004
change in wave height	presence of reef	wave height, water level		Field study	Hawaii	Gerritsen 1981
wave energy reaching shore	reef depth & slope	wave height, water depth		Laboratory study & model	Australia	Gourlay 1994
shore wave energy; wave "set-up"; wave velocity	reef top water depth (reef height); reef friction; reef slope; width of reef flat (distance from shore)	offshore wave height & period		Model	Australia	Gourlay & Colleter 2005
wave height and period; wave spectra; wave breaking	distance along reef flat from reef front; depth over reef flat	wave height		Field study	Australia	Hardy & Young 1996
wave attenuation, spectra	presence of reef flat	tidal level		Field and laboratory studies	Japan	Kono & Tsukayama 1980
change in wave height; rate of wave dissipation	reef roughness (standard deviation in reef height); presence of reef flat; presence of fore reef	fore reef wave height, wave frequency, seawater density, etc.		Model & field study	Hawaii	Lowe *et al.* 2005
wave set-up; wave spectra	presence of reef crest, reef flat, lagoon	tide level		Field Study validation of Tait's model	Caribbean	Lugo-Fernandez *et al.* 1998
loss of wave height, velocity, and acceleration	distance from reef crest; model-calibrated reef friction parameter	wave height, period; tide level		Field validation of model	Australia	Madin *et al.* 2006
wave energy dissipation	presence of mangroves, sea grass, patch reef, *Acropora*, algal, gorgonians, or *Montastraea*			Field study & literature review	Caribbean	Mumby *et al.* 2008
wave energy dissipation spectra over range of frequencies	presence of reef crest, reef flat			Field study	Caribbean	Roberts *et al.* 1975
% offshore energy reaching the shore	reef top water depth (reef height); reef friction; reef slope; width of reef flat (distance from shore); relative area of live, dead, eroded coral, sand, rubble, seagrass, or algal turf	offshore wave height & period		Model	Indian Ocean	Sheppard *et al.* 2005

Ecosystem Service Endpoint	Reef Attributes	Physical Variables	Socioeconomic Variables	Method	Location	Citation
Physical processes (con't)						
reduction in wave height	presence of reef front, reef flat; distance from reef front; depth at reef crest; fore reef slope	offshore wave height & period; beach slope		Model	Hawaii	Tait 1972
wave dynamics; hydrodynamic processes	reef slope, height, depth	offshore wave height & period		Model	Australia	Wolanski 1994
wave attenuation; wave spectra; area of influence	presence of reef flat, fore reef; reef flat water depth; reef area	incident wave height		Field study	Australia	Young 1989
Biological processes processes						
damage to coral by hurricane	reef profile (depth, slope, & shelf width); presence of reef crest			Model	Jamaica	Woodley *et al.* 1981
low energy environment favorable for growth of mangroves and seagrasses	presence of reef			Anecdotal (review)	Caribbean & Pacific	Birkeland 1985
loss of seagrass vegetation	presence of reef; gap in reef			Field observations	Florida	Fourqurean & Rutten 2004
low energy environment favorable for growth of mangroves and seagrasses	presence of reef			Workshop summary	Caribbean	Ogden & Gladfelter 1983
presence of mangroves	presence of reef flats			Review, anecdotal	Global	Sheaves 2009
presence of seagrasses	presence of reef	wave sheltered		Mapping, anecdotal	Global	Short *et al.* 2007
presettlement fishes	presence of reef	tidally generated eddies		Field study	Australia	Burgess *et al.* 2007
larval fish densities	presence of reef	wind/wave exposure		Field study	Hawaii	DeMartini *et al.* 2009
fish assemblages	sheltered reef vs. wave-exposed fore-reef	water motion (flow velocity & rates of direction change)		Field study	Australia	Fulton & Bellwood 2005
Ecosystem services						
shift in shoreline due to erosion	hydrographic profile of seabed composition [reef face vs. sand], reef depth	waves (height, direction, period), current, sediment (grain size), water depth		Model	Egypt	Frihy *et al.* 2004
beach sand erosion	presence of reef	wave energy (height & period of waves at beach); beach elevation; height of sand deposition; beach elevation; sediment grain size		Field study	U.S. Virgin Islands	Hayden *et al.* 1978
formation of salients and tombolos	ratio of length of reef along shoreline to distance of reef from undisturbed shoreline; completely submerged	wave climate		Statistical analysis	Australia	Black & Andrews 2001

Ecosystem Service Endpoint	Reef Attributes	Physical Variables	Socioeconomic Variables	Method	Location	Citation
Ecosystem services (con't)						
tsunami run-up relative to no reef	depth and width of reef flat; width of lagoon (offshore distance to the reef); bottom drag coefficient ("reef health"); presence, width, and location of a gap	tsunami wavelength and amplitude		Model	Indian Ocean	Kunkel *et al.* 2006
reduction in wave height during cyclone	presence of reef			Field study and model	Australia	Young & Hardy 1993
coastal flooding	% coral protection; % seagrass; % mangrove; reef orientation	distance from tsunami fault line, sea bed depth 10 km offshore, length of slope		Statistical analysis	Indian Ocean	Chatenoux & Peduzzi 2007
tsunami height & inundation; tsunami damage (structures destroyed, deaths)	presence of reef or gap in reef			Observational	Sri Lanka	Fernando *et al.* 2005
coastal flooding	reef profile (depth, slope, & shelf width); reef continuity; reef area; reef topography; terrace width; species distribution, geometry, & ecology; species at reef front more resistant	extreme storm events; distance from hurricane event		Review	Global	Lacambra *et al.* 2008
tsunami run-up, height	gap in reef			Observational	Sri Lanka	Liu *et al.* 2005
tsunami movement to coast	gaps in reef				Australia	Nott 1997
tsunami wave run-up	presence of reef			Review	Global	UNEP-WCMC 2006
Coastal inundation during extreme events	presence of reef	coastal bathymetry		Observational	Indonesia	Baird *et al.* 2005
probability of indirect or direct consequences due to damage from exposure ($p[C_{ID}|D,EX]$)	presence of reef; fragmentation of reef (size & orientation of channels); seagrass or mangrove vegetation structure; orientation to coastline; vegetation relation to landscape morphology; presence of rivers	source distance & coastal geomorphology; type of coastline; profile of coastline; seabed depth; distance to tsunami source; coastline orientation; probability of geologic event	location of human inhabitants relative to hazard & vegetation	Framework	Indian Ocean	Cochard *et al.* 2008
Socioeconomic benefits						
human deaths & loss of property	presence of intact reefs			Review	Indian Ocean	EJF 2005
damage to human lives & livelihoods	presence of reefs			Review	Global	Sudmeier-Rieux *et al.*
damage to human lives & livelihoods	absence of reefs			Observational	Indonesia	UNEP 2005
loss of human life	presence of reefs			Observational	Indonesia	WI 2005
loss of village	presence of reef	cyclone		Observational	India	Whittingham *et al.* 2003
avoided damages				Economic analysis	SE Asia	Burke *et al.* 2002

Ecosystem Service Endpoint	Reef Attributes	Physical Variables	Socioeconomic Variables	Method	Location	Citation
Socioeconomic benefits (con't)						
length of coastline within 2 km of mapped coral reef	presence of healthy coral reef; presence of degraded coral reef	length of coastline		Economic analysis	Caribbean	Burke & Maidens 2004
avoided damages	reef loss		level of shoreline development	Economic analysis	Indonesia	Cesar 1996
avoided damages				Economic analysis	Worldwide	Cesar *et al.* 2003
avoided property damage due to presence of reef	coral reef locations, "role of coral reefs"	coastal profile, susceptible flood zones, shoreline stability, storm regime	historical property damage, property values	Economic analysis	Bermuda	Beukering *et al.* 2010
dollar value of coastal protection	presence of reef			Economic analysis	Philippines	White *et al.* 2000
dollar value of coastal protection	coral loss			Economic analysis	Indonesia	Pet-Soede *et al.* 1999
relative contribution of reefs to shoreline stability	reef type; reef continuity; reef distance from shore	wave energy; hurricane frequency; coastal geology & elevation; coastal vegetation		Economic analysis	Caribbean	WRI 2009
cost of replacement breakwaters				Economic analysis	Sri Lanka	Berg *et al.* 1998
cost to restore eroded beach	damage to reef due to mining			Economic analysis	Indonesia	Riopelle 1995
cost to replace with concrete breakwaters	presence of reefs			Case Study	Maldives	Talbot & Wilkinson 2001
cost of replacement artificial reef	reef loss			Observational	Maldives	Weber 1993
eroding coastline	presence of undamaged reefs	breakwaters	presence of low lying homes, cost to repair breakwaters	Observational	Maldives	Wells & Edwards 1989

5
Coral Reefs: Natural Products

The flora and fauna of coral reef ecosystems are the source for a large number of pharmaceuticals and biochemicals and the inspiration for a wide variety of chemical and structural models. This chapter describes some of these natural products, the ecological forces that create them, and how they can be quantified as an ecosystem service.

5.1 Natural products as sources and templates for pharmaceuticals, biochemicals, and biomaterials

Relative to their terrestrial counterparts, marine ecosystems are latecomers as sources and templates of pharmaceuticals, biochemicals, and other biomaterials. This tardiness is mainly due to their inaccessibility, especially as compared to the easy availability of terrestrial flora and fauna. Consequently, there is no indigenous medicine tradition to draw upon, because there are so few instances (southern China being one) where marine species were used for medicinal purposes (Fenical 1996).

However, advances in undersea technology in the past few decades have gradually opened up marine ecosystems to more systematic exploration. This exploration has revealed marine ecosystems to be complex and species-rich with a vast array of predator-prey relationships that, coupled with the challenges of living in an aqueous medium, have resulted in a myriad of secondary metabolites[1] with extraordinarily complex, and hitherto unseen, structures (Fenical 1997; Gerwick 2008). From 1977–1987, the first decade of intensive marine exploration, about 2,500 previously unknown metabolites were reported (Newman *et al.* 2000). Among the relatively small percentage of marine biochemicals that have been isolated, identified, and tested are pharmaceuticals, nutraceuticals, cosmetics, food additives, antifouling agents, adhesives, and physical and chemical templates in a variety of fields.

5.1.1 Pharmaceutical uses of marine natural products

Natural products have long been used for medicinal purposes. India's use of plants for medicinal treatment dates back over 5,000 years and has become codified in the Ayurveda, which contains over 8,000 herbal remedies. This same system of treatment is still used in over 14,000 dispensaries in India today. During the period in which the Ayurveda was created, a Chinese emperor was describing 365 herbal remedies, including ginseng, opium (the source of codeine and morphine), and ephedra (the source of ephedrine). During the subsequent millennium, the Assyrians listed 250 medicinal plants, and the Sumerians recorded 1,000 plants with medicinal properties (Huxley 1984). A Chinese herbal pharmacopoeia written about 2,000 years ago describes the use of marine seaweeds for medicinal purposes (Bowling *et al.* 2007).

More recently, from 2000 to 2006, about 50% of small molecule[2] new chemical entities[3] were natural products or based on natural products (Newman & Cragg 2007). From 1981 through mid-2006, 63% of all new chemical entities were natural products or based on natural products (Newman & Cragg 2007; Cragg & Newman 2009). However, over 50% of marketable pharmaceutical products are consistently natural products or based on natural products (NRC 1999, p. 73), and half of all cancer drug research is devoted to marine natural products (Fenical 1996). Further, about 50% of the drugs introduced from 1994 to the present are either natural products or based on natural products (Harvey *et al.* 2010).

There are over 10,000 marine biochemicals with potentially useful pharmacological properties, and Appendix 5-A lists over 200 of them, showing their biological source, geographic location, chemical name and structure, the nature of their biological activity, and their approval status, where applicable. There were 36 marine-derived natural products that were in clinical trials (Table 5-1) or approved for use as of 2006 (Table 5-2), and 20 or more that were in the preclinical stage of testing (Simmons *et al.* 2005; Wijffels 2007).

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[1] A secondary metabolite is a substance produced by an organism that seemingly has no direct role in the organism's metabolism, though they are often produced via pathways that are derived from primary metabolic pathways. It is believed that they are created because they confer some evolutionary advantage, particularly in nonmotile organisms. Most often secondary metabolites are used by the organism in intraspecies or interspecies interactions usually related to defense or signaling (*e.g.*, for reproduction) (NRC 1999, pp. 74-75; Croteau *et al.* 2000, pp.1250-1, 1316; Seigler 2002, p. 3; Wink 2003).

[2] "In the fields of pharmacology and biochemistry, a small molecule is a low molecular weight organic compound which is by definition not a polymer. The term small molecule, especially within the field of pharmacology, is usually restricted to a molecule that also binds with high affinity to a biopolymer such as protein, nucleic acid, or polysaccharide and in addition alters the activity or function of the biopolymer. The upper molecular weight limit for a small molecule is approximately 800 Daltons which allows for the possibility to rapidly diffuse across cell membranes so that they can reach intracellular sites of action. In addition, this molecular weight cutoff is a necessary but insufficient condition for oral bioavailability." (Wikipedia 2010)

[3] A new chemical entity is a drug that contains no active moiety that has been approved by the FDA (21CFR314.108).

Table 5-1. Testing stages for new pharmaceuticals

Trial Stage	Nature of Testing
Preclinical	*in vitro* tests and *in vivo* animal model tests for preliminary dose ranging, efficacy, toxicity, and pharmacokinetic evaluation
Phase 0	instituted by FDA in 2006; single, subtherapeutic dose; 10–15 human subjects; on-going evaluation of phase's usefulness, ethics, and claimed benefits (to save money and to speed up the approval process)
Phase I	normally, first stage of human testing; trials assess the drug's safety, tolerability (including maximum tolerable dose), pharmacokinetics (effects of drug), and pharmacodynamics (metabolism of drug); 20–100 healthy volunteers or patients with the target disease
Phase II	continues evaluation of the drug's safety in larger groups of subjects (200–300 patients with the target disease); evaluation of the drug's efficacy, optimal dosing regimen, and side effects; often double-blind tests versus placebo
Phase III	multicenter trials involving hundreds or thousands of subjects; trials attempt to establish the drug's efficacy *vis-à-vis* current best practice and an overall risk-benefit ratio in a demographically diverse sample of patients with the target disease; usually drug versus standard treatment
Phase IV	post-approval monitoring of large populations of patients taking the drug; may evaluate drug's usefulness in treating diseases other than the original target

Source: University of Pittsburgh (2002); Wikipedia (2011).

Table 5-2. Status of marine-derived natural products in clinical trials or clinical use

Compound Name	Source	Status (Disease)	Comment
Abyssomicin C	actinobacterium (*Verrucosispora maris*)	Phase I (antibiotic)	
ACV1 (*aka* **α-conotoxin**)	mollusk (cone snail) (*Conus victoriae*)	Phase I (analgesic)	Metabolic Pharma (Australia)(06/2006); conotoxin Vc1.1
Acyclovir (*aka* **Zovirax®**)	sponge (*Cryptothetya crypta*)	Clinically available (antiviral)	Synthetic analog of arabinose nucleotides; antiviral used to treat herpes infections; King Pharmaceuticals discontinued marketing in June 2001, possibly due to superior alternatives
Aplidine † (*aka* **plitidepsin**, **Aplidin®**)	tunicate (*Aplidium albicans*)	Phase II (cancer)	Dehydrodidemnin B; synthetic analog
Ara-A (*aka* **vidarabine, Vira-A®**)	sponge (*Cryptothetya crypta*)	FDA approved in 1976 (antiviral)	Synthetic analog of arabinose nucleotides; antiviral used primarily for ophthalmic infections
Ara-C † (*aka* **cytarabine, Cytosar-U®, DepoCyt®, Tarabine PFS®**)	sponge (*Cryptothetya crypta*)	Clinically available; FDA approved in 1969; Phase I/II (cancer)	Approved by FDA in 1969; first marine anticancer drug; synthetic analog of arabinose nucleotides; sold by Pharmacia & Upjohn
AZT (*aka* **Retrovir®**, **zidovudine**)	sponge (*Cryptothetya crypta*)	Clinically available (antiviral)	Synthetic analog of arabinose nucleotides; first drug licensed for treatment of HIV; sold by GlaxoSmithKline
Bryostatin 1 †	bryozoan (*Bugula neritina*)	Phase I/II (cancer); Phase II (Alzheimer's)	Now in combination therapy trials; licensed to GPC Biotech by Arizona State Univ.
Cematodin † (*aka* **LU103793**)	mollusk (sea hare) (*Dolabella auricularia*) cyanobacterium (*Symploca* sp.)	Phase I/II (cancer)	Synthetic analog of dolastatin 15; some positive effects in melanoma; studies discontinued in 2004
Contulakin-G (*aka* **CGX-1160**)	mollusk (cone snail) (*Conus geographus*)	Phase I (analgesic); Phase II late 2005	Cognetix and Elan Corporation (Ireland)
Diazepinomicin (*aka* **ECO-4601**)	actinobacterium (*Micromonospora* sp.)	Phase I (antibiotic, cancer)	Ecopia BioSciences (Canada)
Discodermolide †	sponge (*Discodermia dissoluta*)	Phase I (cancer)	Licensed to Novartis by Harbor Branch Oceanographic Institution; studies may have been discontinued in 2005
DMXB (*aka* **GTS-21, DMXB-A**)	marine worm	Phase II (Alzheimer's, schizophrenia)	Licensed to Taiho by the Univ. of Florida
Ecteinascidin 743 † (*aka* **trabectedin**, **Yondelis®**)	tunicate (*Ecteinascidia turbinata*)	Phase II/III (cancer) in 2003-2005; approved by EMA* for treatment of soft tissue sarcoma	Licensed to Ortho Biotech (J&J/Janssen Pharmaceuticals); PharmaMar currently makes and sells Yondelis® in Europe
Eribulin † & **Eribulin mesylate** (*aka* **E7389, Halaven®**)	sponges (*Halichondria okadai, Axinella sp., Phakellia carteri,* & *Lissodendoryx* sp.) (or possibly their symbiotic[4] bacteria)	Phase II/III (cancer); FDA approved for late-stage breast cancer in 2010.	Eisai's synthetic halichondrin B derivative; breast, prostate, & nonsmall cell lung cancer (NSCLC) cancers
Hemiasterlin † (*aka* **E7974)**	sponges (*Hemiasterella minor, Auletta* sp., *Cymbastela* sp. & *Siphonochalina* sp.)	Phase I (cancer)	Eisai's synthetic analog of hemiasterlin; being tested against colorectal cancer
IPL-576,092 (*aka* **HMR-4011A**)	sponge (*Petrosia contignata*)	Phase II (anti-asthmatic) successfully completed	Derived from contignasterol; Inflazyme Pharma

[4] Symbiosis is a close relationship between two or more organisms of different species. There are four forms: amensalism, commensalism, mutualism, and parasitism: amensalism is when one species is harmed while the other is unaffected; commensalism is when one species benefits while causing little or no harm to the other; mutualism is when both species benefit from the relationship; and, parasitism is when one species benefits and the other is harmed. We use symbiosis throughout this chapter, because the exact nature of the relationship is often unknown or unspecified.

Table 5-2. (continued)

Compound Name	Source	Status (Disease)	Comment
IPL-512,602 **(*aka* AVE 0547)**	Synthetic analog	Phase II (anti-asthmatic)	Derived from IPL576,092; with Aventis;. no further data as of 08/2005
IPL-550,260	Synthetic analog	Phase I (anti-asthmatic)	Derived from IPL576,092; with Aventis;. no further data as 08/2005
Irvalec® † (*aka* **elisidepsin, PM02734)**	mollusk (sea slug) (*Elysia rufescens*) green algae (*Bryopsis* sp.)	Phase II (cancer)	Synthetic analog of kahalalide F created to insure sufficient supply; licensed to PharmaMar by Univ. of Hawaii
KRN-7000 † (*aka* **α-GalCer, α-galactosylceramide**)	sponge (*Agelas mauritianus*)	Phase I/II (cancer)	An agelasphin derivative
LAF-389 †	sponge (*Jaspis* sp.)	Phase I (cancer)	Synthetic analog of bengamide B; may have been withdrawn in 2006
LBH-589 (*aka* Faridak®, **panobinostat)**	*Psamaplysilla* spp. (sponge)	Phase III (cancer)	Synthetic analog of psammaplin; with Novartis
Marizomib † (*aka* **salinosporamide A** & **NPI-0052**)	actinobacterium (*Salinispora tropica*)	Phase I (cancer)	Proteasome inhibitor; Nereus Pharma
Neovastat † (*aka* **Æ-941**)	shark	Phase II/III (cancer)	Defined mixture of <500 kDa from cartilage; anti-angiogenic; possibly withdrawn March 2007
NVP-LAQ824 † (*aka* **dacinostat)**	Synthetic combination of three natural products	Phase I (cancer)	Derived from psammaplin, trichostatin, and trapoxin structures; possibly withdrawn in 2006
Plinabulin † (*aka* **NPI-2358)**	fungus (*Aspergillus* sp.)	Phase I/II (cancer)	Synthetic analog of marizomib; selective tumor vascular disrupting agent (VDA)
Pseudopterosins	gorgonian (sea whip) (*Pseudopterogorgia elisabethae*)	Phase II (anti-inflammatory)	Used in Estée Lauder's Resilience skin cream
Soblidotin † (*aka* **auristatin PE** & **TZT-1027**)	mollusk (sea hare) (*Dolabella auricularia*) cyanobacteria (*Symploca hydnoides* *Lyngbya majuscula*)	Phase III (cancer)	Synthetic derivative of dolastatin 10; no positive effects found in Phase II trials, but appears to be effective in combination therapy with vinca alkaloids and bryostatin
Spisulosine (*aka* **ES-285**)	mollusk (arctic surf clam) *Spisula polynyma* (aka *Mactromeris polynyma)*	Phase I (cancer)	*Rho*-GTP inhibitor
Squalamine † (*aka* **Evizon**™)	shark (spiny dogfish) (*Squalus acanthias*)	Phase II (cancer & macular degeneration)	Anti-angiogenic activity is basis for its use to treat both cancer and wet form age-related macular degeneration; Evizon™ is the name used for the ophthalamic formulation
Synthatodin † (*aka* **ILX651, tasidotin**)	mollusk (sea hare) (*Dolabella auricularia*) cyanobacteria (*Symploca* sp.)	Phase I/II (cancer)	Synthetic analog of dolastatin 15; for melanoma, breast, and nonsmall cell lung cancer (NSCLC)
Taltobulin † (*aka* **HTI-286**)	sponges (*Hemiasterella minor, Auletta* sp., *Cymbastela* sp. & *Siphonochalina* sp.)	Phase I/II (cancer)	A synthetic analog of hemiasterlin; studies may have been discontinued in 2005
Trodusquemine (*aka* **MSI-1436)**	shark (spiny dogfish) (*Squalus acanthias*)	Phase I (diabetes treatment; weight loss)	Genaera started Phase I in 2007 and reported promising results in 2009. Shortly after, Genaera was dissolved, and trodusquemine was sold to Ohr Pharmaceuticals; current status unknown
Zalypsis® † (*aka* **PM1004**)	mollusk (nudibranch) (*Jorunna funebris*)	Phase II (cancer)	A synthetic analog of jorumycin, safracin B, & saframycin B; made by PharmaMar
Ziconotide (*aka* **Prialt**®)	mollusk (cone snail) (*Conus magus*)	Clinically available (neuropathic pain)	Licensed by Elan to Warner Lambert; approved by FDA in Dec 2004; also approved by EMA*; chronic use does not result in tolerance

* EMA: European Medicines Agency

† The 20 anticancer products used as a basis for the charts in Figure 5-3.

Source: primarily Fenical (2006), Simmons & Gerwick (2008), and Mayer *et al* (2010). Also Baerga-Ortiz (2009), Butler (2005), Dumez *et al.* (2007), Glaser (2007), Gross & König (2006), Gullo *et al* (2006), Hunt & Vincent (2006), Lam (2006), Nereus (2010), Newman & Hill (2006), Sashidhara *et al* (2009), UN (2007, pp. 26-27), and Yuan *et al* (2006).

Identifying the optimum process of drug discovery has been the subject of a fairly contentious debate over the past three decades. Although natural products have long been the primary source of new drugs, the difficulty of finding biologically active chemicals, isolating and testing them, and then maintaining a steady supply of the chemical's source created an impetus in the pharmaceutical industry to turn to synthetic combinatorial chemistry, which was later coupled with high-throughput screening methods. The allure of *de novo* synthesis of new drugs induced most pharmaceutical firms to shift resources from natural products research to combinatorial chemistry, and many firms shuttered their natural products research entirely. However, despite large investments in combinatorial chemistry, it has yielded only one new drug that has been approved for use (Nexavar® [*aka* sorafenib] in 2005) (Newman & Cragg 2007). Müller *et al.* (2004) show that natural products are much more likely than combinatorial chemistry products to yield a drug approved for clinical use (Table 5-3).

Table 5-3. Number of candidate drugs reaching different stages of clinical trials

	Natural Products (Secondary Metabolites)	Combinatorial Chemistry (Synthesized Chemicals)
Available for study	200	5,000 – 10,000
Preclinical	200	200
Phase I trials	>>10	10
Clinical use	>>1	~1

Source: Müller *et al.* (2004).

The situation is nicely explained by Firn (2003):

> In contrast to the chemists, organisms use enzymes instead of chemical reagents to bring about chemical transformations. The crucial advantage of using enzymes in biosynthetic sequences is that enzymes can bring about specific structural changes to very specific sites in a complex molecule. This facility of microbes and plants to make structurally complex molecules with relative ease means that humans inevitably find it hard to manufacture natural products.

The difficulty of creating new pharmaceuticals using only combinatorial chemistry was made abundantly clear by GlaxoSmithKline's announcement that a six-year effort to discover broad-spectrum antibiotics failed because of the limited chemical diversity of their synthetic screening libraries (Williams 2008). The best strategy may be to combine these two approaches by seeking bioactive chemical structures from natural sources and then optimizing those structures5 via combinatorial chemistry. By acknowledging the prominent role of natural products in drug discovery, this joint discovery-then-optimization strategy may highlight the importance of preserving marine biochemicals.

Despite its potential, marine drug discovery faces some difficult challenges, not the least of which is acquiring a sufficient quantity of the marine source material to allow extraction of a testable quantity. While the quantities of end product may seem small, steps in the development of the end product require much more raw material, and the quantity of source material needed rapidly escalates as the chemical proceeds through the discovery and testing process (Table 5-4). A vivid example of how much source material is required is that of bryostatin. For the initial clinical trials, 13,000 kg of *Bugula neritina* were collected and processed using large-scale chromatographic techniques, yielding 18 g of bryostatin 1 (about 1.4 mg per kg or 1.4 ppm) (Newman & Cragg 2004). Such small yields are not uncommon: the concentration of halichondrin B in *Lissodendoryx* spp. is ~0.4 mg per kg, and of halistatin in sponges is 8.8 μg per kg (Molinski *et al.* 2009). It seems likely that these secondary metabolites appear in such minute quantities because of their extremely potent biological activity (Gerwick 2008).

In some rare instances, a bioactive chemical can be used directly as a drug and can be obtained in quantities sufficient for therapeutic use. Ziconotide (Prialt®), a toxin from *Conus* snails, is such a rarity; it was the first "direct from the sea" approved drug (Donia & Hamann 2003; Newman & Cragg 2007). For terrestrial sources of pharmaceutical natural products, cultivation of the drug's source to produce marketable quantities is usually feasible, but there has been little success in attempts to cultivate marine sources to produce such quantities (Donia & Hamann 2003). As a result, chemical synthesis of the natural product is often the only available option for producing sufficient quantities of the bioactive chemical. Even so, synthesis is not always an option, as succinctly stated by Donia and Hamann (2003):

> Unfortunately, the structural complexity of marine molecules, which suggests novel mechanisms of action and high selectivity, has also resulted in few economically feasible strategies for total chemical synthesis.

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[5] It is often the case that an effective dose of a bioactive natural product is either too toxic or produces unacceptable side effects. These undesirable effects can usually be reduced by selectively modifying the chemical structure of the natural product (Newman *et al.* 2000). For example, salicylic acid from willow trees was acylated to form acetylsalicylic acid (aspirin), which is less irritating to the gastrointestinal tract than the natural product.

Table 5-4. Timeline of drug development and amount of raw material and pure product needed at each stage

Stages	Length of Stage (approx.)	Raw Material Needed	Pure Chemical Needed
Collection of field samples & bioactivity screening	1–2 years	~0.1–1 kg	—
Identification, isolation, & purification of bioactive compound	1–2 years	~1–5 kg	1–10 µg
Determination of chemical structure			1–10 mg
Identification of mechanism of action and potential for synthesis			1–10 g
Preclinical trials	2–4 years	>5 kg (could be >10,000 kg)	100 g
Clinical trials	4–6 years		

Source: Koehn & Carter (2005); Hunt & Vincent (2006).

A steady progression of advances in chemical synthesis methods combined with the joint discovery-then-optimization strategy described above may make more of these syntheses economically feasible. It is worth noting that even when synthesis is achieved, the synthetic product may not have the same structure and biological activity as the natural product. Pettit and Taylor (1996) report an instance where the natural product (stylopeptide 1), despite seeming to be pure based on all physicochemical measurements, was in fact in association with a halistatin-like polyether compound that was a highly active anticancer agent. The presence of this polyether eluded the usual physical, chromatographic, and NMR tests and could only be detected using biological methods. As a result, synthetic stylopeptide 1 had none of the biological activity attributed to the natural product even though the two were structurally identical (Newman & Cragg 2004).

Although marine microbes[6] have long been considered a likely and potentially significant source of bioactive chemicals (Fenical 1982; Kaul & Daftari 1986; Franco & Coutinho 1991; Fenical 1993), recent discoveries suggest that their importance could exceed expectations. Initially, marine microbes were viewed as likely counterparts to terrestrial microbes, which are the source of many antibiotics. However, in the past decade, it has become apparent that many of the bioactive chemicals attributed to higher order flora and fauna (*e.g.*, sponges and nudibranchs) are in fact created by symbiotic microorganisms (often algae, actinomycetes, cyanobacteria, or fungi) (Donia & Hamann 2003; Leeds *et al.* 2006; Wase & Wright 2008).

Marine microbes represent a surprisingly large amount of biomass: they can account for more than 60% of a sponge's wet weight (Wilkinson [1978] as cited by Bowling *et al.* [2007]). In total, marine prokaryotes (bacteria and archaea) outnumber their terrestrial counterparts; Whitman *et al.* have estimated that there are about 3.67 x 10^{30} prokaryotic cells in marine ecosystems (give or take a few billion), and that there are about 305 Pg of carbon in these cells.

Marine microbes demonstrate a surprising degree of host specificity, both with respect to different species in the same location and to the same species in different locations. Of the 100 bacterial species found on three nearby sessile organisms, only two were common to all three (Longford *et al.* [2007] as cited by Penesyan *et al.* [2010]). Further, the microbial community found in the coral *Montastraea franksi* had almost no overlap with the microbes found in the surrounding seawater (Rohwer *et al.* [2001] as cited by Penesyan *et al.* [2010]).

Despite their great potential as sources of new drugs or structural templates, marine microbes pose a considerable challenge, because fewer than five percent of them can be grown in standard laboratory or industrial conditions. To overcome this problem, it may be possible to use metagenomic techniques to move the section of the microbe's genome responsible for creating the bioactive chemical into the genome of a microbe that is already used in large-scale fermentation processes (Donia & Hamann 2003). However, many microbes will not produce the bioactive compounds of interest if they are not in contact with their symbiont host (Wijffels 2007), so a means must be devised to replace the biochemical signaling between microbe and host that activates the transferred genetic sequence. It seems likely that metagenomic techniques could solve this problem, but it has yet to be demonstrated. Although it has great promise and has already been successfully used, metagenomics is still early in its development, and it would be imprudent to depend on it exclusively. As pointed out by Udwary *et al.* (2008, p. 521), metagenomics has its drawbacks (including cost and complexity) and has had its failures (discodermolide). Metagenomics is probably best seen as one of the arrows in the quiver rather than the only arrow.

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[6] The term "microbe" is used throughout this chapter to refer collectively to unicellular or colonial microorganisms, including bacteria, fungi, archaea, or protists.

5.1.2 Marine natural products as structural templates for synthesis

The many unique chemical structures found in marine species provide templates that can be used in the synthesis of new drugs and for insight into structural possibilities. One of the more significant contributions to medicinal chemistry was the discovery that sugars other than ribose or deoxyribose were constituents of naturally occurring nucleosides. This discovery resulted from the isolation of spongouridine and spongothymidine from marine sponges in the early 1950s, and it heavily influenced drug development for the next 30 years. According to Newman *et al.* (2000):

> These two compounds can be thought of as the prototypes of all of the modified nucleoside analogues made by chemists that have crossed the antiviral and anti-tumor stages since then. Once it was realized that biological systems would recognize the base and not pay too much attention to the sugar moiety, chemists began to substitute the 'regular pentoses' with acyclic entities, and with cyclic sugars with unusual substituents. These experiments led to a vast number of derivatives that were tested extensively as antiviral and anti-tumor agents over the next thirty plus years…such structures evolved in the (then) Wellcome laboratories, leading to AZT and, incidentally, to Nobel Prizes for Hitchens and Elion, though no direct mention was made of the original arabinose-containing leads from natural sources.

5.1.3 Marine natural products as molecular probes

Molecular probes are chemicals that are used to explore and elucidate biochemical structures and processes at the cellular and molecular levels. A great many marine biochemicals that are biologically active but unusable as drugs are used extensively as molecular probes (some examples are shown in Table 5-5). Marine neurotoxins, including tetrodotoxin, saxitoxin, conotoxin, and lophotoxin, have been used with great success to advance our understanding of a wide variety of receptors and ion channels in the operation of nervous systems. "The importance of molecular probes in resolving the complexities of diseases and cellular processes has often outweighed any value that they would have as commercial drugs." (NRC 1999, p. 79)

Table 5-5. Marine biochemicals used as molecular probes

Chemical	Use	Reference
adociasulfate-2	selectively inhibits the intracellular molecular motor protein kinesin	NRC 1999; Brier *et al.* 2006
brevitoxin	sodium channel inhibitor in nerves and muscle	Al-Sabi *et al.* 2006; Karunasagar & Karunasagar 2008
conotoxins	calcium channel inhibitor (ω-conotoxins); block voltage-gated sodium channels (μ- & μO-conotoxins); delay inactivation of sodium channels (δ-conotoxins); potassium channel inhibitor (κ-conotoxins); inhibits norepinephrine transporter (χ-conopeptides); nicotinic acetylcholine receptor (α-conotoxins); blocks type 3 serotonin receptors (σ-conotoxins); inhibits α_1-adrenergic receptor (ρ-conopeptides); inhibits NMDA receptor (conantokins); vasopressin receptor agonist (conopressins); neurotensin receptor agonist (contulakins)	NRC 1999; Layer & McIntosh 2006; Lewis 2009
jaspamide (jasplakinolide)	selective binding agent to the intracellular actin network	Senderowicz *et al.* 1995; Saito 2009; Robinson *et al.* 2010
latrunculin A	selective binding agent to the intracellular actin network; used to explore the role of phospholipase A_2 in inflammation	Matthews *et al.* 1997; Amagata *et al.* 2008 Karunasagar & Karunasagar 2008
lophotoxin	irreversible nicotinic receptor antagonist	Fusetani & Kem 2009
manoalide	selective inhibitor of the inflammation enzyme phospholipase A2	Glaser & Jacobs 1986; Yasuhara-Bell *et al.* 2006
okadaic acid	potent and selective inhibition of phosphatases	NRC 1999
saxitoxin	inhibits calcium, potassium, & sodium channels in nerves and muscles	Hay & Fenical 1996; NRC 1999; Al-Sabi *et al.* 2006
swinholide A	selective binding agent to the intracellular actin network; severs F-actin filaments; binds G-actin filaments	Bubb *et al.* 1995; Saito 2009
tetrodotoxin	inhibits calcium, potassium, & sodium channels in nerves and muscles	Hay & Fenical 1996; NRC 1999; Al-Sabi *et al.* 2006; Fusetani & Kem 2009

5.1.4 Nonpharmaceutical uses of marine natural products

Marine natural products have a wide variety of nonpharmaceutical uses, both as products and as templates or sources of insight that may lead to innovative new products (Table 5-6). Perhaps the largest and most economically significant use at this time is in antifouling coatings. In a review of the literature, Chambers *et al.* (2006) found that potential antifouling products had been found in 160 marine species from a wide variety of phyla (Figure 5-1).

Table 5-6. Current and potential nonpharmaceutical uses for marine natural products

Source	Use	Reference
algae	cultured for production of jet fuel	Guardian 2010
algae (green) (*Chlamydomonas reinhardtii*)	surrogate production of drugs	Rasala *et al.* 2010
algae (green, cryptophyte)	more efficient light-harvesting in photosynthesis	Collini *et al.* 2010
annelid (sandcastle worms) (*Phragmatopoma californica*)	medicinal glues and adhesives that function under water	Fountain 2010
cnidarian (corals) (*Porites* spp.) echinoderm (various)	highly interconnected microporous structures of calcium carbonate (*aka* aragonite from corals) or calcite (from echinoderms) used as hard tissue prostheses, cardiovascular material, and tracheal prostheses	White & White 2002
echinoderm (brittle stars) (*Ophiocoma wendtii*)	development of biomimetic compound lenses that minimize optical aberrations while maximizing focal length or field of view	Lee & Szema 2005
fish (sharks)	shark-skin textured material stops bacterial growth	Sharklet Technologies 2010
fish (sharks)	shark-skin textured surface improves fuel economy by reducing drag	Bhushan 2009
fish (zebrafish) (*Danio rerio*)	gene expression activation to repair and replace damaged cardiac cells damaged	Jopling *et al*. 2010; Kikuchi *et al.* 2010
fish (zebrafish) (*Danio rerio*)	use of zebrafish model to identify genes and proteins that promote melanoma	Ceol *et a*l. 2008; Ceol *et al.* 2011; White *et al*. 2011
mammal (dolphin) (*Tursiops truncatus*)	genetic pathway for controlling blood sugar levels	Venn-Watson & Ridgway 2007
mollusk (abalone) (*Haliotis* spp.)	nacre (the inside lining of abalone shells) is a template for tough, lightweight structural coatings for buildings and airplanes	Mayer 2005
mollusk (mussels) (*Mytilus californianus*, *M. galloprovincialis*)	medicinal glues and adhesives that function under water	Messersmith 2010 Harrington *et al.* 2010
mollusk (mussels) (*Mytilus edulis*)	medicinal glues that bonds to living tissue and adheres in wet environ-ments; used to repair human fetal membranes	Benedict 2002 Bilic *et al.* 2010
mollusk (scaly-foot snail) (*Crysomallon squamiferum*)	unique shell structure (fortified with iron sulfide) in a deep-sea snail found near hydrothermal vents will improve helmets & body armor	Yao *et al*. 2010
porifera (sponge) (*Agelas spp.*)	ageliferin renders previously resistant bacterial biofilms susceptible to antibiotics	Huigens *et al.* 2008
tunicate	cellulose from ascidians has a nanoscale structure that can be used to structurally align skeletal muscle tissue grown in the laboratory	Dugan et al. 2010
tunciate (ascidian) (*Pegea confoederata*)	the most efficient filter feeders may help remove carbon from ocean surface water thereby limited CO_2 to atmosphere	Sutherland *et al.* 2010

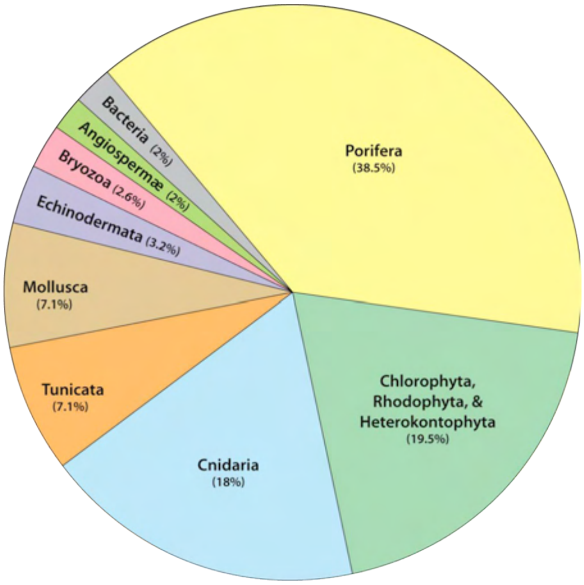

Figure 5-1. Phyletic distribution of 160 reviewed marine species from which potential antifouling natural products have been extracted (figure adapted from Chambers *et al.* 2006)

5.2 Sustaining the presence of natural products in coral reef ecosystems

Maintaining the richly diverse cornucopia of marine natural products requires some understanding of the dynamic ecosystems that drive their creation. Two of the contributing factors are the great diversity of marine life and the density of that life in the marine environment. Of the approximately 35 phyla, every phylum but one has marine species (NRC 1999, p. 74; Davidson & Erwin 2006). In 1999, the NRC (*loc. cit.*) stated that the 200,000 marine species that had been described to that point represented "a small percentage of the total number of species that have yet to be discovered and described." Bouchet (2006) gives a range of 230,000–275,000 marine species, with 1,300–1,500 new species being identified every year. The First Census of Marine Life (CoML 2010, p. 11) states that as of 2010, experts believe that there are about 244,000 cataloged marine species and that this number will rise to about 250,000 in the next few years. However, the CoML goes on to state that the consensus of the CoML scientists is that at least a million marine species are likely to exist. In other words, for every marine species that has been identified, three more species are yet to be discovered.

Coral reefs are thought to have the highest species density of any marine ecosystem, with some areas having about 1,000 species per square meter (Donia & Hamann 2003). This combination of high species diversity and high species density leads to the profusion of secondary metabolites, with over 18,000 unique chemical structures having been identified (Gerwick 2008, p. 428). This may be just the tip of the iceberg. A metagenomic analysis of 1,800 species (primarily unicellular) found in seawater samples collected from the Sargasso Sea near Bermuda predicts more than six million proteins, more than double the number that have been identified (Yooseph *et al.* 2007; Cragg & Newman 2009). Hunt and Vincent (2006) have attempted to map the global distribution of previously unknown marine biochemicals, but the resulting map may better represent the location and frequency of natural product explorations than where novel chemicals are to be found.

The species numbers just described do not include microorganisms[7]. This is practical but may be somewhat misleading, because many of the natural products of pharmaceutical interest apparently originate in microorganisms. With respect to marine microorganism diversity, the NRC (1999, p. 78) stated, "Most of the Earth's microbial diversity is found in the ocean." While some can be found in both terrestrial and marine ecosystems, many taxonomic classes of microorganisms exist only in the sea, including ones that have adapted to a variety of extreme environments, such as hypersaline conditions, enormous hydrostatic pressures, hydrothermal vent temperatures, and high-sulfur environments. Based on what is known from the small areal extent that has been surveyed, it is estimated that several million marine microorganism species exist (Gerwick 2008, p. 427). The CoML (2010, p. 12) research has led to a hundredfold increase in estimates of the number of marine microbe genera and to an estimate that there may be as many as a billion types of marine microbes.

The adaptability of microorganisms may be the reason why different populations of the nearly ubiquitous bryozoan *Bugula neritina* yield very different amounts of bryostatins, a family of potential anticancer drugs. The few *B. neritina* populations that

[7] It should be noted that only microbes that are protists (eukaryotes) are organized into species. Prokaryotes (including bacteria and archaea) are organized by kind, or phylotype (CoML 2010, p. 12).

produce detectable concentrations of the bryostatins are spatially scattered and are at depths greater than 9 m. A metagenomic analysis showed that the symbiotic microorganisms (*Candidatus Endobugula sertula*) from *B. neritina* harvested at greater than 9 m varied by 8% in its mitochondrial carboxylase I sequences from those harvested at less than 9 m (Newman & Cragg 2004). This suggests a pitfall for simplistic or insufficiently informed conservation strategies: implementing a conservation strategy for *B. neritina* (had one been needed) that preserved the wrong populations would have resulted in losing the potential anticancer benefits of the bryostatins (Hay & Fenical 1996).

A healthy reef with high biodiversity may increase the probability that any given species could be the source of a marketable product. As such, the probability of a bioprospecting discovery may be represented as directly proportional to the state of the reef (van Beukering & Cesar 2004). Certain benthic habitats may foster greater sponge diversity and abundance (Mumby *et al.* 2008), which, in turn, may foster the development of secondary metabolites with pharmaceutical potential by the sponges and their symbiont microorganisms.

5.2.1 Ecological role and sources of secondary metabolites

The flora and fauna inhabiting marine ecosystems are confronted with a very complex and stressful environment, and the biochemical adaptations made in response to those stresses have resulted in a vast trove of natural products with unprecedented structural complexity. Marine ecosystems have existed far longer that terrestrial ecosystems—thereby providing greater opportunity for evolutionary adaptation (*e.g.*, cyanobacteria have existed for about 3.5 billion years [Gerwick 2008, p. 428]). The immersion of marine species exposes them to attack by predators and pathogens to a much greater degree than in terrestrial ecosystems. Space is also a significant stressor, though it might not seem so given the oceans' expanse. The shallow coastal zones and infrequent seamounts (places where sunlight can be a useful source of energy) constitute a relatively small area, within which competition can be intense. In particular, sessile organisms not only need room to grow, but they need to prevent other sessile organisms from growing on top of them (Pawlik 1993).

Marine flora and fauna have adapted to the stresses inherent in their complex ecosystems by creating highly unusual and complex secondary metabolites. Faulkner (2000) provides a concise explanation of how these complex biochemicals came to be:

> It is probable that chemical defense mechanisms evolved with the most primitive microorganisms but have been replaced in many more advanced organisms by physical defenses and/or the ability to run or swim away and hide. Sessile, soft-bodied marine invertebrates that lack obvious physical defenses are therefore prime candidates to possess bioactive metabolites. If it is assumed that secondary metabolites evolved from primary metabolites in a random manner, any newly produced secondary metabolite that offered an evolutionary advantage to the producing organism would contribute to the survival of the new strain. The specific evolutionary pressures that led to chemically rich organisms need not be defined but the longer the period of evolution, the more time the surviving organism has had to perfect its chemical arsenal. Sessile marine invertebrates have a very long evolutionary history and have had ample opportunity to perfect their chemical defenses.

In creating these chemical defenses, marine organisms use chemicals and pathways that are distinctly different than their terrestrial counterparts (Hay & Fenical 1996). Secondary metabolites are usually associated with immobility, so in terrestrial ecosystems they are most often found in plants. In marine ecosystems, secondary metabolites occur more widely both because both plants and animals (along with their symbiotic microbes) may be sessile and because of the high rate of predation (Hay & Fenical 1996). Interestingly, it is usually the case that more is known about the effect of a secondary metabolite on human cellular biochemistry than its function in the species from which it was isolated (NRC 1999, pp. 74–75).

The very nature of secondary metabolites (*i.e.*, as biochemicals produced specifically to interact with biological processes) makes them more attractive to natural product chemists and far more likely than a randomly chosen organic structure to be biologically active. As Faulkner (2000) points out,

> Chemical defense mechanisms cannot be directly equated with potential biomedical activity, but it is remarkable how well the two correlate in reality. This could be explained by the fact that targets of the chemical defenses, primary metabolites such as enzymes and receptors, are highly conserved compared with secondary metabolites.

Simmons & Gerwick (2008, p. 433) describe four distinctive characteristics of marine secondary metabolites:

> From the species studied to date, it is clear that marine organisms have been subject to unique adaptive pressures and utilize rather different strategies for producing secondary metabolites compared to their terrestrial counterparts. In some cases, seasoned organic chemists look at the structures of metabolites produced by marine life and characterize them as bizarre, unlike anything found from the land environment. Alternatively, some marine metabolites are of exceptional complexity representing true milestones of human achievement in the characterization of their convoluted multicyclic, and three-dimensional structures, such as maitotoxin…Coupled to the uniqueness of their physical structure are their biological properties, which can be exquisitely potent against some cellular targets. Indeed, some of the most potent natural toxins on the planet derive from marine life…Perhaps even more important than potency is the fact that some of these marine metabolites exert their pharmacological activities through interactions at novel drug sites, such as

> enzymes or receptors not targeted by any current pharmaceutical agent. Hence, the real possibility exists that entirely new drug classes will be discovered that have novel structures and new sites of action…

The potency of marine natural products is probably attributable to their inevitable dilution in seawater; that is, the chemical must be sufficiently powerful to overcome the dilution that will take place en route to its target and still have the desired effect (Newman & Cragg 2004). A fifth distinctive characteristic of marine secondary metabolites is the relatively high frequency with which they incorporate chlorine or bromine in their chemical structure, probably resulting from the easy availability of the halogens in seawater (Gerwick 2008, p. 428). It may also be that the toxicity often conferred by halogenation served to provide an evolutionary advantage.

Historically, marine macroorganisms[8], particularly sponges and seaweeds from tropical waters, were thought to be the greatest source of these secondary metabolites (Gerwick 2008, p. 428). However, several different lines of inquiry have led to the understanding that the source is often one of the multitude of symbiotic microorganisms associated with the macroorganism. Probably the first evidence of this was the discovery of identical secondary metabolites in different species of macroorganisms. In some cases, this was a matter of macroorganisms ingesting the same species of microorganism. However, in other cases the association is symbiotic. Metagenomic analyses have confirmed that the symbiotic microorganisms, not the macroorganisms, possessed the genetic sequences capable of producing the biologically active secondary metabolites in question. It is fascinating that these microorganisms produce secondary metabolites not for their protection, *per se,* but for the protection of their symbiont macroorganisms, suggesting a lengthy co-evolution that may also include sophisticated biochemical signaling between the species (*e.g.,* the bacteria that grow on fish eggs protect the eggs from fungal infection) (Fisher 1983a; Fisher 1983b; Fisher & Clark 1983).

This state of affairs creates several difficulties. The first is that the identification of threatened or endangered ecosystems or species routinely focuses on macroorganisms. The obvious importance of the symbiotic relationship between marine macroorganisms and microorganisms clearly emphasizes the necessity of adopting a holistic perspective towards ecosystem protection, since ecosystems are similar to organisms in that their well-being requires preservation of the whole, not merely a few of the attractive parts (*e.g.,* charismatic megafauna).

The second difficulty is that a macroorganism species growing in different geographic locations may well have quite different symbiont microorganism populations. This possibility complicates strategies for both marine bioprospecting and ecosystem protection. A third difficulty is that culturing symbiont microorganisms apart from their hosts has been very difficult, and even when such cultures do succeed, they often do not produce the desired active natural products. Pharmaceutical screening is consequently more complicated, because it is necessary to analyze the microbial genome, identify and extract the likely sequences used to create the secondary metabolites, and insert those sequences into a culturable microorganism. If a sufficient amount of the secondary metabolite has been isolated from natural sources, another alternative would be to identify the chemical structure for synthesis. Unfortunately, synthesizing these complex secondary metabolites is unlikely to be feasible either with respect to time or cost early in the screening process.

The macroorganisms that have been found with potentially useful secondary metabolites (whether originating from the macroorganism or its symbiotic microorganisms) are predominantly from the phylum Porifera (sponges) (Figure 5-2 and Table 5-7). This observation results from an examination of the U.S. National Cancer Institute's Developmental Therapeutics Program and its Natural Product Extract Cancer Screening Database[9], which appears to have been last updated in 2003. The database contains the results of 236,335 cancer screens for 4,335 marine natural products, 472 from marine plants and 3,863 from marine invertebrates. The predominance of sponges most likely results from several factors. Sponges tend to be fairly prominent and discrete, making them visible and easy to collect. Also, from the earliest marine biochemical research, sponges had developed a reputation for being excellent sources of biologically active chemicals. This may have led researchers to preferentially collect sponges for evaluation. Sponges appear to be a good starting point for investigating symbiotic microorganisms, because those microorganisms can account for greater than 60% of a sponge's wet weight (Bowling *et al.* 2007).

Simmons and Gerwick (2008) used metagenomic analysis to clarify the sources of 20 marine anticancer products (marked in Table 5-2 with a †) currently in clinical trials (Figure 5-3). The current view is that only 20% of these anticancer products (or the natural templates on which they are based) are produced by macroorganisms and that fully 80% are produced by symbiotic microorganisms. Of course, as noted above, if the macroorganisms are not present to host the microorganisms, the microorganisms will not produce the biologically active secondary metabolites.

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[8] A macroorganism is an organism that can be seen with the naked eye.

[9] available at http://dtp.nci.nih.gov/docs/cancer/natural_products/natural_products_data.html (accessed 2010.08.19)

Figure 5-2. Marine phyla contributing secondary metabolites with pharmaceutical potential
(adapted from Hunt & Vincent [2006])

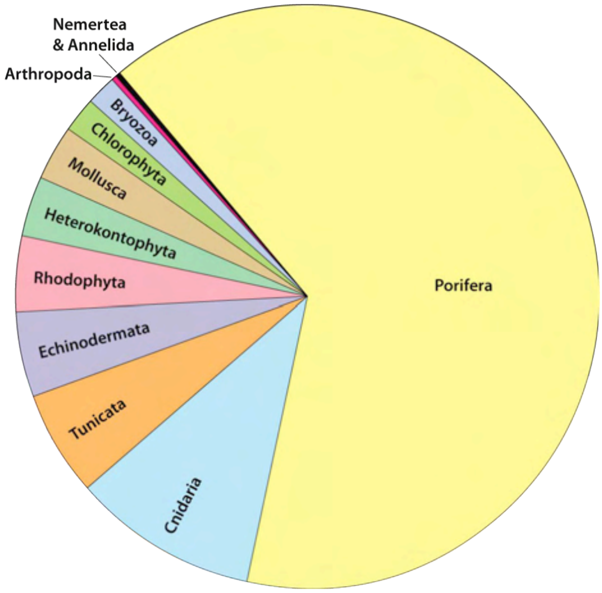

Table 5-7. Percentage of secondary metabolites with pharmaceutical potential from marine phyla
(percentages estimated from Figure 1 in Hunt & Vincent [2006])

Phylum	Phylum Members Include	Percentage of Secondary Metabolites
Porifera	sponges	64.7%
Cnidaria	corals, jellyfish, sea anemones	10.1%
Tunicata	tunicates (ascidians)	6.0%
Echinodermata	starfish, sea urchins	4.7%
Heterokontophyta	brown algae, seaweeds	3.4%
Mollusca	nudibranchs, snails, squid	3.1%
Chlorophyta	green algae	1.8%
Bryozoa	colonial filter feeders	1.7%
Arthropoda	barnacles, crabs, shrimp	0.3%
Nemertea & Annelida	worms	0.2%

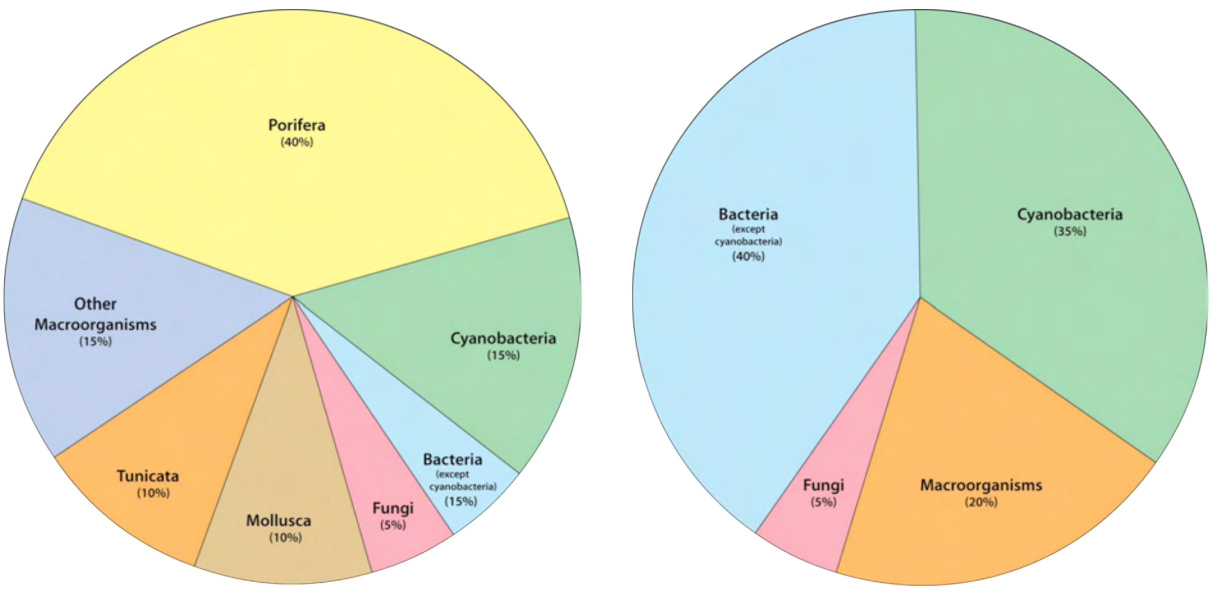

Figure 5-3. Sources of 20 marine anticancer drugs in clinical trials or recently in clinical trials (see Table 5-2): reported (left) versus predicted based on subsequent metagenomic analysis (right)
(adapted from Simmons & Gerwick [2008])

5.3 Measuring and valuing the service

The provision of natural products by marine ecosystems has not been assessed in the same manner as the other ecosystem services discussed in this document, probably because this ecosystem service, being of a distinctly different nature, does not lend itself to commonly employed assessment and valuation methods. For example, there is no easy or straightforward method for estimating either the number of natural products that could be developed or their value. Developing an ecosystem service assessment, particularly for pharmaceutical products, would be greatly impeded by the reticence of companies to discuss their methods, the status of their investigations and clinical trials, or even the specific products being investigated. Given these significant hurdles, it is not especially surprising that there appear to be no reported estimates of the value, or potential value, of marine natural products. There are rare instances where a product's sales may be given for a single year, but such examples tend to be treated (even by authors) as throwaway factoids, rather than reliable data. Creating a list of potential products, such as Table 5-2, requires a wide-ranging review of many journal articles, reports, and web pages, because the information has not been compiled, and the lists that are available are inevitably incomplete and quickly outdated by new developments.

5.3.1 Specific examples

There are few well-documented market values for marine pharmaceutical products. Part of the problem is that there are not very many marine pharmaceutical products currently in commercial production. Another aspect of the problem is that the pharmaceutical industry tends not to make sales and profit figures available that are disaggregated by year or product. When figures are made available, they tend to be provided in ways that make comparisons difficult, if not impossible. In 2005 in the *British Medical Journal*, the following estimates were given:

> The annual profits from a sea sponge compound used to treat herpes, for example, are between $50m and $100m (£27m and £55m; €41m and €81m), and cancer fighting agents derived from marine organisms are worth $1bn (Cole 2005).

The herpes drug is almost certainly acyclovir (*aka* Zovirax®) (see Table 5-2 and Appendix 5-A [listed as acycloguanosine in the Anti-infectives section]).

Another approach is to consider the value of relatively new drugs not of marine origin to gain some sense of the market potential for new marine drugs (Table 5-8).

Table 5-8. Market value of pharmaceutical products

Product	Market Segment	Sales
Avastin®	cancer	$2.7billion/yr
Herceptin®	cancer	$1.3 billion /yr
Prezista®	HIV	$25m (est. for 2006) $181m (est. for 2007)
all products	antibiotics	$5 billion
Lipitor®	cholesterol-lowering	$13.6 billion (2006)
Retrovir® (AZT)	HIV	$23m (2005)
Zovirax®	antiviral (herpes)	~$237m (2006)

Source: UN (2007)

5.3.2 Possible approach

One approach that could be used to approximate the potential value of marine natural products in the pharmaceutical industry would be to rely on assumed values for the following parameters:

1. **the number of marine species**
   for megafauna, the number of species is likely to be about 250,000 (as discussed above), but it will be more difficult to estimate the number of species of microorganisms (the estimates discussed above come with great uncertainty);
2. **the probability that any given species could be the source of a marketable pharmaceutical product**
   estimates of this probability vary for terrestrial species, but it appears that the per species probability may be considerably higher for marine species;
3. **the expected value of a product's revenue**
   revenue estimates have been difficult to find (particularly revenue projections), but in the past decade, there has been more independent research in this area;
4. **the expected cost of a product's development**
   research costs have always been difficult to estimate, primarily because pharmaceutical companies consider them to be competitively important and so rarely release them except in the most aggregated forms. However, research on these costs has resulted in numerous journal articles in the past decade, particularly by DiMasi and colleagues at the Tufts Center for the Study of Drug Development (*e.g.*, DiMasi 2001a; DiMasi 2001b; Grabowski *et al.* 2002; DiMasi *et al.* 2003; Adams & Brantner 2006; DiMasi & Grabowski 2007; DiMasi *et al.* 2010); and,
5. **the expected value of a product's nonmarket benefits**
   the nonmarket benefits are usually the most difficult to estimate and the most difficult on which to reach consensus. These benefits will vary depending on: (a) the disease(s) a drug will be used to treat; (b) the treatment regime (short-term vs. long-term consumption); (c) the number of expected users; and, (d) the age distribution of the user population. Several difficult choices have to be made in arriving at an estimate,

including the value of human well-being (including quality of life), the value of life extensions, the value of palliative treatments, the value of a life saved, and whether the value of life depends on the age of the person saved.

This approach has been used to estimate the potential pharmaceutical value of terrestrial plant biodiversity (Principe 1987; Principe 1996). However, such global values are not very useful for assessments and management of specific marine locales and do not provide the marginal values necessary for a proper economic assessment (Simpson *et al.* 1996; Simpson & Craft 1996; Craft & Simpson 2001).

5.4 Reflections

In considering the coral reef ecosystem and which of its attributes contribute to the creation of the ecosystem services provided by natural products, it seems that one must inevitably conclude that these services are not so easily categorized. This results from the services being exclusively created by the ecosystem as a whole; a single attribute is not responsible for the provision of the service. The services provided by the natural products also do not lend themselves to a disaggregated perspective, as is possible, for example, in shoreline protection. Consequently, the table of final ecosystem services and supporting features (Table 5-9) is a brief one.

Marine natural products possess several characteristics that make them compellingly attractive for pharmaceutical purposes. First, the structural complexity of marine secondary metabolites is far greater than from terrestrial sources. Second, marine-derived compounds seem to possess a far higher probability of success than the one in ten thousand expected from traditional sources of potential pharmaceuticals (Principe 1987; Principe 1996). Third, marine-derived compounds have demonstrated biological activity against a wide variety of diseases, afflictions, and pathogens. Fourth, only a small percentage of marine secondary metabolites have been investigated for pharmacological use to date, so there remains an extremely large pool of marine biochemicals to investigate for pharmaceutical use. The utility for humans from marine-based pharmaceuticals is potentially so large that its economic value could surpass that of all other coral reef benefits combined. Consequently, the estimation of this utility will be a vital, if not determinative, element of analyses conducted to support policy decisions that affect the health and integrity of coral reefs.

Even once one gets past the stage of gawping, touristic wonder when viewing the complex structures and strategies created by the denizens of marine ecosystems, the tremendous potential of marine natural products to benefit humans remains mind-numbingly large. Unfortunately, what also remains is the discouraging possibility that the degradation or destruction of coral reef ecosystems will result in these being mind-numbingly large *foregone* benefits. This outcome could be forestalled if the potential benefits of marine natural products could be better characterized and quantified, and this should be one of the goals of the ESRP research program.

Table 5-9. Final ecosystem services and supporting features for natural products

Ecosystem Service(s)		Natural Features	Social Values	Complementary Goods & Services	Ecosystem-Derived Benefits	Potential Indicators of Final Ecosystem Service(s)
Final (FES)	Intermediate					
Pharmaceuticals from natural products						
Marketable natural product or a template that results in a marketable product	Unique biologically active secondary metabolite	Shallow, marine biodiverse, species-dense ecosystem	Desirability of good health and well-being	Pharmaceutical research programs for both field collection and laboratory analysis	Increased revenues from pharmaceuticals; increased health and well-being	Species density, biological integrity, sponge diversity, rare species

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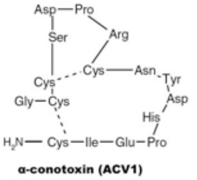
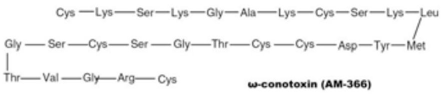
Appendix 5-A
Marine pharmaceutical products

This table contains a small subset of the marine biochemicals possessing biological activity that have been investigated as potential pharmaceutical products or as molecular probes for exploring biochemical pathways and reactions. The biochemicals are grouped into the following categories:

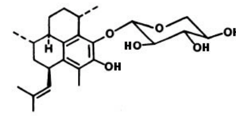
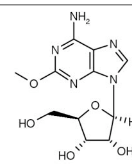
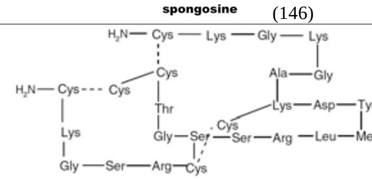
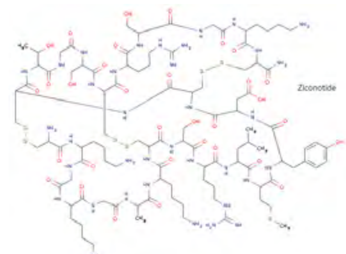
- Analgesic drugs
- Antiasthmatic drugs
- Anticancer drugs
- Antidiabetic drugs
- Anti-infective drugs
- Cardiac & circulatory system drugs; Anti-angiogenesis drugs
- Immunological drugs
- Molecular probes
- Neurological drugs
- Templates

Some of the chemicals have duplicate entries if they have multiple uses.

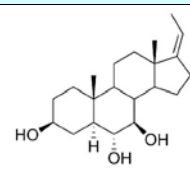
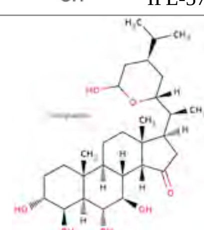
Analgesic drugs

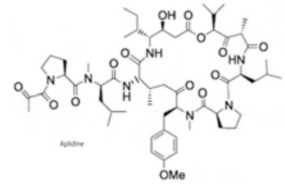
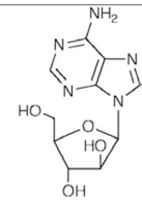
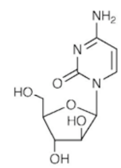
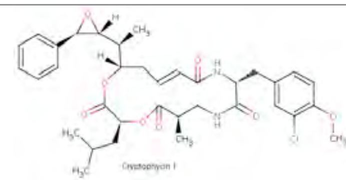
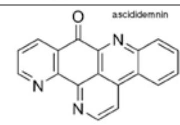
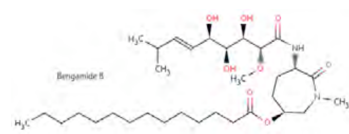
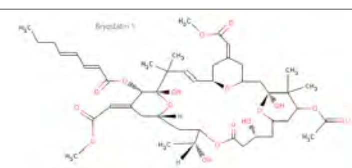
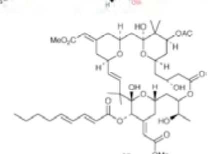
Chemical	Source	Uses & Status	Structure	Citations
conantokin G	mollusk (cone snail) (*Conus geographus*) Indo-Pacific 	analgesic & anti-seizure; 17-amino-acid competitive antagonist of N-methyl-D-aspartate (NMDA) receptors; Phase I trials discontinued	precursor amino acid sequence shown at (128, Figure 2, p. 275)	1,2,18 photo:3
α-conotoxin Vc1.1 (ACV1)	mollusk (cone snail) (*Conus victoriæ*) Australia, Japan	α-conotoxins inhibit the postsynaptic acetylcholine receptor; preclinical studies	 (146)	18,146
χ-conotoxin MR1A/B	mollusk (cone snail) (*Conus* sp.) Indo-Pacific	χ-conotoxins selectively inhibit the activity of neuronal noradrenaline transporter; preclinical studies		4,18
ω-conotoxin CVID (AM-336)	mollusk (cone snail) (*Conus catus*) Indo-Pacific 	ω-conotoxins inhibit voltage-activated entry of calcium into the presynaptic membrane, inhibiting the release of acetylcholine; preclinical studies	 (146)	18,146 photo: 5
contulakin G (CGX-1160)	mollusk (cone snail) (*Conus geographus*) Indo-Pacific 	a 16-amino acid peptide with an *O*-glycosylated threonine residue; a neurotensin agonist; Phase I trials		6,18 photo: 3
Thr 10-contulakin G (modified toxin)	mollusk (cone snail) (*Conus* sp.) Indo-Pacific	preclinical studies		7,8,18

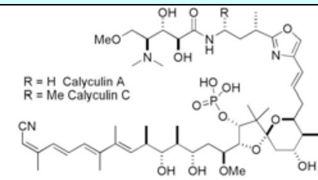
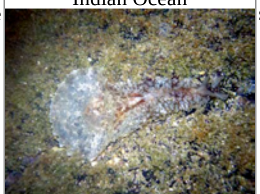
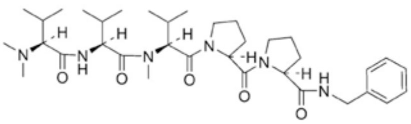
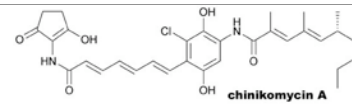
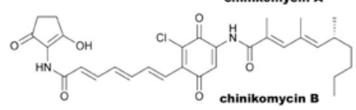
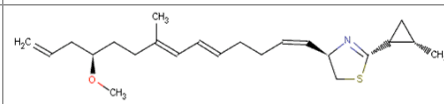
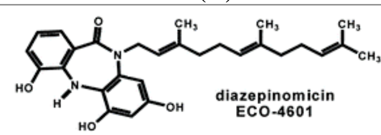
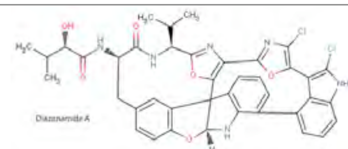
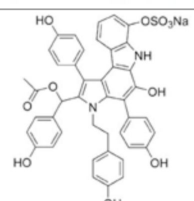
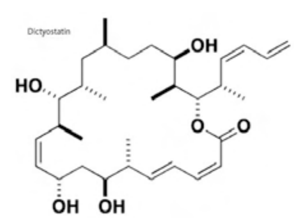
Analgesic drugs

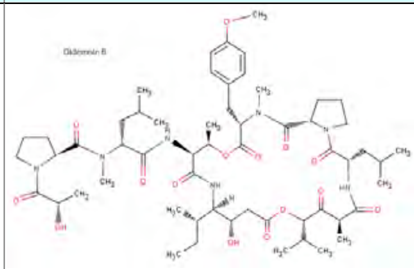
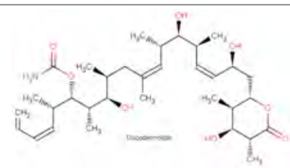
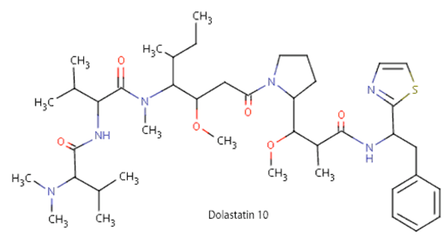
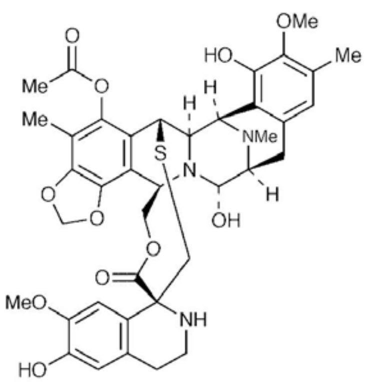
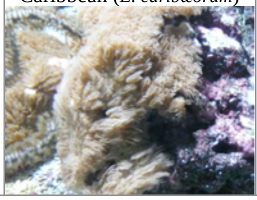
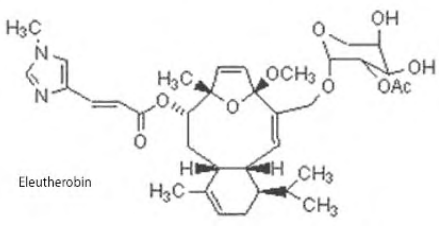
Chemical	Source	Uses & Status	Structure	Citations
pseudopterosins (including methopterosin, a derivative)	gorgonian (sea whip) (*Pseudopterogorgia elisabethæ*) Caribbean 	arthritis, anti-inflammation, & analgesic; affect the arachidonic acid cascade; inhibit synthesis of eicosanoids, (locally functioning hormone-like substances) in specific white blood cells; pharmacologically distinct from other NSAIDs & their MOA seems novel; preclinical; sold as a cosmetic anti-wrinkle cream by Estee Lauder under the name	 (9) pseudopterosin A	9,10,24,25 photo: 11
spongosine (2-metoxyadenosine)	sponge (*Tectitethya crypta*) (synonym: *Cryptotethya crypta*) Caribbean	analgesic; neuropathic & inflammatory pain	 spongosine (146)	146
ziconotide (Prialt®)	mollusk (cone snail) (top:*Conus geographus*, bottom: *Conus magus*) Indo-Pacific  	inhibits N-type voltage-dependent calcium channels to short-circuit neurotransmitter release in nerves that transmit pain signals; the precisely targeted MOA effectively blocks pain while still allowing the rest of the nervous system to function properly; the effect of ω-conotoxin M VII A is 100 to 1000 times that of morphine; FDA approval in December 2004; licensed to Warner Lambert	 ω-conotoxin (ziconotide) (146)  (13)	12,13,14, 18,102,106, 146 photos: 3 (top) 15 (bottom)

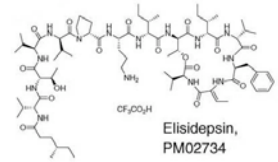
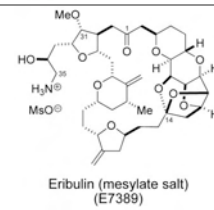
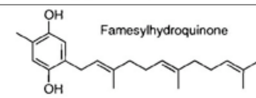
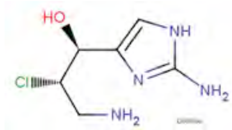
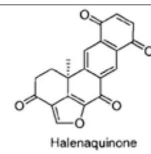
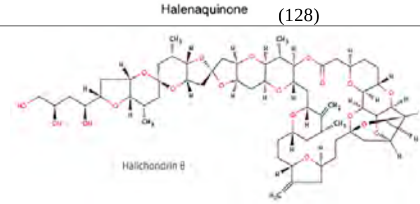
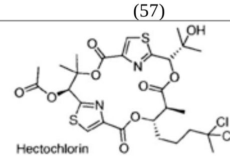
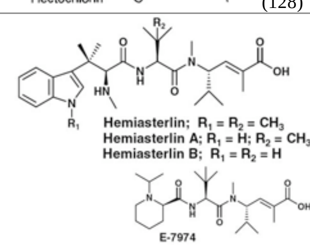
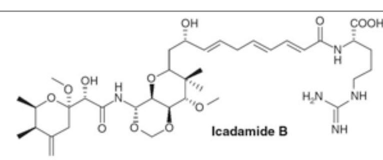
Antiasthmatic drugs

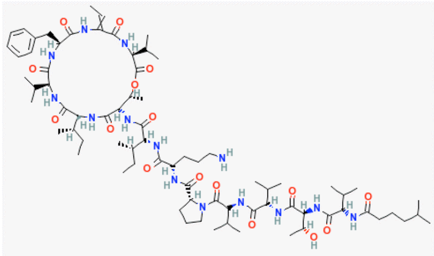
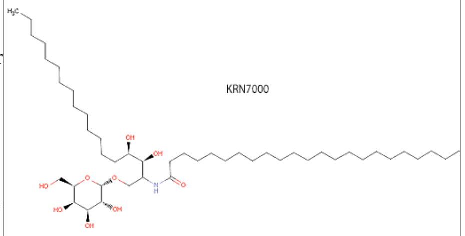
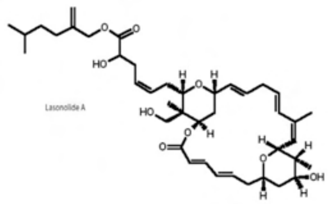
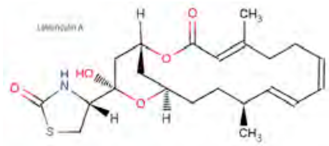
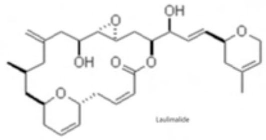
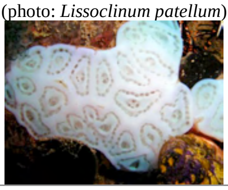
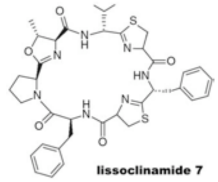
Chemical	Source	Uses & Status	Structure	Citations
IPL-576,092 (HMR-4011A) IPL-550,260 IPL-512,602 (contignasterol derivatives)	sponge (*Neopetrosia contignata*) (synonym: *Petrosia contignata*) Indonesia	antihistamine & antiasthmatic; IPL-576,092 completed Phase II trials successfully (by Inflazyme Pharma); IPL-512,602 in Phase I trials (by Avantis); IPL-512,602 in Phase II trials (by Avantis)	 IPL-576,092 (18)	16,18
contignasterol	sponge (*Neopetrosia contignata*) (synonym: *Petrosia contignata*) Indonesia	antihistamine & antiasthmatic	 (16)	16,18

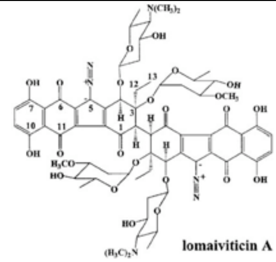
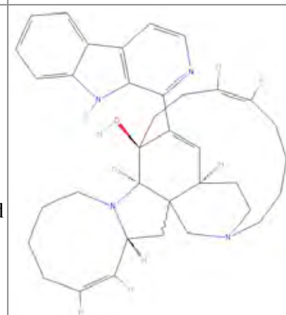
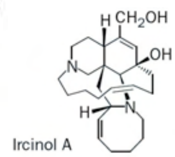
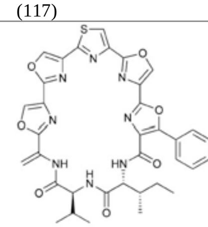
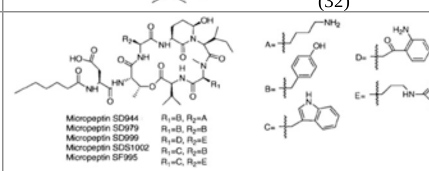
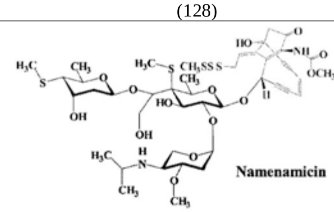
Anticancer drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
aplidine (total synthetic of dehydrodidemnin B) (Aplidin®)	tunicate (*Aplidium albicans*) Mediterranean	anticancer; differs chemically from didemnin B and the other didemnins only in the structure of its side chain; MOA is unclear; a multifactorial apoptosis inducer; Phase II trials underway for various cancers; PharmaMar	 (17)	17,18
Ara-A (vidarabine, Vira-A®) (derived from spongouridine & spongothymidine)	sponge (*Tectitethya crypta*) (synonym: *Cryptotethya crypta*) Caribbean	antiviral & anticancer; clinical use	 (102)	18,19,102
Ara-C (Cytosar-U®, DepoCyt®, Tarabine PFS®, cytarabine, 1-β-D-arabinosylcytosine) (derived from spongouridine & spongothymidine)	sponge (*Tectitethya crypta*) (synonym: *Cryptotethya crypta*) Caribbean	antiviral & anticancer; clinical use	 (102)	18,19, 102,103
arenastatin A (cryptophycins)	sponge (*Dysidea arenaria*) Palau Islands	anticancer; tubulin interactive agent; Phase I trials; synthetic derivative licensed to Lilly by Univ. of Hawaii; withdrawn in 2002	 (20)	18,20
ascididemnin	tunicate (*Leptoclinides* sp.) Central Pacific	anticancer; reductive DNA-cleaving agents; preclinical studies	 (18)	18,21
azaspiracid-1	algæ	anticancer; shows toxicity to lymphocytes & neuroblastoma cells		128
bengamide derivative; LAF-389	sponge (*Jaspis* sp.) Fiji 	anticancer & antihelminthic; methionine aminopeptidase (Met-AP1) inhibitor; licensed to Novartis; withdrawn from Phase I trials in 2002; LAF-389 is a synthetic bengamide B derivative; Phase I trial may have been suspended in 2006	 (22)	18,22 photo: 23
bistratene	tunicate	anticancer; induces cell-cycle arrest in G_0/G_1 & G_2/M		128
bryostatin 1	bryozoan (*Bugula neritina* [photo]) (chemical possibly from commensal bacterium [*Endobugula sertula*]) worldwide 	anticancer; inhibits leukemia via immunostimulation & binding to the receptor, protein kinease C (PKC), displacing tumor promoting phorbol esters that bind to the same place; seems to enhance other drugs but not effective by itself; Phase II trials; in combination therapy trials in 2004; licensed by Arizona State Univ to GPC Biotech., which stopped development in 2003	 (27)  (102)	18,24,25,26, 27,102 photo: 28

Anticancer drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
calyculin A & calyculin C	sponge (*Discodermia calyx*)	anticancer; strong serine/threonine protein phosphatase inhibitors	 (29)	30
cematodin (synthetic derivative of dolastatin 15) (LU-103793)	sea hare (*Dolabella auricularia* [photo]) (chemical possibly from commensal cyanobacteria [*Symploca hydnoides* & *Lyngbya majuscula*]) Indian Ocean 	anticancer; Phase II trials for malignant melanoma, meta-static breast cancer & non-small-cell lung cancer; Phase II trials for melanoma, breast, & NSCLC; appears to stabilize melanoma & breast cancers; increase in QoL for NSCLS	 (18)	18,44 photo: 31
chinikomycin A & chinikomycin B (chlorine-containing manumycin derivatives)	sediment actinobacterium (*Streptomyces* sp.) China	anticancer; antitumor activity against several cancer lines	 (32)  (32)	32
coscinosulfate	sponge	anticancer; cell cycle regulation		128
curacin A	cyanobacterium (*Lyngbya majuscula*) Caribbean	anticancer; antimitotic activity; tubulin interactive compound; preclinical; synthetic derivatives with better solubility being evaluated	 (34)	18,24,25, 33,34
diazepinomicin (ECO-4601)	actinobacterium (*Micromonospora* sp.)	antibiotic & anticancer; Phase I trials (antibiotic & anticancer)	 (35)	35,36
diazonamide	ascidian (*Diazona angulata*) Phillipines	anticancer; inhibits microtubule assembly, arresting the process of cell division; preclinical studies; synthesized & new structure elucidated	 (37)	18,37
dictyodendrins	sponge (*Dictyodendrilla verongiformis*) Japan	anticancer; telomerase inhibitors; has shown 100% inhibition; preclinical studies	 **dictyodendrin A** (18)	18
dictyostatin	*sponge* *(*Spongia *sp.)* Caribbean 	anticancer; inhibits the growth of human cancer cells; active against certain Taxol-resistant tumors; MOA appears to be prevention of the breakdown of tubulin during mitosis (like Taxol) ; preclinical studies	 (38)	38 photo: 126

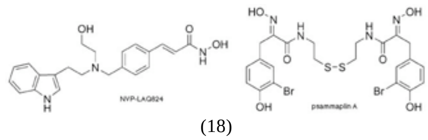
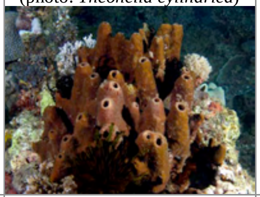
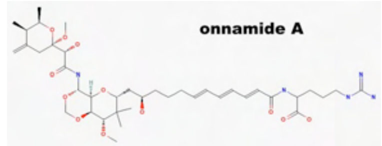
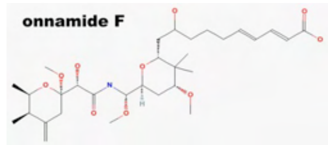
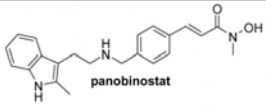
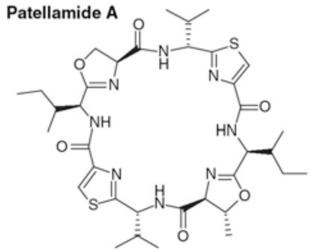
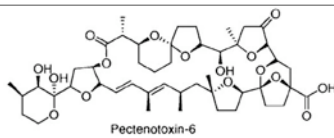
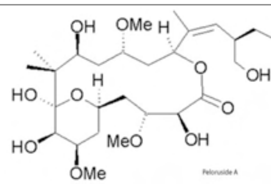
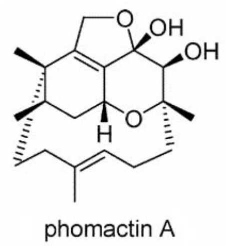
Anticancer drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
didemnin B	tunicate (*Tridideмium solidum*) Caribbean	anticancer & antiviral interrupts protein synthesis in target cells by binding noncompetitively to palmitoyl protein thioesterase; cytotoxic for lymphomas, some leukemias & melanomas; antiviral for herpes simplex and several others; Phase II trials showed significant toxicity at efficacious doses; dropped in middle 1990s	 (41)	18,24, 39,40,41
discodermolide	deep-water sponge (*Discodermia dissoluta*) Caribbean	anticancer & immunosuppressive; tubulin polymer stabilizer (like taxol); essentially arresting cells at a specific stage in the cell cycle and halting cell division; Phase I trials; licensed to Novartis by Woods Hole; may be used in combination with Taxol	 (43)	24,25,42,43
dolastatin 10	sea hare (*Dolabella auricularia*) (chemical possibly from commensal cyanobacteria [*Symploca hydnoides* & *Lyngbya majuscula*]) Indian Ocean 	anticancer; mitotic inhibitor; interferes with tubulin formation & thereby disrupt cell division by mitosis; binds to tubulin at the vinca/peptide region, the target for several structurally complex natural products, including hemiasterlin; cytotoxic for B-16 and LOX melanomas; no positive effects in Phase II trials, but may find use in combination drug therapy with vincas or bryostatin; many derivatives made synthetically (see next entries)	 (46)	18,24,25, 44,45,46 photo: 31
ecteinascidin 743 (trabectedin, ET-743, Yondelis®)	tunicate (Caribbean sea squirt, a mangrove ascidian) (*Ecteinascidia turbinata*) Caribbean 	anticancer; cytotoxic for several types of cancer; binds to target cell DNA & inhibits cell division, leading to apoptosis; induces apoptosis only during active gene transcription, which is much more frequent in cancer cells; keeps tumors from becoming resistant to chemotherapy by interfering with the gene that produces P-glycoprotein, a membrane protein that enables drug resistance; Phase I trials showed effectiveness against advanced-stage breast, colon, ovarian and lung cancers, melanoma, mesothelioma and several types of sarcoma; Phase II/III trials in 2003; licensed by Ortho Biotech (J&J); partial synthesis from microbial metabolite; approved by EC for soft tissue sarcoma	 (102)	18,24,25, 44,47,48,49, 102 photo: 50
eleutherobin (related to sarcodicytins)	alcyonarian (*Eleutherobia* sp.) gorgonian (*Eunicella stricta*) coral (*Erythropodium caribæorum* [photo]) W. Australia, Caribbean (*E. caribæorum*) 	anticancer; mimics pacilitaxel's activity against tubulin; synthesized and derivative structures created	 (51)	18,51,102 photo: 52

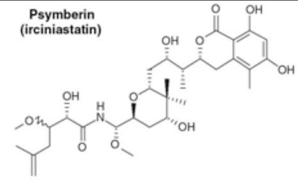
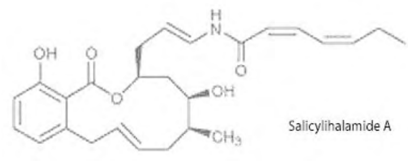
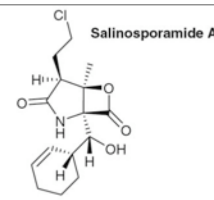
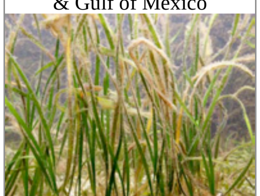
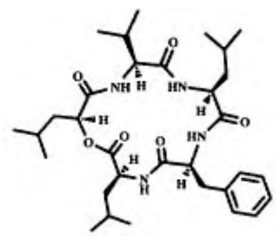
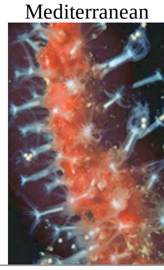
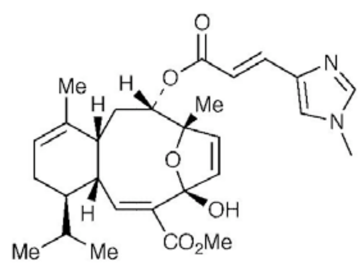
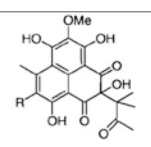
Anticancer drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
elisidepsin (Irvalec®, PM02734)	sacoglossan sea slug (*Elysia rufescens*) that grazed on green macroalgæ (*Bryopsis pennata*) Pacific	Synthetic analog of kahalalide F created to insure sufficient supply; licensed to PharmaMar by Univ. of Hawaii; Phase II trials	 (53)	53
eribulin & eribulin mesylate (E7389, Halaven®)	sponge (*Halichondria okadai*, *Axinella* sp., *Phakellia carteri*, & *Lissodendoryx* sp.) Japan, W. Pacific, Eastern Indian Ocean, & New Zealand	Eisai's synthetic halichondrin B derivative; breast, prostate, & non-small cell lung cancer (NSCLC) cancers; Phase II/III trials; FDA approved for late-stage breast cancer in 2010	 (54)	18,44,54
farnesylhydro-quinone	fungus	anticancer & antimalarial	 (128)	128
girolline	sponge (*Pseudaxinyssa cantharella*) (synonym: *Cymbastela cantharella*) New Caladonia	anticancer; inhibits protein synthesis at termination the process rather than at the initiation or chain elongation steps like other known inhibitors; Phase I trials discontinued due to hypertension	 (55)	18,55
halenaquinone	sponge	anticancer; induces apoptosis	 (128)	128
halichondrin B	sponge (*Halichondria okadai*, *Axinella* sp., *Phakellia carteri*, & *Lissodendoryx* sp.) Japan, W. Pacific, Eastern Indian Ocean, & New Zealand	anticancer; binds tubilin at a site close to the so-called vinca site and altered tubulin depolymerization; in clinical trials; see eribulin	 (57)	24,25,56,57
hectochlorin	bacterium	anticancer; inhibits cell growth; induces actin polymerization	 (128)	128
hemiasterlin (hemiasterlin analog E-7974)	sponge (*Hemiasterella minor*, *Auletta* sp., *Siphonochalina* sp., *Cymbastela* sp.) South Africa	anticancer; cytotoxic, anti-tubulin; mitotic inhibition occurs through binding to tubulin at the vinca/peptide region in a manner similar to dolastatin and the vinca alkaloids; Phase II trials; licenses to Wyeth by Univ. of British Columbia; a closely related chemical, E7974, from Eisai is currently in Phase I trials	 (both 44)	18,44,58
hermitamide A & hermitamide B	cyanobacterium (*Lyngbya majuscula*) Papua New Guinea	anticancer;		114
icadamides	sponge (*Leiosella* sp.) Phillipines	anticancer, antiviral, & immunostimulant	 (106)	59,106

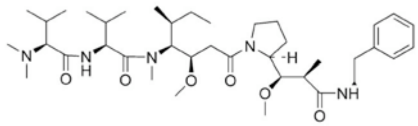
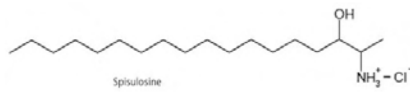
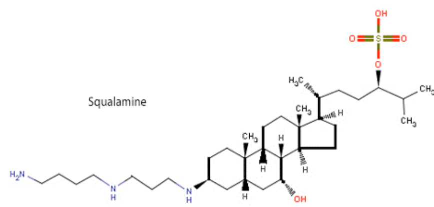
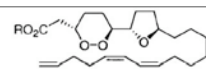
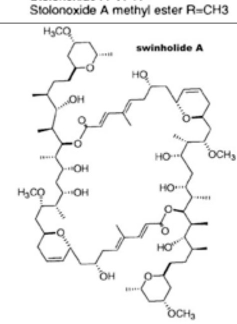
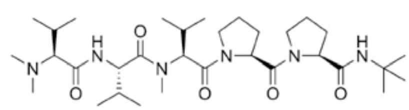
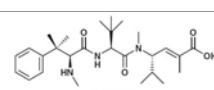
Anticancer drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
kahalalide F (revised structure) (see elisidepsin, above)	sacoglossan sea slug (*Elysia rufescens*) that grazed on green macroalgæ (*Bryopsis pennata*) Hawaii 	anticancer; disrupts lysosome [def] membranes within certain target cells, thereby initiating apoptosis (programmed cell death); inhibits gene expression related to DNA replication & cell proliferation; Phase II trials for NSCLC, melanoma & androgen-independent prostate cancer; also being studied for use on androgen-resistant prostate cancer, liver cancer, & advanced solid tumors; licensed to PharmaMar by U. Hawaii	 (61)	18,44,60,61 photo: 60
KRN-7000 (α-GalCer, α-galactosyl-ceramide) (agelasphin derivative)	sponge (*Agelas mauritiana*) Red Sea, Indian Ocean	anticancer; stimulates lymphocytic proliferation under certain conditions; appears to stimulate the production of natural killer T (NKT) cells in the body; Phase I trial showed effects with patients having high levels of NKT cells. Phase II trial ongoing	 (62)	18,62
lasonolides	deep-water sponge (*Forcepia* sp.) Gulf of Mexico 	anticancer & antifungal; kills cancer cells in a different way than most other cancer drugs; the exact mode of action is not yet fully understood, and is an area of active research; preclinical studies	 (63)	63 photo: 64
latrunculins	sponge (*Latrunculia magnifica*) Red Sea	cytotoxic actin-active agent; disrupts actin polymerization, microfilament organization, etc; cell shape, cytokinesis, and microfilament-mediated processes such as fertilization and early development are altered; preclinical; early tests show low in vivo activity; may require novel drug delivery strategies; also used as a probe for studying the role of actin in maintaining cell shape	 (65)	18,65
laulimalide	sponge (*Cacospongia mycofijiensis*) Pacific	anticancer; microtubule stabilizer; activity profiles are clearly different than other microtubule-binding agents such as paclitaxel; preclinical studies	 (66)	18,66
lissoclinamide 7	commensal bacterium found on tunicate (*Lissoclinum* sp.) Indo-West Pacific (photo: *Lissoclinum patellum*) 	anticancer	 (106,67)	67,106 photo: 68

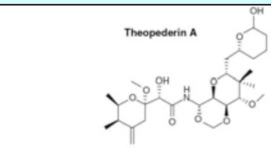
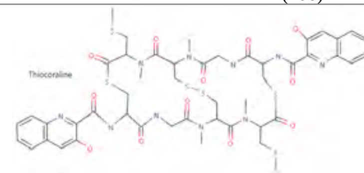
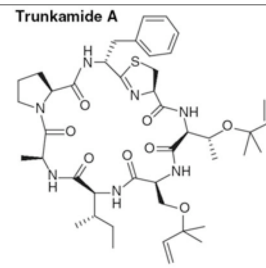
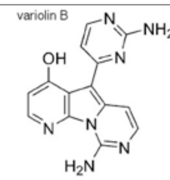
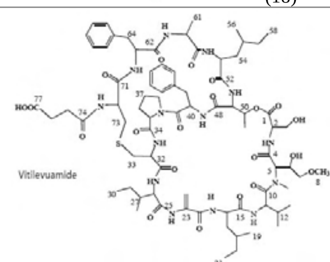
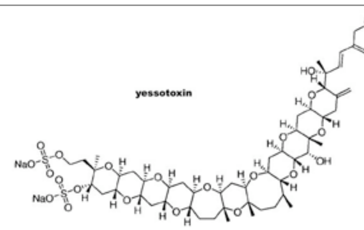
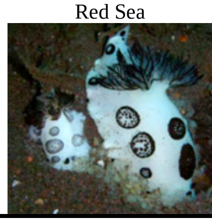
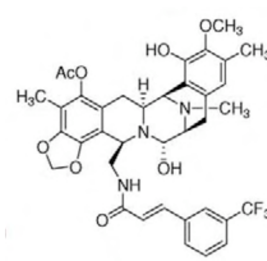
Anticancer drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
lomaiviticin A	commensal bacterium (*Micromonospora lomaivitiensis*) found on tunicate Fiji	anticancer; potent DNA damaging activity	 (69)	69
makaluvamines	sponge (*Zyzzya fuliginosa*) Indo-West Pacific	anticancer; cytotoxic through inhibition of DNA topoisomerase II		70,114
manzamine A & Ircinol A (its likely biogenic precursor, which lacks the β-carboline moiety)	sponges (*Haliclona* sp., *Pachypellina* sp.) with commensal bacterium (*Micromonospora* sp.) Indo-Pacific (photo: *Haliclona sarai*) 	antitumor, antimalarial, anti-infective, antituberculosis, antitoxoplasmosis, & antineurogenic inflammation; has shown activity against malaria, tuberculosis, HIV, and other inflammatory diseases; preclinical studies	 (117)  (103)	103,117 photo: 71
mechercharmycin A	sediment actinobacterium (*Thermoactinomyces* sp.) Palau	anticancer; active against lung cancer & leukemia cell lines; a patent claims cytotoxicity	 (32)	32
micropeptins	bacterium	anticancer; inhibition of trypsin & chymotrypsin	 (128)	128
namenamicin	commensal bacterium found on tunicate (*Polysyncraton lithostrotum*) Australia, New Zealand	antitumor & antibiotic; the enediyne moiety is very reactive with DNA, making these chemicals extremely cytotoxic for all cells & among the most potent antitumor agents known	 (72)	72
Neovastat (Æ-941) (a derivative of shark cartilage extract; not a specific mono-molecular compound, Æ-941 is a defined standardized liquid extract comprising the <500 kDa (kilodaltons, a unit of mass) fraction from shark cartilage)	shark (photo: *Carcharhinus amblyrynchos*) 	anticancer; inhibits the binding of Vascular Endothelial Growth Factor (VEGF) to its receptors; normally, VEGF binds to target endothelial receptors & directs the profusion of new capillaries to nourish the tumor; by blocking the receptor sites, AE-941 preempts the formation of the new blood supply; Phase II & III trials for renal carcinoma and NSCLC	a mixture	18 photo: 73

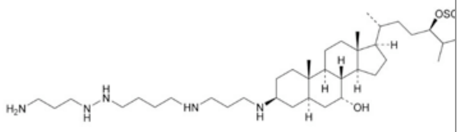
Anticancer drugs

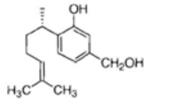
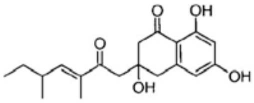
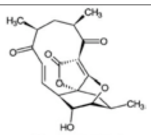
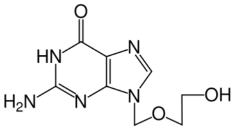
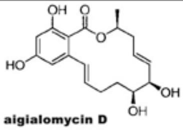
Chemical	Source	Uses & Status	Structure	Citations
NVP-LAQ824 (dacinostat) (synthetic using structures from psammaplin, trichostatin, & trapoxin)	sponge (*Psammaplysilla* [*also found in a 2-sponge association of Poecillastra* sp. & *Jaspis* sp.]) Indo-West Pacific	antibiotic, anti-tumor, DNA methyltransferase inhibitor; extremely potent histone deacetylase (HDAC) inhibitor; Phase I trial for hematologic malignancies	 (18)	18,74
onnamide A onnamide F	sponges (*Theonella* sp. and *Trachycladus lævispirulifer*) Okinawa, Australia (photo: *Theonella cylindrica*) 	anticancer, antifungal, & anthelmintic	 (75)  (76)	75,76, 114,128 photo: 77
panobinostat (LBH-589, Faridak®)	sponge (*Psammaplysilla spp.*) Indo-West Pacific	anticancer; synthetic analog of psammaplin; with Novartis; Phase III	 (78)	78
patellamides	commensal bacterium found on tunicate (*Lissoclinum patella*) Indo-West Pacific 	anticancer; cytotoxic; patellamides B, C, & D appear to reverse multidrug resistance	 (106)	79,80,106 photo: 68
pectenotoxin-6	algæ	anticancer; induces F-actin depolymerization	 (128)	128
peloruside A	sponge (*Mycale hentscheli*) New Zealand	anticancer; appears to bind tubulin and arrests target cell development at the G2-M transition stage of the cell cycle, triggering apoptosis (cell suicide) before mitosis can begin; preclinical studies	 (81)	18,81
phomactins	fungus (*Phoma* sp.) found on shell of crab (*Chinoecetes opilio*) Japan 	anticancer; platelet activating factor (PAF) antagonists	 (82)	83 photo: 84
plinabulin (NPI-2358)	fungus (*Aspergillus* sp.)	anticancer; synthetic analog of marizomib; selective vascular disrupting agent (VDA); Phase I/II	 (53)	53

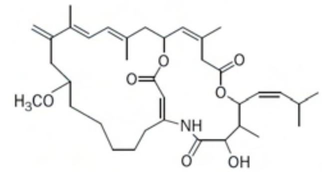
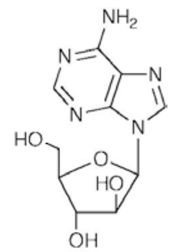
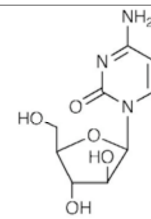
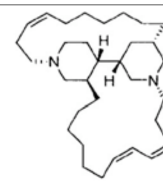
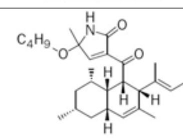
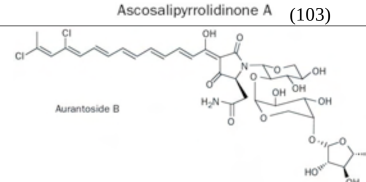
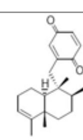
Anticancer drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
psymberin (irciniastatin)	sponges (*Psammocinia* sp. & *Ircinia ramosa*) Indo-West Pacific	anticancer; showed extremely potent toxicity toward several cancer cell lines (>10^4 more potent than usually observed))	 (106)	85,106
salicylihalimides	sponge (*Haliclona* sp.) Indo-Pacific (photo: *Haliclona sarai*) 	anticancer & anti-osteoporosis; first marine Vo-ATPase inhibitor (Vo-ATPases are eukaryotic enzymes whose principal role is to pump hydrogen ions across cell vacuolar membranes); may mediate bone resorption; preclinical studies	 (86)	18,86,87 photo: 71
saliniketal A & saliniketal B	actinobacterium (*Salinispora arenicola*) worldwide	chemopreventive		
salinosporamide A (NPI-0052, marizomib)	actinobacterium (*Salinispora tropica*) tropics	antibiotic & cytotoxin; very potent proteasome inhibitor; A & B inhibited colon cancer cells in vitro; A was extremely potent against NSCLC, CNS, & breast cancer lines; in Phase I trials with Nereus Pharma	 (44)	32,44
sansalvamide	fungus (*Fusarium* sp.) found on seagrass (*Halodule wrightii*) western tropical Atlantic & Gulf of Mexico 	anticancer; selective cytotoxicity towards colon & melanoma cell lines	 (88)	88,114 photo: 89
sarcodicytin (related to eleutherobins & eleuthosides)	alcyonarians (soft corals) (*Sarcodictyon roseum* [photo], *Eleutherobia aurea*, & *Bellonella albiflora*) Mediterranean 	anticancer; tubulin interactive agent; synthetic combinatorial research using base structures of sarcodicytins & eleutherobins; preclinical testing of derivatives	 (102)	18,86,102 photo: 90
sculezonone A & sculezonone B	bacterium	anticancer; inhibits DNA polymerase	 (128)	128

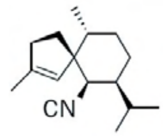
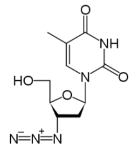
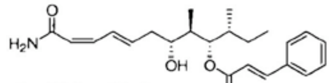
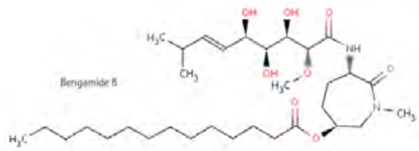
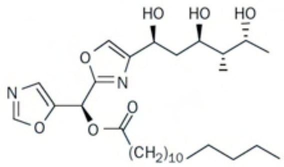
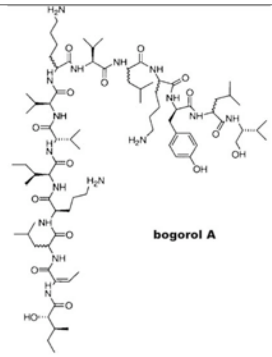
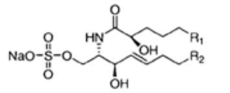
Anticancer drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
soblidotin (auristatin PE, TZT-1027) (synthetic analog of dolastatin)	sea hare (*Dolabella auricularia*) (chemical possibly from commensal cyanobacteria [*Symploca hydnoides* & *Lyngbya majuscula*]) Indian Ocean 	anticancer; exhibits potent antivascular effects in addition to antitublin activity; Phase III trials; Phase II trials showed no positive results when used alone, but it appears to be effective in combination therapy with vinca alkaloids and bryostatin	 (18)	18,44 photo: 31
spisulosine (ES-285)	Arctic surf clam (*Spisula polynyma*) North Atlantic, North Pacific, Arctic Seas, Japan	anticancer; *Rho*-GTP inhibitor; appears to alter cell morphology: treated cells appear to lose actin stress fibers, (bundles of actin filaments that appear & disappear in response to mechanical stimuli); Phase I trials	 (91)	18,91
squalamine (opthalamic formulations are called Evizon™)	spiny dogfish (*Squalus acanthias*) Northwest Atlantic 	anticancer, antiangiogenic, & antibiotic; broad spectrum antibiotic; also shows anti-angiogenic activity and may be useful to treat wet-form age-related macular degeneration; Phase II trials for nonresponding solid tumors as part of combination therapy and for advanced ovarian cancer as primary treatment; Phase III trials for wet macular degeneration show significant activity	 (92)	18,44, 92,103 photo: 93
stolonoxides	tunicate	anticancer; mitochondrial respiratory chain inhibition	 Stolonoxide A R=H Stolonoxide A methyl ester R=CH3 (128)	128
swinholide A	sponge	anticancer; facilitates outflow in eye	 (128)	128
synthatodin (ILX 651, tasidotin) (3rd gen. derivative of dolastatin 15)	sea hare (*Dolabella auricularia*) (chemical possibly from commensal cyanobacteria [*Symploca hydnoides* & *Lyngbya majuscula*]) Indian Ocean 	anticancer; orally-active 3rd generation analog; Phase I/II trials for melanoma, breast, NSCLC; licensed by Ilex from BASF Pharma	 (18)	18,44,46 photo: 31
Taltobulin (HTI-286) (hemiasterlin analog)		Phase I/II trials	 HTI-286 (44)	44

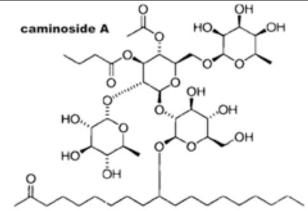
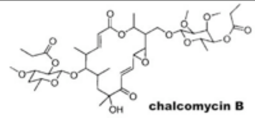
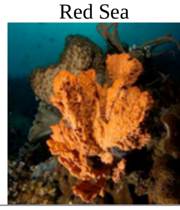
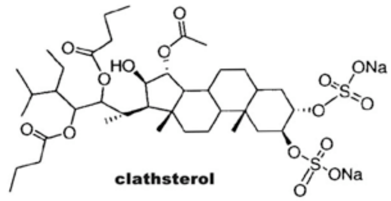
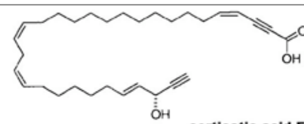
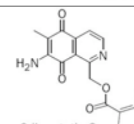
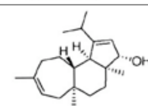
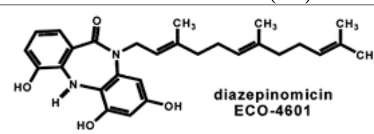
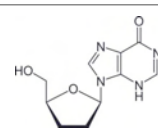
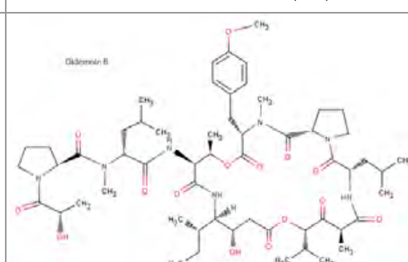
Anticancer drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
theopederins	sponge (*Theonella swinhoei*) Indo-Pacific	anticancer	 (106)	106
thiocoraline	actinobacterium (*Micromonospora marina*)	anticancer; DNA polymerase α inhibitor; preclinical studies	 (94)	18,94
trunkamide	commensal bacterium found on tunicate (*Lissoclinum patella*) Indo-West Pacific 	anticancer; has specific & unusual activity against the multidrug-resistant UO31 renal cell line	 (106)	80,106 photo: 68
variolins	Antarctic sponge (*Kirkpatrickia variolosa*) Antarctic	anticancer; Cdk inhibitors; preclinical studies	 (18)	18
vitilevuamide	tunicates (*Didemnum cucliferum* & *Polysyncraton lithostrotum* [photo]) Australia, New Zealand	anticancer; inhibits tubulin polymerization & can arrest the cell cycle in the G2/M phase; tubulin binding & inhibition occurs at a different site on the tubulin molecule than used by dolastatin 10, colchicine, & the vinca alkaloids; preclinical studies	 (95)	18,95
yessotoxin	algæ	anticancer; lymphocyte homeostasis modulation	 (128)	128
Zalypsis® (PM1004)	nudibranch (*Jorunna funebris*) Western Indian Ocean, Red Sea 	anticancer; synthetic analog of jorumycin, safracin B, & saframycin B; made by PharmaMar; Phase II trials	 (53)	53 photo: 96

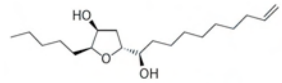
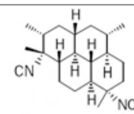
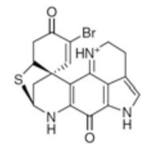
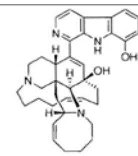
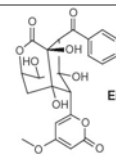
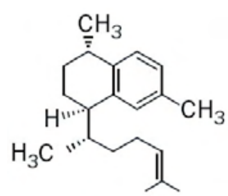
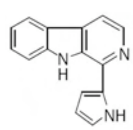
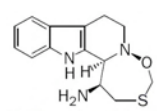
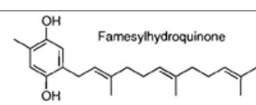
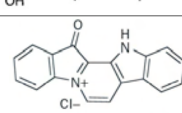
Antidiabetic drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
insulin	European spotted dogfish (*Scyliorhinus canicula*) & hammerhead shark (*Sphyrna lewini* [photo]) North Atlantic, Indian Ocean, Red Sea 	antidiabetic; high affinity binding to human insulin receptor; although markedly different than human insulin the binding sites for the human receptor in the same location	A Chain GIVDHCCHNTCSLYDLEGYCNQ B Chain LPSQHLCGSHLVETLYFVCGQKGFYYVPKI Insulin - AA sequence from insulin of the hammerhead shark (128)	128 photo: 97
trodusquemine (MSI-1436)	spiny dogfish (*Squalus acanthias*) worldwide 	antidiabetic; causes fat-specific weight loss; Phase I trials had very promising results; Genaera started Phase I in 2007 and reported promising results in 2009. Shortly thereafter, Genaera was dissolved, and trodusquemine was sold to Ohr Pharmaceuticals; current status unknown	 (98)	92,98 photo: 93

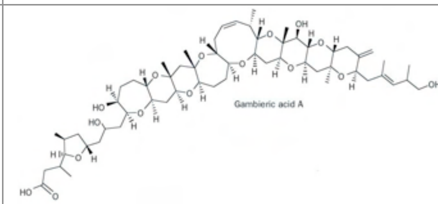
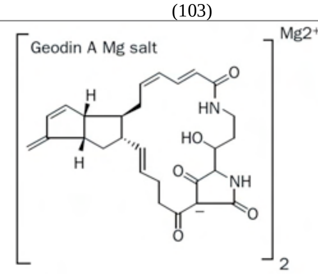
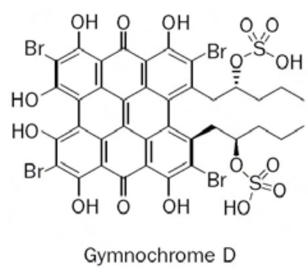
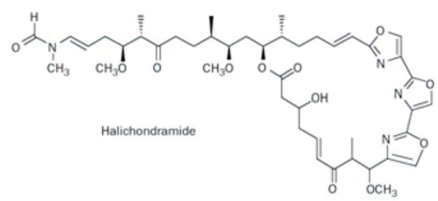
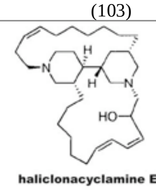
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
(*S*)-(+)-15-hydroxy-curcuphenol	sponge (*Didiscus oxeata*) Jamaica	antimalarial; *P. falciparum* inhibition	 (S)-(+)-hydroxycurcuphenol (128)	128
3,3'-oxybis[5-methyl-phenol]	fungus (*Keissleriella* sp.)	antifungal; *C. albicans*, *T. rubrum* & *A. niger* inhibition	 3,3'-oxybis[5-methyl-phenol] (128)	128
abyssomicin C	actinobacterium (*Verrucosispora maris*)	antibiotic; inhibits biosynthesis of p-aminobenzoate (pABA), a pathway not found in humans; Phase I trials	 Abyssomicin C (99)	99,100,101
Acyclovir (ACV, acycloguanosine, Zovirax®) (derived from spongouridine & spongothymidine)	sponge (*Tectitethya crypta*) (synonym: *Cryptotethya crypta*) Caribbean	antiviral; Acyclovir differs from previous nucleoside analogues in that it contains only a partial nucleoside structure: the sugar ring is replaced by an open-chain structure; clinical use	 (102)	102
aigialomycin D	mangrove fungus (*Aigialus parvus* BCC 5311) tropics	antimalarial; *P. falciparum* inhibition	 aigialomycin D (128)	128

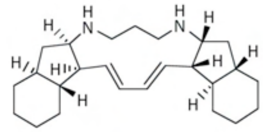
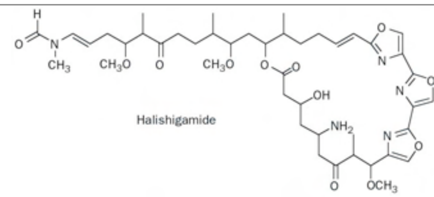
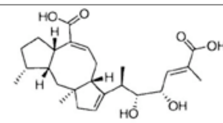
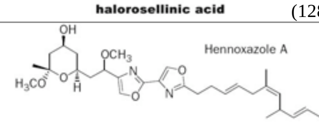
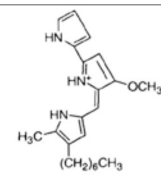
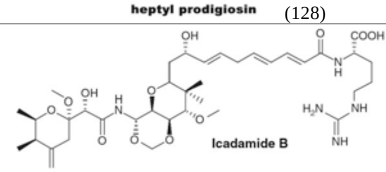
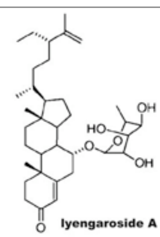
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
amphilactams	sponge (Amphimedon *sp.*) Australia (photo: *A. queenslandica*) 	antiparasitic	 Amphilactam D (103)	103 photo: 104
Ara-A (vidarabine, Vira-A®) (derived from spongouridine & spongothymidine)	gorgonian (*Eunicella cavolini*) Mediterranean 	antiviral & anticancer; clinical use	 (102)	18,19, 105,102 photo: 105,
Ara-C (Cytosar-U®, DepoCyt®, Tarabine PFS®, cytarabine, 1-β-D- arabinosylcytosine) (derived from spongouridine & spongothymidine)	sponge (*Tectitethya crypta*) (synonym: *Cryptotethya crypta*) Caribbean	antiviral & anticancer; clinical use	 (102)	18,19, 102,103
arenosclerins (similar to haliclonacyclamine)	sponge (*Arenosclera brasiliensis*) Brazil	antibacterial	 arenosclerin A (128)	128
ascosali- pyrrolidinone A	green algæ *(Ulva* sp.) with commensal fungus (*Ascochyta salicorniæ*) worldwide	antiparasitic	 Ascosalipyrrolidinone A (103)	103
aurantoside B	sponge (*Siliquariaspongia japonica*) Japan	antifungal	 Aurantoside B (103)	103
avarol	sponge (*Dysidea avara*) Mediterranean	antibiotic & anticancer; Cytostatic agent with potent antileukemic activity both *in vitro* & *in vivo* (mice); antibacterial & antifungal activities for a limited range of microbes; inhibits HIV-1 reverse transcriptase	 averol (107)	106,107
avarone	sponge (*Dysidea avara*) Mediterranean	antiviral	 Avarone (103)	103

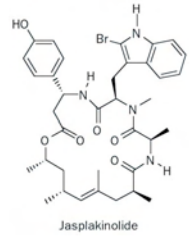
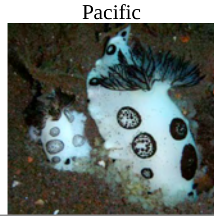
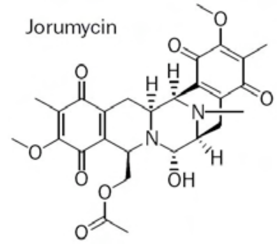
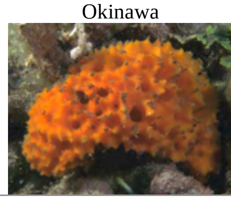
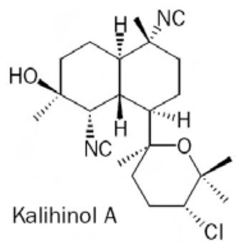
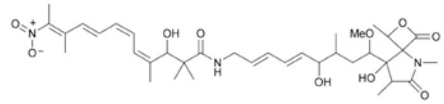
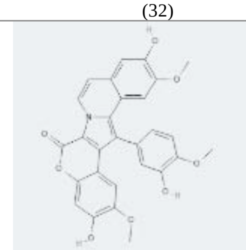
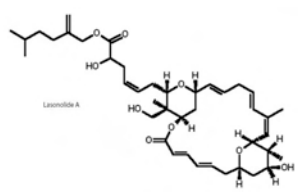
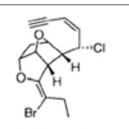
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
axisonitrile-3	sponge (*Acanthella klethra*) Australia 	antituberculosis	 Axisonitrile-3 (103)	103 photo: 108
azidothymidine (AZT, zidovudine, Retrovir®) (derived from spongouridine & spongothymidine)	sponge (*Tectitethya crypta*) (synonym: *Cryptotethya crypta*) Caribbean	antiviral; reverse-transcriptase inhibitor; clinical use	 (109)	18,19,102 106,109
basiliskamide A & basiliskamide B	bacterium (*Bacillus laterosporus*)	antifungal; *C. albicans* & *A. fumigatus* inhibition	 basiliskamide A (128)	128
bengamide derivative	sponge (*Jaspis* sp.) Fiji 	anticancer & antihelminthic; methionine aminopeptidase (Met-AP1) inhibitor; licensed to Novartis; withdrawn from Phase I trials in 2002	 (22)	18,22 photo: 23
bengazole A	sponge (*Jaspis* sp.) Fiji 	antifungal	 Bengazole A (103)	103 photo: 23
bogorol A	bacterium (*Bacillus* sp.)	antibacterial; inhibits antibiotic-resistant *S. aureus* & enterococci	 (128)	128
bromosphaerone	red algæ (*Sphærococcus coronopifolius*) Atlantic coast of Morocco	antibiotic	 Bromosphaerone (103)	103
calyceramides A–C	sponge (*Discodermia calyx*) Japan	antiviral; neuraminidase inhibition	 Calyceramide A $R_1 = C_{10}H_{22}$ $R_2 = C_{12}H_{26}$ Calyceramide B $R_1 = C_9H_{20}$ $R_2 = C_{13}H_{28}$ Calyceramide C $R_1 = C_{11}H_{24}$ $R_2 = C_{11}H_{24}$ (128)	128

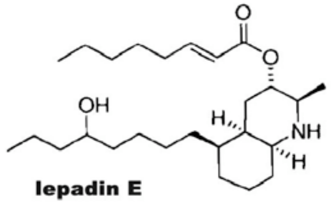
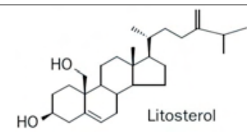
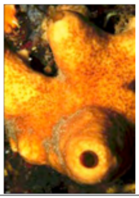
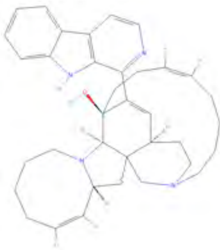
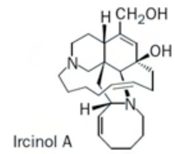
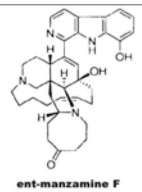
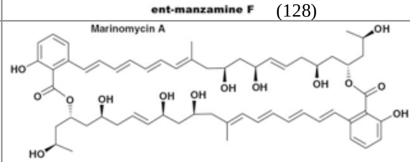
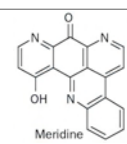
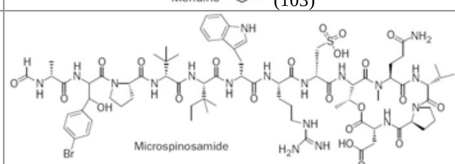
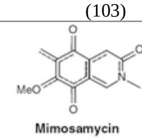
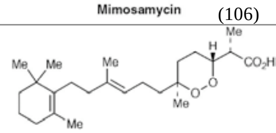
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
caminoside A	sponge (*Caminus sphæroconia*) Caribbean, Brazil	antibacterial; inhibits antibiotic-resistant *S. aureus* & enterococci	 caminoside A (128)	128
chalcomycin B	actinobacterium (*Streptomyces* sp.)	antibacterial; inhibits antibiotic-resistant *S. aureus*	 chalcomycin B (128)	128
clathsterol	sponge (*Clathria* sp.) Red Sea 	antiviral; HIV reverse transcriptase inhibition	 clathsterol (128)	128 photo: 110
corticatic acid A & corticatic acid B	sponge (*Petrosia corticata*) Western Pacific	antifungal; *C. albicans* & *A. fumigatus* inhibition; selective GGTase 1 inhibition (enzyme is involved in fungal cell wall biosynthesis)	 corticatic acid E (128)	128
cribrostatin 3	sponge (*Cribrochalina* sp.) worldwide	antibiotic & anticancer	 Cribrostatin 3 (103)	103
cyanthiwigin C	sponge (*Myrmekioderma rea*) (synonym: *Myrmekioderma styx*) Jamaica	antituberculosis	 cyanthiwigin C (128)	128
diazepinomicin (ECO-4601)	actinobacterium (*Micromonospora* sp.)	antibiotic & anticancer; Phase I trials (antibiotic & anticancer)	 diazepinomicin ECO-4601 (35)	36
dicynthaurin	tunicate (*Halocynthia aurantium*) North Pacific	antibacterial; gram negative & gram positive inhibition	ILQKAVLDCLKAAGSSLSKAAITAIYNKIT **dicynthaurin** (128)	128
didanosine (2',3'-dideoxy-inosine, ddI, DDI) (derived from spongouridine & spongothymidine)	sponge (*Tectitethya crypta*) (synonym: *Cryptotethya crypta*) Caribbean	antiviral; clinical use	 (102)	102
didemnin B	tunicate (*Trididemium solidum*) Caribbean	anticancer & antiviral interrupts protein synthesis in target cells by binding noncompetitively to palmitoyl protein thioesterase; cytotoxic for lymphomas, some leukemias & melanomas; antiviral for herpes simplex and several others; Phase II trials showed significant toxicity at efficacious doses; dropped in middle 1990s	 (41)	18,24, 39,40,41,41

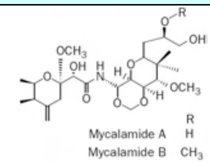
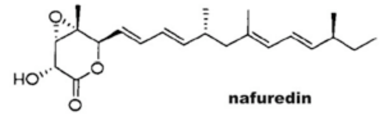
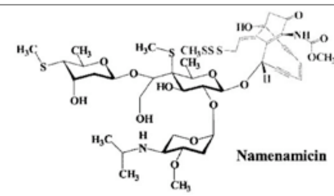
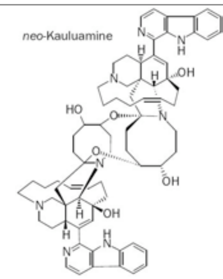
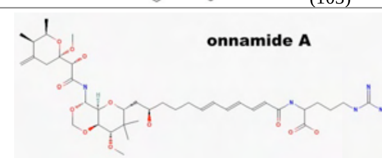
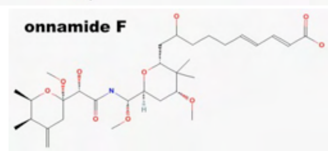
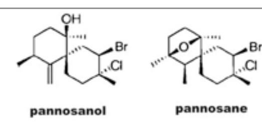
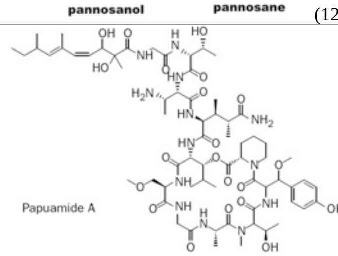
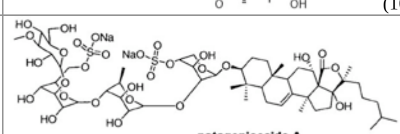
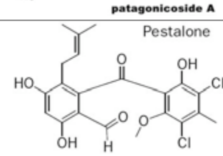
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
dihydroxytetra-hydrofuran	brown algæ (*Notheia anomala*) Australia	antiparasitic; *in vivo* tests did not duplicate *in vitro* success, probably because drug is strongly hydrophobic	 *Trans*-dihydroxytetrahydofuran (103)	103
di-isocyano-adociane	sponge (*Pipestela hooperi*) (synonym: *Cymbastela hooperi*) Australia	antimalarial	 Diisocyanoadociane (103)	103
discorhabdins	sponges (*Latrunculia* sp.) New Zealand	antibacterial, antifungal, & antitumor	 **Discorhabdin A** (106)	106,111
ent-8-hydroxy-manzamine A	sponge Indo-Pacific	antimalarial; *P. berghei* inhibition	 **ent-8-hydroxymanzamine** (128)	128
enterocin	actinobacterium (*Streptomyces maritimus*)	antibiotic & antiviral	 **Enterocin** (106)	106,112
ergorgiaene & 7-hydroxy-ergorgiaene	gorgonian (sea whip) (*Pseudopterogorgia elisabethæ*) Caribbean 	antituberculosis	 Ergorgiaene (103)	12,103 photo: 11
eudistomins	shallow water tunicate (*Eudistoma* sp.) Caribbean 	antiviral; Four types of eudistomins: unsubstituted, pyrrolyl-substituted, pyrrolinyl-substituted, & tetrahydro-β-carbolines	 Pyrrolyl-substituted eudistomins (103)  Eudistomins with oxathiazepine ring (103)	103 photo: 113
farnesylhydro-quinone	fungus	anticancer & antimalarial	 (128)	128
fascaplysin	sponge (*Fascaplysinopsis* sp.) Indo-West Pacific	antifungal	 Fascaplysin (103)	103

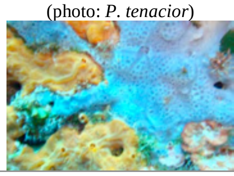
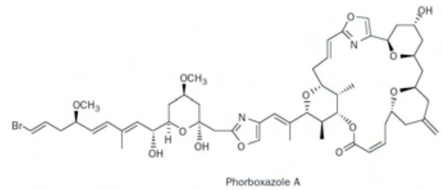
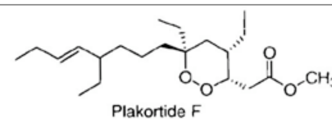
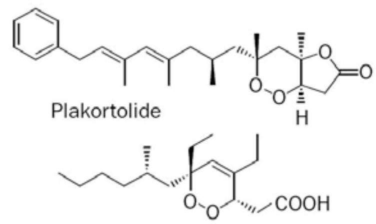
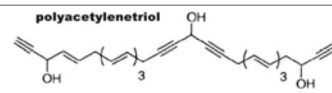
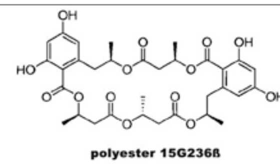
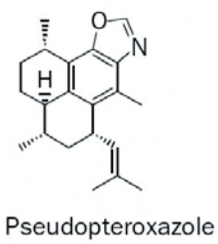
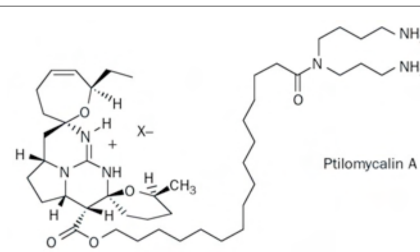
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
fumiquinazoline	epiphytic fungus (*Acremonium* sp.) on tunicate (*Ecteinascidia turbinata*) Caribbean 	antifungal		114 photo: 50
gambieric acids	dinoflagellate (*Gambierdiscus toxicus*) Central Pacific, Gulf of Mexico	antifungal	 (103)	103
geodin A Mg salt	sponge (*Geodia* sp.) Australia 	antiparasitic	 (103)	103 photo: 115
gymnochrome D	stalked crinoid (sea lily) (*Neogymnocrinus richeri*) (synonym: *Gymnocrinus richeri*) New Caledonia 	antiviral	 (103)	103 photo: 116
halichondramide	sponge (*Halichondria* sp.) Indo-West Pacific	antifungal & antimalarial	 (103)	103
haliclona-cyclamines (similar to arenosclerins)	sponge (*Arenosclera brasiliensis*) Brazil	antibacterial	 (128)	128

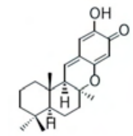
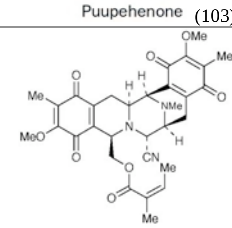
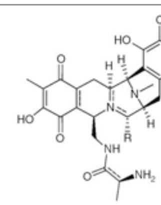
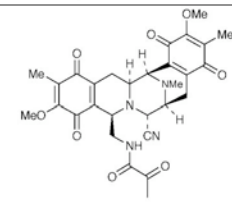
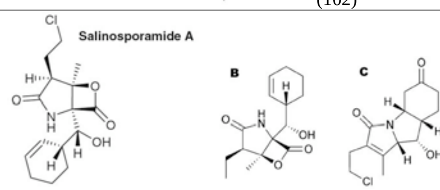
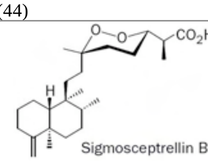
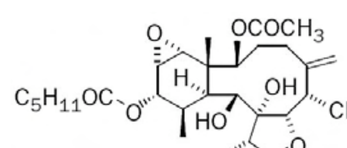
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
haliclonadiamine	sponge (*Haliclona* sp.) Indian Ocean (photo: *Haliclona sarai*) 	antifungal	 Haliclonadiamine (103)	117 photo: 71
halishigamide A	sponge (*Halichondria* sp.) Indo-West Pacific	antifungal	 (103)	103
halocidin	tunicate (*Halocynthia aurantium*) Northern Pacific	antibacterial; inhibits antibiotic-resistant *S. aureus* & MDR-resistant *P. æruginosa*	WLNALLHHGLNCAKGVLA | ALLHHGLNCAKGVLA Two amino acid sequences (one 18-unit & one 15-unit) joined by a disulfide bond between a cysteine residue in each unit halocidin (128)	128
halorosellinic acid	fungus (*Halorosellinia oceanica* BCC 5149) Thailand	antimalarial; *P. falciparum* inhibition	 halorosellinic acid (128)	128
hennoxazole A	sponge (*Polyfibrospongia* sp.) Indo-Pacific	antiviral	 (103)	103
heptyl prodigiosin	commensal bacterium found on tunicate Phillipines	antimalarial; *P. falciparum* & *P. berghei* inhibition	 heptyl prodigiosin (128)	128
icadamides	sponge (*Leiosella* sp.) Phillipines	anticancer, antiviral, & immunostimulant	 (106)	59,106
iyengaroside A	algæ (*Codium iyengarii*) Arabian Sea	antibacterial; gram negative & gram positive inhibition	 Iyengaroside A (128)	128

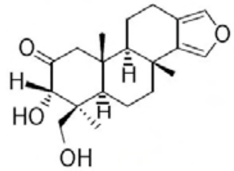
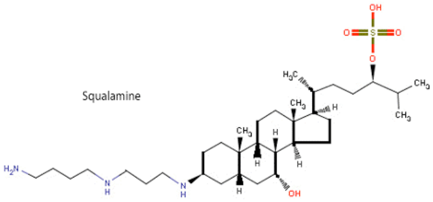
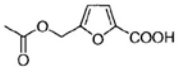
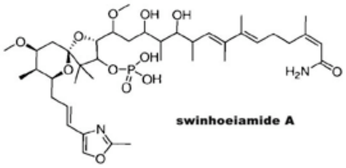
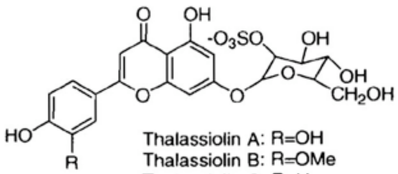
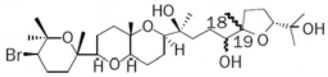
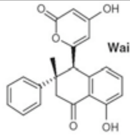
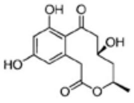
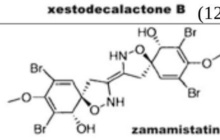
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
jasplakinolide (jaspamide)	sponge (*Jaspis* sp.) Fiji 	antifungal & antiparasitic; *P. falciparum* inhibition	 (103)	103,128 photo: 23
jorumycin	nudibranch (*Jorunna funebris*) Pacific 	antibiotic	 (103)	103 photo: 96
kalihinol A	sponge (*Acanthella* sp.) (photo: *A cavernosa*) Okinawa 	antimalarial	 (103)	103 photo: 118
lajollamycin	sediment actinobacterium (*Streptomyces nodosus*) California	antibiotic & anticancer; active against both drug-sensitive & drug-resistant Gram positive microbes; inhibited growth in murine melanoma cell line	 (32)	32
lamellarins (lamellarin α 20-sulfate)	tunicate (*Didemnum obscurum*) Indo-West Pacific	antiviral; HIV-1 integrase inhibitor; inhibits early steps of HIV replication	 (119)	114
lasonolides	deep-water sponge (*Forcepia* sp.) Gulf of Mexico 	anticancer & antifungal; kills cancer cells in a different way than most other cancer drugs; the exact mode of action is not yet fully understood, and is an area of active research; preclinical studies	 (63)	63 photo: 64
lembyne A	red algæ (*Laurencia* sp.) Malaysia	antibacterial	 (128)	128

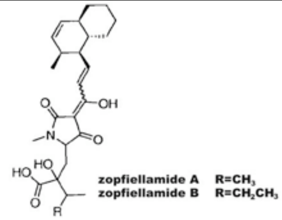
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
lepadin E & lepadin F	tunicates (*Clavelina lepadiformis* [photo], *Aplidium tabascum, Didemnum* sp.) Mediteranean, Indo-West Pacific 	antimalarial; *P. falciparum* inhibition	 (128)	128 photo: 120
litosterol	alcyonarian (soft coral) (*Litophyton viridis*) Okinawa	antituberculosis	 (103)	103
manzamine A & ircinol A (its likely biogenic precursor that lacks the β-carboline moiety)	sponge (*Haliclona* sp., *Pachypellina* sp.) Indo-Pacific (photo: *Haliclona sarai*) 	antitumor, antimalarial, anti-infective, antituberculosis, antitoxoplasmosis, & antineurogenic inflammation; has shown activity against malaria, tuberculosis, HIV, and other inflammatory diseases; preclinical studies	 (117)  (103)	103,117 photo: 71
manzamine F	sponge Indo-Pacific	antimalarial; *P. berghei* inhibition	 (128)	128
marinomycins A–D	actinobacterium (*Marinispora* sp.)	antibiotic; potent activity against drug-resistant bacterial pathogens & some melanomas	 (44)	44
marinone	bacterium	antibiotic		25
meridine	sponge (*Corticium* sp.) Bahamas	antifungal	 (103)	103
microspinosamide	sponge (*Sidonops microspinosa*) Philippines	antiviral; HIV-growth inhibition	 (103)	103,121,128
mimosamycin	commensal actinobacterium (*Streptomyces lavendulæ*) found on sponge (*Petrosia* sp.) Western Pacific	antibiotic; a neutral antibiotic mainly active against mycobacteria	 (106)	106
muqubilin	sponge (*Prianos* sp.) Red Sea	antimalarial	 (102)	102

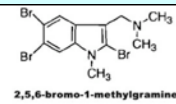
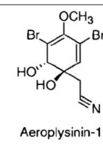
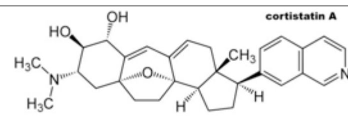
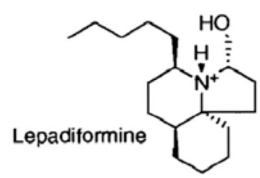
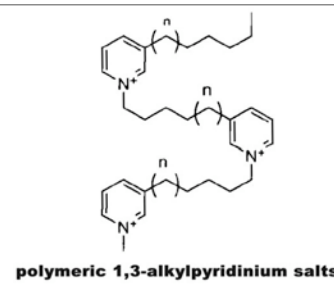
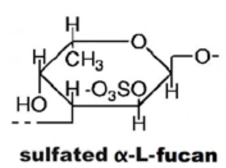
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
mycalamide A & mycalamide B	sponge (*Mycale* sp.) New Zealand	antiviral; protein synthesis inhibitors; mycalamide B has shown greater antiviral activity	 (103)	103
nafuredin	fungus (*Aspergillus niger*)	anthelmintic; inhibition of helminth NADH-fumarate reductase; competes for the quinone-binding site	 (128)	128
namenamicin	commensal bacterium found on tunicate (*Polysyncraton lithostrotum*) Australia, New Zealand	antitumor & antibiotic; the enediyne moiety is very reactive with DNA, making these chemicals extremely cytotoxic for all cells & among the most potent antitumor agents known	 (72)	72
neo-kauluamine	sponge Indo-Pacific	antimalarial; *P. berghei* inhibition	 (103)	103,128
onnamide A & onnamide F	sponges (*Theonella* sp. & *Trachycladus lævispirulifer*) Okinawa, Australia (photo: *Theonella cylindrica*) 	anticancer, antifungal, & anthelmintic	 (75)  (76)	75,76, 114,128 photo: 77
pannosanol & pannosane	red algæ (*Laurencia pannosa*) Malaysia	antibacterial	 (128)	128
papuamide A	sponges (*Theonella mirabilis* & *T. swinhoei* [photo]) Indo-West Pacific	antiviral	 (103)	103
patagonicoside A	echinoderm (sea cucumber) (*Psolus patagonicus*) Southern Ocean	antifungal; *Cladosporium cucumerinum* inhibition	 (128)	128
pestalone	marine fungus (*Pestalotia* sp.) found on brown algæ (*Rosenvingea* sp.) Bahamas	antibacterial	 (103)	103,128

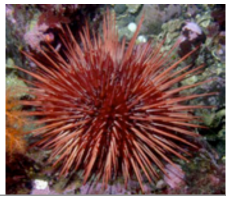
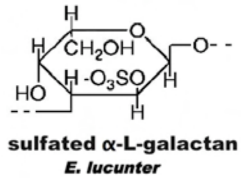
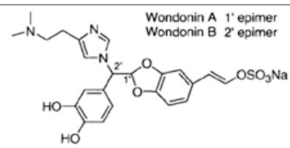
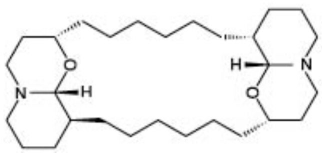
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
phorboxazole A	sponge (*Phorbas* sp.) Australia (photo: *P. tenacior*) 	antifungal	 (103)	103 photo: 122
plakortide F	sponge (*Plakinastrella onkodes*) Jamaica	antimalarial; *P. falciparum* inhibition	 (128)	103,128
plakortolide & plakortolide G (a 2nd cyclic peroxide)	sponges (*Plakortis* sp. [photo] & *Plakinastrella onkodes*) Pacific (*Plakortis* sp.) Jamaica (*P. onkodes*) 	antiparasitic & antiprotozoal; active against *Leishmania* spp. parasites	 2nd cyclic peroxide (103)	103,128 photo: 123
polyacetylenetriol	sponge (*Petrosia* sp.) Mediteranean	antiviral; RNA- & DNA-directed DNA polymerase inhibition	 (128)	128
polyester 15G256β	fungus (*Halorosellinia oceanica*) (synonym: *Hypoxylon oceanicum*) Indian Ocean	antifungal; cell wall biosynthesis inhibition	 (128)	128
pseudopter-oxazole	gorgonian (sea whip) (*Pseudopterogorgia elisabethæ*) Caribbean 	antituberculosis	 (103)	12,103 photo: 11
ptilomycalin A	sponge (*Ptilocaulis spiculifer*) Australia 	antifungal	 (103)	103 photo: 124

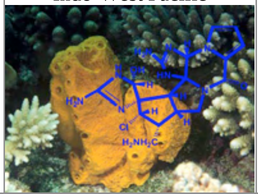
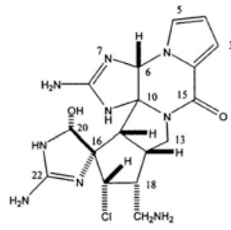
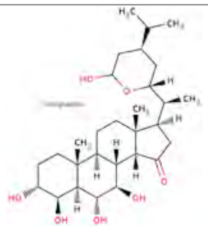
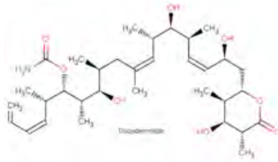
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
puupehenone	sponges (from Order Verongida & Order Dictyoceratida) Hawaii	antituberculosis	 Puupehenone (103)	103
renieramycins	sponge (*Reniera* sp.) Pacific	antibiotic;	 (102)	102
safracins	bacterium (*Pseudomonas fluorescens*)	antibiotic & antitumor	 (106)	106
saframycins	actinobacterium (*Streptomyces lavendulæ*)	antibiotic & anticancer	 (102)	102
salinosporamide A	actinobacterium (*Salinispora tropica*) tropics	antibiotic & cytotoxin; very potent proteasome inhibitor; A & B inhibited colon cancer cells in vitro; A was extremely potent against NSCLC, CNS, & breast cancer lines; in Phase I trials	 (44) (32)	32,44
sigmosceptrellin & sigmosceptrellin B	sponges (*Sigmosceptrella* sp. & *Diacarnus erythrœanus*) Red Sea	antimalarial & antiparasitic	 Sigmosceptrellin B (103)	102,103
solenolide A	gorgonian (*Briareum asbestinum*) Gulf of Mexico 	antiviral	 Solenolide A (103)	103 photo: 125

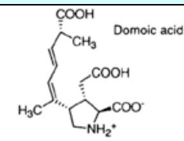
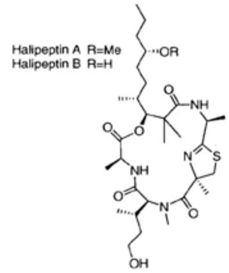
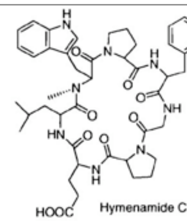
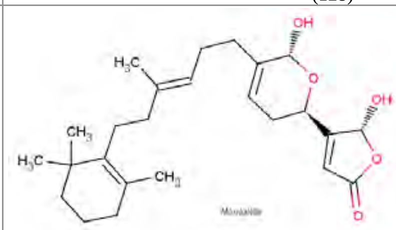
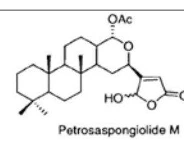
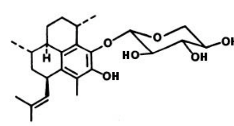
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
spongiadiol	deep-water sponge (*Spongia* sp.) (photo: *S. officinalis*) Caribbean 	antiviral	 Spongiadiol (103)	103 photo: 126
squalamine	spiny dogfish (*Squalus acanthias*) worldwide 	anticancer, antiangiogenic, & antibiotic; broad spectrum antibiotic; also shows anti-angiogenic activity and may be useful to treat age-related macular degeneration; Phase II trials for nonresponding solid tumors as part of combination therapy and for advanced ovarian cancer as primary treatment; Phase III trials for wet macular degeneration show significant activity	 (92)	18,44, 92,103 photo: 93
Sumiki's acid (acetyl derivative)	fungus	antibacterial; *B. subtilis* & *S. aureus* inhibition	 (128) **Sumiki's acid**	128
swinhoeiamide A	sponge (*Theonella swinhoei*) Indo-West Pacific	antifungal; *C. albicans* & *A. fumigatus* inhibition	 **swinhoeiamide A** (128)	128
thalassiolins A–C	sea grass (*Thalassia testudinum*) Gulf of Mexico 	antiviral; HIV-1 integrase inhibition	 Thalassiolin A: R=OH Thalassiolin B: R=OMe Thalassiolin C: R=H (128)	128 photo: 127
thyrsiferol	red algæ (*Laurencia venusta*) Indian Ocean	antiviral	 Thyrsiferol 18*S*, 19*R* (103)	103
wailupemycins	actinobacterium (*Streptomyces maritimus*)	antibiotic & antiviral	 Wailupemycin D (106)	106
xestodecalactone B	fungus (*Penicillium* cf. *monanense*) found on sponge (*Neopetrosia exigua*) (synonym: *Xestospongia exigua*) Indian Ocean	antifungal; *C. albicans* inhibition	 **xestodecalactone B** (128)	128
zamamistatin	sponge (*Pseudoceratina purpurea*) Okinawa	antibacterial; *Rhodospirillum salexigens* inhibition	 **zamamistatin** (128)	128

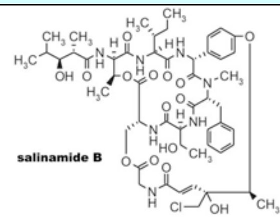
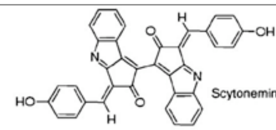
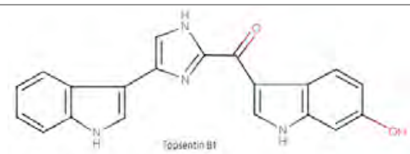
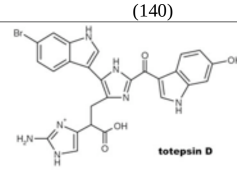
Anti-infective drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
zopfiellamide A & zopfiellamide B	fungus (*Zopfiella latipes*)	antibacterial; gram negative & gram positive inhibition	 (128)	128

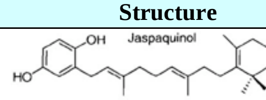
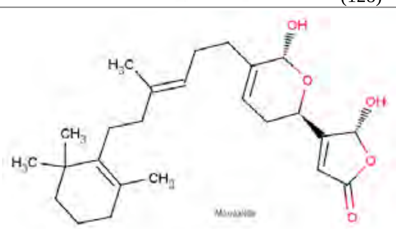
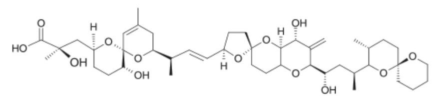
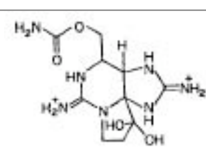
Cardiac & circulatory system drugs; Anti-angiogenesis drugs				
Chemical	**Photo of Source**	**Uses & Status**	**Structure**	**Citations**
2,5,6-tribromo-1-methylgramine (TBG)	bryozoan (*Zoobotryon verticillatum*) (synonym: *Z. pellucidum*) worldwide	cardiovascular; vasorelaxation; Ca^{2+} inhibition & increase cyclic AMP	 (128)	128
aeroplysinin-1	sponge	antiangiogenic	 (128)	128
bryoanthra-thiophene	bryozoan	inhibits angiogenesis		128
cortistatins	sponge (*Corticium simplex*) Australia	possesses a highly selective & perhaps mechanistically unique antiangiogenic activity	 (129)	129
lepadiformine	tunicates (*Clavelina moluccensis* & *C. lepadiformis* [photo]) Mediteranean, Indo-West Pacific 	cardiovascular; inhibition of cardiocirculatory system; reduction in inward K^+ current	 (128)	128 photo: 130
polymeric 1,3-alkylpyridinium salts	sponge (*Haliclona (Rhizoniera) sarai*) (synonym: *Reniera sarai*) Mediteranean 	blood coagulation & platelet aggregation; induces blood coagulation, platelet aggregation, & cytotoxicity in rats; previously found to be cholinesterase inhibitors	 (128)	128 photo: 71
sulfated *α-L*-fucan	sea urchins (*Echinometra lucunter* [photo] & *Strongylocentrotus franciscanus*) Brazil & Gulf of Mexico 	anticoagulant	 (128)	128 photo: 131

Cardiac & circulatory system drugs; Anti-angiogenesis drugs				
Chemical	**Photo of Source**	**Uses & Status**	**Structure**	**Citations**
sulfated *α-L*-galactan	sea urchins (*Echinometra lucunter* & *Strongylocentrotus franciscanus* [photo]) Brazil & Gulf of Mexico 	anticoagulant	 (128)	128 photo: 132
wondonin A & wondonin B	sponge	modulation of angiogenesis	 (128)	128
xestospongin C	sponge (*Xestospongia* sp.) (photo: *Xestospongia testudinaria*) Okinawa 	vasodilation; a potent, cell-permeable inhibitor of Ca; inhibits voltage-dependent Ca & K currents	 (133)	133 photo: 134

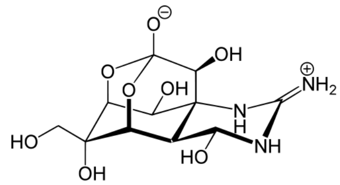
Immunological drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
(–)-palau'amine	sponge (*Stylissa massa*) (synonym: *Stylotella aurantium*) Indo-West Pacific 	immunosuppressant; strongly cytotoxic; antibiotic	 (–)-palau'amine (135)	135 photo: 136
contignasterol	sponge (*Neopetrosia contignata*) (synonym: *Petrosia contignata*) Indonesia	antihistamine & antiasthmatic	 (16)	16,18
discodermolide	deep-water sponge (*Discodermia dissoluta*) Caribbean	anticancer & immunosuppressive; tubulin polymer stabilizer (like taxol); essentially arresting cells at a specific stage in the cell cycle and halting cell division; Phase I trials; licensed to Novartis by Woods Hole; may be used in combination with Taxol	 (43)	24,25,42,43

Immunological drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
Domoic acid (causes amnesic shellfish poisoning in humans)	diatom (*Pseudo-nitzschia* sp.) worldwide	immune system; limits TNF-a & matrix metalloproteinase-9 release from brain microglia	 (128)	128
halipeptin A & halipeptin B	sponge (*Haliclona* sp.) Indo-Pacific (photo: *Haliclona sarai*) 	anti-inflammatory; inhibition of carrageenan-induced edema	 (103)	103,117 photo: 71
hymenamide C	sponge (*Stylissa carteri*) (synonym: *Axinella carteri*) Indo-West Pacific	anti-inflammatory; neutrophil & macrophage mediator modulation	 (128)	128
manoalide (AGN-190093) (related to the cacospongiolides from the same sponge)	sponge (*Luffariella variabilis*) Indo-Pacific	anti-inflammation; antipsoriatic; nervous system; first substance ever observed to selectively inhibit phospholipase A_2 (PLA2); inhibits seizures & epileptogenic properties of crotoxin; pharmacological probe; commercially available; licensed to Allergan; Phase II trials stopped due to formulation problems (insufficient dermal absorption); research continuing	 (138)	18,24,25,128 137,138
oxepinamide	fungus (*Acremonium* sp.) found on tunicate (*Ecteinascidia turbinata*) Caribbean 	anti-inflammatory		114 photo: 50
petrosaspongiolide	sponge (*Petrosaspongia nigra*) New Caledonia	anti-inflammatory; phospholipase A_2 inhibition	 (128)	128
pseudopterosins (including methopterosin, a derivative)	gorgonian (sea whip) (*Pseudopterogorgia elisabethæ*) Caribbean 	arthritis, anti-inflammation, & analgesic; modify the arachidonic acid cascade; inhibit synthesis of eicosanoids, (hormone-like substances) in specific white blood cells (polymorphonuclear leukocytes); extremely selective; they appear to be pharmacologically distinct from other NSAIDs; novel MOA; Phase II trials; sold as a cosmetic "anti-wrinkle" cream by Estee Lauder under the name *Resilience*	 (9) pseudopterosin A	9,10,12, 24,25 photo: 11

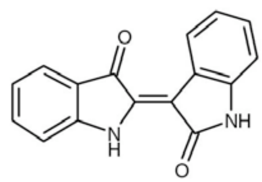
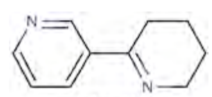
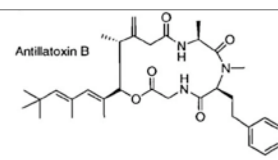
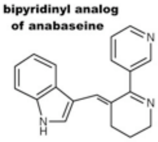
Immunological drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
salinamide A & salinamide B	bacterium	anti-inflammatory	 (139)	25,139
scytonemin	cyanobacterium	anti-inflammatory & anticancer; inhibition of PMA-induced mouse ear edema; inhibits active cell proliferation	 (128)	128
thalassospiramide A & thalassospiramide B	bacterium (*Thalassospira* sp.)	immunosuppressant		44
topsentin B1	deep-water sponges (*Halichondria genitrix* [synomyn: *Topsentia genitrix*], *Hexadella* sp., *Spongosorites ruetzleri*) Mediteranean, North Atlantic, Caribbean	anti-inflammatory; suppresses immunogenic & neurogenic inflammation; early research suggests potential use for colon cancer, Alzheimer's disease, & inflammatory bowel disease; preclinical studies	 (140)	140
totepsin D	sponge (*Spongosorites* sp.)	anti-inflammatory	 (146)	146

Molecular probes				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
jaspaquinol	sponge	molecular probe; human 15-lipoxygenase inhibition	 (128)	128
manoalide (AGN-190093) (related to the cacospongiolides from the same sponge)	sponge (*Luffariella variabilis*) Indo-Pacific	anti-inflammation; antipsoriatic; first substance observed to selectively inhibit phospholipase A_2 (PLA2); inhibits seizures & epileptogenic properties of crotoxin; pharmacological probe; commercially available; licensed to Allergan; Phase II trials stopped due to formulation problems (insufficient dermal absorption); research continuing	 (138)	18,24,25, 128,137,138
okadaic acid	red tide dinoflagellate (*Prorocentrum lima*) Northeast Atlantic, Gulf of Mexico	molecular probe; cellular phosphorylation processes; causes Diahrretic Shellfish Poisoning (DSP); selective inhibitor of the enzyme protein phosphatase; pharmacological probe, commercially available	 (141)	12,24,25, 141
saxitoxin		molecular probe; neurotoxin; ion channel nerve transmission; pharmacological probe	 (142)	12,142

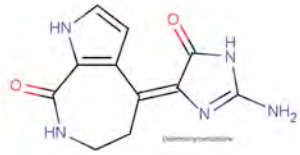
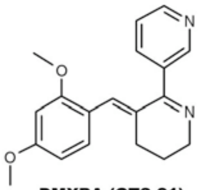
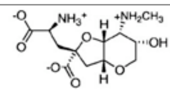
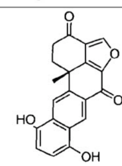
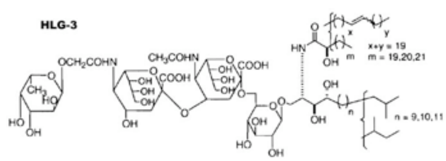
Molecular probes

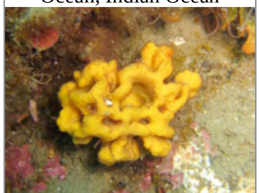
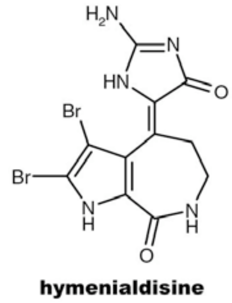
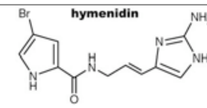
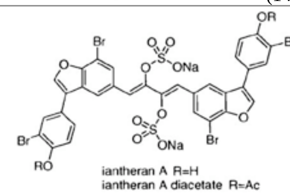
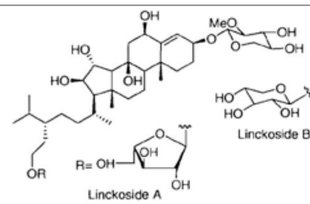
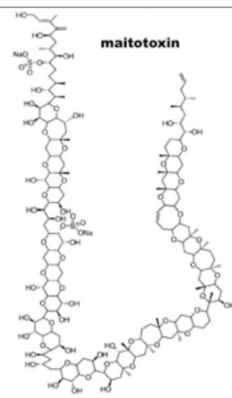
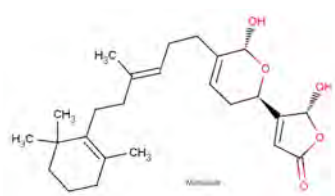
Chemical	Source	Uses & Status	Structure	Citations
tetrodotoxin	horseshoe crab (*Limulus polyphemus* [NW Atlantic & Gulf of Mexico], *Carcinoscorpius rotundicauda* [Asia], Tachypleus sp. [Asia]), blue-ringed octopus (*Hapalochlaena lunulata* [Western Pacific] [photo], *Hapalochlaena maculosa* [Australia]) 	molecular probe; neurotoxin; ion channel nerve transmission; pharmacological probe	 (143)	12,142,143 photo: 144

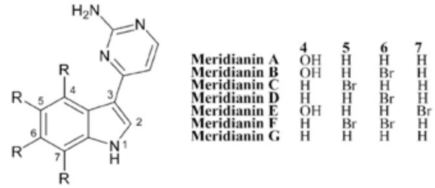
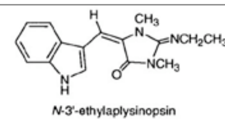
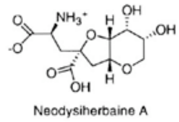
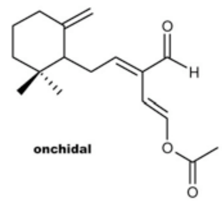
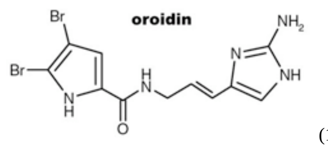
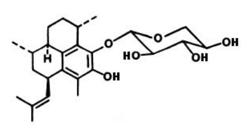
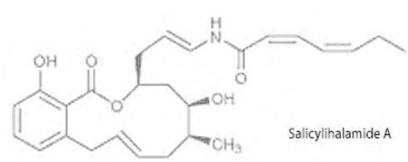
Neurological drugs

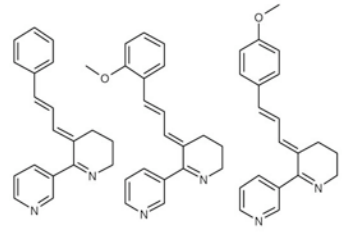
Chemical	Source	Uses & Status	Structure	Citations
6-bromoindirubin	mollusk (sea snail) (*Hexaplex trunculus*) Mediterranean 	anti-Alzheimer's; selective inhibitor of GSK-3β	 **6-bromoindirubin** (146)	146 photo: 145
anabaseine (hoplonemertine toxin)	nemertine worm (*Paranemertes peregrina*) North Pacific	anti-Alzheimer's & memory enhancement; stimulates vertebrate neuromuscular nicotinic receptors & increasing cholinergenic transmission; has potential as a treatment of cognitive function loss	 **anabaseine** (147)	18,146,147
antillatoxin & antillatoxin B	cyanobacterium (*Lyngbya majuscula*) Indian Ocean, Gulf of Mexico, Southeast Atlantic	nervous system; activates voltage sensitive Na channel	 (128)	128
aplysiallene	sea hare	nervous system; Na^{+}, K^{+}– ATPase inhibition		128
bipyridinyl analog of anabaseine (synthetic analog of anabaseine)	nemertine worm (*Paranemertes peregrina*) North Pacific	nervous system; treatment of neurodegenerative diseases; patented by Memory Pharmaceuticals Corp.	**bipyridinyl analog of anabaseine**  (146)	146,147
chlorogentisyl-quinone	fungus	nervous system; neutral sphingomyelinase inhibition		128

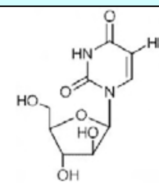
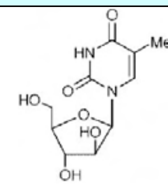
Neurological drugs

Chemical	Source	Uses & Status	Structure	Citations
conantokin G	mollusk (cone snail) (*Conus geographus*) Indo-Pacific 	analgesic & anti-seizure; 17-amino-acid competitive antagonist of N-methyl-D-aspartate (NMDA) receptors; Phase I trials discontinued	precursor amino acid sequence shown at (128, Figure 2, p. 275)	1,2,18 photo: 3
conantokin L	mollusk (cone snail) (*Conus lynceus*) Indo-Pacific 	anti-seizure & neuroprotective; N-methyl-D-aspartate (NMDA) receptor antagonist	precursor amino acid sequence shown at (128, Figure 2, p. 275	128 photo: 148
Debromo hymenialdisine (DBH)	sponge (*Stylotella aurantium*) Palau	anti-Alzheimer's & osteoarthritis; acts as a highly selective inhibitor of a specific target cell DNA damage checkpoint enzyme during the G2 phase of the cell cycle; Phase I trials	 (149)	149 photo: 149
DMXB (DMXB-A, GTS-21) (synthetic analog of anabaseine)	nemertine worm (*Paranemertes peregrina*) North Pacific	anti-Alzheimer's & memory enhancement; stimulates vertebrate neuromuscular nicotinic receptors & increasing cholinergic trans-mission; has potential as a treatment of cognitive function loss; Phase II trial for treatment of Alzheimer's and schizophrenia; licensed to Taiho by U. Florida; only marine drug in trials for pallative treatment of Alzheimer's (2005)	 **DMXBA (GTS-21)** (146)	146,147
dysiherbaine	sponge (*Lamellodysidea herbacea*) (synonym: *Dysidea herbacea*) Indian Ocean	nervous system; induces convulsant action in mice; inhibits kainic acid & mGluR5 glutamate receptors	 Dysiherbaine (128)	128
halenaquinol	sponge	nervous system; Na^+, K^+– ATPase inhibition	 Halenaquinol (128)	128
HLG-1, HLG-2, & HLG-3	echinoderm (sea cucumber) (*Holothuria leucospilota*) Indian Ocean 	nervous system	 (128)	128 photo: 150

Neurological drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
hymenialdisine	sponges (*Axinella damicornis* [photo], *Axinella verrucosa, Stylissa carteri* [synonym: *Acantella aurantiaca*]) Mediteranean, Atlantic Ocean, Indian Ocean 	anti-Alzheimer's & anti-Parkinson's; ATP-competitive kinase inhibitor; inhibits cyclin-dependent kinases & blocks *in vivo* phosphorylation; Potent inhibitor of mitogen-activated protein kinase kinase-1 (MEK-1)	 (146)	146,151,152 photo: 153
hymenidine	sponge (*Hymeniacidon* sp.) Okinawa	anti-Alzheimer's & anti-Parkinson's; a potent antagonist of serotonergic receptors	 (146)	146,154
iantheran A & iantheran B	sponge	nervous system; Na^+, K^+–ATPase and plasmin inhibition	 (128)	128
linckoside A & linckoside B	starfish	nervous system; induces neuritogenesis	 (128)	128
maitotoxin	algæ	nervous system; modulates calcium & sodium influx	 (128)	128
manoalide (AGN-190093) (related to the cacospongiolides from the same sponge)	sponge (*Luffariella variabilis*) Indo-Pacific	anti-inflammation; antipsoriatic; nervous system; first substance ever observed to selectively inhibit phospholipase A_2 (PLA2); inhibits seizures & epileptogenic properties of crotoxin; pharmacological probe; commercially available; licensed to Allergan; Phase II trials stopped due to formulation problems (with dermal application, insufficient amount absorbed through skin); research continuing	 (138)	18,24,25, 128,137,138

Neurological drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
meridianins	tunicate (*Aplidium meridianum*) Southern Ocean 	anti-Alzheimer's; protein kinase inhibitors	 (155)	155 photo: 156
N-3´-ethylaplysinopsin	sponge (*Smenospongia aurea*) Jamaica	nervous system; binds to human serotonin 5-HT_{2C} receptor	 (128)	128
neodysiherbaine A	sponge (*Lamellodysidea herbacea*) (synonym: *Dysidea herbacea*) Indian Ocea	nervous system; induces convulsant action in mice; inhibits kainic acid glutamate receptors	 (128)	128
onchidal	mollusk (sea slug) (*Onchidella binneyi*) Gulf of California (photo: *Onchidella* sp.) 	anti-Alzheimer's; an active site-directed irreversible inhibitor of AChE	 (146)	146 photo: 157
oroidin (related to hymenialdisine)	sponge (*Agelas oroides*) Mediteranean 	anti-Alzheimer's & anti-Parkinson's; a potent antagonist of serotonergic receptors	 (146)	146 photo: 158
pseudopterosins (including methopterosin, a derivative)	gorgonian (sea whip) (*Pseudopterogorgia elisabethæ*) Caribbean 	arthritis, anti-inflammation, & analgesic; appear to modify the arachidonic acid cascade; inhibit synthesis of eicosanoids, (locally functioning hormone-like substances) in specific white blood cells called polymorphonuclear leukocytes; their extreme selectivity intrigues to researchers; they appear to be pharmacologically distinct from other NSAIDs & their MOA seems novel; preclinical studies; sold as a cosmetic anti-wrinkle cream by Estee Lauder under the name *Resilience*	 (9) pseudopterosin A	9,10,12, 24,25 photo: 11
salicylihalimides	sponge (*Haliclona* sp.) Indo-Pacific (photo: *Haliclona sarai*) 	anticancer & anti-osteoporosis; first marine Vo-ATPase inhibitor (Vo-ATPases are eukaryotic enzymes whose principal role is to pump hydrogen ions across cell vacuolar membranes); may mediate bone resorption; preclinical studies	 (86)	18,86 photo: 71

Neurological drugs				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
trans-3-cinnamylidene analogs of anabaseine	nemertine worm (*Paranemertes peregrina*) North Pacific	nervous system; developed by Univ. of Florida; potentially useful for treating brain nicotinic subtype receptors	 trans-3-cinnamylidene analogs of anabaseine (146)	146,147
tridentatol	hydroid (*Tridentata marginata*) Gulf of Mexico	antioxidant & UV protection		114

Templates				
Chemical	**Source**	**Uses & Status**	**Structure**	**Citations**
spongouridine & spongothymidine	sponge (*Tectitethya crypta*) (synonym: *Cryptotethya crypta*) Caribbean	template for antiviral & antitumor agents; template for nucleosides with sugars other than ribose or deoxyribose; led to synthesis of zidovudine (AZT)	 **spongouridine**  **spongothymidine** (102)	19,102

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Chapter 6
Coral Reefs: Summary

The ESRP coral reefs project is intended to advance the understanding of coral reef ecosystem services, how they are affected by human activities, and how management and policy decisions influence their delivery. Clear definitions of the ecosystem services provided, including the reef attributes that support these services are needed.

In the previous chapters, we have provided a review of past studies focused on four primary ecosystem services provided by coral reefs (shoreline protection, fishing, tourism and recreation, and natural pharmaceutical and biochemical products). The chapters have summarized the economic benefits provided by each of the services, the methods used to quantify the services, and how those ecosystem services were linked to characteristics (attributes) of coral reefs. Table 6-1 shows the combined final ecosystem services table.

6.1 Lessons learned

The management of ecosystem services and the establishment of policies that will result in the preservation of coral reefs will require extensive collaboration between natural and social scientists. We need to better understand:

- The physical and biological processes that provide the ecosystem services;
- The nature of the ecosystem services and how they can be quantified;
- Sustainable exploitation of reef services; that is,
  - How do we define sustainable levels of exploitation?
  - How do we estimate a reef's carrying capacity or potential to supply a service? and,
- The social benefits derived from ecosystem services and how they can be measured.

Our decision framework needs to change. Decisions must move towards sustainability (that is, consideration of the "triple bottom line", where economic, social, and ecological aspects receive equal consideration in decision-making). We are currently hindered by our incomplete understanding of all the benefits provided by coral reefs. We need to look at this from two directions:

- On one hand, what does society gain by having the reef.
- On the other hand, what do we lose if the reef goes away. (e.g., "How much of the protein consumption in the USVI or Samoa comes directly or indirectly from their coral reefs?" "How would that be replaced and at what cost.")

Measuring an ecosystem service is often confused with valuing that service. For the past twenty years, economists have been conducting studies to estimate the economic value of coral reefs. These studies have often focused on a single ecosystem service, and data limitations have often precluded comprehensive measurements and valuations. In addition, some services provided by coral reefs have been ignored in these studies. For example:

- Conotoxins provide significant improvement in quality of life as compared to opiate painkillers in some therapeutic situations, because conotoxins reduce pain more effectively than opiates without inducing sleep or impairing cognitive functions. How do we most appropriately capture the value of this improved quality-of-life.
- There are over 10 million surfers. Many of the best surfing locations are provided by reef breaks. This service has not yet been quantified.
- Coral reefs provide protection from flooding during storms. Better quantification of this service could potentially support reduced flood insurance rates for those areas protected by reefs.

Valuation tends to be more accurate at the micro level, where economists are able to apply methods for eliciting individuals' values (both market and nonmarket). However, aggregation and estimation of nonmarket benefits at the macro scale remain a challenge. As a result, coral reef ecosystem services have been undervalued, perhaps significantly. Most studies have not directly measured the ecosystem services.

There is a need to consider all aspects of the ecosystem service that can be provided in the valuation process. The present value of the actual use of the ecosystem service, the service that could potentially be available, and the service that would be available under management for sustainable use should all be determined. For example, current practice does not include services being provided but not exploited because supporting services (*e.g.,* access) are not available. However, the development of supporting infrastructure brings environmental impacts to the reef that must be considered in the light of sustainable use. We recommend that all three aspects of the ecosystem service be quantified, when possible.

6.2 Next steps

The ultimate goal of the ESRP coral reefs project is to identify coral reef indicators that can be used to estimate the quantity of ecosystem services being delivered by coral reef ecosystems and to predict the extent to which the current quantities are likely to change in the future. In 2011, we will fully document the linkages between coral reef condition, function, and ecosystem services and the coral reef attributes that support those services. We will also create the coral reef system model that links the coral reef ecological production functions with policy/management-relevant final ecosystem services. We will identify a manageable suite of candidate indicators of final ecosystem services and directly tie the valuation activities to particular management decision(s).

Our literature review has shown that many of the ecosystem indicators are already being collected. However, the aggregation of the indicators and of the underlying data and relating them to ecosystem services is not being done. Missing items include landscape attributes (both onshore and offshore), many of which have been collected but not analyzed for the purpose of relating them to ecosystem services. We plan to begin research in this area using existing and new ORD expertise and resources.

We intend to design the next generation of survey questionnaires, which will address the value that stakeholders assign to coral reef attributes. In addition, modern technology would support web-based surveys, which could greatly facilitate the ease of collecting and analyzing the survey data. One of our collaborators, NOAA's Bob Leeworthy, successfully used a web-based survey questionnaire in a recent valuation of Hawaii's coral reefs. We are collaborating with Bob to design a web-based study for the Guánica Bay Watershed. This is a longer-term research activity (2012-2013).

Table 6-1. Combined final ecosystem services and supporting features for coral reefs

Ecosystem Service(s)		Natural Features	Social Values	Complementary Goods & Services	Ecosystem-Derived Benefits	Potential Indicators of Final Ecosystem Service(s)
Final (FES)	Intermediate					
Tourism & recreation						
Recreational Fishing Opportunity	Production of benthic and aquatic prey for consumption by recreational fish	Fish diversity and abundance	Desirability of fish species and size for rod-and-reel catches	Adequate infrastructure (boats, marinas, etc.)	Revenues from tourism and recreation activities	Abundance of catchable snappers and groupers
Recreational Diving/Snorkeling Opportunity	Coral reef formation & maintenance; maintenance of water clarity; Production of benthic and aquatic prey for consumption by recreational fish	Coral diversity, abundance and health; fish diversity and abundance; water clarity	Desirability of coral reef for recreation based on physical appearance (color, visibility, etc.)	Access to reef, safe swimming conditions, adequate infrastructure (hotels, dive boat operators, etc.)	Revenues from tourism and recreation activities	Taxa richness, size and density of reef organisms
Recreational Underwater Photography Opportunity	Coral reef formation & maintenance; maintenance of water clarity; Production of benthic and aquatic prey for consumption by recreational fish	Coral diversity, abundance and health; fish diversity and abundance; water clarity	Desirability of coral reef for recreation based on physical appearance (color, visibility, etc.)	Access to reef, safe swimming conditions, adequate infrastructure (hotels, dive boat operators, etc.)	Revenues from tourism and recreation activities	Taxa richness, size and density of reef organisms
Recreational Surfing Opportunity	Reef breaks	3-D reef structure	Desirability based on wave size and speed	Access to reef, adequate infrastructure (hotels, board shops, etc.)	Revenues from tourism and recreation activities	3-D structure and proximity to deep ocean
Opportunity to View Nature and Wildlife	Biological integrity	Biodiversity (birds, marine mammals, turtles)	Desirability of species (rarity, size)	Access to reef and adequate infrastructure (boats, tour guides)	Revenues from tourism and recreation activities	Taxa richness, presence of specific species
Opportunity to Sunbath and Swim at the Beach	Water quality, shoreline protection, sand production	White coralline sands; calm waters	Desirability of coralline sand beach for sunbathing (size, cleanliness, appearance)	Access to beach	Revenues from tourism and recreation activities	Areal extent of beach, color of beach, water temperature, days of sunshine, beach trash
Opportunity to Collect Objects (beachcombing)	Water quality	Wide sandy beaches, biodiversity, occasional storms	Desirability of walking on beach and of finding beautiful & unusual objects	Access to beach	Revenues from tourism and recreation activities	Areal extent of beach, frequency of storms, proximity of reef, taxa richness of invertebrates

Table 6-1 (continued)

Ecosystem Service(s)		Natural Features	Social Values	Complementary Goods & Services	Ecosystem-Derived Benefits	Potential Indicators of Final Ecosystem Service(s)
Final (FES)	Intermediate					
Fishing						
Seafood Products: Fish, shellfish, algae harvested	Biological integrity	Fish diversity and abundance; coral health; seascape connectivity; and structural complexity	Desirability of species based on taste	Adequate infrastructure (boats, marinas, etc.)	Revenue from commercial seafood fisheries	Abundance of commercially desirable fish species
Aquarium Products (live fish & coral taken)	Biological integrity	Coral diversity, abundance and health; fish diversity and abundance; seascape connectivity; and structural complexity	Desirability of species for aquaria based on physical appearance (color, size, etc.), rarity		Revenue from sales of aquarium fish and coral	Species abundance and diversity of target populations
Material for Curios and Jewelry removed	Biological integrity	Coral diversity, abundance and health; water clarity	Aesthetic values and artistic inspiration	Diving and boating infrastructure	Revenue from sales of curios and jewelry	Species abundance and diversity of target populations
Shoreline protection						
Protection from shoreline erosion; Decreased erosion in kg/ha/y	Reduction in wave energy, velocity, or height	Presence of reef; reef height, width, slope, & roughness; reef continuity. *Physical variables:* Offshore wave energy, wave height, tidal depth; beach elevation, sediment grain size	Attractiveness of sandy beaches; desirability of housing near water	Absence of constructed breakwaters	Higher property values; opportunity to use beaches (see Ch. 2)	% reduction in rates of shoreline erosion due to presence of reef
Protection from coastal inundation during extreme events area in hectares protected	Reduction in wave set-up, or storm surge	Presence of reef; reef height, width, slope, roughness; reef continuity. *Physical variables:* Wave energy; distance from hazard event; slope of coastline; frequency & intensity of extreme events	Past history of extreme events	Absence of constructed breakwaters; location, intensity, and value of coastal development	Lower insurance rates; higher property values; lower property damage and loss of life	% reduction in coastal inundation due to presence of reef
Pharmaceuticals from natural products						
Marketable natural product or a template that results in a marketable product	Unique biologically active secondary metabolite	Shallow, marine biodiverse, species-dense ecosystem	Desirability of good health and well-being	Pharmaceutical research programs for both field collection and laboratory analysis	Increased revenues from pharmaceuticals; increased health and well-being	Species density, biological integrity, sponge diversity, rare species

***Definitions** (proposed by the Ecosystem Services Research Program and currently under discussion by the Program)*

- **Final Ecosystem Service** – Output of ecological functions or processes that directly contributes to social welfare or has the potential to do so in the future (broadly based on Boyd & Banzhaff [2007]).
- **Intermediate Ecosystem Service** - Output of ecological functions or processes that indirectly contributes to social welfare or has the potential to do so in the future.
- **Natural Features** – The biological, chemical, and physical attributes of an ecosystem or environment.
- **Social Values** – The social attributes that influence economic demand for an ecosystem service.
- **Complementary Goods & Services** - Inputs (usually built infrastructure or location characteristics) that allow a good or service to be used by complementing the ecological condition. For example, complementary goods and services that allow the presence of fishable fish to become an opportunity for recreational fishing will include aspects of site accessibility, such as road access, available parking and the presence of a fishing pier, all of which make fishing at the site possible and enhance enjoyment of the activity.
- **Ecosystem-Derived Benefits** - The contribution to social welfare of ecosystem goods and services. In the ESRP, the term applies specifically to net improvements in social welfare that result from changes in the quantity or quality of ecosystem goods and services attributable to policy or environmental decisions.
- **Indicator of Final Ecosystem Service** – Biophysical feature, quantity, or quality that requires little further translation to make clear its relevance to human well-being (*i.e.*, “public-friendly” measurement)

Coral Reefs: Glossary

Words in **bold** are defined in this glossary.

A

Acropora	A genus of **stony corals** that contain the elkhorn and staghorn corals (NOAA 2010).
actinomycetes	Gram-positive bacteria of the order Actinomycetales in the phylum Actinobacteria that are mostly aerobic but can be anaerobic. Some resemble fungi, because they produce a characteristic, branched mycelium. Actinobacteria are well-known sources of **secondary metabolites** having pharmaceutical uses. Often found in symbiont relationships with megafauna, notably sponges.
alcyonarian	An **octocoral**.
algæ	A large and diverse group of simple unicellular or multicellular organisms that use chloroplasts for photosynthesis, although they are not plants. Algæ, which are chiefly aquatic, form the basis of the marine food chain. Common algæ include dinoflagellates, diatoms, seaweeds, and kelp.
antifouling agents	Agent that inhibits the growth of barnacles and other marine organisms on a ship's bottom (an antifouling paint or other coating). Organotin compounds have been the most often used agents in this application since they are effective against both soft and hard fouling organisms. However, in spite of their performance, they have a negative impact on the marine environment, and their long half-life in the environment has prompted marine paint manufacturers to look for a nonpersistent alternative.
artificial breakwater	A bank or levee of stones or a timber structure, used to break the force of the sea in its entrance into a harbor or roadstead.
ascidian	Sac-like filter feeders that belong to the class Ascidiacea within the subphylum Tunicata. Often called sea squirts.
atoll reef	A type of coral reef that encircles a lagoon partially or completely.
attribute	Any measurable component of a biological system (Karr & Chu 1999).
Ayurveda	An ancient medical treatise of the Hindu art of healing and prolonging life; sometimes regarded as a 5th Veda.

B

back reef	The landward side of a reef between the **reef crest** and the land.
barrier reef	A type of coral reef near the **shoreline**, but separated from it by a deep lagoon.
Bayesian belief network (BBN)	A graphical network for modeling probabilistic interrelationships between events. Events are represented by nodes in the network and causative relationships are represented by directed arrows between the nodes. A BBN is especially useful when individual nodes of the network will be updated with evidence. For example, a BBN could represent the probabilistic relationships between diseases and symptoms. Given symptoms, the network can be used to compute the probabilities of the presence of various diseases. Decision and utility nodes can be added to a BBN to represent and solve a decision problem following maximum expected value criterion (this is called an influence diagram).
beachcombing	The recreational activity of searching the beach and the intertidal zone for items that have washed in with the tide (*e.g.*, corals, seashells, sponges, sea fans, fossils, pottery shards, artifacts, sea beans, sea glass, and driftwood).
benefit transfer	Techniques to estimate values of **ecosystem goods and services** based on previously conducted valuation studies. Benefit transfer is conducted by either taking average values of existing studies or by using a transfer function to transfer values from primary studies (study sites) to new locations (policy sites). A transfer function is often developed through meta-analysis, which is a statistical (usually regression) technique to model differences in values among primary valuation studies. A transfer function allows values to be transferred from study sites to policy sites based on a set of independent variables that capture the degree of similarity between the study sites and policy sites (Wainger & Mazzotta 2009).
biochemicals	Chemicals that result from biological and chemical processes in living organisms.
biogeography	The study of ecosystem geography to understand why flora and fauna are found in certain places.
biological diversity (biodiversity)	The variability among living organisms from all sources including terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within and among species and diversity within and among ecosystems (MEA 2009).

biophysical	Pertaining to the biological, chemical, and physical attributes of an **ecosystem** or environment.
bombora	A shallow area some distance from the **shoreline** that causes sea waves to break.
bryozoans	Aquatic animals comprising the phylum Bryozoa that form mossy colonies of small polyps each having a curved or circular ridge bearing tentacles; they attach to stones or seaweed and reproduce by budding.

C

carbon dioxide (CO_2)	An odorless colorless gas formed during respiration and by the decomposition of organic substances; absorbed from the air by plants in photosynthesis. It is also a byproduct of burning fossil fuels and biomass, as well as land use changes and other industrial processes. It is the principal anthropogenic greenhouse gas that affects the earth's radiative balance.
charismatic megafauna	Large animal species with widespread popular appeal that environmental activists use to achieve conservation goals well beyond just those species.
clinical trials	A scientifically designed and executed investigation of the effects of a drug (or vaccine) administered to human volunteers. The goal is to define the safety, clinical efficacy, and pharmacological effects (including toxicity, side effects, incompatibilities, or interactions) of the drug.
cnidarian (the *c* is silent)	Multicellular animals comprising the phylum Cnidaria (silent *c*), including the **stony corals** (**scleractinians)**, soft corals (**octocorals**), anemones, sea fans, sea pens, hydroids, and jellyfish.
commercial fishing	Fishing for profit.
complementary goods and services	Inputs (usually built infrastructure or location characteristics) that allow a good or service to be used by complementing the ecological condition. For example, complementary goods and services that allow the presence of fishable fish to become an opportunity for recreational fishing will include aspects of site accessibility, such as road access, available parking and the presence of a fishing pier, all of which make fishing at the site possible and enhance enjoyment of the activity.
connectivity	A topological property relating to how geographical features are attached to one another functionally, spatially, or logically.
contingent valuation method (CVM)	A valuation method that estimates consumers' preferences by asking them how much they are willing to pay for a benefit (**willingness-to-pay** or WTP), or what they are willing to accept by way of compensation to tolerate a loss (**willingness-to-accept** or WTA).
coral	The regulatory definition is: species of the phylum Cnidaria, including: (a) all species of the orders Antipatharia (black corals), Scleractinia (stony corals), Gorgonacea (horny corals), Stolonifera (organpipe corals and others), Alcyanacea (soft corals), and Coenothecalia (blue coral), of the class Anthozoa; and (b) all species of the order Hydrocorallina (fire corals and hydrocorals) of the class Hydrozoa (16 U.S.C. 6401 et seq 2000). Current taxonomy has corals and sea anemones grouped into the class Anthozoa within the phylum Cnidaria. Anthozoa is divided into two subclasses, Octocorallia and Hexacorallia. Soft corals (including **gorgonians**) (order Alcyonacea) and blue corals (order Helioporacea) are under Octocorallia, and **stony corals** (order Scleractinia), black corals (order Antipatharia), and zoanthids (order Zoantharia) are under Hexacorallia. Neither fire corals nor hydrocorals are technically corals: they are classified as phylum Cnidaria, class Hydrozoa, order Capitata.
coral bleaching	The process in which a coral polyp, under environmental stress, expels its symbiotic **zooxanthellæ** from its body. The affected coral colony appears whitened (NOAA 2010).
coral cover	The covering of the sea floor by coral. It can be measured in square miles, square kilometers, or as a percentage of area with cover.
coral reef	Any reefs or shoals composed primarily of **corals**.
coral reef ecosystem	**Coral** and other species of reef organisms (including reef plants) associated with coral reefs, and the nonliving environmental factors that directly affect coral reefs, that together function as an ecological unit in nature.

cultural services	Cultural services are the nonmaterial benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and æsthetic experiences, including: cultural diversity, spiritual and religious values, knowledge systems (traditional and formal), educational values, æsthetic values, social relations, sense of place, cultural heritage values, and, recreation and ecotourism. In the lexicon of the ESRP, many of the elements in the MEA category (*e.g.*, spiritual and religious values) could be considered **ecosystem services** that are best defined specifically in terms of beneficiaries' ethical or cultural value systems, while the benefits derived from others (*e.g.*, certain aspects of recreation and ecotourism) might be valued in more generic terms. See also, **provisioning services**, **regulating services**, and **supporting services** (MEA 2005).
cyanobacteria	Photosynthetic aquatic bacteria that compose the phylum Cyanobacteria. They are often called blue-green algæ, but have no relationship to **algæ**. Cyanobacteria get their name from the bluish pigment phycocyanin, which they use to capture light for photosynthesis. They also contain chlorophyll *a*, the same photosynthetic pigment found in the chloroplasts of plants. Not all "blue-green" bacteria are blue; some common forms are red or pink, resulting from the pigment phycoerythrin (NOAA 2010).
D	
decision maker	Individual(s) or groups of people responsible for making choices or determining policy that impacts the functions, processes, and condition of ecological systems. Decisions may be local, regional, or national in scale.
demand	Generally, the amount of a particular good or service that a consumer or group of consumers will want to purchase at a given price. Demand for a good or service is determined by many different factors other than price, such as the price of substitutability and complementary goods and services. Along with supply, demand is one of the two key determinants of the market price.
direct use values	Economic values derived from direct use or interaction with a biological resource or resource system.
E	
ecological endpoint	A biophysical feature, quantity or quality that requires little further translation to make clear its relevance to human well-being (*i.e.*, "public-friendly" measurements). Ecological endpoints are the ecological inputs that, along with complementary goods and services inputs and demands by people, produce **ecosystem services**. For example, the abundance of watchable birds at a site is an ecological endpoint that, when combined with complementary inputs such as transportation infrastructure and demand by birders, produces the ecosystem service of recreational bird watching. Specified changes in ecological endpoints can be used in economic surveys to gauge people's **willingness-to-pay** for (or **willingness-to-accept**) increases or decreases in potentially valued ecosystem services, thereby providing quantitative information with which to evaluate decision/management mandates (adapted from Boyd [2007], Boyd & Banzhaf [2007], Wainger & Boyd [2009] and Wainger & Mazzotta [2009]).
ecological integrity	The capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region (Frey 1975; Karr and Dudley 1981; Angermeier and Karr 1994; Karr et al. 1986).
ecological production function (EPF)	A description of the type, quantity and interactions of natural features required to generate outputs of natural products and services. For a simple example, the biophysical characteristics of a coastal wetland (flooding regimes, salinity, nutrient concentrations, plant species abundance, prey and predator abundances, etc.) can influence the abundance of a population of watchable wading shorebirds (the **ecological endpoint**). The outputs of ecological production functions, when combined with complementary goods and services and demand by humans, produce ecosystem goods and services (adapted from Wainger & Boyd [2009] and Wainger & Mazzotta [2009]).
ecological resilience	The capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks (Walker *et al*. 2004; Folke 2006).
ecosystem	A dynamic complex of plant, animal, and microorganism communities and their nonliving environment interacting as a functional unit (MEA 2009).
ecosystem functions	Physical, chemical, and biological processes that occur in ecosystems.
ecosystem goods and services	Outputs of ecological functions or processes that directly (**final ecosystem service** broadly based on Boyd & Banzhaff [2007]) or indirectly (**intermediate ecosystem service**) contribute to social welfare or have the potential to do so in the future. Some outputs may be bought and sold, but most are not marketed. Often abbreviated as ecosystem services (modified from EPA [2006]).
ecosystem service	Shorthand notation for an ecosystem good or service.

ecosystem structure	The individuals and communities of plants and animals of which an ecosystem is composed, their age and spatial distribution, and the nonliving natural resources present. The elements of ecosystem structure interact to create ecosystem functions.
effect on production (EoP)	An estimate of the difference in value of productive output before and after the impact of a threat or a management intervention.
emergy	The available energy of one kind previously used-up directly and indirectly to make a product or service. Emergy is expressed in its own unit, the emjoule, which connotes the energy of equivalent quality (*e.g.*, solar emjoules) used in the past to make a product or service (*e.g.*, a wetland), as compared with the energy (J) content of the product or service (Odum 1996).
enzymes	Proteins that catalyze (*i.e.*, increase the rates of) chemical reactions.
erosion	Wearing away of rock or soil by the gradual detachment of soil or rock fragments by water, wind, ice, and other mechanical, chemical, or biological forces.
ex-vessel price	The price received by a commercial fishing captain for the catch (Thayer *et al*. 2005).
F	
fauna	Animal life, especially the animals characteristic of, or endemic to, a region.
final ecosystem service	Components of nature directly enjoyed, consumed, or used to yield human well-being (Boyd & Banzhaf 2007).
financial analysis	Uses the observed current financial activities, revenues, costs, and financial flows in the economy from market-based uses of the reef (such as diving and snorkeling) to analyze the economic activity generated by use of an ecosystem good or service.
flora	Plant life, especially the plants characteristic of, or endemic to, a region, period, or special environment.
fore reef	The seaward edge of a reef that is fairly steep and slopes down to deeper water.
fringing reef	A type of coral reef that borders the **shoreline**, separated from shore by only a shallow lagoon or none at all.
functions	The physical, chemical, and biological processes that occur in ecosystems.
fungi	A kingdom separate from animals, bacteria, and plants consisting of usually multicellular, heterotrophic eukaryotes that have multinucleated cells enclosed within cell walls. Fungi obtain nutrition by decomposing dead and dying organisms and absorbing the decomposition products (NOAA 2010).
G	
gorgonian	An **octocoral** having a horny or calcareous branching skeleton (*e.g.*, sea fans and sea whips).
H	
habitat	A place where the physical and biological elements of ecosystems provide a suitable environment including the food, cover, and space needed for plant and animal livelihood (EPA 2009a).
hardbottom	Shallow and deep-water habitats with solid floor that can provide an attachment surface for sessile (nonmoving) organisms such as corals.
health	Health is the general condition of a person in all aspects, including physical and mental. The term health is also sometimes used to represent the condition of other organisms as well as ecosystems and social structures. Ecosystem health is an element of overall ecosystem integrity (Campbell 2000). Organism and ecosystem health usually implies normal functioning of the system and absence of disease as a dominant factor in the system. Ecosystem health can be thought of as functional integrity. Ecosystems also have structural integrity, which is related to the presence of all the normally expected elements of the system. Overall ecological integrity is a combination of the two (*i.e.*, wholeness and normal functioning). For example, a person with only one arm might be healthy but would not be structurally whole.
herbivore	An animal that feeds on plants (EPA 2010).
I	
index	A usually dimensionless numeric combination of scores derived from biological measures called metrics (EPA 2000).

indicator	Information based on measured data used to represent a particular attribute, characteristic, or property of a system (MEA 2009).
indigenous	A species is defined as native to a given region or ecosystem if its presence in that region is the result of only natural processes, with no human intervention. Every natural organism (as opposed to a domesticated organism) has its own natural range of distribution in which it is regarded as native. Outside this native range, a species may be introduced by human activity, after which it is referred to as an "introduced species" in such locales.
integrity	The extent to which all parts or elements of a system (*e.g.*, an aquatic ecosystem) are present and functioning.
intermediate ecosystem service	Components of nature that are not directly enjoyed, consumed or used to yield human well-being, but that are important for the production of **final ecosystem services**.
L	
landscape	An area of land that contains a mosaic of ecosystems, including human-dominated ecosystems. The term cultural landscape is often used when referring to landscapes containing significant human populations (MEA 2009).
M	
macroalgæ	Macroscopic, multicellular algæ commonly referred to as seaweed.
macroinvertebrate	Animals without backbones of a size large enough to be seen by the unaided eye and that can be retained by a U.S. Standard No. 30 sieve (28 meshes per inch, 0.595 mm openings) (EPA 2009a).
macrophyte	Large aquatic plants that may be rooted or non-rooted, vascular or algiform (such as kelp), including submerged aquatic vegetation, emergent aquatic vegetation, and floating aquatic vegetation (EPA 2000).
mangrove	A general name for several species of halophyte (a plant able to grow in saline conditions) belonging to different families of plants (including trees, shrubs, a palm tree, and a ground fern) occurring in intertidal zones of tropical and subtropical sheltered coastlines and exceeding one-half meter in height. The term is applied to both the individual and the ecosystem (which is termed mangal). Mangroves provide protected nursery areas for juvenile reef fishes, crustaceans, and mollusks. They also provide a feeding ground for a multitude of marine species. Many organisms find shelter either in the roots or branches of mangroves. Mangrove branches are nesting areas for several species of coastal birds. The root systems harbor organisms that trap and cycle nutrients, organic materials and other important chemicals. Mangroves also contribute to higher water quality by stabilizing bottom sediments, filtering water, and protecting **shorelines** from erosion. They protect reefs from land runoff and sedimentation. Conversely, coral reefs protect mangroves and seagrasses from erosion during heavy storms and strong wave action. The nations with the largest mangrove areas include Indonesia (with 21% of global mangroves), Brazil (9%), Australia (7%), Mexico (5%), and Nigeria (5%).The global area of mangroves—150,000 km^2—is equivalent to the area of the state of Illinois, or half the area of the Philippines. About one-fifth of all mangroves are thought to have been lost since 1980, and although loss rates are declining, they are still three to four times higher than average global forest loss estimates (NOAA 2010).
Marine Protected Area (MPA)	Any area of the marine environment that has been reserved by federal, state, territorial, tribal or local laws or regulations to provide lasting protection to part or all of the natural or cultural resources within them. Familiar examples of U.S. MPAs include national parks, national wildlife refuges, national monuments, national marine sanctuaries, fisheries closures, critical habitat, habitat areas of particular concern, state parks, conservation areas, estuarine reserves and preserves, and numerous others. MPAs are sometimes called Marine Managed Areas (MMA). However, "marine protected area" is a broad, inclusive term that includes both multipurpose sites with some restrictions as well as the more restrictive "no-take marine reserves" (NOAA 2010).
marine reserve	An area in the ocean that is protected from uses that remove animals, plants, and other organisms, or alter their habitats (NOAA 2010).
marine tourism	Includes those recreational activities that involve travel away from one's place of residence and that have as their host or focus the marine environment (where the marine environment is defined as those waters that are saline and tide-affected) (Orams 1999).
metabolites	A substance that takes part in the process of metabolism, which involves the breakdown of complex organic constituents of the organism's body with the liberation of energy for use in bodily functioning. The various compounds that take part in, or are formed by, these reactions are called metabolites (NOAA 2010).
model	A physical, mathematical, or logical representation of a system of entities, phenomena, or processes; an abstracted view of a complex reality.
molecular probe	Chemicals that are used to explore and elucidate biochemical structures and processes at the cellular and molecular levels.

Montastraea	A genus of hard (stony) coral (**octocoral**) that includes the boulder coral and the great star coral (NOAA 2010).
N	
National Account Systems (NAS)	NAS provide a complete and consistent conceptual framework for measuring the economic activity of a nation. NAS are derived from a wide variety of source data including surveys, administrative and census data, and regulatory data. Most countries have a national statistical office or central bank that compiles, integrates, harmonizes, and publishes the data. NAS include a number of aggregate measures (*e.g.*, gross domestic product [GDP], disposable income, savings, and investment) and other information (*e.g.*, input-output tables that show how industries interact with each other in the production process).
natural feature	A readily observable characteristic of natural systems such as type of vegetation and arrangement of land use (Wainger & Boyd 2009).
nature and wildlife watching	The practice of observing nature and wildlife (*e.g.*, birds, dolphins, fish, manatees, turtles, whales) in their natural habitat.
nonmarket value	Value recognized by people but not usually expressed in prices because the thing either is not currently, or cannot be, traded in markets.
nonuse value	The value people hold for a service that they do not directly use. (Sometimes referred to as "passive use value".) Early literature in environmental economics split nonuse value into three components: existence value, option value, and bequest value. Nonuse values are theoretically distinct from use values, although the boundary between use and nonuse values is often fuzzy.
North American Industry Classification System (NAICS)	The standard used by Federal statistical agencies in classifying business establishments for the purpose of collecting, analyzing, and publishing statistical data related to the U.S. business economy. NAICS was developed under the auspices of the Office of Management and Budget (OMB), and adopted in 1997 to replace the Standard Industrial Classification (SIC) system. It was developed jointly by the U.S. Economic Classification Policy Committee (ECPC), Statistics Canada, and Mexico's Instituto Nacional de Estadistica y Geografia, to allow for a high level of comparability in business statistics among the North American countries (U.S. Census Bureau 2010).
nudibranch	A marine gastropod mollusk that has no protective covering as an adult. Gills or other projections on the dorsal surface carry on respiration. They comprise the clade Nudibranchia (formerly a suborder).
nutraceuticals	A term that combines the words *nutrition* and *pharmaceutical* and is a food or food product that provides health and medical benefits, including the prevention and treatment of disease (Kalra 2003).
O	
octocoral	Aquatic organisms formed of colonial polyps with 8-fold symmetry. They comprise the subclass Octocorallia. Examples include blue coral, soft corals, and **gorgonians** (sea fans and sea whips). See also **coral**.
opportunity cost	The cost of something in terms of an opportunity forgone (and the benefits that could be received from that opportunity), or the most valuable forgone alternative (*i.e.*, the second best alternative).
overfishing	Occurs when fishing activities reduce fish stocks below a level that is biologically or economically sustainable.
P	
patch reef	Small circular or irregular reefs that arise from the floor of lagoons, behind **barrier reefs**, or within an **atoll**.
pharmaceutical	Biologically active chemicals used to treat diseases, disorders, and illnesses (NOAA 2010).
preclinical stage of testing	Research (sometimes using animal models) to assess whether a candidate drug, procedure, or treatment is likely to be of therapeutic value in humans. Preclinical studies take place before any testing in humans is done.
presence of reef	Quantifies whether or not an offshore reef is present near the coastal area of interest.
protein	A large complex molecule made up of one or more chains of amino acids. A typical protein contains 200–300 amino acids, but some are much smaller and some much larger (*e.g.*, titin, a protein found in skeletal muscle, contains approximately 27,000 amino acids in a single chain). Proteins perform a wide variety of essential activities in cells, including: (1) they largely form the physical structure of cells and cellular matrices; (2) proteins are enzymes, which are the catalysts for all biochemical reactions; (3) the transport of materials in body fluids depends on proteins; (4) the receptors for hormones and other signaling molecules are proteins; (5) motion and locomotion of cells and organisms depends on contractile proteins; (6) the transcription factors that turn genes on and off are proteins; and, (7) proteins are an essential nutrient for heterotrophs. The activities of cells and organisms are largely dependent on the activities of their proteins (NOAA 2010).

provisioning services	A category of **ecosystem services** as described by the *Millennium Ecosystem Assessment*. Provisioning services (ecosystem goods) are the products obtained from ecosystems, including: food; fiber; fuel; genetic resources; biochemicals, natural medicines, and pharmaceuticals; ornamental resources; and, fresh water. In the lexicon of the ESRP and when quantified appropriately, elements in the MEA provisioning services category could be considered ecological endpoints. Also see the other MEA categories of **cultural services**, **regulating services**, and **supporting services** (MEA 2005).
R	
recreation	"Refreshment of strength or spirits after work; also: a means of refreshment or diversion" (Merriam Webster 2010). Recreational activities are enjoyed by both tourists and residents of a given geographic location. However, the common practice of economists is to differentiate between tourism and recreation based upon the source of demand.
recreational (sport) fishing	Fishing for pleasure or competition. It is included as a component of tourism and recreation.
reef break	A wave that breaks over a coral reef or a rock seabed.
reef continuity	The uninterrupted distribution the reef, namely the absence of large gaps or fragmentation due to degradation or coral mining.
reef crest	The sharp break in slope, or peak in **reef height** at the seaward edge of the **reef flat**.
reef depth	The distance from the ocean surface to the top of the reef; may be an assumed or fixed value in simulation models, or an average value from field observations for the reef under consideration.
reef distance	The distance between the **reef crest** and the edge of the **shoreline**; essentially the width of the lagoon.
reef flat	The relatively shallow, flat expanse of coral reef between the **reef crest** and the **shoreline**.
reef height	The distance from the top of the reef to its base; may be an assumed or fixed value in simulation models, or an average value from field observations for the reef under consideration.
reef roughness	The bottom drag coefficient that quantifies friction and may be approximated in field studies by variability in colony height, or other measures of topography, along the **reef flat**.
reef slope	The angle, from gradual to steep, of the reef front where offshore waves are first encountered; may be an assumed or fixed value in simulation models, or an average value from field observations for the reef under consideration.
reef type	Describes the general structure of the reef and its relationship to the **shoreline**, including **fringing reefs** that border the shoreline, **barrier reefs** that are separated from shore by a deep lagoon, **atoll reefs** that form a circular barrier around an island, and **patch reefs** that are small, isolated reef outcrops.
reef width	The length of the **reef flat**, the flat expanse of reef from where offshore waves first crest over the reef to the edge closest to the **shoreline**; may be an assumed or fixed value in simulation models, or an average value from field observations for the reef under consideration.
refugia	An area or refuge where biota can live and breed without suffering excess predation from other organisms.
regulating services	A category of **ecosystem services** as described by the *Millennium Ecosystem Assessment*. Regulating services are the benefits obtained from the regulation of ecosystem processes, including: air quality regulation, climate regulation, water regulation, erosion regulation, water purification and waste treatment, disease regulation, pest regulation, pollination, and natural hazard regulation. In the lexicon of the ESRP, elements in the MEA regulating services category could be considered ecological processes that can produce ecological endpoints, that when combined with complementary goods and services and demand by humans, could produce ecosystem goods and services. See also the other MEA categories of **cultural services**, **provisioning services,** and **supporting services** (MEA 2005).
replacement costs	The amount that an entity would have to pay to replace an asset at the present time.
residents	People who live at a particular place for a prolonged period (Leeworthy 2002; Princeton WorldNet Glossary 2010a).
resilience	The ability of a system to absorb or recover from disturbance and change, while maintaining its **functions** and **services** (Carpenter *et al.* 2001). For example, a reef's ability to recover from a **coral bleaching** event.
revealed preference	The use of the recovery of expenditure to "reveal" the preference of a consumer or group of consumers for the bundle of goods they purchase.

risk assessment	The determination of quantitative or qualitative value of risk related to a concrete situation and a recognized threat (also called hazard).
rugosity	Describes the amount of “wrinkling” or roughness of the reef profile. It is an index of substrate complexity. Areas of high complexity are likely to provide more cover for reef fishes and more places of attachment for algæ, corals, and various sessile invertebrates (2010).
S	
salient	A type of beach morphology in which sediments are deposited and accumulate in the lee of a breakwater structure, growing seaward from the **shoreline** to form a bell-shaped structure.
scleractinians	Corals that have a hard limestone skeleton and belong to the order Scleractinia. See **stony coral**.
scuba	An apparatus carried by a diver that includes a tank holding a mixture of oxygen and other gases, used for breathing underwater. Scuba is an acronym for “self-contained underwater breathing apparatus”.
seagrass	A flowering plant, complete with leaves, a rhizome (an underground, usually horizontally-oriented stem), and a root system. They are found in marine or estuarine waters. Most seagrass species are located in soft sediments. However, some species are attached directly to rocks with root hair adhesion. Seagrasses tend to develop extensive underwater meadows (NOAA 2010).
seascape	A mosaic of interconnected coastal and marine ecosystems (coral reefs, seagrass meadows, and mangrove forests).
secondary metabolite	A substance produced by an organism that seemingly has no direct role in the organism’s metabolism, though they are often produced via pathways that are derived from primary metabolic pathways. It is believed that they are created because they confer some evolutionary advantage, particularly in sessile (nonmoving) organisms. Most often, secondary metabolites are used by the organism in intraspecies or interspecies interactions usually related to defense or signaling (NRC 1999; Croteau *et al.* 2000; Seigler 2002; Wink 2003).
services	The benefits that human populations receive from functions that occur in ecosystems.
shoreline	The intersection of the land, including man-made waterfront structures, with the water surface. The shoreline depicted on NOAA National Ocean Service (NOS) maps and charts represents the line of contact between the land and a selected water elevation. In areas affected by tidal fluctuations, the shoreline is the interpreted mean high water line. In confined coastal water of diminished tidal influence, the mean water level line may be used. In nontidal waters, the line represents the land/water interface at the time of survey. In areas where the land is obscured by marsh grass, cypress or similar marine vegetation, the actual shoreline can not be accurately represented. Instead, the outer limit line of the vegetation area is delineated (where it would appear to the mariner as the shoreline), in this case, it is referred to as the apparent shoreline (NOAA 2010).
shoreline protection	The ability of reefs to attenuate offshore wave energy, to provide sheltered nearshore waters, and to protect coastlines from erosion, flooding, and storm damage.
snorkeling	The practice of swimming while equipped with a diving mask, a shaped tube called a snorkel, and fins.
species	A category of taxonomic classification, ranking below a genus or subgenus and consisting of related organisms capable of interbreeding. Also refers to an organism belonging to such a category.
species diversity	The number of different species in an area and their relative abundance (NOAA 2010).
species richness	The number of species in an area or biological collection (NOAA 2010).
sponge	A sessile (nonmoving), multi-cellular marine animal whose body consists of a jelly-like endoskeleton sandwiched between two layers of cells. Sponges comprise the phylum Porifera.
stony coral	Corals (comprising the order Scleractinia) that form hard, calcium carbonate skeletons. Examples include the brain corals, fungus or mushroom corals, staghorn corals, elkhorn corals, table corals, flower pot corals, bubble corals, and lettuce corals. These corals are largely responsible for the physical form of coral reefs.
subsistence fishing	Fishing for survival. Fishing for food (consumed by the local group of people who do the fishing), not for commercial sale.

supporting service	A category of **ecosystem service** as described by the *Millennium Ecosystem Assessment*. Supporting services are those that are necessary for the production of all other ecosystem services. They differ from **provisioning services**, **regulating services**, and **cultural services** in that their impacts on people are often indirect or occur over a very long time, whereas changes in the other categories have relatively direct and short-term impacts on people. (Some services, like erosion regulation, can be categorized as both a **supporting service** and a regulating service, depending on the time scale and immediacy of their impact on people.) Examples of supporting services include: soil formation, photosynthesis, primary production, nutrient cycling, and water cycling. See also the other MEA categories of cultural services, provisioning services, and regulating services (MEA 2005)
surf break	A permanent obstruction such as a reef, headland, **bombora**, rock, or sandbar that causes waves to break (Silmalis 2007).
surfing	The sport of riding a surfboard toward the shore on the crest of a wave.
sustainability	A characteristic or state whereby the needs of the present and local population can be met without compromising the ability of future generations or populations in other locations to meet their needs (MEA 2009).
T	
tombolo	A type of beach morphology in which sediments are deposited and accumulate in the lee of a breakwater structure, growing seaward from the **shoreline** until they are connected to the structure.
topography	The physical features of a surface area including relative elevations and the position of natural and man-made (anthropogenic) features.
total economic value (TEV)	The sum of the change in all relevant use values and nonuse values for ecosystem goods and services produced by a given change in the ecosystem (*i.e.*, the full social benefits). This is distinct from the "total value" of an ecosystem, which is the value of the entire system (*e.g.*, the value of an entire wetland), but instead is the value of a marginal change to that ecosystem that results form some action.
Tourism Satellite Account (TSA)	A statistical accounting framework in the field of tourism that measures goods and services according to international standards for concepts, classifications, and definitions, that allow valid comparisons from country to country in a consistent manner. A complete TSA contains detailed production accounts of the tourism industry and their linkages to other industries, employment, capital formation, and additional non-monetary information on tourism.
tourists	People who "travel to and stay in places outside their usual environment for more than twenty-four (24) hours and not more than one consecutive year for leisure, business and other purposes not related to the exercise of an activity remunerated from within the place visited" (UNWTO 1995).
travel cost	A valuation method that uses the travel time or travel costs as a proxy "total entry fee", and therefore, a person's **willingness-to-pay** for visiting a particular tourist location.
tunicate	Members of the subphylum Tunicata (also called Urochordata); a group of underwater sac-like filter feeders with incurrent and excurrent siphons that is classified within the phylum Chordata. While most tunicates live on the ocean floor and are commonly known as sea squirts (ascidians) and sea pork, others—such as salps, doliolids and pyrosomes—live above in the pelagic zone as adults.
V	
valuation	The process of expressing a value for a particular good or service in a certain context (*e.g.*, decision-making) usually in terms of something that can be counted, often money, but also through methods and measures from other disciplines (sociology, ecology) (MEA 2009).
value	Generally, the worth, merit, or desirability of something. It can be expressed quantitatively (for example, in monetary terms) or qualitatively. Specifically with respect to ecological benefits, a quantitative or qualitative description of those benefits. Using this definition, the value of an ecosystem might be defined in terms of its beauty, its uniqueness, its irreplaceability, its contribution to life support functions or commercial or recreational opportunities, or its role in supporting wildlife or reducing environmental or human health risks, or providing many other services that benefit humans (Ecosystem Valuation 2009).

W	
wetlands	A type of ecosystem, generally occurring between upland and deepwater areas, that provides many important functions including fish and wildlife habitat, flood protection, erosion control, water quality maintenance, and recreational opportunities. A wetland is an area that is covered by water or has water-saturated soil during a portion of the growing season. In general, it is often considered the transitional area between permanently wet and dry environments. The Ramsar Convention on Wetlands identifies the following marine/coastal wetlands: permanent shallow marine waters; marine subtidal aquatic beds (kelp beds, sea-grass beds, tropical marine meadows); coral reefs; rocky marine shores (including rocky offshore islands and sea cliffs); sand, shingle or pebble shores; estuarine waters; intertidal mud, sand or salt flats; intertidal marshes (includes salt marshes, salt meadows, saltings, raised salt marshes); intertidal forested wetlands (includes mangrove swamps, nipah swamps, and freshwater tidal brackish and freshwater marshes); coastal brackish/saline lagoons; coastal freshwater lagoons; and marine and coastal karst and other subterranean hydrological systems (RAMSAR 2001).
willingness-to-accept (WTA)	The amount of money (or other goods) that a person must be paid to accept the loss of something else.
willingness-to-pay (WTP)	The amount of money (or other goods) that a person is willing to give up to get something else.
Z	
zooplankton	Free-floating or drifting animals with movements determined by the motion of the water.
zooxanthellæ	A group of dinoflagellates living endosymbiotically in association with one of a variety of invertebrate groups (*e.g.*, corals). In corals, they provide carbohydrates through photosynthesis, which are used as one source of energy for the coral polyps. They also provide coloration for the corals and receive a sheltered habitat in return. (NOAA 2010).

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