
Evaluating and Ranking the Vulnerability of Global Marine Ecosystems to Anthropogenic Threats

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Abstract: *Marine ecosystems are threatened by a suite of anthropogenic stressors. Mitigating multiple threats is a daunting task, particularly when funding constraints limit the number of threats that can be addressed. Threats are typically assessed and prioritized via expert opinion workshops that often leave no record of the rationale for decisions, making it difficult to update recommendations with new information. We devised a transparent, repeatable, and modifiable method for collecting expert opinion that describes and documents how threats affect marine ecosystems. Experts were asked to assess the functional impact, scale, and frequency of a threat to an ecosystem; the resistance and recovery time of an ecosystem to a threat; and the certainty of these estimates. To quantify impacts of 38 distinct anthropogenic threats on 23 marine ecosystems, we surveyed 135 experts from 19 different countries. Survey results showed that all ecosystems are threatened by at least nine threats and that nine ecosystems are threatened by >90% of existing threats. The greatest threats (highest impact scores) were increasing sea temperature, demersal destructive fishing, and point-source organic pollution. Rocky reef, coral reef, hard-shelf, mangrove, and offshore epipelagic ecosystems were identified as the most threatened. These general results, however, may be partly influenced by the specific expertise and geography of respondents, and should be interpreted with caution. This approach to threat analysis can identify the greatest threats (globally or locally), most widespread threats, most (or least) sensitive ecosystems, most (or least) threatened ecosystems, and other metrics of conservation value. Additionally, it can be easily modified, updated as new data become available, and scaled to local or regional settings, which would facilitate informed and transparent conservation priority setting.*

Keywords: ecosystem resilience, ecosystem resistance, ecosystem recovery time, ecosystem vulnerability, functional group, global threat analysis, human impact assessment, threat frequency

Evaluación y Clasificación de la Vulnerabilidad a las Amenazas Antropogénicas de los Ecosistemas Marinos Globales

Resumen: *Los ecosistemas marinos están amenazados por un conjunto de factores antropogénicos. La mitigación de amenazas múltiples es una tarea desalentadora, particularmente cuando las restricciones de financiamiento limitan el número de amenazas que pueden ser abordadas. Las amenazas que típicamente son atendidas y priorizadas en talleres de expertos que a menudo no dejan registros del fundamento de las decisiones, lo que dificulta la actualización de recomendaciones con información nueva. Diseñamos un método modificable, repetible y transparente para recolectar la opinión de expertos que describe y documenta los efectos de las amenazas sobre los ecosistemas marinos. Se les pidió a expertos que evaluaran el impacto funcional, la escala y la frecuencia de una amenaza a un ecosistema; la resistencia y el tiempo de recuperación de un ecosistema y la certidumbre de estas estimaciones. Para cuantificar los impactos de 38 amenazas antropogénicas sobre 23 ecosistemas marinos, encuestamos a 135 expertos de 19 países. Los resultados de la encuesta mostraron que todos los ecosistemas están amenazados por lo menos por nueve causas y que*

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nueve ecosistemas están amenazados por >90% de las amenazas existentes- las mayores amenazas (valores de impacto más altos) fueron el incremento de la temperatura de los mares, la pesca demersal destructiva y la contaminación orgánica. Los ecosistemas más amenazados fueron los arrecifes rocosos, arrecifes coralinos, manglares y epipelágicos. Sin embargo, estos resultados generales pueden estar parcialmente influidos por la habilidad específica y la geografía de los encuestados, y deben ser interpretados con cautela. Este método para el análisis de amenazas puede identificar las mayores amenazas (globales o locales), las amenazas más extendidas, los ecosistemas más (o menos) amenazados y otras medidas de valor para la conservación. Adicionalmente, el método puede ser modificado fácilmente, actualizado conforme se disponga de más datos y ajustado para escalas locales o regionales, lo que facilitaría la definición de prioridades de conservación de manera informada y transparente.

Palabras Clave: análisis de amenazas globales, evaluación del impacto humano, frecuencia de amenazas, grupo funcional, resistencia de ecosistemas, tiempo de recuperación de ecosistemas, vulnerabilidad de ecosistemas

Introduction

Human activities now affect nearly every marine ecosystem (e.g., Glover & Smith 2003; POC 2003). The number and variety of threats can be overwhelming to management and conservation efforts. Mapping where threats occur is important for management, but does not explicitly account for differences in the extent and nature of ecosystem responses to threats. For example, bottom-trawl fisheries have significantly more severe and long-lasting impacts on epibenthic communities living on hard versus soft substrates and even greater impact with increasing water depth because individual growth rates decrease and recovery times increase (Watling & Norse 1998; Thrush & Dayton 2002). Understanding these differences in ecosystem response is critical to knowing which threats have the biggest impact on different ecosystems and how to best address them at different scales. Quantifying these differences allows threats to be ranked based on the severity of their impact.

Many conservation organizations are currently developing global prioritization models for conservation action in marine systems (e.g., Olson & Dinerstein 1998) that rely on ranking the impact of threats. For example, it may be efficient and appropriate to ignore land-sea connections if ocean-based threats, such as fishing, have an overwhelming effect on a particular marine ecosystem. In fact, conservation at all scales would benefit from a systematic and transparent method for ranking threats to marine ecosystems. The challenge of ecosystem-specific threat ranking is that hundreds of threat-ecosystem combinations exist. A literature review encompassing all possible threat-ecosystem combinations would be daunting and full of gaps. Consequently, as a substitute, conservation planners traditionally use expert opinion on how threats affect ecosystems. This approach is valid and efficient, but often the methods used and scientific evidence underlying the assessment are not made explicit and the process lacks a paper trail. Thus, it is usually impossible to assess sources of uncertainty in threat assessments.

For instance, how does one determine how experts took information about different facets of threats (e.g., spatial extent, frequency of occurrence, magnitude) into account? We need a quantitative, replicable, and transparent method for determining the impact of any given threat on a particular ecosystem to ensure that information about the ranking process is preserved and to allow for evaluation and revision of resulting decisions as new information becomes available.

Several threat-ranking and evaluation systems have been developed to aid conservation priority setting (e.g., Bryant et al. 1998; TNC 2000; Zacharias & Gregr 2005; Kappel 2005; and innumerable recovery plans for endangered species). Those with a marine focus have addressed only a single ecosystem and a few threats (Bryant et al. 1998), were species (Kappel 2005) or "feature" focused (Zacharias & Gregr 2005), or did not explicitly evaluate or record why threats are problematic (TNC 2000). Our approach differs in several ways. First, in response to the recent emphasis on ecosystem-based management in marine systems (e.g., POC 2003), we assessed the scale of threat impact from single species to the entire ecosystem. Second, we included the full suite of marine ecosystem types and potential threats. Third, we explicitly accounted for the level of certainty in threat rankings. Finally, we used expert opinion and published studies in a transparent and quantitative way so that results would be repeatable and easy to update in the future.

Using this method, we surveyed experts from around the world, and the results allowed us to address a series of critical questions: What are the most important current threats within and across ecosystems? Which ecosystems are most vulnerable to human activities? Which factors drive differences in ecosystem susceptibility, and is it possible to quantify those differences? By developing our method and answering these questions, we devised a flexible tool for systematically assessing the impact of human activities on global marine ecosystems and then implemented it. Local- and regional-scale conservation and resource management efforts can gain significant insight

from a global analysis and can follow our method to conduct finer-scale analyses for region-specific rankings.

Methods

In two workshops that convened academic, nongovernmental, and agency scientists from around the world, we identified 23 distinct marine ecosystems (Table 1) intended to include all major ecosystems commonly recognized by the resource management and conservation communities. The list can be easily modified in future applications to include further subdivisions or alternate classifications. We also identified 20 categories of threats to marine ecosystems, building on previously published lists (Bryant et al. 1998; Kappel 2005), with an additional 18 subcategories (Table 1; complete descriptions of all threats are available from <http://www.nceas.ucsb.edu/~halpern/html/explanations.html>). Although threats could be subdivided further, this list captures the major regional and global anthropogenic threats. We subdivided fishing because different types of fishing can have dramatically different consequences for marine ecosystems. Climate change and pollutant input were subdivided because the sources of different subthreats differ in their consequences for ecosystems. Freshwater and sediment input were subdivided because humans can either increase or decrease both (e.g., the effects of dams versus channelization) with potentially different consequences. Finally, we subdivided nutrient input because nutrient-rich upwelling zones are less likely to be affected by nutrient addition than oligotrophic systems in which nutrients generally limit plant growth.

The impact of a threat on a species or ecosystem is determined by the ecosystem's vulnerability to that threat. Wilson et al. (2005) reviewed and synthesized various methods for assessing ecosystem vulnerability. Expanding on their framework, we evaluated vulnerability by considering the spatial scale, frequency, and functional impact of each threat in each marine ecosystem; the resistance of the ecosystems to disturbance by each threat; and the resilience (i.e., recovery time) of the ecosystems following such disturbance. We included a measure of certainty that allowed the ranks selected for each vulnerability factor to be qualified by the level of certainty in the survey response.

Vulnerability Factors

We defined *spatial scale* as the average scale at which a threat event affects the ecosystem, based on a logarithmic system ranging from zero (ecosystem unaffected) to six (scale >10,000 km²; Table 2). Spatial scale was not the scale at which threats exist (most can be found almost everywhere). For example, a single pass of a demersal trawl may cover approximately 1–10 km², whereas de-

mersal trawling overall affects 1000s of km² of continental shelf ecosystems each year. The vulnerability measure focuses on the first scale. The second would be captured by mapping actual spatial distributions of threats. Scale was intended to include both direct and indirect impacts. For example, dredging a channel within the mouth of a bay may directly affect only a small area but indirectly affect an entire estuary by altering tidal flow. In this case the scale of the threat encompasses the entire bay.

We used *frequency* to describe how often discrete threat events occur in a given ecosystem. Values ranged from “never occurs” to “persistent threat” (Table 2). For those threats that occur as discrete events, frequency represented how often new events occur, not duration of a single event. Furthermore, some threats affect only a few species, whereas others affect entire ecosystems. To capture these differences in what we have termed *functional impact* we used a four-category ranking scheme that ranged from species to ecosystem levels (Table 2).

We used *resistance* to describe the average tendency of a species, trophic level, community, or ecosystem to resist changing its “natural” state in response to a threat. Because of the difficulty of developing a common metric that could be used across multiple levels of organization from species to ecosystems and across widely varying threat-by-ecosystem combinations, we used qualitative ranks for this vulnerability measure (Table 2). These ranks referred to the resistance of the ecosystem components that react to the threat (i.e., the functional level identified above). *Recovery time* was the average time required for the affected species, trophic level(s), or ecosystem to return to its prethreat state (Table 2). Because populations, communities, and ecosystems are dynamic in nature, they need not (and are unlikely to) return to their exact prethreat condition to be deemed “recovered” (Beisner et al. 2003). For persistent threats we considered recovery time following removal of the threat. Finally, we included a qualitative measure of certainty that allowed respondents to indicate the depth of knowledge used to determine vulnerability (Table 2).

Threat Modifier Model

In an ideal world empirical studies would exist for every threat-ecosystem combination so that quantitative, experiment-based rankings of the relative impact of threats could be produced. Nevertheless, with 874 threat-ecosystem combinations in our study (38 threats times 23 ecosystems), data that readily translated into our vulnerability ranking system were available for only a small percentage of these combinations. Thus, to ensure comparable evaluations of all threat-ecosystem combinations, we called on scientists who have evaluated and published work on threats to ecosystems to translate their knowledge into the vulnerability rankings.

Table 1. Overall weighted-average scores for ecosystem vulnerability to each threat for each marine ecosystem.^a

Threat ^b	Intertidal					Coastal				
	Rocky intertidal	Intertidal mud	Beach	Mangrove	Salt marsh	Coral reef	Seagrass	Kelp forest	Rocky reef	Suspension-feeder reef ^c
	13	5	7	7	14	24	6	7	9	5
Freshwater input										
increase	1.6	1.3	0.3	1.8	1.9	1.5	1.6	0.0	1.5	1.7
decrease	1.1	1.1	0.0	2.6	1.9	0.4	1.4	0.0	0.6	1.2
Sediment input										
increase	2.4	2.0	1.1	2.2	2.2	2.8	2.9	1.2	2.0	2.2
decrease	0.6	1.6	0.7	1.3	1.7	0.4	0.5	0.0	0.0	1.5
Nutrient input ^d										
into oligotrophic water	1.8	1.1	0.2	1.4	1.4	2.4	2.1	0.0	1.7	0.0
into eutrophic water	1.3	2.1	0.6	2.1	2.3	1.1	2.0	0.8	1.5	2.8
Pollutant input										
atmospheric	0.8	0.7	0.0	0.9	1.6	0.9	0.6	0.0	0.5	1.8
point, organic	2.4	2.1	1.9	2.0	1.5	2.2	1.9	0.8	2.1	2.4
point, nonorganic	2.2	1.7	0.8	1.1	2.0	1.9	0.4	0.2	1.6	2.4
nonpoint, organic	2.1	2.8	0.1	1.4	1.7	1.2	1.0	1.0	2.2	2.8
nonpoint, nonorganic	2.1	1.6	0.6	0.5	2.0	0.7	0.8	0.0	2.2	2.7
Coastal engineering	2.7	2.1	2.8	3.1	2.3	2.3	2.4	0.0	1.9	3.0
Coastal development	2.7	2.9	3.2	3.4	2.8	2.9	3.3	1.2	2.5	3.2
Direct human	2.8	2.2	2.7	3.3	1.6	2.3	2.5	1.6	2.5	3.0
Aquaculture	2.0	2.0	0.1	3.1	1.7	1.8	2.1	0.0	1.9	1.5
Fishing										
demersal, destructive	1.2	1.4	0.2	0.0	1.0	1.2	0.2	1.5	2.7	3.1
demersal, nondestructive	0.8	1.9	0.9	0.9	1.0	1.6	1.1	2.1	2.9	0.7
pelagic, high bycatch	0.9	0.0	0.1	0.0	0.5	0.5	0.0	0.0	2.6	0.0
pelagic, low bycatch	0.0	0.0	0.0	0.0	0.4	0.7	0.0	0.0	2.6	0.0
aquarium	1.4	0.0	0.0	0.7	0.5	1.6	0.4	0.0	1.8	0.0
illegal/unregulated/unreported	1.2	0.0	0.7	0.0	0.4	1.0	0.6	0.0	1.2	0.0
artisanal, destructive	1.1	0.5	0.8	1.2	0.5	2.0	0.0	1.5	2.3	1.2
artisanal, nondestructive	1.4	0.3	0.5	2.2	0.6	2.5	0.6	0.0	2.1	0.7
recreational	2.0	1.7	0.4	2.1	0.5	2.1	2.2	2.3	2.6	1.3
Climate change										
sea level	2.5	1.9	2.1	3.0	3.1	2.4	2.6	1.6	1.5	1.8
sea temperature	2.8	1.4	0.6	2.4	1.4	2.8	2.1	2.0	1.9	0.8
ocean acidification	0.9	1.0	0.0	1.2	1.3	1.1	1.4	0.0	1.1	0.7
ozone/UV	0.9	1.3	0.0	0.2	1.1	0.8	0.5	0.1	0.7	0.0
Species invasion	2.8	2.9	0.9	1.0	2.8	1.5	1.2	1.3	2.5	2.6
Disease	1.3	1.8	0.0	1.7	1.1	2.2	1.0	0.7	1.8	2.1
Harmful algal blooms	1.9	2.2	0.9	1.6	2.0	1.8	2.3	0.4	1.7	2.5
Hypoxia	1.2	2.1	0.6	0.6	1.9	0.8	1.3	1.0	1.6	2.9
Ocean-based pollution	1.3	0.8	0.5	1.2	1.2	1.2	0.5	0.1	1.7	0.0
Commercial activity	0.3	1.9	1.9	2.0	1.4	1.5	1.9	0.0	1.4	0.0
Ocean mining	0.9	0.0	0.3	0.0	1.1	0.8	0.4	0.0	1.3	0.0
Offshore development	0.7	0.0	0.4	0.0	0.7	0.2	0.0	0.5	0.7	0.0
Benthic structures	1.0	0.9	0.8	1.3	0.9	0.5	1.6	0.0	1.7	0.4
Ecotourism	1.6	0.0	1.0	2.3	1.3	1.8	1.5	0.8	1.7	0.3
Summed threat	58.9	51.4	28.4	55.7	54.9	57.2	48.9	22.4	66.6	53.2
Average threat	1.5	1.4	0.7	1.5	1.4	1.5	1.3	0.6	1.8	1.4

continued

Table 1. (continued)

Subtidal soft bottom ^e	Coastal						Oceanic						Sum	Average
	Ice	Soft sbelf (30-200 m)	Hard sbelf (30-200 m)	Soft slope (200-2000 m)	Hard slope (200-2000 m)	Soft benthic (deep)	Deep seamount	Vent	Soft canyon	Hard canyon	Surface water	Deep water		
5*	2*	8	5	4*	2*	5*	2*	5*	1*	1*	6	3*		
1.4	2.5	2.0	0.7	0.1	0.0	1.1	0.0	0.0	0.0	0.0	0.8	0.0	21.7	0.9
1.8	0.0	1.3	1.4	0.1	0.0	0.8	0.0	0.0	0.0	0.0	1.0	0.0	16.7	0.7
1.5	3.2	2.8	1.7	1.5	1.8	1.8	0.0	0.1	1.9	2.0	1.2	0.0	40.4	1.8
1.0	DK	1.0	0.3	0.7	0.5	1.0	0.0	0.0	1.9	2.0	0.8	0.0	17.4	0.8
1.3	0.0	1.0	1.4	2.2	0.6	2.0	0.0	0.0	2.4	2.5	1.1	0.0	26.7	1.2
2.6	0.0	1.7	2.0	1.7	0.5	0.6	0.0	0.0	1.9	2.0	1.3	0.0	30.8	1.3
1.0	0.0	2.5	0.6	0.9	0.7	3.3	1.2	0.0	1.5	1.7	1.1	1.5	23.8	1.0
2.6	2.6	2.3	1.6	1.1	0.2	2.9	0.0	0.2	2.4	2.7	2.3	1.6	41.7	1.8
2.3	0.0	1.8	1.1	1.0	0.2	2.5	0.0	0.3	1.8	DK	0.8	1.6	27.5	1.3
1.2	2.2	1.4	0.0	2.0	0.2	1.7	0.0	0.0	2.4	2.7	1.9	1.6	33.7	1.5
1.5	0.0	2.1	0.2	2.1	0.2	1.8	0.0	0.0	1.8	DK	2.3	1.6	26.7	1.2
2.3	3.1	1.2	1.5	0.0	0.0	1.6	0.0	0.0	0.0	0.0	1.2	0.0	33.4	1.5
2.4	2.9	1.8	3.8	0.0	0.1	1.6	0.0	0.0	0.0	0.0	1.3	0.0	42.0	1.8
2.0	2.6	1.1	2.9	0.0	0.0	1.6	0.0	1.4	0.0	0.0	0.9	0.0	37.0	1.6
1.8	0.0	1.8	3.0	0.1	0.0	1.0	0.0	0.2	0.0	0.0	0.9	0.0	24.9	1.1
2.1	0.0	3.0	3.1	3.2	2.8	2.3	3.5	0.7	2.6	3.4	2.1	0.8	42.2	1.8
2.1	0.0	2.0	3.2	2.3	2.4	2.0	0.0	0.5	0.0	0.0	1.6	0.0	30.0	1.3
0.0	0.0	1.1	2.8	0.2	0.0	1.6	0.0	0.0	0.0	0.0	3.0	2.2	15.5	0.7
0.6	0.0	0.8	2.8	0.2	0.0	0.5	0.0	0.1	0.0	0.0	2.2	0.6	11.4	0.5
0.0	0.0	0.0	1.9	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.6	0.0	9.2	0.4
0.0	0.0	0.0	1.8	1.0	1.7	0.0	1.7	0.0	2.6	3.4	1.5	1.0	19.8	0.9
0.0	0.0	0.6	1.9	0.0	0.0	0.6	0.9	0.0	0.0	0.0	0.6	0.0	15.6	0.7
0.0	0.0	1.2	1.9	0.0	0.8	0.0	0.8	0.0	0.0	0.0	1.4	0.0	17.0	0.7
0.4	0.0	1.4	3.4	0.4	0.8	0.8	0.4	0.0	0.0	0.0	1.9	0.0	26.8	1.2
2.2	0.0	2.0	1.5	0.0	0.0	1.6	1.3	0.0	0.0	0.0	2.4	0.0	33.5	1.5
0.5	3.8	2.5	2.9	2.3	0.9	2.5	1.8	0.9	2.8	3.5	3.3	2.3	48.4	2.1
0.1	0.0	1.7	2.5	2.1	1.6	2.2	2.7	0.7	1.7	4.0	1.8	0.0	29.8	1.3
0.3	2.7	1.9	1.8	0.0	0.0	1.3	0.0	0.0	0.0	0.0	1.5	0.0	15.2	0.7
2.7	3.2	1.6	1.5	0.2	0.5	1.5	0.0	0.1	0.0	0.0	2.3	0.0	32.9	1.4
1.2	0.0	1.1	1.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	1.6	0.0	19.4	0.8
2.2	0.0	1.4	2.5	0.1	0.2	1.1	0.0	0.0	0.0	0.0	2.2	0.0	26.9	1.2
1.8	0.0	1.5	3.2	2.3	1.7	2.5	1.7	0.4	2.6	3.4	2.1	2.8	40.0	1.7
1.1	0.0	1.2	0.3	1.4	1.7	2.3	1.2	0.0	1.5	1.9	1.7	0.4	23.1	1.0
0.3	0.0	1.7	0.9	0.1	1.0	0.9	0.0	0.0	0.0	0.0	1.9	0.0	19.0	0.8
0.9	0.0	2.2	1.3	0.9	0.0	1.0	0.0	1.3	0.0	0.0	1.1	0.0	13.4	0.6
0.0	0.0	1.2	1.1	1.7	0.8	1.5	1.6	0.1	1.7	2.1	1.1	0.4	16.5	0.7
0.1	0.0	0.5	2.1	1.6	2.2	1.9	1.4	0.1	1.7	2.1	1.5	0.0	24.1	1.0
0.2	0.0	1.3	1.8	0.0	0.0	0.7	0.0	0.4	0.0	0.0	1.0	0.0	17.7	0.8
45.2	28.9	57.7	69.3	33.8	24.3	55.3	20.0	7.6	35.1	39.3	59.5	18.4		
1.2	0.8	1.5	1.8	0.9	0.6	1.5	0.5	0.2	0.9	1.1	1.6	0.5		

^aShading highlights the range of values in which each threat-by-ecosystem score lies: black > 3.0; gray 2.0-3.0; light gray 1.0-2.0; and white < 1.0. These shades should not be used to identify strict categories of threat (i.e., a gray score of 2.99 is essentially the same as a black score of 3.01). The numbers at the top of each column are the number of respondents for that ecosystem type and an asterisk (*) shows an ecosystem for which a literature survey was conducted.

^bSee <http://www.nceas.ucsb.edu/~halpern/html/explanations.html> for a full explanation of each threat type.

^cSuspension reefs are ecosystems defined by suspension feeders, such as oyster reefs.

^dOligotrophic waters are nutrient poor, whereas eutrophic waters are nutrient rich. Nutrient input into these different waters is expected to have different impacts.

^eSubtidal soft bottom includes all shallow, soft bottom ecosystems.

Table 2. Ranking systems for each vulnerability measure used to assess how threats affect marine ecosystems.

<i>Vulnerability measure</i>	<i>Category</i>	<i>Rank</i>	<i>Descriptive notes</i>	<i>Example</i>
Scale (km ²)	no threat	0		
	<1	1		anchor damage
	1-10	2		single trawl drag
	10-100	3		sediment run-off from deforestation
	100-1,000	4		land-based pollution from run-off of large rivers
	1,000-10,000 >10,000	5 6		an invasive species sea surface temperature change
Frequency	never occurs	0		
	rare	1	infrequent enough to affect long-term dynamics of a given population or location	large oil spill
	occasional annual or regular	2 3	frequent but irregular in nature frequent and often seasonal or periodic in nature	toxic algal blooms runoff events due to seasonal rains
	persistent	4	more or less constant year-round, lasting through multiple years or decades	persistent hypoxic zones
Functional impact	no impact	0		
	species (single or multiple)	1	one or more species in a single or different trophic levels	ship strikes on whales
	single trophic level	2	multiple species affected; entire trophic level changes	overharvest of multiple species within the same trophic guild
	>1 trophic level	3	multiple species affected; multiple trophic levels change	overharvest of key species from multiple trophic guilds
entire community	4	cascading effect that alter the entire ecosystem	ocean temperature increase and fatal bleaching of coral reefs	
Resistance	no impact	0		
	high	1	no significant change in biomass, structure, or diversity until extreme threat levels	trawling on soft-sediment communities
	medium	2	moderate intensities or frequencies of a threat lead to change	effects of industrial pollution run-off on coastal species
	low	3	slightest occurrence of a threat causes a change, or all-or-nothing threats	blast fishing in coral reefs
Recovery time (years)	no impact	0		
	<1	1		kelp recovery after disturbance
	1-10	2		short-lived species recovery from episodic toxic pollution
	10-100	3		long-lived species recovery from overfishing
	>100	4		deep sea coral recovery after trawl damage
Certainty	none	0		
	low	1	very little or no empirical work exists	
	medium	2	some empirical work exists or expert has some personal experience	
	high	3	body of empirical work exists or the expert has direct personal experience	
	very high	4	extensive empirical work exists or the expert has extensive personal experience	

Web Survey of Experts

We used an on-line, annotated survey of experts to quantify how each threat affects the ecosystem(s) in geographic region(s) where their expertise was strongest, based on the five vulnerability factors (www.nceas.ucsb.edu/~halpern/html/expert_survey.htm). The survey instrument was tested on a core group of five experts and modified for clarity based on their input. Experts were identified by searching the Web of Science for literature on each threat-ecosystem combination (e.g., pollution and mangrove), and all authors with listed email addresses were contacted about the survey. We requested these people to pass our invitation on to other experts in one or more ecosystems. Although respondents represented a mix of academic, agency, and nongovernmental organization (NGO) scientists, our sample contained more academic experts because we used publication in the peer-reviewed literature as a source of identification. We sent surveys to 370 experts on all 23 marine ecosystems and received responses from 135 of them (37% response rate) from 19 different countries (Table 3). Reminder emails were sent up to three times over a 2-month period. Affiliation, geographic distribution, and gender of respondents were similar to those of the experts contacted (Table 3), indicating low likelihood of nonrespondent bias for these variables. Participants were provided descriptions of the vulnerability factors in a language similar to that above and in Table 2 (http://www.nceas.ucsb.edu/~halpern/html/Matrix_Instructions.pdf). Participants were asked to fill in vulnerability values for all 38 potential threats for an ecosystem and could annotate their responses. At the end of the survey, participants were asked to state which three threats they thought were most important (termed *stated answers*), in order of importance, without making explicit reference to our vulnerability measures.

Literature-Based Surveys

For the 10 ecosystems for which we received fewer than five completed surveys, we supplemented the data with a thorough literature review that counted as a single additional survey response. Thus, survey sample sizes were still small, suggesting caution in interpreting results for these ecosystems (although sample size did not correlate with variance in responses). For many threat-ecosystem combinations, relevant published empirical research was not available. We set vulnerability to zero when logically justifiable (e.g., effects of sea level rise on deep-water ecosystems), but left the vulnerability rankings blank in all other cases for which we had insufficient information on effects of threats (14.5% of the time).

Modifier Model

We combined the five vulnerability measures and the certainty measure into a single weighted-average vulnerabil-

ity score that represents (in relative terms) how vulnerable a given ecosystem is to a given threat. The weighted-average vulnerability score was calculated in two steps: averaging across replicate survey responses, and combining the five factors into one weighted-average score. For each threat-ecosystem combination, we rescaled "scale" and "resistance" values to range from 0 to 4 (multiplied by 4/6 and 4/3, respectively), so all vulnerability measures were comparable. Then each 0–4 rank was multiplied by the certainty value, and the sum of these weighted values for each vulnerability measure was divided by the sum of the certainty values. This weighted average gives greater importance to values with higher certainty (and presumably higher precision), but may lower weighted scores for poorly studied threat-ecosystem combinations. Additionally, it may be sensitive to the scale of the categories used for each vulnerability measure.

Assuming equal weighting of the five vulnerability measures, we took the grand mean of their weighted averages to get a single rank (from 0 to 4) that indicated how a given threat affects a particular ecosystem. This assumption seems reasonable because an extreme value in any single vulnerability measure could lead to ecosystem demise, and it decreases the sensitivity of the average to the categorical scales used. However, weighting could easily be adjusted if a given vulnerability measure was thought to play a larger role in determining ecosystem vulnerability. Because experts occasionally did not know how a particular threat affected an ecosystem and therefore left vulnerability scores blank, several threat-by-ecosystem combinations had smaller sample sizes than reported for the entire ecosystem.

We tested whether ecosystems differed significantly in their average vulnerability scores across all threats with analysis of variance. Similarly, we determined whether threats differed significantly by comparing average vulnerability scores across all ecosystems.

Expert Versus Model Output

We wanted to know whether simply asking experts to state the top three threats affecting a given ecosystem would result in different outcomes for the final ranking of threats compared with the survey's quantitative assessment. Using the aggregate data for each ecosystem, we compared the three threats most frequently listed by respondents at the end of the survey to the three threats with the highest vulnerability scores based on the weighted average of all responses for that ecosystem. In addition, for coral reefs, one of our best-sampled ecosystems, we examined consistency within individual survey responses by examining the frequency of matches between individuals' stated top threats and the top threats based on individual vulnerability scores. We did not examine the specific ranking (first, second, or third); rather, we determined whether both methods identified a given

Table 3. Institutional affiliation, geographic expertise, and geographic location of respondents to the survey of how different threats affect marine ecosystems.^a

	Rocky intertidal	Intertidal mud	Beach	Coral reef	Mangrove	Seagrass	Salt marsh	Kelp forest	Rocky reef	Suspension-feeder reef	Subtidal mud	Soft shelf	Hard shelf	Soft slope	Hard slope	Soft benthic	Deep seamount	Vent	Surface water	Deep water	Ice	Experts contacted (%)	Survey respondents (%)
Institutional type																							
academic	10	4	3	13	4	3	9	7	8	5	3	5	3	2	1	3		3	4	2	1	81.6	68.1
NGO	3		2	4		2						1		1		1	1	1	1			9.5	12.6
agency		1	2	7	3	1	5		1		1	2	2			1			1			8.9	19.3
Geographic location^b																							
Asia																							
India			1	1	1	1	1																
Singapore				1																			
Europe																							
UK	1			3					1														
Norway																1							
Sweden									1														
Germany																	1						
Spain							1																
Greece				1																			
Italy	1			1																			
Africa																							
South Africa	1																						
Tanzania				1																			
North/Central America																							
USA	7	5	3	12	5	4	12	7	5	5	4	5	5	3	1	3		4	4	2	1		
Canada				1			1																
Mexico				1																			
South America																							
Chile	2																						
Brazil				1					1			1											
Australasia																							
Australia	1			3	1								1							1			
New Zealand													1										
Middle East																							
Israel	1			1																			
Geographic expertise^c																							
Caribbean		1	3	8	5	4	1		1	1			2										
Indian Ocean	1		2	8	3	1	1						1	1		1		1	1				
W. Pacific			1	10	3	1	1						1			1		2					
S. Pacific	3		1	10	3		1	1	2			1	1	1		2		1	1				
N. Pacific	6	2	2	8	2		7	6	4	3	1	4	3	3	1	2		3	4	2			
Mid-East	1		1	1																			
S. Atlantic	2		1	1				1					1				1		1	1			
N. Atlantic	1	3	1		2	1	7	1		2	2		2	1		3	1	1					
Arctic							1					3				2			1		1		
Southern Oceans							1		1		1	2				1			1				
Mediterranean	4		3			1			1										1				

^aNumbers show how many experts had that trait for that ecosystem. The final two columns are summary statistics. Seven people responded for two ecosystems, one person responded for three ecosystems, and two people responded for five ecosystems.

^bCountries represented in the contacted list but not in the response list include Indonesia, Korea, Japan, Poland, Finland, Netherlands, Denmark, Belgium, France, Portugal, Ireland, Greece, Sao Tome, South Africa, Fiji, Vietnam, Hong Kong, Oman, and Argentina.

^cRespondents often identified more than one area of geographic expertise, so the sum of these values is often greater than the number of respondents.

threat in the top three. When volunteered top threats were more general than the subcategories we used (e.g., “fishing” vs. “pelagic fishing with high bycatch”), we matched them to the most relevant specific threat from the vulnerability survey.

Results

Expert opinion and literature surveys produced overall vulnerability scores (on a continuous scale) for each threat-ecosystem combination (Table 1). Summing all scores across threats essentially ignores zero values and provides ranks based only on threats that have an impact, whereas average scores account for zero values. By either measure, the survey results identified increasing sea temperature, demersal destructive fishing, coastal development, point-source and nonpoint-source organic pollution, increasing sediment input, hypoxia, and direct human impact as the greatest threats (i.e., highest 20% of impact scores), in decreasing order of importance (Table 1; Supplementary Material). In contrast, the threats with the least impact on ecosystems were aquarium-trade fishing, ocean mining, and ozone depletion. Nevertheless, even threats with low overall impact scores can have severe impacts on certain ecosystems; indeed, survey results showed that both high- and low-bycatch pelagic fishing have large effects on pelagic ecosystems in particular.

Hard shelf, rocky reefs, epipelagic offshore waters, and rocky intertidal ranked as the ecosystems most vulnerable to threats (Table 1; Supplementary Material). Several deep-ocean ecosystems ranked as least threatened, including hydrothermal vents, deep water, and seamounts. The most threatened ecosystems ranked high because they are afflicted by many threats, particularly multiple types of fishing (Table 1). In contrast, experts considered some ecosystems to be imperiled by only a few high-impact threats. Comparisons across ecosystems allowed for ranking the relative impact of a threat to different ecosystem types. For example, demersal destructive fishing had the highest impacts on hard-shelf and canyon ecosystems, deep seamounts, and suspension-feeder reefs, whereas sea level rise was the greatest threat to intertidal ecosystems, coral reefs, and seagrasses.

We used comparisons of values within a single ecosystem to identify the threats with the most and least impact on a particular ecosystem. In most cases the survey responses confirmed results of previous analyses for specific ecosystems. The top three threats to coral reefs were coastal development, increased sediment input, and changes in sea temperature, with increased nutrient input, sea level rise, and artisanal fishing also posing major threats (Table 1; Bryant et al. 1998). Experts considered kelp forests threatened primarily by demersal and recreational fishing (Steneck et al. 2002) and salt marshes most threatened by sea level rise, coastal engineering and de-

velopment, and species invasions (Adam 2002). Results for some ecosystems were surprising: coastal development and recreational fishing were the highest threats within hard-shelf ecosystems and ecotourism was ranked as a threat to hard- and soft-shelf ecosystems. Our approach allowed us to determine the primary drivers of results in Table 1 by examining individually the five vulnerability factors (Supplementary Material). Functional impact had the highest average vulnerability value among the five measures for most threats (23 of 38 threats), and it was a close second for nine others (Table 4), indicating that high overall scores were largely driven by functional impact. In contrast, recovery time and scale most often had the lowest scores (for 20 and 16 threats, respectively), indicating that in general most systems were considered resilient to threats and a majority of threats act at fairly small spatial scales. There were of course notable exceptions to this, for example, the large-scale effects of climate change and relatively slow recovery from destructive demersal fishing in many systems.

Average vulnerability scores (Table 4) also provided insight into why particular threats are greater than others. The largest-scale threats were climate-change-based threats, species invasion, and hypoxia. Highest-frequency threats were increasing sea surface temperature, coastal development, and point-source organic pollution, which all tend to be persistent rather than episodic. The threats with greatest functional impact were increasing sedimentation, point-source organic pollution, and hypoxia, and all threats that tend to affect abiotic characteristics of ecosystems. Experts considered ecosystems least resistant to and to have the longest recovery times from demersal destructive fishing, point-source organic pollution, coastal development, and increasing sea surface temperature.

Ecosystems differed in the drivers of their vulnerability. For instance, coral reefs and deep soft benthic ecosystems were considered vulnerable to threats primarily because of low resistance to and slow recovery from threats (Table 5). On the other hand, hard-shelf ecosystems were considered highly threatened because of vulnerability to the scale, frequency, and functional impact of threats (see Supplementary Material).

Across all ecosystem-threat vulnerability measures, only half (50.3%) had standard deviations for rescaled values <1.0. This high variance was largely consistent for each ecosystem type, even for ecosystems with large numbers of respondents. There was no relationship between survey sample size within an ecosystem and the variance in response values (Fig. 1). Some of this variance was likely due to regional variation in how ecosystems respond to threats: although all ocean basins and seas were represented in survey responses, experts reported basing their responses on knowledge of the Indian, West Pacific, South Atlantic, Arctic, southern oceans, or the Mediterranean <10% of the time. Many more responses were

Table 4. Average values across all marine ecosystem types for each of the five measures of ecosystem vulnerability for each threat type and the certainty of respondents to the survey on how threats affect marine ecosystems.*

<i>Threat</i>	<i>Scale</i>	<i>Frequency</i>	<i>Functional impact</i>	<i>Resistance</i>	<i>Recovery time</i>	<i>Certainty</i>
Freshwater input						
increase	0.9	1.1	1.4	0.8	0.6	1.8
decrease	0.7	0.8	1.1	0.7	0.5	1.7
Sediment input						
increase	1.2	2.0	2.7	1.7	1.2	1.7
decrease	0.4	0.9	1.4	0.7	0.5	1.4
Nutrient input						
oligotrophic	0.8	1.2	1.6	1.4	0.8	1.6
eutrophic	1.0	1.6	2.0	1.1	0.9	1.8
Pollutant input						
atmospheric	1.1	1.3	1.0	0.8	1.0	1.4
point, organic	1.1	2.0	2.5	2.1	1.4	1.7
point, nonorganic	0.9	1.5	1.4	1.5	1.1	1.5
nonpoint, organic	1.2	1.7	1.7	1.5	1.1	1.5
nonpoint, nonorganic	1.1	1.5	1.2	1.5	1.0	1.4
Coastal engineering	0.9	1.5	1.9	1.8	1.2	2.2
Coastal development	1.3	2.1	2.2	2.0	1.5	2.3
Direct human	1.1	1.9	1.9	1.8	1.3	2.4
Aquaculture	0.8	1.4	1.3	1.2	0.8	2.0
Fishing						
demersal, destructive	1.3	1.8	2.2	2.1	1.8	2.0
demersal, nondestructive	1.0	1.5	1.4	1.4	1.2	1.7
pelagic, high bycatch	0.7	0.7	0.7	0.6	0.6	1.8
pelagic, low bycatch	0.6	0.5	0.6	0.4	0.4	1.7
aquarium	0.3	0.5	0.5	0.4	0.3	1.7
IUU	0.6	0.9	1.0	1.0	0.8	1.3
artisanal, destructive	0.4	0.7	0.9	0.8	0.6	1.9
artisanal, nondestructive	0.5	1.0	0.8	0.7	0.7	1.9
recreational	0.9	1.5	1.2	1.2	1.0	2.0
Climate change						
sea level	1.7	1.7	1.8	1.2	0.9	2.0
sea temperature	2.2	2.3	2.2	2.0	1.7	1.5
acidification	1.5	1.4	1.4	1.2	1.0	1.5
ozone/UV	0.8	0.8	0.7	0.6	0.4	1.8
Species invasion	1.4	1.5	1.7	1.4	1.0	1.5
Disease	0.9	0.8	0.9	0.9	0.7	1.3
Harmful algal blooms	1.1	1.2	1.6	1.2	0.8	1.7
Hypoxia	1.5	1.6	2.3	2.1	1.2	1.5
Ocean-based pollution	0.7	1.1	0.9	1.2	1.0	1.5
Commercial activity	0.8	1.0	0.9	0.8	0.7	1.7
Ocean mining	0.6	0.5	0.8	0.5	0.5	1.5
Offshore development	0.5	0.8	0.9	0.8	0.7	1.6
Benthic structures	0.6	1.0	1.3	1.2	1.0	1.4
Ecotourism	0.6	1.1	0.9	0.7	0.5	2.0

*High values for resistance and recovery time represent low resistance and long recovery times.

based on knowledge of the North Pacific (28.3%), North Atlantic (12.6%), South Pacific (12.6%), and Caribbean (11.7%) oceans. Sample sizes for each region within an ecosystem type were not large enough to test whether variance was lower within versus among regions (Table 3).

Consistency between the top three threats volunteered by experts and the top three threats revealed by average vulnerability scores was low (Table 6). In the overall analysis consistency ranged from no overlap for rocky intertidal, subtidal mud, and soft deep benthic habitats to complete agreement for kelp forest, with an average

consistency of 51.7%. This inconsistency existed within ecosystems as well. Consistency between individual respondents' volunteered versus surveyed top threats for coral reefs was only 39%, much lower than the overall average for coral reefs (67%), with individual consistency ranging from 0% to 100%.

Discussion

Human activities are affecting nearly every part of the world's oceans, creating a difficult challenge for

Table 5. Average scores for each of the five measures of ecosystem vulnerability and the certainty of respondents to the survey on how threats affect each marine ecosystem.*

Vulnerability measure	Rocky intertidal	Intertidal mud	Beach	Coral reef	Mangrove	Seagrass	Salt marsh	Kelp forest	Rocky reef	Suspension-feeder reef	Subtidal mud	Soft shelf	Hard shelf	Soft slope	Hard slope	Soft benthic (deep)	Deep seamount	Vent	Soft canyon	Hard canyon	Surface water	Deep water	Ice
Scale	1.0	0.9	0.5	0.9	0.9	1.0	1.2	0.5	1.5	0.9	0.9	1.4	2.1	0.9	0.4	1.4	0.4	0.2	0.0	0.7	1.7	0.5	0.7
Frequency	1.7	1.4	1.0	1.5	1.5	1.5	1.6	0.6	1.8	1.3	1.1	1.4	2.2	1.0	0.8	1.4	0.6	0.1	1.1	1.1	1.6	0.6	0.5
Functional impact	1.8	1.7	1.0	1.7	1.8	1.4	1.8	0.6	2.0	1.4	1.3	1.9	2.0	1.1	0.9	1.6	0.6	0.4	1.2	1.3	2.1	0.4	0.6
Resistance	1.5	1.2	0.9	1.5	1.5	1.4	1.2	0.5	1.8	1.4	1.1	1.4	1.5	1.0	0.8	1.5	0.7	0.3	1.4	1.3	1.2	0.5	0.5
Recovery time	1.1	0.8	0.5	1.1	1.1	1.0	1.2	0.2	1.3	0.9	0.8	1.2	1.1	0.7	0.8	1.4	0.7	0.2	0.9	1.3	1.2	0.4	0.3
Certainty	1.8	1.6	1.5	1.5	1.7	1.4	1.4	1.2	1.6	2.0	1.3	1.4	1.6	1.4	2.3	1.9	1.8	1.7	2.4	2.3	1.5	1.7	1.5

*The three highest values for each measure are coded by shades of gray (black, dark gray, and light gray, respectively). Because of rounding, values may appear equal but are not exactly the same.

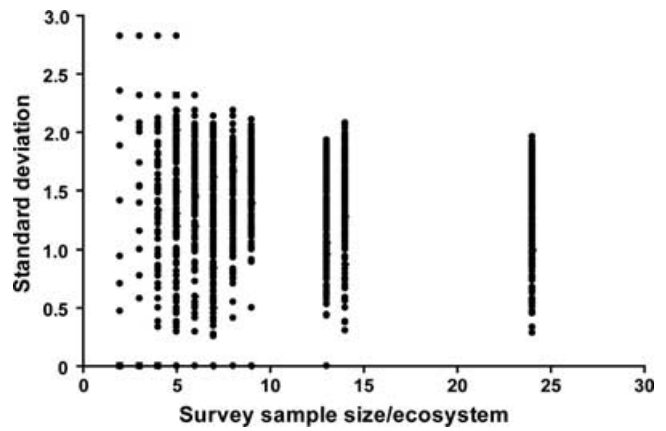


Figure 1. Variance around weighted average scores from survey responses within each marine ecosystem relative to the number of experts surveyed for that ecosystem. Ecosystems with only one survey response were excluded. Each point is a particular ecosystem vulnerability measure for a threat-ecosystem combination ($n = 3800$). About one-quarter of the data are at $SD = 0$ ($n = 1027$).

conservationists and managers. How does one decide which threats or ecosystems to focus on first, or where one might achieve the greatest return on conservation investment? Our method for assessing ecosystem vulnerability to current threats allows scientists and managers to catalog and compare anthropogenic threats to marine ecosystems and explicitly identify why a threat affects a particular ecosystem in a quantifiable, transparent, and repeatable way. This allows for clear communication of the basis for a threat ranking and provides a relatively easy means to modify the overall ranking as additional information becomes available.

We used this method to provide the first systematic and comprehensive assessment of how current threats affect the world's marine ecosystems. Our results indicate that every marine ecosystem is affected by multiple threats and that many ecosystems are affected at some level by every identified threat. Somewhat surprisingly, only one of the greatest threats (highest impact scores) was ocean based (demersal destructive fishing); others (sea temperature rise, coastal development, point-source organic pollution, increased sediment input, hypoxia, and direct human impact) are all driven by land-based activities. Consequently, effective marine conservation and management will have to address terrestrial, freshwater, and marine-based threats simultaneously. These general results should be interpreted with caution because scarcity of information for many of the threat-by-ecosystem combinations, geographic biases in the expertise of respondents, and variation in how respondents may have interpreted the vulnerability factors likely influenced results in some cases. Nevertheless, our results provide an initial assessment of ecosystem vulnerability, illustrate the potential of

Table 6. Consistency (% similarity) between the top three threats to marine ecosystems calculated from the expert survey (average ecosystem vulnerability scores) and the most frequently stated threats by respondents to the survey on how threats affect each marine ecosystem.*

<i>Habitat</i>	<i>Consistency</i>
Intertidal	
rocky intertidal	0.00
intertidal mud	0.67
beach	0.67
salt marsh	0.67
mangrove	0.67
seagrass	0.67
Coastal	
coral reef	0.67
kelp forest	1.00
rocky reef	0.33
suspension-feeding reef	0.33
subtidal mud	0.00
ice	0.33
soft shelf	0.67
hard shelf	0.33
Oceanic	
soft slope	0.67
hard slope	0.67
soft benthic (deep)	0.00
deep seamount	N/A
vent	0.67
soft canyon	N/A
hard canyon	N/A
surface water	0.67
deep water	0.67
Overall	0.52

*Survey respondents were asked to state what they believed were the top three threats (stated threats) without evaluating them by the five measures of ecosystem vulnerability. See methods on how nonidentical terms for threats were compared. N/A indicates either there were no survey respondents or no respondent indicated the top three threats.

our approach for conducting comparisons across threats and ecosystems, and point out important gaps in knowledge and areas for future research.

Understanding the ways in which particular threats affect ecosystems (Table 4) can aid in prioritization of the most important or most manageable threats. Some threats act at very large scales (e.g., climate change) or have large functional impacts (e.g., increased sedimentation), whereas ecosystems are generally much less resistant to and have longer recovery times from other threats (e.g., demersal destructive fishing). Addressing such threats can be challenging but may provide more return on conservation or management investment. Ultimately, threat ranking and prioritization will ultimately depend on the scale at which decisions need to be made. Threats such as climate change primarily need to be addressed at regional to global spatial scales, whereas threats such as coastal development require local to regional management. Our approach can be easily modified to provide guidance at different spatial scales and even for specific locations.

Surprisingly, rocky reefs and hard-bottom shelf areas were ranked as most threatened. Yet other ecosystems, such as coral reefs and mangroves, are widely recognized as being highly imperiled. There are at least two possible explanations for these results. First, we did not account for the global rarity of an ecosystem type or the amount of the total ecosystem affected. Ecosystems with lower average threat ranks may actually be more at risk of local or global extinction than higher-ranked ecosystems. For example, the majority of the world's mangroves and coral reefs are threatened (Bryant et al. 1998; Valiela et al. 2001), whereas large regions of rocky reef and hard-bottom shelf may be relatively unaffected by anthropogenic activities (even though more threats can affect them). Mapping impacts spatially will provide this assessment, an effort we have undertaken elsewhere (B. S. H. et al., unpublished data).

Second, threats almost certainly interact in a multiplicative rather than additive manner. For example, when nutrient input coincides with overharvest of herbivores, macroalgal blooms are enhanced in rocky intertidal and coral reef ecosystems (e.g., Hughes 1994; Worm et al. 2002). Although many threats clearly interact in ways that can amplify their consequences for ecosystems, the nature and magnitude of this synergism are unknown for most threats and ecosystems. Consequently, we conservatively assumed threats are additive. We also ignored potential linkages that could allow impacts to propagate between ecosystems. For example, destruction of mangroves or seagrass beds could affect fauna on nearby coral reefs that depend upon these nursery habitats (e.g., Mumby et al. 2004).

Although most of our results make intuitive sense, several emerge as surprising. Destructive fishing was scored as a lesser threat than nondestructive fishing for both demersal and artisanal fishing in many of the ecosystems (Table 1). This result likely emerged from many experts reporting that destructive fishing was not a threat for the region(s) of their expertise, whereas nondestructive fishing was. When both threats existed within a region the experts generally ranked destructive fishing as being much worse. A lower value for destructive artisanal fishing emerged globally, therefore, even though it clearly is a higher impact threat than nondestructive artisanal fishing where both occur. Another surprising result is that recreational fishing and coastal development were considered the highest impacts in hard-shelf ecosystems, even though these activities primarily occur near shore. This result is possibly explained by the broad depth range of the hard-shelf ecosystem, which includes the sublittoral zone to the continental shelf break (30–200 m depth). Activities that occur near shore have the potential to influence the shallower shelf but likely do not affect deeper areas; this distinction is lost when depths are pooled. Indeed, for some ecosystem types finer subdivisions may be needed. If improbable results persist after

further scrutiny, additional surveys or even experimental studies could be conducted to refine the impact values for that particular threat-ecosystem combination. In general, it is wise to consider the results of this analysis as hypotheses about relative vulnerability that should be tested with further research.

The global results of our study provide a valuable big picture, but the relative importance of particular threats depends in part on which threats are present at particular locations, the magnitude of the threats, and the specific attributes of the location. For example, areas with greater local species and/or genetic diversity may have greater resistance to some threats than less diverse areas (e.g., Steneck et al. 2002; Hughes et al. 2003). Connectivity within and among ecosystems will affect the scale and functional impact of a threat in a particular location, both positively (via dispersal-mediated recovery) and negatively (via threat transport).

Because most management happens at regional or local scales, finer-scale threat assessment will probably be most relevant to managers, and caution should therefore be used when applying specific impact scores and threat ranks from our global survey to regional management. Nevertheless, for threats and ecosystems that are present in a region, our global results provide reasonable estimates of the relative importance of threats. Future regional assessments could be directly compared with our global results.

Error in the results may stem from small survey sample sizes in some ecosystems or potential survey biases toward academic scientists. For example, experts from different backgrounds (e.g., academic and agency) may have different perceptions of how threats affect ecosystems, a possibility we are testing elsewhere (B.S.H., unpublished data). Variance among responses was fairly high, even for ecosystems with large survey sample sizes, a result we attribute to four sources. First, valid differences in perspectives and knowledge base exist. Second, regional differences in ecosystem response to threats most likely created differences in expert responses, although within-ecosystem sample size was too small to test for such differences. Third, paucity of data on some threat-ecosystem combinations forced experts to rely on intuition. Finally, despite efforts to carefully explain each concept, misinterpretation of instructions may have led to respondent error. Misinterpretation may be minimized through the use of one-on-one interviews in which the interviewer can explain terms and concepts in a consistent way, take notes on the reasoning and evidence behind responses, and proofread entries. Nevertheless, a survey similar to ours conducted through interviews had the same mean standard deviation (1.1) as our survey (K.A.S., unpublished data), which indicates that respondent error was not necessarily larger in our Web-based survey relative to the interview method.

The surprisingly large inconsistency between the lists of top three threats derived from the survey versus the volunteered responses, both across all respondents and for each individual expert, emphasizes the need for conducting quantitative and transparent threat analyses. Experts may have a feeling about which threats are most serious, but when asked to consider each possible threat systematically based on a suite of factors, a different picture may emerge. Our approach allows one to examine why and where these discrepancies emerge.

Our survey method is not an exercise in management or conservation priority setting because different groups have different goals (e.g., protect most threatened vs. most pristine area). The strength of the approach is that it can be used in almost any management or conservation priority-setting effort tasked with identifying key threats or priority ecosystems. Our ecosystem perspective, however, may not be the most appropriate if species are the focus of management. Results from species-based approaches (Wilcove et al. 1998; Kappel 2005) show that habitat degradation, pollution, invasive species, and overharvest (for marine species) are the greatest threats. This difference is not surprising because loss of habitat, increased mortality rates, and increased competition (from non-natives) should have greater impacts on populations than on entire ecosystems.

Our results also provide important guidance on where the greatest information gaps and research needs exist. The threats and ecosystems with lowest certainty scores are in clear need of more research. Illegal, unregulated, and unreported (IUU) fishing, disease, and decreases in sediment input had the lowest average certainty scores, whereas direct human impact, coastal engineering and development, and recreational and destructive commercial fishing had the greatest certainty scores. Not surprisingly, understudied soft-bottom ecosystems generally had the lowest certainty scores, but it was surprising that kelp forests also had among the lowest certainty scores. This result may indicate that even for relatively well-studied ecosystems, field studies have concentrated on a small subset of possible threats, with large uncertainties remaining for many others. In particular, threats with high impacts (e.g., point and nonpoint inorganic pollution and acidification due to climate change) and heavily affected ecosystems (pelagic surface water, soft shelf, and mangroves) that have low certainty scores need more research effort.

Several threats that have received broad attention for being particularly bad for many marine ecosystems did not emerge as the greatest threats in our results. Most notably, species invasions are commonly cited as a major threat to particular ecosystems (e.g., Mack et al. 2000), yet they were ranked 14th in our study. Artisanal fishing ranked 30th and 33rd (nondestructive and destructive, respectively) even though it has a significant impact in

a variety of ecosystems (e.g., Ruttenberg 2001; Hawkins & Roberts 2004). These differences suggest a need for further work to refine our understanding of these threats or potentially that people's impressions of these threats differ from their actual relative impact on ecosystems.

There are multiple ways our threat analysis method and results could be useful to managers and conservation organizations. First, ranking diverse threats and ecosystems in a comparable way can help organizations prioritize how to spend limited time and money. This is particularly true for organizations working on a global scale and interested in choosing focal areas and/or threat abatement strategies, with the caution that the global results are an average of responses from various regions with uneven representation in our survey. Regional organizations would be best served by adopting our method and redoing the ranking process for the region. Second, survey results allow for identification of the ecosystems that are most and least difficult to manage (e.g., with the highest or lowest number of threats). Conservation and management effort focused on the latter type of ecosystem (e.g., deep seamounts, beaches) may produce more substantial return on an investment because those efforts can target a few key threats, whereas efforts focused on the former type of ecosystem will likely require greater investment to produce similar results. Third, our inclusion of scale as a vulnerability measure provides a method for assessing the necessary spatial scale at which management needs to act. It is encouraging that most threats act at fairly small spatial scales, although the sources of some of these localized threats can be large (e.g., a large watershed that drains into a small estuary) and their overall spatial distribution may be extensive.

Fourth, recovery time estimates can be used to set expectations for approximate response time of ecosystems to management activities. Average recovery time from nearly all of the threats we surveyed was <1 year, which if accurate suggests that if threats are effectively mitigated, most ecosystems will respond relatively quickly. Of course, exact recovery times depend on threat type, magnitude, and extent and local and regional biological and oceanographic conditions. There are clearly some threats—such as those with ecosystem-scale impacts—that will have longer recovery times than a year. In addition, recovery times were estimated by respondents for single threats, but ecosystems face multiple, potentially interacting threats, which will likely lead to more complicated, slower trajectories of recovery in the real world. Finally, functional impact vulnerability scores can help discriminate instances where single-species approaches are sufficient from those where threats need to be addressed at the level of species assemblages or whole ecosystems. The generally high levels of functional impact support the recent focus on ecosystem-based management, indicating that such holistic approaches are needed to address threats across a majority of marine ecosystem types.

The future will inevitably usher in new types of threats and allow access to new empirical data or additional expert opinion. Because this method for evaluating how threats affect marine ecosystems is transparent and replicable, this survey mechanism can be easily and quickly updated to include new sources of information and refine the results from this analysis. Our results provide global guidance on how and where to act now, although local and regional management plans could develop more exact and tailored strategies if this method were repeated for the specific areas. Our aim is for resource managers to use these results to help prioritize threat mitigation and abatement efforts that will prove most productive in meeting their particular goals.

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Supplementary Material

Pairwise comparison results from analyses of variance of threats across ecosystem type (Appendix S1) and of ecosystems across threats (Appendix S2) are available as part of the on-line article from <http://www.blackwell-synergy.com/>. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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