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A Global Map of Human Impact on Marine Ecosystems

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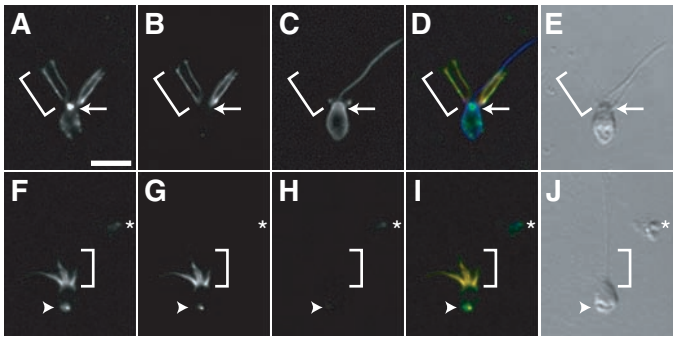

Fig. 2. Subcellular localization of MBCDH1 and MBCDH2 (**A** and **F**), compared with polymerized actin stained with rhodamine-phalloidin (**B** and **G**), or antibodies against β-tubulin (**C** and **H**). Cells were exposed to antibodies against MBCDH1 after (A to E) or before (F to J) permeabilization. Overlay of MBCDH1 and MBCDH2 (green), actin (red), and β-tubulin (blue) reveals colocalization of MBCDH1 and MBCDH2 with actin (yellow) on the collar and at the basal pole (**D** and **I**). Differential interference contrast microscopy shows cell morphology (**E** and **J**). Brackets, collar of microvilli; arrow, apical organelle; arrowhead, basal pole; asterisk, cluster of autofluorescent bacterial detritus.

MBCDH1 and MBCDH2 lack the CCD and the *M. brevicollis* genome lacks a β-catenin ortholog.

Metazoan E-cadherins and flamingo cadherins are bound by pathogenic bacteria which exploit them as extracellular tethers during host cell invasion (*31–33*). It is possible that choanoflagellate cadherins fill an equivalent role in binding bacterial prey for recognition or capture, functions consistent with the enrichment of MBCDH1 and MBCDH2 on the feeding collar (Fig. 2). If ancient cadherins bound bacteria in the unicellular progenitor of choanoflagellates and metazoans, cadherin-mediated cell adhesion in metazoans may reflect the co-option of a class of proteins whose earliest function was to interpret and respond to cues from the extracellular milieu. Indeed, the transition to multicellularity likely rested on the co-option of diverse transmembrane and secreted proteins to new functions in intercellular signaling and adhesion.

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A Global Map of Human Impact on Marine Ecosystems

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The management and conservation of the world's oceans require synthesis of spatial data on the distribution and intensity of human activities and the overlap of their impacts on marine ecosystems. We developed an ecosystem-specific, multiscale spatial model to synthesize 17 global data sets of anthropogenic drivers of ecological change for 20 marine ecosystems. Our analysis indicates that no area is unaffected by human influence and that a large fraction (41%) is strongly affected by multiple drivers. However, large areas of relatively little human impact remain, particularly near the poles. The analytical process and resulting maps provide flexible tools for regional and global efforts to allocate conservation resources; to implement ecosystem-based management; and to inform marine spatial planning, education, and basic research.

Humans depend on ocean ecosystems for important and valuable goods and services, but human use has also altered the oceans through direct and indirect means (*1–5*). Land-based activities affect the runoff of pollutants and nutrients into coastal waters (*6*, *7*) and remove, alter, or destroy natural habitat. Ocean-based activities extract resources, add pollution, and change species composition (*8*). These human activities vary in their intensity of impact on the ecological condition of communities (*9*) and in their spatial distribution across the seascape. Understanding and quantifying, i.e., mapping, the spatial distribution of human impacts is needed for the evaluation of tradeoffs (or compatibility) between human uses of the oceans and protection of ecosystems and the services they provide (*1*, *2*, *10*). Such mapping will help improve and rationalize spatial management of human activities (*11*).

Determining the ecological impact of human activities on the oceans requires a method for translating human activities into ecosystem-specific impacts and spatial data for the activities and ecosystems. Past efforts to map human impacts on terrestrial ecosystems (*12*), coral reefs (*13*), and coastal regions (*14–16*) used either coarse categorical or ad hoc methods to translate human activities into impacts. We developed a standardized, quantitative method, on the basis of expert judgment, to estimate ecosystem-specific differences in impact of 17 anthropogenic drivers of ecological change (table S1) (*9*). The results provided impact weights (table S2) used to

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combine multiple drivers into a single comparable estimate of cumulative human impact on 20 ecosystem types (*17*). We focused on the current estimated impact of humans on marine ecosystems (within the last decade), as past impacts and future scenarios of human impacts are less tractable, though also important (*17*).

Predicted cumulative impact scores (I_C) were calculated for each 1 km^2 cell of ocean as follows: $I_C = \sum_{i=1}^{n} \sum_{j=1}^{m} D_i * E_j * \mu_{i,j}$ where D_i is the log-transformed and normalized value [scaled between 0 and 1 (*17*)] of an anthropogenic driver at location i, E_j is the presence or absence of ecosystem j (either 1 or 0, respectively), and $\mu_{i,j}$ is the impact weight for the anthropogenic driver i and ecosystem j [range 0 to 4 (table S2)], given $n = 17$ drivers and $m = 20$ ecosystems (fig. S1). We modeled the distribution of several intertidal and shallow coastal ecosystems lacking global data (*17*). Weighting anthropogenic drivers by their estimated ecological impact in this way resulted in a different picture of ocean condition compared with simply mapping the footprints of human activities or drivers (fig. S1). Summing across ecosystems allows cells with multiple ecosystems to have higher potential scores than areas with fewer ecosystems; sensitivity analyses showed that summing or averaging across ecosystems within cells resulted in similar global pictures of human impacts on marine ecosystems (*17*). The global impact of a particular driver (I_D) is $I_D = \sum_{i=1}^{n} D_i * E_j * \mu_{i,j}$ and of all drivers on a particular ecosystem type (I_E) is $I_E = \sum_{j=1}^{m} D_i * E_j * \mu_{i,j}$. This method produced I_C scores ranging from 0.01 to 90.1. The I_C scores were significantly correlated with independent estimates of ecological condition in 16 mixed-ecosystem regions containing coral reefs (*17*, *18*). The linear equation relating the two scores [$R^2 = 0.63$, $P = 0.001$ (fig. S5)] was then used to divide I_C scores into six categories of human impact ranging from very low impact ($I_C < 1.4$) to very high impact ($I_C > 15.5$) (*17*).

Predicted human impact on the oceans shows strong spatial heterogeneity (Fig. 1) with a roughly bimodal distribution of per-cell I_C scores (Fig. 2), but with every square kilometer affected by some anthropogenic driver of ecological change. Over a third (41%) of the world's oceans have medium high to very high I_C scores [>8.5 (*17*)], with a small fraction (0.5%) but relatively large area (~2.2 million km^2) experiencing very high impact ($I_C > 15.5$). Most of the highest predicted cumulative impact is in areas of continental shelf and slope, which are subject to both land- and ocean-based anthropogenic drivers. Large areas of high predicted impact occur in the North and Norwegian seas, South and East China seas, Eastern Caribbean, North American eastern seaboard, Mediterranean, Persian Gulf, Bering Sea, and the waters around Sri Lanka (Fig. 1).

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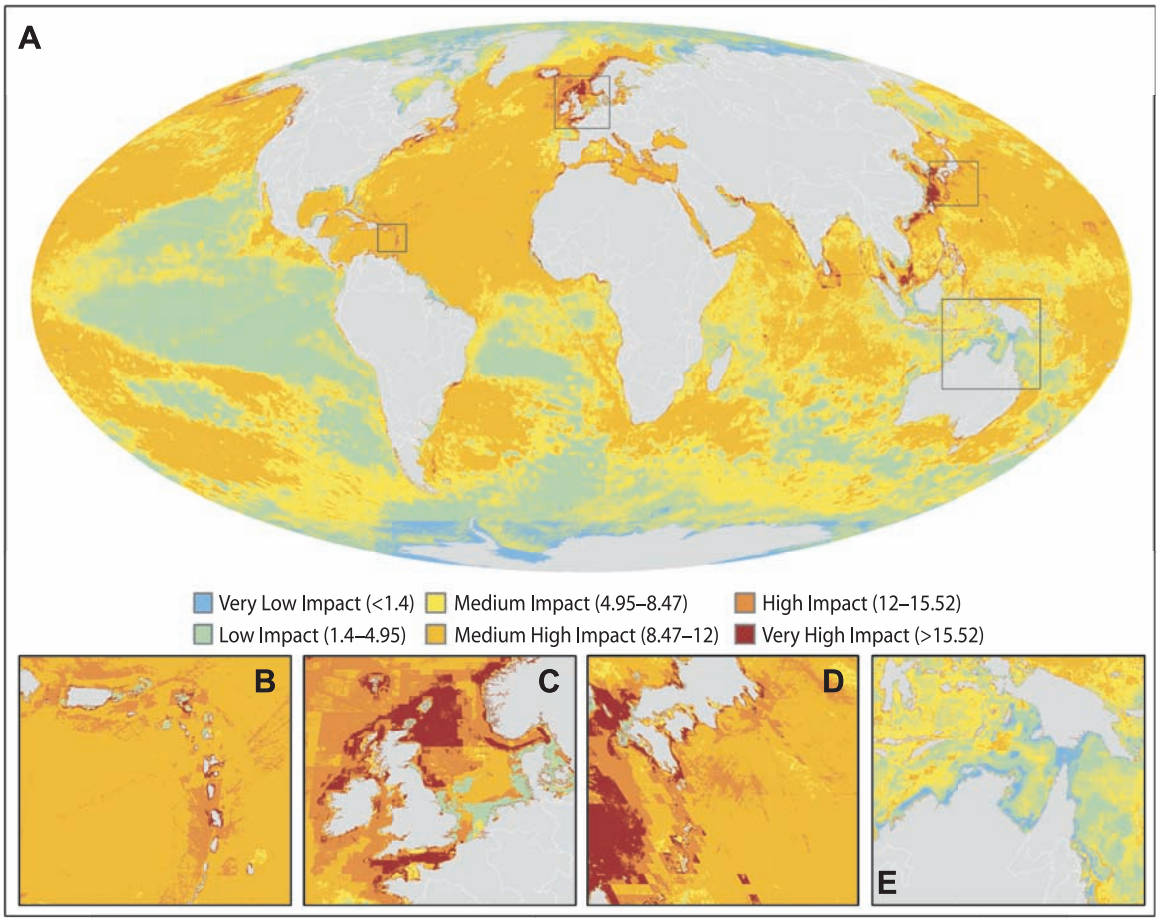

Fig. 1. Global map (**A**) of cumulative human impact across 20 ocean ecosystem types. (Insets) Highly impacted regions in the Eastern Caribbean (**B**), the North Sea (**C**), and the Japanese waters (**D**) and one of the least impacted regions, in northern Australia and the Torres Strait (**E**).

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Ecoregions, a classification of coastal (<200 m depth) areas based on species composition and biogeography (*19*), also showed variation in scores indicating differential risks to unique marine assemblages (table S3).

The majority of very low impact areas (3.7% of the oceans) occurs in the high-latitude Arctic and Antarctic poles (Fig. 1), in areas with seasonal or permanent ice that limits human access. However, our analyses did not account for illegal, unregulated, and unreported (IUU) fishing, which may be extensive in the Southern Ocean (*20*), or atmospheric pollution, which may be particularly high in the Arctic (*21*). Furthermore, projections of future polar ice loss (*22*) suggest that the impact on these regions will increase substantially. In general, small human population and coastal watershed size predict light human impact (Fig. 1E) but do not ensure it, as shipping, fishing, and climate change affect even remote locations—e.g., impact scores are relatively high in the international waters of the Patagonian shelf. In some places, predicted impact scores may be higher than anticipated because many anthropogenic drivers are not readily observable. Conversely, impact scores may seem unexpectedly low in other locations because a more abundant but less-sensitive ecosystem (e.g., soft sediment) surrounds a sensitive, but rare, ecosystem (e.g., coral reefs).

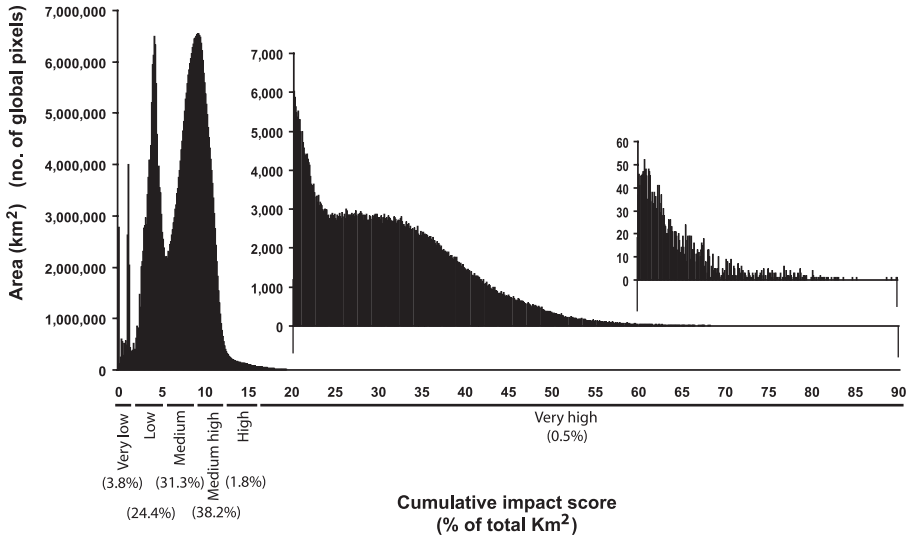

Fig. 2. Histogram of cumulative impact scores depicting the fraction of global area that falls within each impact category. There are no zeros; histogram bars are in bins of 0.1. Categories described in (*17*). (Insets) Expanded views of the tail of values.

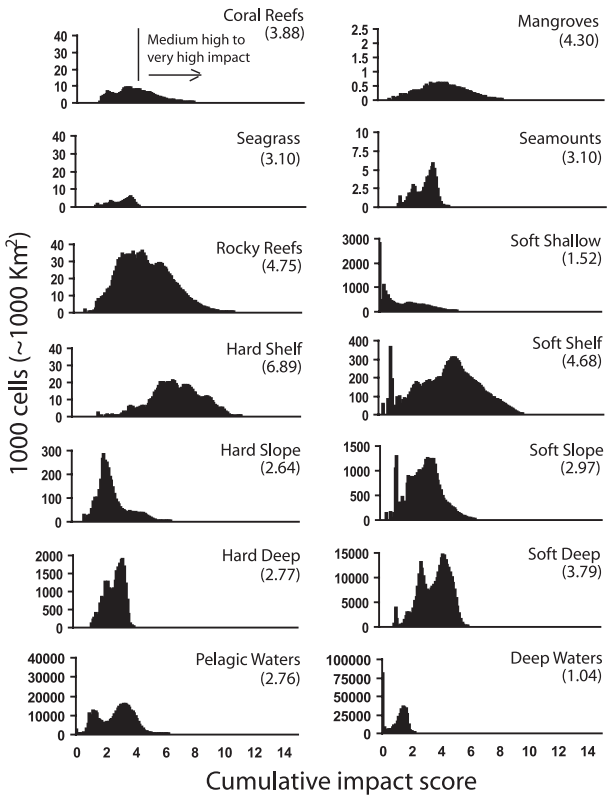

Fig. 3. The distribution of cumulative impact scores for each ecosystem in our analyses (means in parentheses). Individual ecosystem scores have a smaller range of values than cumulative impact scores (Fig. 2) because the latter sum all ecosystem-specific scores within a cell. Ground-truthed estimates of coral reef condition (*17*) were used to identify I_E values at which coral reefs experience medium high to very high impact, as indicated on the coral reef histogram. Note differences in *y*-axis scales.

Ecosystems with the highest predicted cumulative impact scores include hard and soft continental shelves and rocky reefs (Fig. 3). Coral reefs, seagrass beds, mangroves, rocky reefs and shelves, and seamounts have few to no areas remaining anywhere in the world with $I_C < 1.5$ (Fig. 3). Indeed, our data suggest that almost half of all coral reefs experience medium high to very high impact (*13*, *17*, *23*). Shallow soft-bottom and pelagic deep-water ecosystems had the lowest scores (>50% of these ecosystems have $I_C < 1.1$ and 1.2, respectively), partly because of the lower vulnerability of these ecosystems to most anthropogenic drivers (table S2). Overall, these results highlight the greater cumulative impact of human activities on coastal ecosystems.

Perhaps not surprisingly, anthropogenic drivers associated with global climate change are distributed widely (Fig. 4A) and are an important component of global cumulative impact scores, particularly for offshore ecosystems. Other drivers, in particular commercial fishing, are also globally widespread but have smaller cumulative impacts because of their uneven distribution. Land-based anthropogenic drivers have relatively small spatial extents and predicted cumulative impacts (Fig. 4A), but their cumulative impact scores approach those of other more widespread drivers within coastal areas where they occur (Fig. 4B). The spatial distribution of land-based impacts is highly heterogeneous but positively spatially correlated. Therefore, management of coastal waters must contend with multiple drivers in concert. Coordination with regulating agencies for urban and agricultural runoff is warranted, although such efforts can be challenging when watersheds cross jurisdictional boundaries. Where anthropogenic drivers tend to be spatially distinct (uncorrelated), as with commercial shipping versus pelagic high-bycatch fishing, management will require independent regulation and conservation tools. Assessing positive and negative spatial correlations among drivers can help anticipate potential interactions (*24*) and provides guidance in adjusting spatial management accordingly.

Our approach may be used to identify regions where better management of human activities could achieve a higher return-on-investment, e.g., by reducing or eliminating anthropogenic drivers with high impact scores (fig. S2). It may also be used to assess whether or how human activities can be spatially managed to reduce their negative impacts on ecosystems. For example, fishing zones have been shifted to decrease impacts on sensitive ecosystems (*25*), and navigation lanes have been rerouted to protect sensitive areas of the ocean (*26*). Wide-ranging fish stocks

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and those that occur primarily in international waters present challenges in determining who must take responsibility for management. If ecosystem-specific weighting values ($\mu_{i,j}$) are excluded, we can also evaluate the distribution, or footprint, of summed anthropogenic drivers of ecosystem change. This global footprint of drivers correlates with the distribution of cumulative impact scores (R^2 = 0.83), but ignores the important small-scale spatial patterns that emerge when accounting for ecosystem vulnerability (fig. S1) (*17*).

Our results represent the current best estimate of the spatial variation in anthropogenic impacts. Although these estimates are conservative and incomplete for most of the ocean, they potentially inflate human impacts on coastal areas because we used an additive model (*17*). Averaging impacts across ecosystems produced highly correlated results, very similar to those from the additive model (*17*), which suggests such inflation is limited, if it exists. Furthermore, the large extent of the ocean that our model predicts to be negatively affected by human activities will likely increase once additional drivers, their historical effects, and possible synergisms are incorporated into the model. Key activities with significant impacts on marine ecosystems but without global data include recreational fishing (*27*), aquaculture (*28*, *29*), disease (*30*), coastal engineering (habitat alteration), and point-source pollution (*31*). Most of these activities primarily affect intertidal and nearshore ecosystems rather than offshore ecosystems, which suggests that our estimates for nearshore areas are particularly conservative. In addition, the spatial data for many anthropogenic drivers were derived from valid but inexact modeling approaches (*17*). Ecosystem data were highly variable in quality, both within and among ecosystem types, and in many cases, we may have underestimated the full extent of these ecosystems and, therefore, the cumulative impact scores. Furthermore, many changes occurred in the past with lasting negative effects, but the drivers no longer occur at a particular location, e.g., historical overfishing (*4*) or past coastal habitat destruction (*32*). Although we used a conservative, additive model, some drivers may have synergistic effects (*24*). Despite these limitations, this analysis provides a framework and baseline that can be built upon with future incorporation or refinement of data. It is noteworthy that the data gaps emphasize the need for research on the most basic information, such as distribution of habitat types and whether and how different anthropogenic drivers interact.

Humans depend heavily on goods and services from the oceans, and these needs will likely increase with a growing human population (*10*). Our approach provides a structured framework for quantifying the ecological tradeoffs associated with different human uses of marine ecosystems and for identifying locations and strategies to minimize ecological impact and maintain sustainable use. In some places, such strategies can benefit both humans and ecosystems, for example, using shellfish aquaculture both to provide food and to improve water quality. Our analytical framework can easily be applied to local- and regional-scale planning where better data are available and can be extended by incorporating other types of information, such as species distribution or diversity data (*33*–*35*) to identify hot spots with both high diversity and high cumulative human impacts that perhaps deserve conservation priority. A key next research step will be

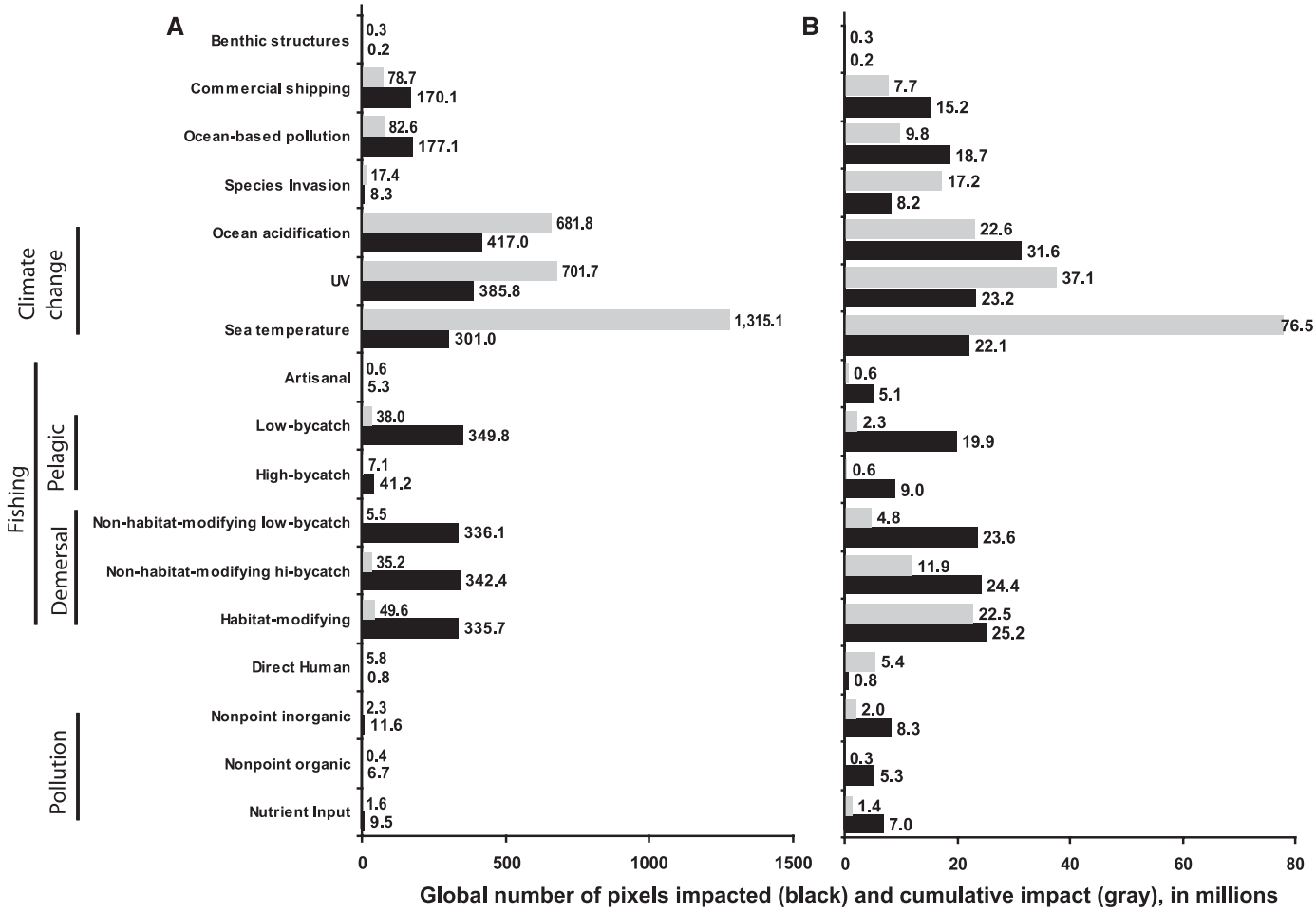

Fig. 4. Total area affected (square kilometers, gray bars) and summed threat scores (rescaled units, black bars) for each anthropogenic driver (**A**) globally and (**B**) for all coastal regions <200 m in depth. Values for each bar are reported in millions.

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to compile regional and global databases of empirical measurements of ecosystem condition to further validate the efficacy of our approach.

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Effects of Predator Hunting Mode on Grassland Ecosystem Function

Oswald J. Schmitz

The way predators control their prey populations is determined by the interplay between predator hunting mode and prey antipredator behavior. It is uncertain, however, how the effects of such interplay control ecosystem function. A 3-year experiment in grassland mesocosms revealed that actively hunting spiders reduced plant species diversity and enhanced aboveground net primary production and nitrogen mineralization rate, whereas sit-and-wait ambush spiders had opposite effects. These effects arise from the different responses to the two different predators by their grasshopper prey—the dominant herbivore species that controls plant species composition and accordingly ecosystem functioning. Predator hunting mode is thus a key functional trait that can help to explain variation in the nature of top-down control of ecosystems.

Species are most likely to have strong effects on ecosystems when they alter factors that regulate key ecosystem functions such as production, decomposition, and nitrogen mineralization (*1*). These effects can be direct, as when selectively feeding herbivores alter plant community composition and hence alter the quality and quantity of plant material entering the soil organic matter pool to be decomposed and mineralized (*1–6*); or indirect, as when predators alter the way in which herbivores affect plant community composition (*7–10*). The exact nature of a species' effect will, however, depend on traits that determine the way it functions (*1*, *11*). Explaining such trait dependency is an important hurdle to overcome in developing predictive theories of species effects on ecosystem function (*1*). This endeavor is currently hampered by a limited understanding of what kinds of species' traits control functioning (*11–15*).

Here I report on a 3-year experiment quantifying the effect of one important functional trait of top predator species—their hunting mode—on the nature of indirect effects emerging at the ecosystem level (Fig. 1). Predators can propagate indirect effects down trophic chains in at least two ways (*16*). They can alter the numerical abundance of herbivore prey by capturing and consuming them. Alternatively, their mere presence in a system can trigger herbivore prey to modify foraging activity in a manner that reduces predation risk. A general rule, derived from empirical synthesis, is that these different kinds of effect are related to predator hunting mode, irrespective of taxonomic identity (*17*). Sit-and-wait ambush predators cause largely behavioral responses in their prey because prey species respond strongly to persistent point-source cues of predator presence. Widely roaming, actively hunting predators may reduce prey density, but they produce highly variable predation risk cues and are thus unlikely to cause chronic behavioral responses in their prey. These hunting mode–dependent herbivore responses should lead to different cascading effects on the composition and abundance of plant species within ecosystems (*9*, *18*) that should further cascade to affect ecosystem function (*10*). Predator effects do indeed cascade to influence ecosystem functions, and they vary with predator species (*10*, *19–22*). But the basis for variation in predator species effects remains unresolved.

This study was carried out in a grassland ecosystem in northeastern Connecticut. The important plant species in this ecosystem (determined by their interaction strengths) may be effectively represented within three functional groups of plants: (i) the grass *Poa pratensis*, (ii) the competitively dominant herb *Solidago rugosa*, and (iii) a variety of other herb species, including *Trifolium repens*, *Potentilla simplex*, *Rudbekia hirta*, *Crysanthemum leucanthemum*, and *Daucus carota*. The important animal species are the generalist grasshopper herbivore *Melanopuls femurrubrum* and the spider predators *Pisaurina mira* and *Phidippus rimator* (*23*). *Pisaurina mira* is a sit-and-wait predator in the upper canopy of the meadow.

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