Science Advances

AUGUST 2018

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SPECIAL COLLECTION: Science of the High Seas

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Today, researchers, enterprise owners, and policy makers are working together in haste to understand and manage human influence on the living and mineral resources of the high seas. This effort is a formable challenge. The oceans represent one-and-a-half times the total land area on the planet and their dynamics play critical—yet poorly understood—roles in regulating climate and biogeochemical cycles, supporting biodiversity, and providing rare habitats to rare species. At the same time, development of ocean resources is moving forward at breakneck pace, putting the sustainable health of the high seas at risk.

This Special Collection of open access articles, curated by *Science Advances* Deputy Editor Dr. Jeremy Jackson & Associate Editor Dr. Jennifer Jacquet, has been compiled in the hope that the research presented can be used to better understand ecological, geological and other systems underlying the functional health of global oceans, and inform those concerned with the exploration and use of living and mineral resources found in the high seas.

The data and analyses in this collection highlight the challenges in balancing the long-term imperatives of preserving global ocean resources with shorter-term economic and political interests that seek to quickly and vigorously draw value from them. The eight papers in the collection range from a study of the ownership of marine genetic resources, to work exploring effective management of deep sea mineral mining, to studies investigating the impacts of expanding large-scale fishing in international waters, including how catch is transported and where it is consumed.

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ENVIRONMENTAL STUDIES

High stakes on the high seas

Today, "the high seas" are generally understood to refer to the vast expanses of open oceans that are not under the formal jurisdiction of any nation. Legally, the high seas are defined as the 60% expanse of the oceans that lie beyond national exclusive economic zones, which are within 200 nautical miles (370 km) of coastlines. Despite legal definitions, however, the expanses of the high seas are neither well-defined nor well-understood from ecological or geological perspectives. The surface area of these waters is one-and-a-half times the total land area on the planet and the dynamics in their depths play critical roles in regulating climate and biogeochemical cycles, supporting incalculable biodiversity and providing rare habitat to some of the most charismatic species on Earth. Like the continent of Antarctica and the canopy of the Amazon, the high seas are places that few will experience but remain sources of wonder and imagination for people of all nations and cultures.

Today, the sustainable health of the high seas is at risk. Industrial activities are already draining the oceans of their natural capital including valuable minerals, new genetic resources, and wild animals. This set of research articles on the science of the high seas has been compiled to underscore some of the major challenges and risks that nations face as ocean exploitation accelerates. Each study explores a particular facet of human influence on the high seas and highlights economic interests in bioprospecting, mining, and fishing. We hope that these can serve to inform researchers and policy makers concerned with sustainable management and international governance of the high seas.

A major concern regarding sustainable use of ocean resources includes how to equitably share benefits derived from marine genetic resources. Blasiak *et al.* (2018) set the stage by looking at the institutional actors that have been acquiring patents on marine genetic resources over the last 30 years, finding that only 30 institutions hold a full 84% of all patents related to marine species, and a single transnational corporation holds almost half of all patent sequences. A little more than 10% of patent sequences are derived from 91 species associated with deep-sea and hydrothermal vents, many of which are found on the high seas—although there is rarely disclosure about where the species were collected.

Another concern about the sustainable use of ocean resources is the increased mining of mineral deposits on mid-ocean ridges, all of which fall beyond any national jurisdiction. Dunn *et al.* (2018) propose a series of metrics that could be used when planning for mining, including a discussion of the value of no-mining areas. They apply their criteria to a case study of the northern and equatorial Mid-Atlantic Ridge, where contractors are already exploring for sulfides. They underscore the need to set aside large areas to protect deep-sea populations, to create conservation corridors for genetic exchange, and to close areas around all active hydrothermal vents to protect the very rare and precious life forms there.

While high seas mining is early in expansion, intensive fishing operations are already well-established on the high seas, in part due to the overfishing in nearshore waters. Tickler *et al.* (2018) use reconstructed catch data to present a historical view of the expansion of fishing offshore starting in 1950. They found that China, Taiwan, Japan, South Korea, and Spain are the most active fishing nations on the high seas. Using newly available satellite data, McCauley *et al.* (2018) found that boats flagged to the same five countries represent the greatest fishing effort on the high seas and these five countries are also among the top countries fishing in the nearshore waters of other countries. Although these new data do not represent all boats on the high seas, they do provide the best view of global, spatial view of fishing activities around the planet.

Three additional studies use satellite data to suss out other views of the impacts of fishing on the high seas. Sala *et al.* (2018), for example, used several large-scale data sets to build a global economic model of high seas fishing costs and revenues and found that without government subsidies more than half of high seas fisheries would be unprofitable. Work on the economics of high seas fisheries is relevant not only to sustainability researchers but also to policy makers at international institutions including the United Nations and the World Trade Organization, where there is talk of decreasing or banning fishing subsidies. Crespo *et al.* (2018) used satellite data to develop a model to detect patterns and potential locations of longline fishing. They showed that this model can be used to predict fishing effort and potential bycatch, as well as indicate where to place additional monitoring and enforcement resources. Boerder *et al.* (2018) also used satellite data to monitor transshipment-at-sea, which is when fishing boats offload their catch, restock, and resume fishing without returning to port. At present, transshipment is a common practice that allows fishing boats to evade monitoring and enforcement and facilitates both illegal fishing and related human rights abuses. In response, many Regional Fisheries Management Organizations (RFMOs) have taken steps to regulate transshipment, and one RFMO, the South East Atlantic Fisheries Organization (SEAFO), has banned transshipment altogether. Despite these efforts, Boerder and her colleagues found more than 100 probable transshipments between 2012 and 2017 in the SEAFO area, demonstrating that satellite data will be essential for detecting violations.

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This collection also includes work by Schiller *et al*. (2018), who used catch and trade data to examine the contribution of high seas fisheries to global food security. They found that total catch from the high seas accounts for only 4% of annual marine capture fisheries by volume and consists of species primarily destined for luxury markets in Japan, the European Union, and the United States. There is only one species, Antarctic toothfish, caught exclusively on the high seas while the remaining 38 fish and invertebrate species, which represent almost the entire high seas catch, are captured in both national and high seas waters. Policy makers may find these data useful in debating the merits of creating no-fishing areas on the high seas and the possible implications of such action on global food security.

These studies, along with many others, provide concrete evidence that, at present institutions or governments, do not have adequate tools to keep pace with those who work to overexploit the high seas. The data and analyses in this collection highlight the challenges in balancing the long-term imperatives of preserving the ocean's vast resources with shorter-term economic and political interests that seek to quickly and vigorously profit from the oceans. The high seas, like everything on Earth, are a limited resource. How we choose to protect and use its precious resources will test our humanity, our cooperation, and our collective vision for the future.

– Jennifer Jacquet and Jeremy B. C. Jackson

10.1126/sciadv.aau8235

Citation: J. Jacquet, J. B. C. Jackson, High stakes on the high seas. *Sci. Adv*. **4**, eaau8235 (2018).

ENVIRONMENTAL STUDIES

Corporate control and global governance of marine genetic resources

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Who owns ocean biodiversity? This is an increasingly relevant question, given the legal uncertainties associated with the use of genetic resources from areas beyond national jurisdiction, which cover half of the Earth's surface. We accessed 38 million records of genetic sequences associated with patents and created a database of 12,998 sequences extracted from 862 marine species. We identified >1600 sequences from 91 species associated with deep-sea and hydrothermal vent systems, reflecting commercial interest in organisms from remote ocean areas, as well as a capacity to collect and use the genes of such species. A single corporation registered 47% of all marine sequences included in gene patents, exceeding the combined share of 220 other companies (37%). Universities and their commercialization partners registered 12%. Actors located or headquartered in 10 countries registered 98% of all patent sequences, and 165 countries were unrepresented. Our findings highlight the importance of inclusive participation by all states in international negotiations and the urgency of clarifying the legal regime around access and benefit sharing of marine genetic resources. We identify a need for greater transparency regarding species provenance, transfer of patent ownership, and activities of corporations with a disproportionate influence over the patenting of marine biodiversity. We suggest that identifying these key actors is a critical step toward encouraging innovation, fostering greater equity, and promoting better ocean stewardship.

INTRODUCTION

The prospect of the ocean generating a new era of "blue growth" is increasingly finding its way into national and international policy documents around the world and has spurred a rush to claim ocean space and resources (*1*, *2*). If economic activities in coastal and offshore areas are to expand in an equitable and sustainable manner, in line with the Sustainable Development Goals (SDGs), progress is needed toward addressing multiple and potentially conflicting uses of ocean space within national jurisdictions, in addition to developing a consistent and transparent legal framework for the vast areas beyond national jurisdiction (ABNJ) (*3*, *4*). These areas cover 64% of the world's ocean and 47% of the Earth's surface yet remain poorly understood or described (*5*).

Marine organisms have evolved to thrive in the extremes of pressure, temperature, chemistry, and darkness found in the ocean, resulting in unique adaptations that make them the object of commercial interest, particularly for biomedical and industrial applications (*6*–*8*). By 2025, the global market for marine biotechnology is projected to reach $6.4 billion, spanning a broad range of commercial purposes for the pharmaceutical, biofuel, and chemical industries (*9*, *10*). One way to ensure exclusive access to these potential economic benefits is through patents associated with "marine genetic resources" (MGRs). Although the term MGRs has never been formally described (*10*), it suggests a subset of "genetic resources," which have been defined under the Convention on Biological Diversity (CBD) as "genetic material of actual or potential value" (*11*). The registration of patent claims involving MGRs constitutes an opaque and rapidly evolving frontier where the worlds of science, policy, and industry meet (*12*). The adoption of the Nagoya Protocol in 2010 represented an important step within the international policy arena to define obligations associated with monetary and nonmonetary benefit sharing of genetic resources and their products sourced from within national jurisdictions (*13*). No such mechanism currently exists for ABNJ.

Transnational corporations have a unique ability to capitalize on and monopolize markets characterized by global scope and complexity. The recent identification of "keystone actors" in the seafood industry, for instance, illustrates how a handful of transnational corporations and their subsidiaries have a disproportionate influence on production volumes and revenues, as well as on governance processes and institutions (*14*). The global scope of the marine biotechnology sector and its expanding size seem conducive to the emergence of a similar pattern of dominance by a small number of transnational corporations. Their substantial financial resources enable them to develop commercial applications despite uncertain timelines and returns on investment while also facilitating the acquisition or collection of samples (for example, chartering vessels for a week-long sampling cruise of deep-water corals was estimated in 2013 at $455,000) (*15*). Past research has focused on countries where patents have been registered (*16*) rather than the individual actors registering them. Identifying the entities in control of MGRs, however, is of crucial importance, given the rapidly evolving legal and political landscapes associated with marine biodiversity.

Here, we investigate how many and what types of marine species are being included in patent claims, by whom, and when. We suggest that identifying the key actors registering patents involving MGRs is a critical step toward ensuring more equitable ocean stewardship, whether through regulation, voluntary industry action, or other mechanisms. These findings are discussed in relation to global governance of MGRs, in particular in light of the Nagoya Protocol and the ongoing international negotiations on the conservation and sustainable use of biodiversity in areas beyond national jurisdiction (BBNJ).

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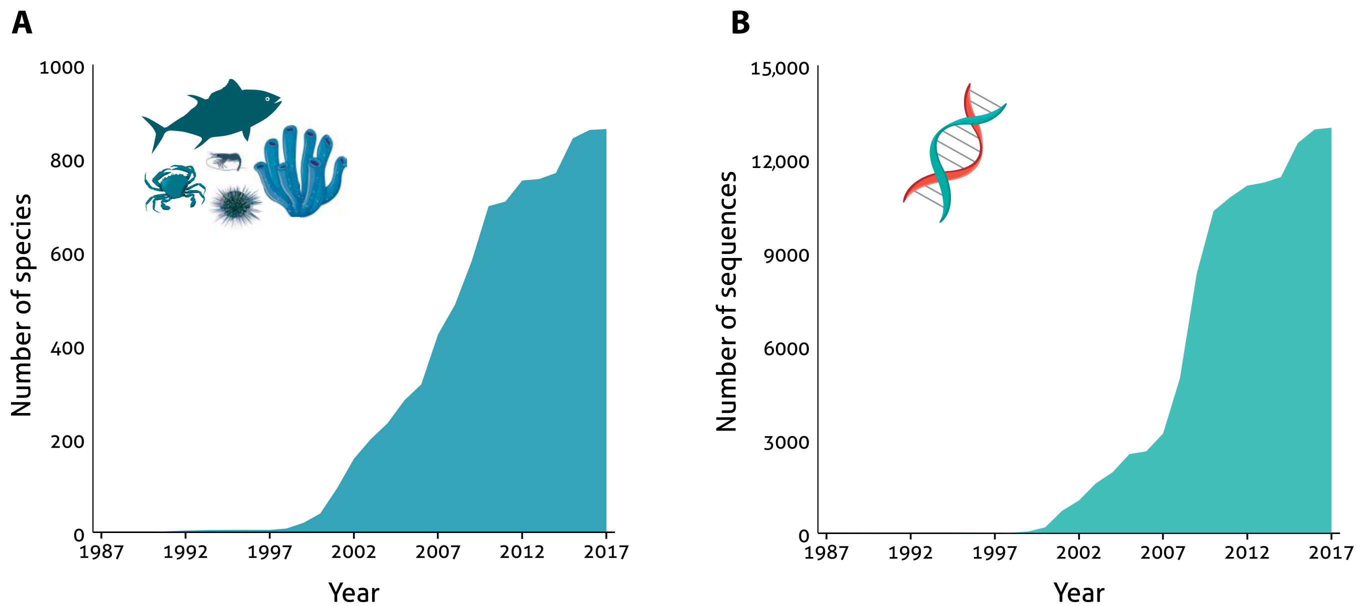

Fig. 1. Growing commercial interest in MGRs. Cumulative number over time (1988–2017) of (A) marine species with patent sequences and (B) patent sequences from marine species.

RESULTS

We identified 862 marine species, with a total of 12,998 genetic sequences (see the Supplementary Materials) associated to patents with international protection filed under the Patent Cooperation Treaty (see the Supplementary Materials), as of October 2017. The first such patent related to a marine species was traced to 1988, resulting in a database spanning 30 years. The vast majority of patents were registered in the last 15 years, in terms of both the number of marine species used as a source for gene patents (Fig. 1A) and the actual number of genetic sequences included in patent claims (Fig. 1B).

What is being patented?

Sequences from a wide range of species have been the focus of patents, extending from the sperm whale (*Physeter macrocephalus*) and giant oceanic manta ray (*Manta birostris*) to microscopic archaea and plankton (fig. S1). The majority of patents are associated with microbial species, which constitute 19% of named species in the World Register of Marine Species (WoRMS), yet account for more than 73% of all patent sequences in our database. Fish and mollusks represent 16 and 3%, respectively (fig. S1B). Other forms of ocean life have drawn less commercial interest. For instance, of the 3057 tunicate (sea squirt) species in WoRMS, only 6 have been the subject of patents (*5*). A considerable portion of all patent sequences (11%) are derived from species associated with deep-sea and hydrothermal vent ecosystems (91 species, 1650 sequences), many of which are found in ABNJ.

Who is registering the patents?

We found that 221 companies had registered 84% of all patents. Public and private universities accounted for another 12%, while entities such as governmental bodies, individuals, hospitals, and nonprofit research institutes registered the remaining 4% (Fig. 2). A single transnational corporation had registered 47% of all patent sequences: BASF, the world's largest chemical manufacturer, headquartered in Germany. With posted sales exceeding $79 billion in 2017 and a network of 633 subsidiaries and offices in 94 countries, BASF is a truly global actor. Not only did BASF register more patent sequences than the other 220 companies combined (37%), but it also exceeded the second and third companies by an order of magnitude: Japanese biotechnology firm Kyowa Hakko Kirin Co. Ltd. (5.3%) and U.S.-based biofuel company Butamax Advanced Biofuels LLC (3.4%) (fig. S2). More than half (56%) of all university patents were registered by the Yeda Research and Development Co. Ltd., the commercial arm of the Weizmann Institute of Science (Israel), exceeding the combined claims of the 77 other universities.

Entities located or headquartered in three countries registered more than 74% of all patents associated with MGR sequences: Germany (49%), United States (13%), and Japan (12%). This figure rises to more than 98% when one considers the top 10 countries (see the Supplementary Materials). In total, international patent claims have been made by entities in 30 countries and the European Union (EU), while the remaining 165 countries are unrepresented.

Trends over time

The annual record of published patents reveals a striking temporal pattern (Fig. 3). Following an extended period of negligible growth from 1988 to 1998, patent claims gradually increased to a plateau of roughly 500 patent sequences annually until 2006, before abruptly peaking in 2009 at 3354 claims and declining just as sharply to 367 in 2012. More than half of the sequences registered to date were included in claims during the period 2007–2010. This peak in activity appears to coincide with key stages in the negotiations and adoption of the Nagoya Protocol (Fig. 3).

DISCUSSION

Corporate control over MGRs

The dramatic asymmetries in patent registration resemble trends in resource use and industry dominance that have been observed in multiple sectors, where high levels of consolidation have resulted in

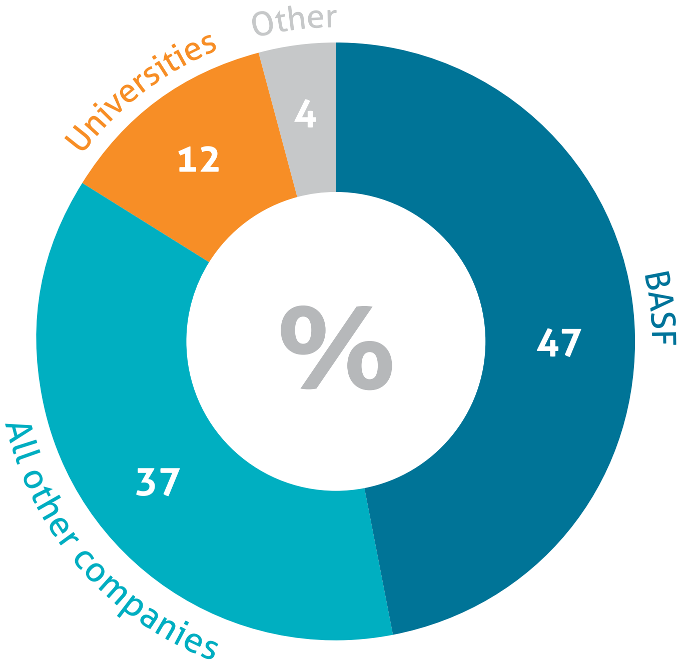

Fig. 2. Percentage of patents with international protection associated with MGRs that were registered over the period 1988–2017 by BASF, all other companies (*n* = 220), universities (*n* = 78), and other actors (*n* = 26; including governmental bodies, individuals, hospitals, and nonprofit research institutes).

the emergence of a handful of keystone actors (*14*, *17*). In the seeds industry, for instance, the so-called Big Six (BASF, Bayer, Dow, DuPont, Monsanto, and Syngenta) have dominated the sector for years (*18*). The merging of Dow and DuPont (in 2015) and current (2018) negotiations by Bayer to acquire Monsanto illustrate a pattern of further consolidation and have increased concerns about an emerging oligopoly characterized by reduced competition, forms of collusion, and inflated prices for consumers (*18*, *19*). Our findings show that the corporate landscape with regard to MGRs is already far more consolidated than the seeds industry, although this development has not drawn public attention or scrutiny. BASF is a keystone actor with 5701 MGR patent sequences (fig. S2), while the participation of the remaining Big Six companies is remarkably modest: DuPont (180), Bayer (34), Monsanto (17), Syngenta (4), and Dow (1). The existence of large transnational corporations with global networks of subsidiaries increases the complexity and difficulty of keeping track of patent contracts (*20*). Large corporations are known to acquire smaller companies for the primary purpose of claiming ownership of their patent portfolios (*21*) while also taking advantage of branches located in countries with weaker institutions and limited monitoring or enforcement capacity (*20*). The full extent of consolidation in ownership of patents related to MGRs will likely not be known until the disclosure of transfers in patent ownership becomes a legal obligation.

Many patents associated with MGRs have been registered by public and private universities, or by their commercialization centers. Existing for the primary purpose of monetizing university innovations and discoveries, commercialization centers operate as companies owned by the respective universities. A keystone pattern is evident here as well, with the Yeda Research and Development Co. Ltd. (the commercial arm of the Weizmann Institute of Science) exceeding the combined claims of all the other universities. Commercialization centers, particularly those associated with publicly funded universities, operate in an ethically ambiguous area, as they are under no legal obligation to disclose how they are monetizing these patents (for example, through transfer of ownership).

The Nagoya Protocol and its obligations

The prospect of the Nagoya Protocol and its obligations heralding a new set of international regulations governing access and benefit sharing appears to have spurred a rush to patent marine biodiversity (Fig. 3). Registering patents through the Patent Cooperation Treaty takes around 30 months from the date of application filing (*22*). In 2004, the seventh Conference of the Parties to the CBD defined the scope of an ad hoc open-ended working group "to elaborate and negotiate the nature, scope and elements of an international regime on access and benefit-sharing" (*23*). Negotiations started in February 2005. Patent registration had peaked by 2009 when a draft text emerged, and fell within 3 years by an order of magnitude. This trend is primarily driven by the activities of BASF and may or may not have been associated with the timing of the Nagoya Protocol. In an interview, a BASF contact suggested that this trend could be linked to patent applications on algae sequences for a research project on cultivating canola plants fortified with polyunsaturated omega-3 fatty acids and consequently unrelated to the Nagoya Protocol negotiations. Moreover, this contact suspected that while the Nagoya Protocol created an obvious regulatory burden, it would not have altered the scope or extent of BASF's patenting activities during this period. Its annual corporate and financial reports underscore a strategic focus on patents and innovation, which suggests continuity and long-term planning, with 2006 research and development investments already being tied to expectations of two- to fourfold returns in annual sales starting in 2015. Since 2004, BASF has continuously expanded its investments in research and development, reaching a new record of €1.9 billion in 2017 (*24*). BASF has also highlighted the fact within its annual reports that it has consistently occupied the top position on the Patent Asset Index since it was launched in 2009 to identify the comparative value of corporate patent portfolios (*24*, *25*).

The Nagoya Protocol's drafting and adoption were driven by an international interest in "levelling the playing field," and the agreement was never meant to stifle innovation. However, concerns have been raised that the lack of user guidance on how to adequately exercise the obligations of legislation to implement the Nagoya Protocol at the national level (*26*) and the consequences of failure to comply with these obligations may be indirectly restricting access to biological material for research purposes (*27*, *28*). Since 2012, patent claims have remained at comparable levels to those seen before the drafting of the Nagoya Protocol, suggesting a damper effect on innovation or a rush to register patents before signatories to the Nagoya Protocol established corresponding compliance mechanisms. The outcome has been a reduced pool of benefits to share, as the Nagoya Protocol does not apply retroactively.

The Nagoya Protocol, like all international agreements, represents a compromise among diverse interests. The African Group, for instance, lobbied unsuccessfully for retroactive application of benefit-sharing provisions and legally mandatory disclosure of the country of origin of the genetic resources. The final language associated with the latter issue references the Bonn Guidelines: "countries could consider, *inter alia*, the following: [...] measures to encourage the disclosure of the country of origin of the genetic resources" (*29*). The origin requirement specified within Article 4 of the EU implementing regulation (no. 511/2014) is currently a nonmandatory provision. Consequently,

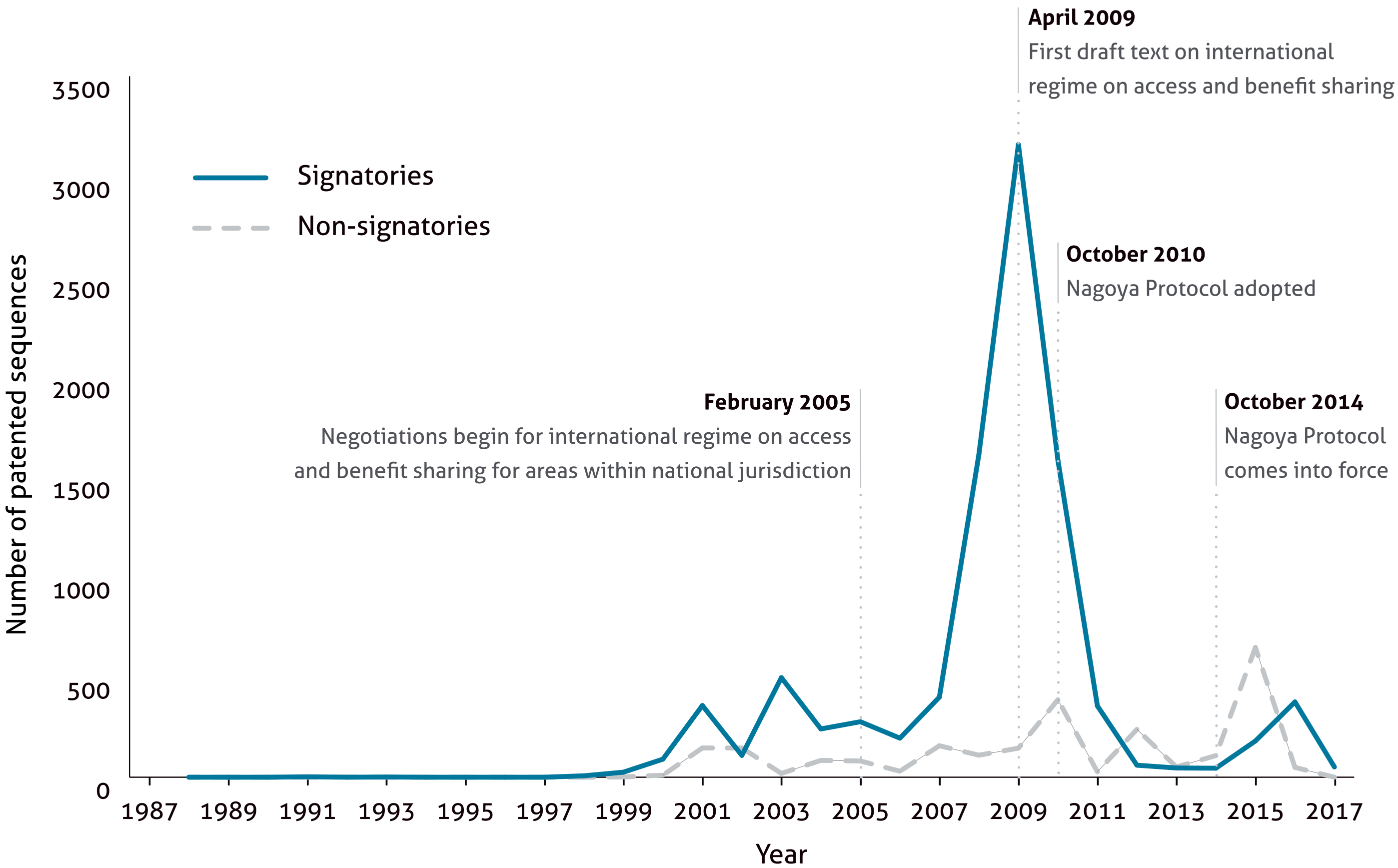

Fig. 3. Timeline of the number of marine genetic sequences associated with claims for international patent protection. Note that registering patents through the Patent Cooperation Treaty entails a roughly 3-year process from the date of filing. A distinction is made between contracting parties to the Nagoya Protocol (n = 20; solid blue line) and non-signatories (n = 10; dashed gray line). Key stages in the negotiations, adoption, and entry into force of the Nagoya Protocol are also included. The protocol remained opened for signature between February 2011 and February 2012 but mostly was not passed into law in national parliaments until 2015 (for example, EU, UK, and Germany).

close to 90% of patent applications do not provide such information—nondisclosure rates being the highest among private corporations (95%) (*30*). This opacity constitutes a serious hurdle to access and benefit sharing of MGRs from ABNJ and would render any potential future retroactive application of such mechanisms largely unfeasible (*16*). The extent to which organisms collected in ABNJ are the subject of gene patents will remain unclear until patent authorities require and verify the MGR origin or until voluntary disclosure becomes an industry norm.

Negotiations on biological diversity beyond areas of national jurisdiction

The nondisclosure of species provenance in patents associated with MGRs has implications for international governance. The United Nations Convention on the Law of the Sea (UNCLOS) distinguishes between two geographical zones in ABNJ: the water column (the High Seas) and the seabed, ocean floor, and subsoil thereof (the Area). An international legal regime exists to govern the exploitation and benefit sharing of mineral resources in the Area, which are considered the common heritage of mankind. While the Nagoya Protocol addresses access and benefit sharing for genetic resources within national waters (*31*), no such mechanism currently exists for MGRs in ABNJ (as of June 2018). Addressing this gap was the focus of one of four "package" issues addressed by a BBNJ Working Group (2006–2015) and Preparatory Committee (2016–2017) (*32*) and will be a key element of the BBNJ treaty negotiations set to start in September 2018. A challenge in these negotiations has been the insistence by some states that MGRs in the Area should, like mineral resources, fall under the common heritage of mankind principle, which would require that their exploitation be subject to some form of benefit sharing. Other states interpret the corresponding articles in UNCLOS to exclude biological resources, resulting in application of the principle of freedom of the High Seas, implying that no legal obligation exists to share the benefits of their exploitation (*10*, *33*).

Developing states have identified MGRs sourced from ABNJ as a top priority within the BBNJ negotiations (*34*). The lack of participation and continuity among delegations of developing countries, however—particularly small island developing states—hampers equitable engagement by these states (*34*). Coupled with a comparatively low level of legal and technical expertise with regard to MGRs, this situation has represented a serious obstacle to progress and has delayed the BBNJ negotiations (*35*). To ensure that the process moves forward in an inclusive manner, states need to increase their commitments to capacity building, including scientific training and collaboration, and make greater use of mechanisms like a voluntary fund that was established to support participation of delegates during the BBNJ Preparatory Committee (*36*). Likewise, greater focus on UNCLOS Part XIV on the development and transfer of marine technology could lay the foundations for more equitable participation by states in efforts to explore and exploit MGRs found in ABNJ (*37*). The findings of this paper, along with the creation of a publicly accessible database (see the Supplementary Materials), represent a practical tool for negotiators engaged in the BBNJ process.

Transformative capacity for ocean stewardship

The existence of keystone actors involved in the patenting of MGRs suggests not only the need to track corresponding lobbying efforts within the BBNJ process but also an opening for more direct engagement with corporations for ocean stewardship (*38*). As private entities, participation by major patent holders like BASF, Kyowa Hakko Kirin Co. Ltd., Butamax Advanced Biofuels LLC, and Yeda Research and Development Co. Ltd. has likely been limited to opaque intersessional engagement with national delegations or trade associations like the International Chamber of Commerce (*22*). Formal participation by major patent holders would render their influence more transparent, enable direct industry reaction to potential rule changes, help outline steps to realistically comply with obligations, and foster greater accountability. Such entities are likewise in a unique position to discuss the implications of various potential monetary and nonmonetary benefit-sharing mechanisms or the practical consequences of regulatory changes.

In addition to the BBNJ process, other mechanisms could also influence change in business standards and practice. Examples include informal governance mechanisms such as advocacy campaigns, changes in consumer and employee interest, engagement with the scientific community, and shareholder activism (*39*). BASF, for instance, is among the world's largest publicly owned companies (ranked 127 on the Fortune 500 list in 2017), with >500,000 individual shareholders, >100,000 employees, and private investors holding some 28% of the company's share capital (*40*). BASF is also participating in the World Business Council for Sustainable Development, is a member of the UN Global Compact, and follows the Global Reporting Initiative guidelines. These are just three of a growing landscape of "voluntary environmental programs," which bring together companies that voluntarily go beyond what is required by government regulation, for instance, with regard to transparency or accounting for externalities (*38*, *41*). There is a possibility that major patent holders would see open engagement with the BBNJ process as purely a risk or liability. Yet, such engagement could also help companies distinguish themselves through their proactive behavior and contribute to providing new norms and standards associated with transparency, capacity building, and benefit sharing (*41*).

Conclusion

Of the 30 countries involved in patenting MGRs, 27 are Parties to UNCLOS and have thereby committed to promoting the development and transfer of marine technology "for the benefit of all parties concerned on an equitable basis" (*42*). The promotion of equity is also deeply embedded within the language of the SDGs. BBNJ negotiations surrounding a new legal regime for MGRs sourced from ABNJ provide countries with an opportunity to follow through on commitments, to increase transparency by requiring disclosure of the geographic origin of MGRs, and to promote greater international participation toward discovering and using the benefits of marine biodiversity (*34*). The scale of patenting to date suggests the need for a greater sense of urgency to ensure a successful conclusion to the negotiation of a new legal regime. Regardless of whether monetary or nonmonetary benefit-sharing mechanisms ultimately emerge through formal agreement or voluntary commitments, it is clear that the potential for commercialization of the genetic diversity in the ocean currently rests in the hands of a few corporations and universities, primarily located or headquartered in the world's most highly industrialized countries. Constructive cooperation among scientists, policymakers, and industry actors is needed to develop appropriate access and benefit-sharing mechanisms for MGRs that serve the triple purpose of encouraging innovation, fostering greater equity, and promoting better ocean stewardship.

MATERIALS AND METHODS

We first created a database of 38 million records of sequences of genetic material associated with patents by accessing the publicly available records of the patent division of GenBank from the National Center for Biotechnology Information on 10 October 2017 (ftp://ftp.ncbi.nih.gov/genbank/). Drawing on a previously described process (*16*), all files (gbpat1.seq.gz to gbpat294.seq.gz) were downloaded and processed to create individual database entries with information on species name, patent number, patent data, and the party (parties) registering the patent. This was done by splitting each file into individual sequences and by extracting the data in the ORGANISM field (species name) and JOURNAL field (patent type, year, and registering party) for each sequence. Data processing was done using the Anaconda Python distribution (version 2.4.1 for Python 2.7). Jupyter notebooks with the data extraction code as well as an SQLite database with the 38 million records are both available on request.

Only those patents issued through international patent applications (those marked "WO") were considered in the analysis that we report on here (7.3 million records). Such applications can facilitate patent recognition throughout some or all of the 152 contracting states to the Patent Cooperation Treaty of the World Intellectual Property Organization (see the Supplementary Materials) (*43*).

The majority of patent sequences relate to identified species (59.3%) and synthetic constructs (39.5%), while a small number are associated with unidentified species (1.2%). Sequences from a total of 8032 different species are included in the database (see the Supplementary Materials). To determine the marine origin of named species, the taxon match tool of the WoRMS, which is estimated to include 98% of described species (*5*), was used for all database hits (*44*), resulting in a conservative filtered list of 1720 species (see the Supplementary Materials). Web searches were conducted for each of these 1720 species to verify the marine origin and to collect further information about the nature of each species. Nearly half of the matched species were subsequently excluded, resulting in a final list of 862 marine species (see the Supplementary Materials). Species were excluded if a literature search revealed that they were associated with freshwater or terrestrial environments; seabirds were also excluded. A final filtering process was carried out to remove a small number of cosmopolitan microbes found in diverse environments, including marine systems. This is due to the high costs typically associated with the collection of genetic resources from marine environments, meaning that cosmopolitan microbes would more likely have been isolated from other more easily accessible sources. In some cases, it was possible to collect information about whether microbes had been isolated from sediments or seawater, and whether this signified a likely deep-sea or hydrothermal vent provenance (see the Supplementary Materials for list and references).

Records of patent sequences from the 862 marine species were extracted from our database and analyzed with regard to patent applicants, resulting in 12,998 relevant sequences. A total of 12,169 (94%)

sequences were registered to a sole entity and formed the basis for the ownership analysis. Analysis of species provenance, date of patent, and number of patent sequences was carried out on the full sample (see the Supplementary Materials). A total of 559 entities were recorded as sole or joint applicants on patents, and web searches were used to collect information about each, including their web presence and the type of entity that they represent, leading to the subsequent definition and classification into three broad categories: companies, universities and their commercialization centers, and others (national institute or agency or government body, individuals, hospitals, nonprofit research institutes) (see the Supplementary Materials).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/6/eaar5237/DC1
Basics of gene patents
fig. S1. Number of marine species and marine sequences associated with patents.
fig. S2. Top 30 largest patent holders.
data file S1. Raw data, species data, patent registration data, owner data, and data aggregations section (Excel file).
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Acknowledgments: We thank K. Bavikatte, M. W. Tvedt, M. Taylor, and other colleagues for their constructive input and insightful feedback. **Funding:** R.B., C.C.C.W., and H.Ö. were supported by the Nippon Foundation Nereus Program, a collaborative initiative by the Nippon Foundation and partners including Stockholm University and the University of British Columbia. J.-B.J. was funded by the Erling-Persson Family Foundation and the Swedish Research Council Formas (project number 2015-743). H.Ö. received additional support from the David and Lucile Packard Foundation, Gordon and Betty Moore Foundation, and Walton Family Foundation. This research was supported by Mistra, through a core grant to Stockholm Resilience Centre. Guidance for Resilience in the Anthropocene: Investments for Development (GRAID), provided by the Swedish International Development Agency (SIDA), provided additional support. **Author contributions:** R.B. and E.S. collected the raw data. All authors contributed to the preparation of the manuscript and were involved in the interpretation of the results. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 12 January 2018
Accepted 27 April 2018
Published 6 June 2018
10.1126/sciadv.aar5237

Citation: R. Blasiak, J.-B. Jouffray, C. C. C. Wabnitz, E. Sundström, H. Österblom, Corporate control and global governance of marine genetic resources. *Sci. Adv.* **4**, eaar5237 (2018).

OCEANOGRAPHY

A strategy for the conservation of biodiversity on mid-ocean ridges from deep-sea mining

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Mineral exploitation has spread from land to shallow coastal waters and is now planned for the offshore, deep seabed. Large seafloor areas are being approved for exploration for seafloor mineral deposits, creating an urgent need for regional environmental management plans. Networks of areas where mining and mining impacts are prohibited are key elements of these plans. We adapt marine reserve design principles to the distinctive biophysical environment of mid-ocean ridges, offer a framework for design and evaluation of these networks to support conservation of benthic ecosystems on mid-ocean ridges, and introduce projected climate-induced changes in the deep sea to the evaluation of reserve design. We enumerate a suite of metrics to measure network performance against conservation targets and network design criteria promulgated by the Convention on Biological Diversity. We apply these metrics to network scenarios on the northern and equatorial Mid-Atlantic Ridge, where contractors are exploring for seafloor massive sulfide (SMS) deposits. A latitudinally distributed network of areas performs well at (i) capturing ecologically important areas and 30 to 50% of the spreading ridge areas, (ii) replicating representative areas, (iii) maintaining along-ridge population connectivity, and (iv) protecting areas potentially less affected by climate-related changes. Critically, the network design is adaptive, allowing for refinement based on new knowledge and the location of mining sites, provided that design principles and conservation targets are maintained. This framework can be applied along the global mid-ocean ridge system as a precautionary measure to protect biodiversity and ecosystem function from impacts of SMS mining.

INTRODUCTION

Mid-ocean ridges are located at divergent oceanic plate boundaries, where volcanism associated with seafloor spreading creates new oceanic crust. In these regions, seawater percolates through seafloor cracks and fissures to depths where it reacts with host rock at high temperature and pressure, stripping the rock of metals such as copper and zinc. The heated, chemically modified fluid is thermally buoyant and rises to exit the seafloor through hydrothermal vents, where metal sulfides precipitate and can accumulate as seafloor massive sulfides (SMS; also referred to as polymetallic sulfides). Where uplifted and exposed as ophiolite complexes on land, SMS deposits have long been exploited for their ores (*1*). They are now targeted for mining at the seabed (*2*). At slow seafloor spreading rates (<4 cm year^{-1}), SMS deposits may accumulate over thousands of years and can be of sufficient size and ore quality to be of commercial interest (*2*, *3*). Some large SMS deposits on the seabed are located at "active" hydrothermal vents, operationally defined as vents that emit diffuse and/or focused hydrothermal fluid and support symbiont-hosting invertebrate taxa that rely on uptake of inorganic compounds in the hydrothermal fluid to support microbial chemosynthesis (*4*). Large inactive, or "extinct" SMS accumulations on mid-ocean ridges are less studied than active vent systems. They generally lack biomass-rich assemblages of vent-endemic taxa but likely support highly diverse and complex benthic communities (*5*, *6*). SMS deposits at inactive vents may be the preferred target for commercial mining based on environmental considerations (*7*), estimated size of the ore bodies (*8*–*10*), and the practicalities of avoiding equipment exposure to the high-temperature, acidic conditions at active vents (*11*).

The United Nations Convention on the Law of the Sea (UNCLOS) sets out the legal framework for seabed mining beyond the limits of national jurisdiction (referred to as "the Area"). The convention, along with the 1994 Implementing Agreement, established the International Seabed Authority (ISA) as the regulatory agency for deep-sea mining in the Area. The ISA is also charged with, among other things, ensuring effective protection of the marine environment from harmful effects arising from mining-related activities on the seabed (UNCLOS article 145). These responsibilities include the need to adopt and periodically review environmental rules, regulations, and procedures for the

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prevention, reduction, and control of pollution and other hazards to the marine environment, the protection and conservation of the natural resources of the Area, and the prevention of damage to the flora and fauna of the marine environment (UNCLOS article 145). Current regulatory efforts by the ISA focus on three mineral resources: SMS on mid-ocean ridges, polymetallic nodules on abyssal plains, and ferromanganese crusts on seamounts. Each occurs in different geological and ecological settings, with ecosystem processes that operate on different spatial and temporal scales (*12*) and with communities with varying degrees of resilience to mining activities (*13*). Environmental impacts from exploitation of SMS deposits are predicted to include loss of biological diversity resulting from direct habitat destruction and modification of vent fluid geochemistry, as well as degradation of surrounding benthic and pelagic environments through indirect impacts such as toxic and particle-rich sediment plumes, noise, vibration, and light created by the mining activity (*4*, *12*, *14*, *15*). Any given SMS mine site on a mid-ocean ridge will encompass only a small area, with direct impacts covering up to a few square kilometers, but a series of small mines may be required to provide an overall profitable enterprise within a single mining contract area (*3*). Potential cumulative impacts of multiple or long-duration SMS mining events on regional scales are of concern. These impacts will result from direct and indirect effects and include disruption of population connectivity, loss of ecosystem functions and services, and the potential for regional and global extinctions (*4*).

To address potential impacts from deep-sea mining, the ISA is developing regional environmental management plans (EMPs) as a best practice (*16*). In 2012, the ISA approved its first EMP (*17*) for abyssal polymetallic nodule fields in the Clarion-Clipperton Zone (CCZ) in the central Pacific Ocean. The goals of the CCZ-EMP include facilitation of exploitation and cooperative research, monitoring of the environment, area-based management, application of an ecosystem-based approach to management, and broad stakeholder participation. Area-based planning to support management of the Area through EMPs should include, but should not be limited to, the design of networks of no-mining areas, consideration of vulnerable habitats at risk of serious harm outside of these conservation areas, and the identification of preservation and impact reference (*18*).

Operationally, the CCZ-EMP uses a network of no-mining areas (referred to by the ISA and, herein, as "Areas of Particular Environmental Interest" or APEIs) for preservation of unique and representative ecosystems and for protection of biodiversity and ecosystem structure and function (*17*). APEI networks contribute to a precautionary approach to environmental management of deep-sea mining by ensuring that representative benthic habitats and associated ecosystems are protected from serious harm on regional scales, particularly given uncertainties regarding the severity, frequency, and spatial extent of mining impacts (*16*). Establishment of these conservation areas does not preclude the need for additional regional environmental management actions that consider both benthic and pelagic ecosystems including, inter alia, environmental impact assessments, site-based conservation, transparent monitoring, and mitigation measures (*18*).

The CCZ-EMP adopts principles for area-based conservation used elsewhere (*19*) as elaborated by Wedding *et al.* (*16*, *20*). These include "the principle that 30 to 50% of the total management area should be protected, that the network of protected areas should capture the full range of habitats and communities, and that each [APEI] should be large enough to maintain minimum viable population sizes for species potentially restricted to a subregion" (*21*). The APEI network design process for the CCZ polymetallic nodule beds used a regional benthic classification system where, in the absence of detailed data on the composition and distribution of benthic communities, surrogate measures and drivers of alpha and beta diversity, such as nodule abundance, particulate organic carbon (POC) flux to the seafloor, seamount distributions, bathymetry, and macrobenthic abundance, were assessed in the context of existing mining exploration claims. Biophysical surrogates of biodiversity have also been used to aid design of conservation networks [for example, in the Northeast Atlantic (*22*)] and have been tested at least once and proven to be effective (*23*). Through this surrogate approach, the CCZ was divided into nine representative subregions, each with a "no-mining" APEI of sufficient area (400 km × 400 km comprising a 200 km × 200 km core area surrounded by a 100-km-wide buffer zone) to support self-sustaining populations in each APEI core (*20*). To avoid overlap with existing exploration claim areas, the ISA positioned two of the APEIs from subregions within the core of the CCZ to the CCZ periphery (www.isa.org.jm/files/images/maps/CCZ-Sep2012-Official.jpg) (*20*). Together, the nine APEIs represent ~24% of the total CCZ management area. At the 22nd Session of the ISA in 2016, consideration was given to creation of two additional APEIs in the CCZ region, which would yield a total APEI coverage of ~29% of the CCZ management area.

The United Nations General Assembly (UNGA), in its resolution 68/70 adopted in 2013, encouraged the ISA to develop and approve EMPs for other seabed regions with potential to support deep-sea mining, in particular regions where exploration contracts had been granted. The UNGA reiterated this recommendation in subsequent annual resolutions on oceans and law of the sea (UNGA 69/245 and UNGA 70/235). The ISA followed with a call for EMPs "in particular where there are currently exploration contracts" (Council decisions ISBA/20/C/1 §9, ISBA/21/C/20 §10, and ISBA/22/C/28 §11). The ISA has yet to consider a regional EMP for any SMS deposits but has encouraged the scientific community to support the development of these EMPs. In response, an international initiative was begun in 2015 to advance a framework for the development of networks of APEIs on mid-ocean ridges using a portion of the Mid-Atlantic Ridge (MAR) as a case study. This region includes three SMS exploration contracts, covering a total area of 30,000 km^2, granted by the ISA to France, the Russian Federation, and Poland (Fig. 1). This scientific initiative adopted an inclusive, expert-driven consultative process like that used for the CCZ APEI network design (*20*, *24*). Two large international workshops were convened in June 2015 and November 2016 with deep-sea biologists, geospatial ecologists, lawyers, and mining contractors to discuss network designs. Supporting activities also fed into the workshops, including a comprehensive data report, a smaller working group that drafted design principles and assessed multiple network options, and outreach activities to obtain input from a larger scientific community. Through this process, a framework was developed for the design and assessment of various APEI network scenarios for the MAR. As reported below, this framework includes a conservation goal, specific conservation objectives and targets, and performance metrics.

The CCZ-EMP served as a starting point for area-based planning for networks of no-mining areas on mid-ocean ridges. However, key features of ridge systems—including their quasi-linear nature, their along- and cross-axis bathymetric complexity, their complex and turbulent flow environments, and the patchy occurrence of hydrothermal vents and SMS on ridges—differ substantially from those of the abyssal plains of the CCZ and required de novo considerations for network

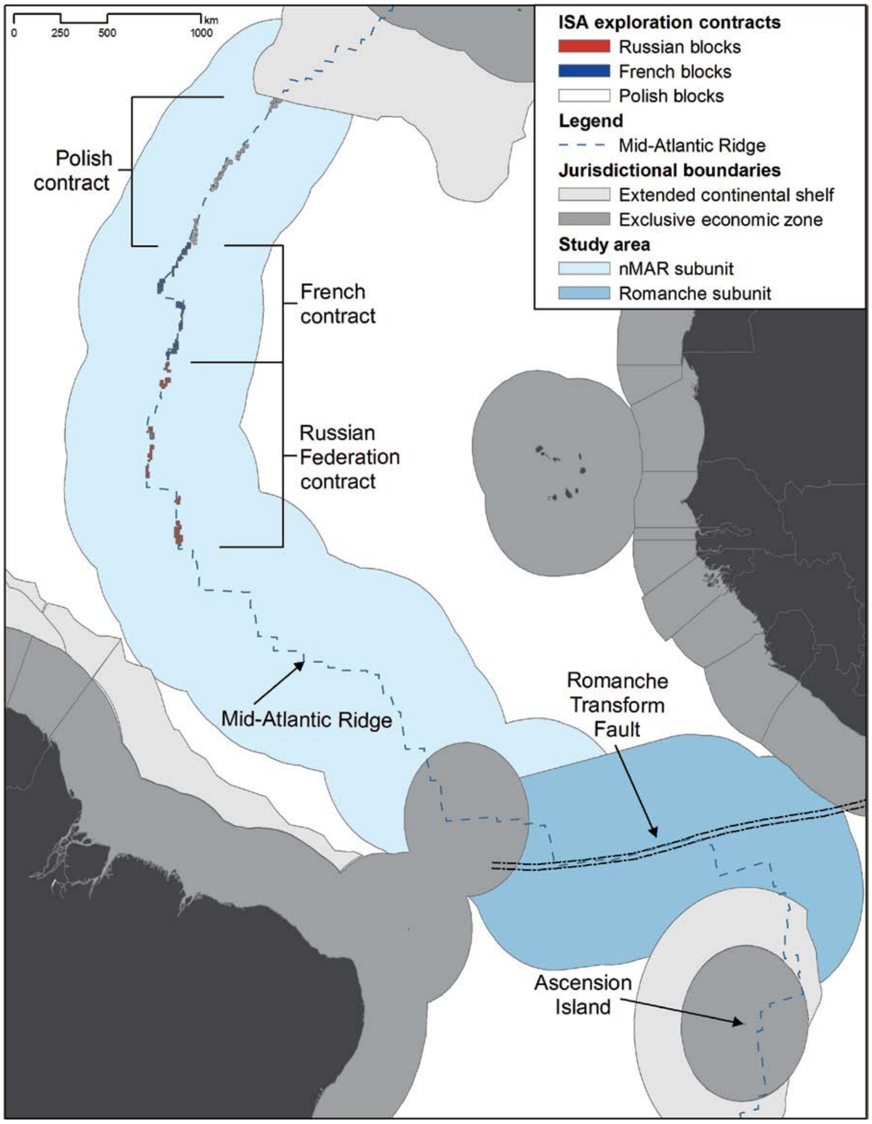

Fig. 1. Study area and management context. The case study area is centered on the ridge axis from the southern boundary of the Portuguese ECS claim to the northern boundary of the UK ECS claim at Ascension Island and extends 500 km to either side of the axis. Two management subunits are proposed here: nMAR and the RTF. Existing French, Polish, and Russian Federation exploration contracts for SMS are from the ISA database (www.isa.org.jm).

design (*25*). A list of habitat indicators and biodiversity drivers on and around mid-ocean ridges was refined (table S1), and metrics for climate-change stressors based on model projections were introduced. In addition to the biodiversity variables of bathymetry and seamount distribution by Wedding *et al.* (*20*), this MAR case study included other variables for performance metrics, including biogeographic region, latitude, POC flux to the seafloor [replacing particulate organic nitrogen flux used by Wedding *et al.* (*20*)], slope, other habitat types (transform faults and hydrothermal vents), and future in situ environmental conditions (pH, temperature, dissolved O_2 concentrations, and POC flux to the seafloor) derived from climate-change projections for the year 2100 (Table 1). Consideration was given to applying a more quantitative approach, including use of optimization tools such as MARXAN (*26*, *27*), but given the limited available data on species distributions and alpha and beta diversity, a MARXAN or related approach would have conveyed a greater level of certainty with respect to the optimal placement of APEIs than is warranted. Furthermore, such an approach would indicate preferred placement of APEIs, which is counter to our intent to develop a framework and not to presuppose a specific solution before the ISA develops one.

The development of the network of APEIs in the CCZ was based on scientific (ecological and biogeographic) principles and included both legal and socioeconomic considerations related to existing exploration contracts and commitments (*20*). Here, the linear nature of the mid-ocean ridge and the distribution of existing exploration contracts (Fig. 1) precluded the design of network of adequately sized and scientifically justifiable APEIs that avoided existing contracts. We thus use a solely science-based, ecological approach to adapt marine reserve design principles to the distinctive ridge setting. In doing so, we consider the APEI network design to be fungible, recognizing that mineral exploration will inform placement of networked APEIs that can meet conservation and exploitation objectives.

Table 1. Network criteria, conservation targets, and metrics. CBD network criteria (bold) including definitions quoted from CBD (*29*), metrics (italics), conservation targets, and metric equations used in this study, with relevant comments.

Network criteria *Metrics*	Definitions and metric equations (normalized to 0 to 5 range)	Conservation targets and comments
Important areas	"[Important Areas are] geographically or oceanographically discrete areas that provide important services to one or more species/populations of an ecosystem or to the ecosystem as a whole, compared to other surrounding areas…"	
Major transform faults *Biogeographic transition zones* *Genetic hybrid zones*	APEI percent coverage/100% × 5.	The objective is to protect 100% of important areas. Scores are based on percent area conserved (for transition zones), percent by number of features conserved (for hybrid zones), and percent of length conserved (for transform faults).
Representativity	"Representativity is captured in a network when it consists of areas representing the different biogeographical subdivisions of the global oceans and regional seas that reasonably reflect the full range of ecosystems, including the biotic and habitat diversity of those marine ecosystems."	
Discrete habitat variables: *Spreading ridge* *Active vents* *Inactive vents* *Fracture zones* *Seamounts*	APEI percent coverage/50% × 5, where any score greater than 5 was set to 5.	The objective is to protect a representative amount (30 to 50%) of key habitat within the study region. Scores are based on percent area conserved (for spreading ridges), percent by number of features conserved (for active and inactive vents, and seamounts), and by percent of length conserved (for transform faults). Note: Active hydrothermal vents and other vulnerable marine ecosystems are at risk of serious harm from SMS mining activities. We expect 100% of active hydrothermal vent ecosystems and other habitats at risk of serious harm to be protected through conservation measures, including, but not limited, to APEIs.
Continuous variables that describe the regional seascape: *Slopes* *Depth* *Seafloor POC flux*	5 − (RMSE × 5)	The objective is to mimic the distribution of variables determined to be key drivers of biodiversity in proportion to their occurrence in the management subunit. Root mean square error (RMSE) was calculated as the difference between cumulative frequency distributions within the APEI scenario and the study region. All variables were classified into 10 to 15 bins to remove the effect of the number of bins on RMSE.
Connectivity	"Connectivity in the design of a network allows for linkages whereby protected sites benefit from larval and/or species exchanges, and functional linkages from other network sites. In a connected network individual sites benefit one another."	
Regional connectivity	6 − (max distance between cores/75th percentile median dispersal distance), where any score greater than 5 was set to 5.	The objective is to ensure that there is no major disruption to dispersal across the network of APEIs. The maximum distance between APEIs compared to median faunal dispersal distances is an indicator of the potential for disrupting dispersal within the entire management subunit.
Network population persistence	6 − mean gap ratio (that is, the mean distance between cores/mean core length), where any score greater than 5 was set to 5.	The objective is to promote the viability of populations by self-seeding within APEIs and/or dispersal between APEIs. By minimizing the difference in length of APEI core areas versus distance between core areas, species that on average disperse beyond the APEI have a good chance of being able to disperse to adjacent APEIs. Minimizing this "gap ratio" should enhance persistence of species across the network, as well as within individual APEIs, and increase resilience across the network to localized disturbances.
Replication	"Replication of ecological features means that more than one site shall contain examples of a given feature in the given biogeographic area. The term "features" means "species, habitats and ecological processes" that naturally occur in the given biogeographic area."	
Replication	Number of APEIs where any score greater than 5 was set to 5.	The objective is to have three to five replicate APEIs within a management unit, to decrease the likelihood of local catastrophes causing systemic biodiversity loss.
Viability and adequacy	"Adequate and viable sites indicate that all sites within a network should have size and protection sufficient to ensure the ecological viability and integrity of the feature(s) for which they were selected."	
Total area	(APEI percent coverage/50%) × 5, where any score greater than 5 was set to 5.	The objective is to conserve an adequate portion (30 to 50%) of the management unit to ensure the viability of populations within it. Total area conserved is a proxy for overall adequacy of a network. The total area metric was calculated similarly to the habitat representativity metrics above.

continued on next page

Network criteria Metrics	Definitions and metric equations (normalized to 0 to 5 range)	Conservation targets and comments
Within APEI persistence	5 × (APEI core length/200 km), where any score greater than 5 was set to 5.	The objective is to ensure that APEIs are large enough to maintain minimum viable populations, and metapopulations, within a single APEI. The larger the APEI, the greater the probability self-recruitment within the APEI, and the lower the percentage of larval export from the APEI, which should enhance the persistence of populations, metapopulations, and communities within an APEI. 200 km was used as the minimum scale required to encompass two times the median dispersal distance of 75% of deep-sea fauna with known dispersal scales (*53*).
Climate Change: Absolute similarity	5 − (RMSE × 5)	The objective is to conserve areas where climate impacts would be minimized. The more close distributions of key climate variables (pH, temperature, dissolved O_2 concentrations, and seafloor POC flux) in the future (that is, 2100) APEI cores mimic the current (that is, 2013) distribution in the management unit, the less impact is expected. RMSE was calculated as the difference between cumulative frequency distributions within the APEI scenario and the study region. All variables were classified into 10 to 15 bins to remove the effect of the number of bins on RMSE.
Climate change: Relative local change	(APEI percent coverage/50%) × 5, where any score greater than 5 was set to 5.	The objective is to conserve 30 to 50% of the areas projected to be least affected by climate change. Least affected cells were defined as the 10% of cells with the lowest percent change between current (2013) and predicted (2100) values of the four key climate variables (pH, temperature, dissolved O_2 concentrations, and POC flux to the seafloor). The percent of those cells falling in APEI cores for each scenario was calculated following the approach used for representativity metrics (continuously distributed variables).

Article 4 of the Convention on Biological Diversity (CBD) states that the convention applies to Areas Beyond National Jurisdiction (ABNJ) "in the case of processes and activities, regardless of where their effects occur, carried out under its jurisdiction or control." The CBD is also charged with "provision of scientific and, as appropriate, technical information and advice related to marine biological diversity" (*28*). In designing APEI network scenarios, we apply five network criteria identified by the CBD (*29*): important areas, representativity, connectivity, replication, and adequacy and viability. For each of these criteria, we propose conservation objectives for APEI networks (Box 1) that are used in an assessment of network performance. Our approach closely resembles that suggested in Annex III of the above CBD decision (albeit in a different order) and involved (i) delineation of a study area based on biogeographical considerations, (ii) identification of known ecologically or biologically important areas [analogous to Ecologically or Biologically Significant Areas (EBSAs) (*29*, *30*)], (iii) iterative site selection, and (iv) consideration of ecological coherence (for example, ecological connectivity and viability), including viability under climate change. We then developed three network scenarios and assessed the performance of the scenarios. This approach allowed the development of scenarios that meet the current understanding of what an ecologically robust network of APEIs on a mid-ocean ridge would look like.

Although we focus our study on the northern and equatorial MAR, the general principles, design criteria, and evaluation approach should be applicable to mid-ocean ridge systems (and potentially other deep-sea settings) worldwide. Our intent was to develop a framework for the design and assessment of networks of no-mining areas based on internationally agreed conservation network criteria to inform the sustainable use of SMS mineral resources. While we consider networks of APEIs to be necessary elements of sustainable use of these resources, we emphasize that they are not sufficient on their own; additional environmental management tools will be needed to protect and preserve the marine environment. For mid-ocean ridges and exploitation of SMS deposits, one such additional tool may be site-based closures to protect all active hydrothermal vent ecosystems, which have been identified as vulnerable and at risk of serious harm (*7*, *12*). Vulnerable marine ecosystems, including cold-water corals and sponges outside of APEIs, will also need protection. Non–area-based tools might include, for example, management of the frequency and timing of mining activities in a region or monitoring of environmental thresholds for turbidity and toxicity.

Building on the conservation goal reported by Wedding *et al.* (*20*) for the CCZ, the conservation goal for the design of an APEI network on the MAR is to contribute to "the protection of the natural diversity, ecosystem structure, function, connectivity, and resilience of deep-sea communities in the context of seabed mining in the region."

RESULTS

Study area and biogeographic approach

To inform governance of deep-sea mining on the seafloor in the Area, the UNGA and ISA call for regional EMPs in areas that contain exploration contracts. We focus on ABNJ on the northern MAR with existing exploration contracts, and an extension to the south that illustrates how regional management units may be defined by biogeography. The study area is centered on the axis of the MAR and extends latitudinally from the southern boundary of the Portuguese extended continental shelf (ECS) claim at 32.84°N to the northern boundary of the UK ECS claim for Ascension Island at 02.43°S, exclusive of the Brazilian Exclusive Economic Zone (EEZ) (Fig. 1). The study area extends 500 km on either side of the axis of the MAR (unless restricted by national jurisdictions) to include the range of representative benthic habitats that might be affected by deep-sea mining of SMS or other seabed resources and provide a zone of sufficient size for population connectivity through larval dispersal.

To ground the study of ecological principles underpinning ecosystem-based management (*31*, *32*), we apply a biogeographic approach using

Box 1. Network criteria and conservation objectives for APEIs on a mid-ocean ridge based on CBD Marine Protected Area network criteria. Viability under climate change is newly integrated into the adequacy/viability criterion.

(1) Important areas

(a) Placement of APEIs within the network should capture areas considered to be ecologically and/or evolutionarily important based on best available science. APEIs should conserve 100% of identified important areas.

(2) Representativity

(a) APEI should conserve 30 to 50% of each habitat type (for example, the spreading ridge, seamounts, and transform faults) within each management unit.

(b) APEIs should be representative of the biophysical seascape (for example, depth, slope, and POC flux to the seafloor) within each management unit.

(3) Connectivity

(a) The APEI network should minimize the average and maximum distances between core areas to the greatest extent possible to conserve all dispersal scales and to ensure exchange across the entire network.

(4) Replication

(a) APEIs should be replicated within biogeographic provinces (where the size of the management unit permits) to capture along-axis variation in faunal composition and protect against localized catastrophes.

(5) Adequacy/viability

(a) The APEI network should protect 30 to 50% of the total management unit.

(b) Each APEI unit within the network should include a core area of sufficient length and width to maintain viable populations and ecosystem function.

(c) Each APEI unit within the network should include an appropriately sized buffer zone to protect core areas from indirect mining effects.

(d) Viability under climate change

(i) Projected biophysical conditions (temperature, pH, dissolved O_2 concentrations, and POC flux to the seafloor) in APEIs should include the range of current conditions across the study area.

(ii) APEIs should include at least 30% of the area projected to be least affected by reasonable climate change scenarios (based on predicted changes in temperature, pH, dissolved O_2 concentrations, and POC flux to the seafloor).

the most recent classification scheme for ocean floor biogeography (*33*). The primary management feature is the spreading axis of the MAR, which, for most of its length in the study area, is encompassed by the lower bathyal (800 to 3500 m) and abyssal (3501 to 6500 m) North Atlantic biogeographic provinces by Watling *et al.* (*33*). There is an isolated hadal (>6500 m) biogeographic unit [HD9 by Watling *et al.* (*33*)] and a bathyal (North Atlantic/South Atlantic) biogeographic transition zone at the southern margin of the study area. The study area was thus partitioned into two subunits: (i) the northern MAR (nMAR) subunit, north of the Brazilian EEZ, and (ii) the Romanche Transform Fault (RTF) subunit, south of the Brazilian EEZ (Fig. 1).

Identification of important areas

APEI network design should incorporate features of ecological importance. For the MAR, these features include (i) major transform faults that serve as conduits for deep-water circulation between west and east basins of the Atlantic (*34*, *35*) and support a diverse set of habitats and fauna (*36*); (ii) transition zones between biogeographic units (so-called "biogeographic crossroads" or "suture zones"), where there is high species richness, beta diversity (*37*), and hybridization that may foster evolution (*38*); and (iii) recognized genetic hybrid zones [for example, Won *et al.* (*39*)]. As noted above, all active hydrothermal vent ecosystems on the mid-ocean ridge are vulnerable and at risk of serious harm and thus deserve protection (*7*, *12*); some of these ecosystems will fall within APEI units, while the others will need to be protected through other area-based conservation measures.

Placement of APEIs in the MAR region was designed to capture the following important ecological features (Fig. 2A):

nMAR subunit:

(1) The Vema Transform Fault, a major water-mass transport pathway between the deep western and eastern Atlantic Basins (*34*) and an area with presumed reducing habitats as suggested by the record of the indicator species *Abyssogena southwardae* (Krylova *et al.*, 2010).

(2) The hybrid zone at Broken Spur (*39*, *40*). While multiple mussel hybrids are known along the MAR (the symbiont-bearing mussels *Bathymodiolus azoricus* and *Bathymodiolus puteoserpensis*), Broken Spur has the greatest proportion of hybrid individuals in a stabilized population with indications of local adaptation (*41*, *42*); this region also corresponds to a biogeographic sub-boundary between northern "bathyal" and southern "abyssal" vent faunas (*43*).

RTF subunit:

(1) The bathyal biogeographic transition zone between the North Atlantic and South Atlantic units (*33*).

(2) The RTF, which includes a hadal biogeographic unit (*33*). The Romanche is a major transport pathway between the western and eastern Atlantic basins for dense water masses originating in polar regions (*34*, *35*, *44*). The proposed RTF subunit also overlaps substantively with the EBSA known as the "Atlantic Equatorial Fracture Zone and High Productivity System" (*45*).

Iterative site selection: Orientation, size, and spacing of APEI units

The cross-axis bathymetric profile of the MAR incudes a central axial valley with ridge flanks, canyons, seamounts, flat sedimented areas, and abyssal hills extending laterally from the axis. To capture cross-axis habitat heterogeneity, APEIs are recommended as rectangular bands with their length following the strike of the ridge axis and their width oriented perpendicular to the ridge axis. The cross-axis orientation of a banded-APEI approach also captures the special characteristics of transform faults, which represent extremes in depth and other environmental variables, including hydrographic regimes that support diverse deep-sea habitats and thus merit protection.

Latitudinal variation in POC flux to the seafloor (*46*, *47*), a primary determinant of biodiversity and ecosystem structure and function in the deep sea (*22*, *48*–*51*), indicates that a network of APEIs should be distributed along the entire length of the ridge axis in the study area to capture this and other latitudinal variations in biophysical characteristics. Such a network of APEIs provides replication that protects against catastrophic loss of habitat in any locality and increases demographic stability by promoting inter-APEI connectivity.

Core length along the ridge axis

APEIs consist of core and buffer areas, where mining should not occur. Each core should be large enough to maintain a minimum viable population size for a large percentage of deep-sea invertebrates through self-replenishment (*20*). The 75th percentile median dispersal distance for deep-sea benthic invertebrates is used to define the distance from the core-area center point required to capture ecological dispersal within the APEI. This distance is calculated from both genetic, reflecting evolutionary time scales (*52*), and larval dispersal models, reflecting contemporary time scales (*53*–*55*). These calculated distances were 103 km for vent invertebrates and 74 km for nonvent deep-sea invertebrates

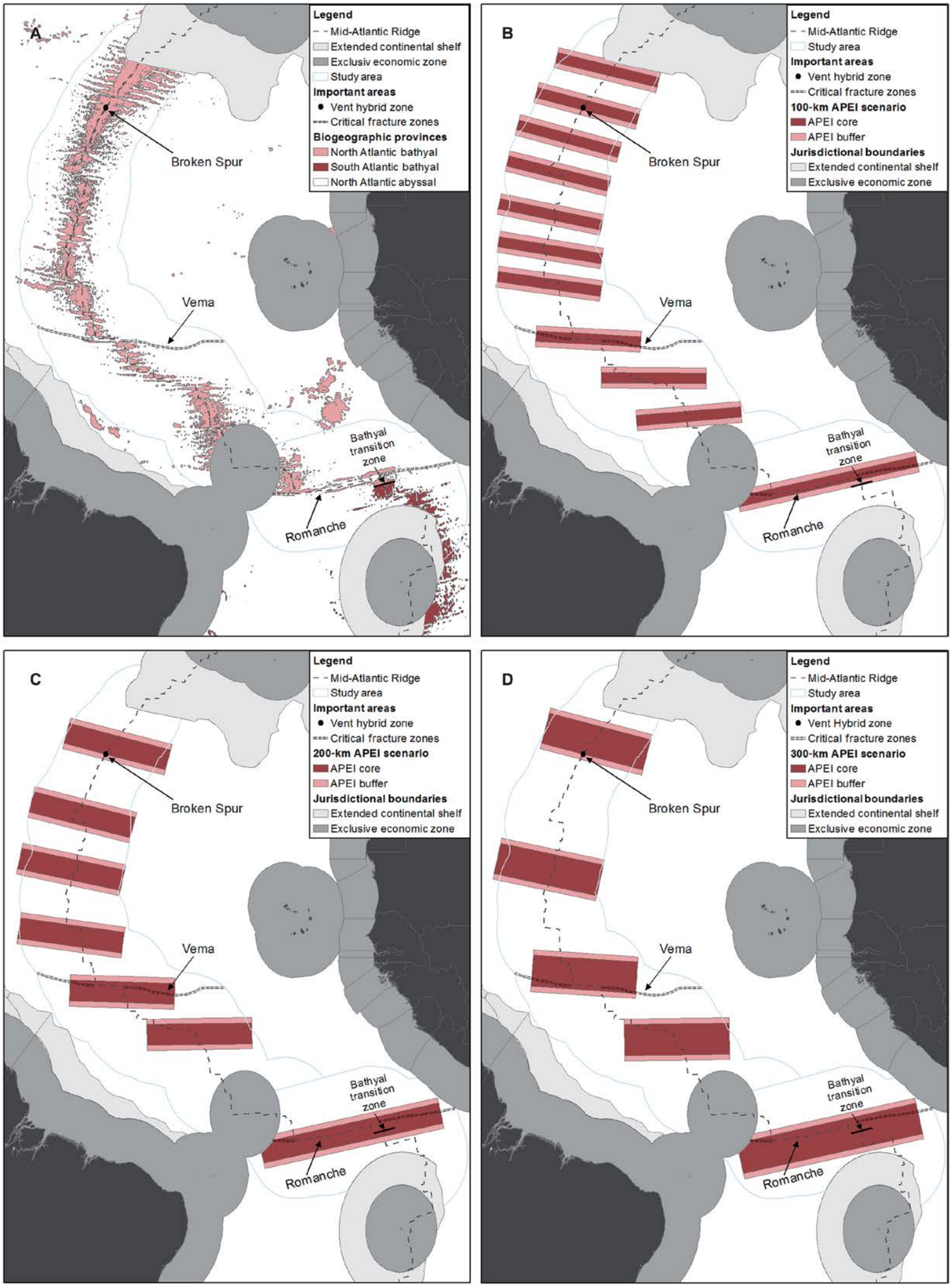

Fig. 2. Biogeographic context, important areas, and APEI scenarios. APEI scenarios were anchored by important areas identified by expert opinion before scenario development began. Important areas include (**A**) critical transform faults (that is, Vema and Romanche), biogeographic transition zones (that is, the bathyal transition zone in the region of the RTF), and genetic hybrid zones (that is, Broken Spur). Three APEI network scenarios were developed for the nMAR subunit, with core lengths along the ridge axis of (**B**) 100 km, (**C**) 200 km, and (**D**) 300 km; each APEI also has a 50-km buffer on the northern and southern sides of the core zone.

(*52*). A nominal 100-km dispersal distance thus captures estimated dispersal distances for vent and nonvent deep-sea invertebrate datasets, within the 75th percentile allowance. This 100-km dispersal distance matches the dispersal distance used in the APEI network design for the CCZ (*20*), but was derived using a new synthesis of dispersal distances for deep-sea (rather than shallow-water) organisms (*52*). As in the case of the CCZ-EMP, the length (and width) of the core conservation area is at least two times the median faunal dispersal distance (*20*, *56*). This indicates that the minimum APEI core length along the ridge axis should be 200 km. Large-scale genetic connectivity over evolutionary time (*57*) is possibly the result of temporally discontinuous short-distance (for example, <26 km) dispersal mediated by stepping stone habitats (*55*). These short dispersal distances that occur discontinuously at contemporary time scales should also be contained well within the minimum core length of 200 km.

Core width across the ridge axis

The mid-ocean ridge has complex, cross-axis physical characteristics (including depth gradients and hydrographic regimes) that drive ecosystem processes, and there is evidence for differentiation in the faunal composition of the eastern and western flanks of the MAR (*58*, *59*). Near-bed currents on the flanks of the ridge axis can be channeled in canyons and faults, resulting in a topographically forced flow toward the ridge crest (*60*, *61*). Because large, buried SMS deposits are expected on the flanks of the ridge crest (*3*, *62*–*65*), flow toward the ridge crest enhances the potential for mining plumes from flank SMS deposits to affect habitats closer to the crest. Where species' distributions extend across ridge flanks, protecting cross-ridge swaths will be important for internal connectivity within an APEI. To capture representative habitats that vary with depth (from upper bathyal to abyssal) and other biophysical characteristics along the flanks (*33*), we extend the width of the core area to 500 km on either side of the ridge axis. Such an approach protects the bathyal-abyssal biogeographic transition areas on the ridge flanks and the ridge axis, helps meet the conservation target of 30 to 50% of each habitat type in the management unit, and accommodates future exploitation of buried SMS deposits and of other minerals on ridge flanks.

Buffer zones

SMS mining is expected to produce plumes of particulates at the seabed during mining activities and plumes at some height above the seabed during discharge of water and fine particles from the shipboard dewatering plant (*12*). While details of SMS mining plume structure and dispersion are not constrained well at present, SMS plumes are expected to affect a smaller region than those created by polymetallic nodule mining, where dispersion distances may extend to 100 km (*66*). Test mining of deep-sea sulfides was undertaken in 2017 off Japan, but the results of the associated environmental monitoring program have not yet been made publicly available. Given that passive particles suspended in the water at 1000 m on the MAR travel on average more than 2 km/day (based on Argo float data and models), we assume that plume dispersal may be on the order of tens of kilometers. Until more data are available on plume dispersal and toxicity, we use a buffer zone of 50 km on the northern and southern borders of the APEI cores. We assume an absence of exploitable mineral resources beyond 500 km on the western and eastern flanks of the ridge axis and thus do not indicate buffer zones on these borders of the core area.

Spacing

All conservation networks involve trade-offs between (i) promoting larval connectivity between closed areas (improved by smaller spacing between closures); (ii) providing spillover of larvae (or emigrants) from closed areas to unprotected areas, thus enhancing productivity/recovery outside protected zones (improved by creating many small closures); and (iii) maintenance of self-sustaining populations within APEI cores (improved by increasing the size of individual closures). We adopt a common design guideline for conservation networks, namely, to minimize the difference between the maximum dispersal distance protected by the core area and the distance between core areas (*67*). Using this approach, species with larval dispersal distances greater than the length of the core areas should be able to disperse to adjacent APEIs, while those with dispersal distances less than the core length are likely to maintain populations (including metapopulations) within a single APEI core. Consideration also needs to be given to the maximum distance between adjacent core areas. Large gaps between core areas can result in core areas effectively acting as separate units rather than as a network. To address this issue, we minimize the maximum distance between adjacent core areas to ensure network functionality. Spacing between APEIs is also necessarily affected by the overall percentage of the management unit to be protected (in this case, 30 to 50%).

nMAR management subunit APEI network design

On the basis of the size and spacing requirements outlined above, network scenarios of APEIs with 100-, 200-, and 300-km core lengths along the ridge axis (oriented approximately north-south), with 1000 km width (centered on the ridge axis), and spaced at distances as near as possible to the length of the APEI core were placed in the nMAR subunit (Fig. 2, B to D). These APEI network scenarios were "anchored" by two important areas identified on the nMAR: the Broken Spur hybrid zone and the Vema transform fault. While our premise is that the 200-km core length scenario is a minimum core length, the 100- and 300-km core length scenarios allow us to understand what ecological performance might be lost (or gained) by changing the core length of an APEI.

RTF management subunit

Assuming that APEI core lengths should be 200 km or more and the identification of the RTF as an important area, the areal extent of the RTF subunit does not allow for a replicated network of APEIs. We proposed a single APEI centered on the RTF. The width of the RTF APEI is extended to protect the full extent of the transform offset and the hadal biogeographic unit between the ridge axes. In addition, the APEI extends 500 km to either side of the adjacent northern and southern ridge axes, as for the nMAR APEIs.

APEI network performance assessment: nMAR management subunit

The guidelines for size and spacing of APEIs described above are based on scientific theory but do not guarantee that such a network would meet the network criteria set out by the CBD, that is, that the network would be ecologically coherent (*68*, *69*). We assessed ecological coherence of APEI network scenarios with core lengths of 100, 200, and 300 km by evaluating performance against conservation targets for 17 metrics developed to quantify the five CBD network criteria (Fig. 3, bottom). The representativity criterion is subdivided into metrics for discrete habitats and for continuous biological or physical oceanographic variables that describe the regional seascape. We also reported summary scores for each scenario for each network criterion (Fig. 3, top).

All scenarios met the target for important areas in this management subunit and did well at representing current biophysical seascape conditions (Representativity: Continuous). Each scenario also outperformed the other scenarios in at least one criterion (Fig. 3, top). The 100-km scenario performed better in the connectivity and replication criteria. The 200-km core scenario outperformed in representing key discrete habitat types and replication. The 300-km scenario did slightly better in achieving targets to represent the regional biophysical seascape and in mitigating effects from projected changes under climatic conditions (Fig. 3). While the 200-km scenario performed well across all criteria, the 100-km scenario underperformed in adequacy and viability, and the 300-km scenario underperformed in connectivity. As noted in the Introduction, the 100-km scenario also does not meet our critical design requirement for a ≥200-km core length.

APEI network performance assessment: RTF management subunit

For the RTF management subunit, all scenarios protect the hadal biogeographic province. Two of the important areas identified by experts are in the RTF management subunit, namely, the RTF itself and the biogeographic transition zone between the North Atlantic and South Atlantic bathyal biogeographic provinces. Only the 300-km scenario completely protected both the RTF and the biogeographic transition zone within a single APEI. The 200-km scenario performed

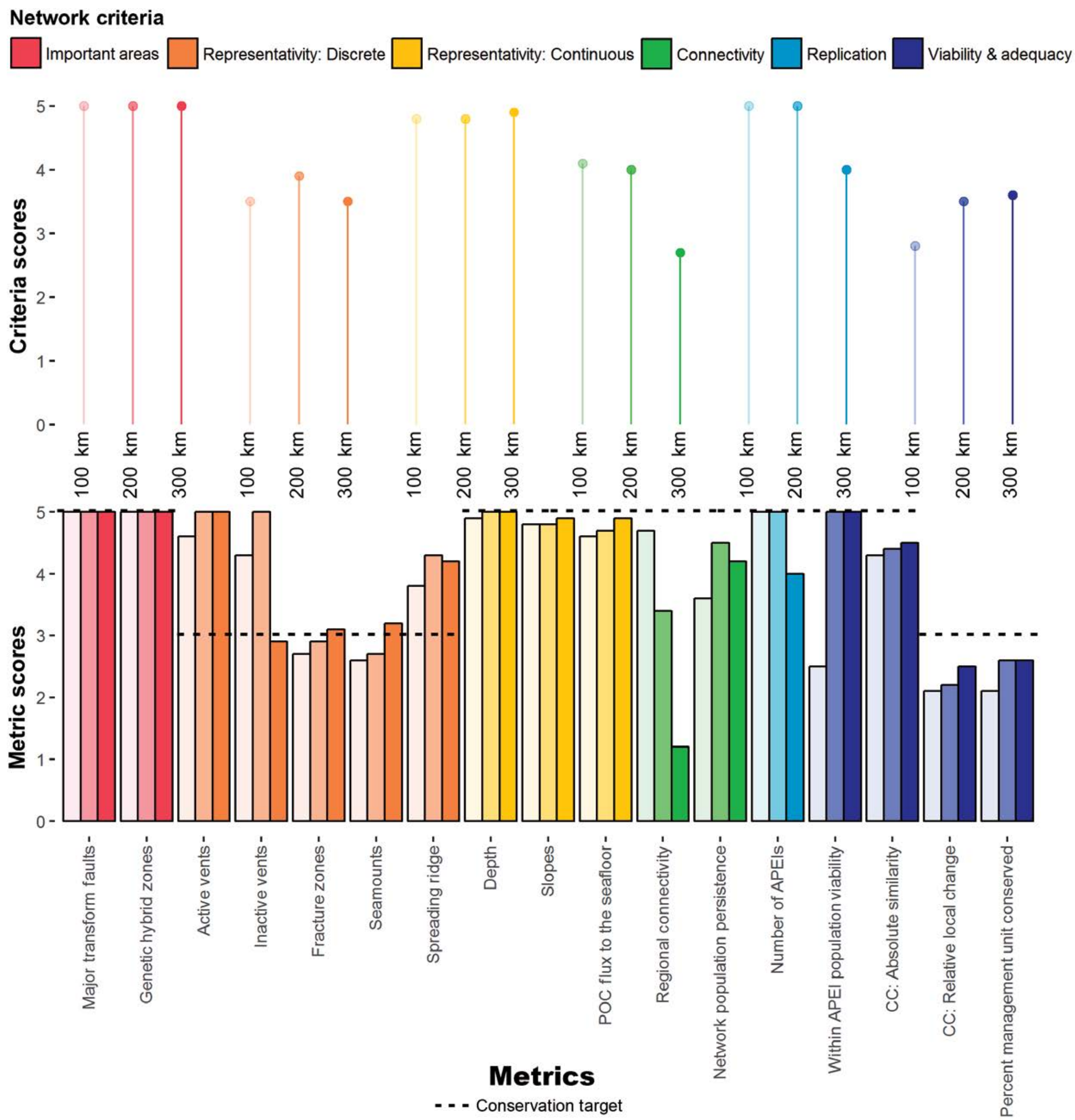

Fig. 3. APEI network performance assessment (nMAR management subunit). Bottom: Scores for 17 metrics derived to capture performance (5 being the best) of scenarios against the five CBD network criteria (see legend for color code; light shading, 100-km scenario; medium shading, 200-km scenario; dark shading, 300-km model). Table 1 defines the metrics and metric equations. Table S2 shows the raw values and commentary. Dotted line, conservation targets for each score; CC, climate change. **Top**: Summary scores for each network criterion (calculated by taking the average scenario score of the metrics for a criterion). Scenario core lengths are provided on the *x* axis.

well, protecting the RTF and greater than 70% of the biogeographic transition zone, but the 100-km scenario was unable to adequately conserve either the RTF or the biogeographic transition zone. Other network criteria were not evaluated, as there was only one APEI and, thus, consideration of metrics for network criteria was inappropriate.

DISCUSSION

From the assessment above, it is evident that there are trade-offs in scenario performance across network criteria. While all scenarios performed well in certain criteria, each criterion must be met to support an ecologically coherent network. The poor performance of the 100-km scenario in the viability and adequacy criterion and the 300-km scenario in the connectivity criterion raise questions about the ecological coherence of those network scenarios. Furthermore, the 100-km scenario failed to meet the basic target to conserve the 75th percentile median dispersal distance for deep-sea benthic invertebrates within core areas and was unable to fully conserve the important areas in the RTF management unit. Given the need to place buffers around core areas, smaller APEIs are a less-efficient mechanism with which to meet conservation targets. Therefore, we recommend the use of a 200-km core length for APEIs but recognize that the size of an APEI is contingent on the characteristics of the management unit (for example, the need to use an APEI with a 300-km core length to fully conserve important areas in the RTF subunit).

The nMAR network scenarios described here do not take into account locations of existing exploration contracts. Exploration contracts influenced decisions by the ISA regarding the placement of APEIs in the CCZ, leading to a network of APEIs that are not necessarily representative of the local and regional biodiversity (*16*, *20*). Exploration contracts on the MAR continue to be granted, with the most recent contract awarded in 2017. Before applying for exploitation contracts, contractors will have to relinquish 75% of the area under the exploration contract. Future exploration and exploitation contracts may also need to consider what other management measures with overlapping objectives have been introduced by other intergovernmental organizations with mandates to regulate human activities (for example, fisheries). Thus, the legal and geographic landscape in which networks of APEIs are being developed continues to (and is designed to) change. Given this situation, the size and spacing of core areas is flexible, and the network development process can be adaptive to accommodate mineral extraction (*16*), as long as the overall regional conservation goal and design targets are not compromised. Critically, lengths of APEIs along the ridge axis can be varied to fit between existing exploration or exploitation contracts, provided that these conditions are met.

More important than the precise dimensions of each APEI is the distribution of those APEIs along the ridge axis; size and spacing of APEIs along the ridge must deliver a network of areas that maintain population connectivity. Connectivity is not merely a function of the mean and maximum distance between APEIs but also of the size of individual APEIs and the percent of habitat protected (*67*). Thus, any network design should ensure that (i) habitat conservation targets are met, (ii) the average length of a core area is at least 200 km, (iii) the distance between APEIs is as close as possible to the core lengths of adjacent APEIs, and (iv) the maximum distance between adjacent APEIs is minimized. Maintaining average core lengths of 200 km should promote self-sustaining populations within APEIs. Limiting what we refer to as the "gap ratio" (the ratio of the APEI core length to the distance to adjacent APEIs) will help ensure connectivity between APEIs. Given the highly linear nature of mid-ocean ridge systems, the maximum distance between APEIs is a critical factor in determining whether the design will act as a network or whether it will simply be multiple isolated conservation areas with concomitant losses in resilience. This becomes more critical as the average size of APEIs decreases, resulting in more larval export from the no-mining area.

The conservation targets, network criteria, and performance assessment framework applied here can provide the scientific basis for the design of banded APEIs on mid-ocean ridges across the globe, facilitating broad applications of a precautionary approach for the protection of biodiversity and ecosystem function in the context of SMS mining. This process can be readily adapted for design of APEI networks on the other mid-ocean ridges where there are, or may be, mining interests. These include the spreading ridges in the Indian Ocean, where the ISA has already awarded SMS exploration leases to India, Germany, Korea, and China, and the southern and more northern extensions of the MAR.

Our APEI design process also considered, for the first time in the deep sea, mitigation of projected climate-induced changes. Projected climate-driven changes in pH, temperature, dissolved O_2 concentrations, and POC flux to the seafloor will occur throughout the water column and at the sea floor (*70*). These environmental shifts could alter connectivity regimes (*71*), induce species range shifts, change latitudinal or depth distributions of species, alter food webs, weaken carbonate skeletons, and ultimately alter biodiversity and ecosystem functions (*72*). In the context of area-based planning in the deep sea, conservation areas should incorporate existing syntheses and future projections of warming, deoxygenation, acidification, and POC flux to the seafloor into the evaluation of habitat vulnerability and resilience (*73*). We used projected changes in these variables to capture current biogeochemical habitat conditions (and their associated biota) within APEI networks in the future (specifically in the year 2100). Climate-induced changes in ecosystem structure and function are critical to include in the design of APEI networks to ensure that the goals of the protected area networks are sustainable as deep-sea ecosystems are altered by climate change.

Although change in seafloor conditions appears inevitable, it is unknown exactly how much change might be physiologically stressful. POC flux is a proxy for food supply, with effects on species diversity, trophic interactions, and other ecosystem attributes (*51*), and POC flux to the seabed is projected to decrease in some parts of the management area by as much as 10 to 25%. Projected increases in temperature (0.1° to 0.2°C) and reductions in O_2 seem modest (*74*) but could raise metabolic energy demands of resident species, and when combined with decreased POC flux to the seafloor, even small increases might be detrimental (*75*). Impacts of climate change are not restricted to metazoan life. Microbial and microbial-metazoan systems in the deep sea are also expected to be influenced by climate-induced changes in temperature, O_2 concentration, POC flux, and pH, with the potential for consequences that modify or disrupt ecosystem structure and function (*76*). Climate-induced stressors will not act alone; changes in environmental conditions will co-occur (*77*) and may interact in unpredictable ways (*78*), highlighting the need for a precautionary approach. Uncertainty in climate projections and their ecological impacts should not preclude, considering climate issues in ongoing spatial planning for APEIs. The analysis undertaken here represents a first attempt to assess how APEI scenarios will reflect or resist change in key environmental variables under future climate change and demonstrated the relatively poor performance of the 100-km core length APEI network scenario in these metrics (Fig. 3, bottom). We strongly encourage future studies to expand on the climate change–related metrics developed here and test their ecological relevance [for example, (*74*)].

Our current knowledge of deep-sea ecosystems is sparse and spatially biased (*79*). The development of validated models of potential habitat suitability (*80*) and other methods to predict the distribution of deep-sea habitats in unsurveyed areas (*81*) can be an important next step in refining network design. Higher resolution and more comprehensive data sets of habitat and species' distributions, important ecological drivers, population genetic structure, connectivity at ecological and evolutionary time scales, oceanographic currents, and higher resolution of earth system models to describe future change and ecological response are needed. In the near term, it is critically important to validate plume dispersal models to inform adaptive management of the size of buffer zones around APEIs to better understand the impacts on the deep pelagic and interlinkages between benthic and pelagic systems in the deep sea (*82*). The designation and valuation of ecosystem services for high-sea and deep-sea ecosystems are just beginning (*83*–*86*) and will also be important for refining APEI network design in the future. With sufficient data, it should be possible to map the supply and demand of ecosystem services to guide area-based planning (*87*–*89*). Network criterion 1 (Box 1) should then be revised so that those areas providing multiple or highly valued ecosystem services would receive priority for protection from activities that may deteriorate these services. Because of the prohibitive costs of sampling in deep and distant locations under extreme environmental conditions, meeting the data needs for these management approaches will require engagement with mining contractors, who must collect high-quality baseline environmental data as part of their exploration contract, as well as the scientific research community.

The ultimate design and timing of implementation of regional APEI networks on mid-ocean ridges remain to be resolved. Regional EMPs, including area-based tools, are within the aegis of the ISA. Placement of APEI networks on the ridge axis before awarding exploration contracts is, at face value, an optimal precautionary approach for protection of the marine environment. However, given that few commercially viable mine sites are thought to exist even over many thousands of kilometers of ridge axis (*3*), such a strategy reduces the likelihood of discovering a commercially viable mine along the ridge axis or identifying important biodiversity areas. Furthermore, large extents of ridge axis in the Atlantic and Indian oceans are already under exploration contracts, potentially compromising the ability to design networks to meet the conservation goal, objectives, and design targets, if these contracted areas must be excluded from APEI network design.

We encourage the ISA and civil society to consider incentives for regional-scale environmental baseline surveys to identify commercially viable mine sites and important biodiversity areas. Our knowledge of deep-sea ecosystems is scant and, without investment in regionally intensive baseline data collection, will likely remain so for decades. Partnerships involving the ISA, contractors, and the scientific community in the environmental planning process, including baseline surveys, are critical if we are to ensure that mining activities can proceed with due regard to the environment. For now, we recommend that the best approach is for regional EMPs, including APEI networks based on a representative approach such as the one described here, to be implemented as soon as possible. The ISA recently released a preliminary strategy for the development of these plans especially for areas where there are current contracts for exploration (*90*), with supporting activities proposed through 2020.

MATERIALS AND METHODS

Data

To ensure repeatability, only published data were used. Biogeographic units of interest were the abyssal, bathyal, and hadal regions extracted from (*33*). Depth and slope were derived from the General Bathymetric Chart of the Oceans 2014 Grid (v. 20150318; www.gebco.net). The spreading ridge feature was extracted from GRID-Arendal's Global Seafloor Geomorphic Features data set (*91*). Locations of known and inferred active and inactive hydrothermal vents sites were taken from the InterRidge Vent Database (*92*). Seamounts were clipped from the Global Seamount Database (*93*). Transform faults were obtained from the Global Seafloor Fabric and Magnetic Lineation Data Base (*94*). Data for contemporary (2013) pH, temperature, dissolved O_2 concentrations, and POC flux to the seafloor were those used by Sweetman *et al.* (*70*), as were the projected (2100) variables generated from Coupled Model Intercomparison Project Phase 5 (CMIP5) (*95*, *96*).

All geospatial analyses were carried out in ArcGIS 10.4.1, and all data layers were clipped to the case study area using a custom projection (Mollweide, with the central meridian set to −36.00°) that allowed for the best compromise between exact area calculations and exact distance calculations.

Derived variables

Distance, total area, and area by habitat coverage

Pairwise distances between APEI core areas in each scenario were calculated by running the "Near" tool using geodesic distances between nearest edges of cores. The area of the management unit conserved in each scenario was calculated by summing the core areas of the APEIs and dividing by the area of the management subunit to describe the percent area conserved. To analyze the degree to which targets for areal coverage of specific habitat types (that is, area of spreading ridges and biogeographic units, number of active and inactive hydrothermal vents and seamounts, and length of transform faults) were achieved, habitats falling within the core areas of each scenario were computed using the "Identify" tool; area of the habitat within the cores was divided by the total area of the management subunit to get the percent conserved by each network scenario.

Geomorphologic, oceanographic, and climate change variables

Distributions of depth and slope (geomorphological features) within APEI core areas were compared to their distributions within the entire management subunit for each scenario. Core and management subunit areas were converted to 1-km resolution rasters to ensure that the succeeding calculations in ArcMap were not performed at a coarser resolution. Variables were then binned by depth (100-m bins) or slope (1° bins) before extracting values. The "Zonal Histogram" tool was used to generate frequency histograms for each variable within APEI cores and for the management units. The same process was used to calculate histograms for the current (2013) and future (2100) distributions of four oceanographic variables at the seafloor, each binned into 20 equal-interval variables: acidity (pH), temperature (°C), O_2 (ml liter^{-1}), and POC flux to the seafloor (mg of C m^{-2} day^{-1}). Percent change between current and future conditions for pH, temperature, dissolved O_2 concentrations, and POC flux to the seafloor was calculated for each grid cell in the study area.

Performance assessment of APEI network scenarios: nMAR management subunit

Eighteen quantifiable metrics were developed to gauge network performance against the conservation targets identified in Box 1 (Table 1).

The three APEI scenarios with core lengths of 100, 200, or 300 km were evaluated to assess how size and spacing of APEIs influence the degree to which the conservation targets were met. Each scenario was scored on the basis of how well it achieved specific conservation goals for individual metrics and each criterion. Equations and conservation targets for all metrics are included in Table 1. For ease of interpretation and to allow summarizing within a criterion, all scores were normalized to a range of 0 to 5, with 5 being the best score.

The metrics used in each criterion were linked by their properties and objectives. Hence, we opted to include a summary metric for each criterion to improve ease of interpretation of the results. The criteria scores were calculated by taking the average of the scores across the metrics included in that criterion. Because of differences in what the criteria measure, and in accordance with current consensus on multicriteria analytical methods, no effort was made to average across all criteria.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/7/eaar4313/DC1

Table S1. Surrogate parameters related to biodiversity and deep-sea ecosystem structure and function and examples.

Table S2. Raw values and performance metric scores.

Table S3. Climate change metric results.

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Acknowledgments: We thank F. Cardigos, G. Carreira, D. Freestone, M. Jungwiwattanaporn, M. King, P. Lourinho, C. Mann, H. Marques da Silva, G. Menezes, F. Porteiro, R. Serrao Santos, I. Shepherd, M. Silva, R. Tinch, S. van den Hove, and V. Zykov for the contributions to the development of the framework described in this paper. We also thank A. Sweetman for supplying the climate change models used in the performance assessment. We extend our appreciation to G. Le Gurun, S. Mulsow, and M. Lodge of the International Seabed Authority for the contributions to the SEMPIA process. **Funding:** The SEMPIA Workshops were supported by funding from the European Union Seventh Framework Programme (FP7/2007-2013) under the Managing Impacts of Deep-Sea Resource Exploitation (MIDAS) Project (grant agreement no. 603418), Direção Regional dos Assuntos do Mar, Governo Regional dos Açores, the Deep-Sea Conservation Coalition, the Pew Charitable Trusts, the Deep Sea Conservation Coalition, the Kaplan Fund, and Oceans 5. Work on the manuscript was supported through funding received by C.L.V.D., D.C.D., and P.N.H. from the Pew Charitable Trusts and, for these authors and D.J., from the Global Ocean Biodiversity Initiative through a grant from the International Climate Initiative (IKI). The Federal Ministry for the Environment, Nature Conservation, Building and Nuclear Safety supports IKI on the basis of a decision adopted by the German Bundestag. D.C.D. was also supported, in part, by the NF-UBC Nereus Program. T.M. was funded by Programa Investigador Fundação para a Ciência e Tecnologia (FCT) (IF/01194/2013/CP1199/CT0002 and UID/MAR/04292/2013). A.G. was supported, in part, by Russian Science Foundation grant 14-50-00095. A.C. is supported by Program Investigador (IF/00029/2014/CP1230/CT0002) from FCT. This study had also the support of FCT through the strategic project UID/MAR/04292/2013 granted to the Marine and Environmental Sciences Center (MARE). J.A.A.P. was supported by the National Council for Scientific and Technological Development–CNPq (process 310504/2016-3). M.C.R. was supported by CORAL–Sustainable Ocean Exploitation: Tools and Sensors (CIIMAR-NORTE 2020-ERDF). L.L. was supported, in part, by the JM Kaplan Foundation and was a co-lead of Deep-Ocean Stewardship Initiative and Deep Ocean Observing Strategy. **Author contributions:** C.L.V.D., T.M., A.C., D.C.D., and P.W. conceived the project. D.C.D., T.M., and P.N.H. undertook the Geographic Information System (GIS) mapping. D.C.D. extracted the feature data for performance assessment. R.J.E., C.R.S., L.A.L., D.C.D., and C.L.V.D. undertook the performance assessment. All authors contributed to iterative discussions, writing, and editing to the manuscript. D.D. and C.L.V.D. led those discussions and the writing and editing. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All geospatial information used in this analysis is publicly available. All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

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Submitted 9 November 2017
Accepted 23 May 2018
Published 4 July 2018
10.1126/sciadv.aar4313

Citation: D. C. Dunn, C. L. Van Dover, R. J. Etter, C. R. Smith, L. A. Levin, T. Morato, A. Colaço, A. C. Dale, A. V. Gebruk, K. M. Gjerde, P. N. Halpin, K. L. Howell, D. Johnson, J. A. A. Perez, M. C. Ribeiro, H. Stuckas, P. Weaver, SEMPIA Workshop Participants, A strategy for the conservation of biodiversity on mid-ocean ridges from deep-sea mining. *Sci. Adv.* **4**, eaar4313 (2018).

ENVIRONMENTAL STUDIES

Far from home: Distance patterns of global fishing fleets

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Postwar growth of industrial fisheries catch to its peak in 1996 was driven by increasing fleet capacity and geographical expansion. An investigation of the latter, using spatially allocated reconstructed catch data to quantify "mean distance to fishing grounds," found global trends to be dominated by the expansion histories of a small number of distant-water fishing countries. While most countries fished largely in local waters, Taiwan, South Korea, Spain, and China rapidly increased their mean distance to fishing grounds by 2000 to 4000 km between 1950 and 2014. Others, including Japan and the former USSR, expanded in the postwar decades but then retrenched from the mid-1970s, as access to other countries' waters became increasingly restricted with the advent of exclusive economic zones formalized in the 1982 United Nations Convention on the Law of the Sea. Since 1950, heavily subsidized fleets have increased the total fished area from 60% to more than 90% of the world's oceans, doubling the average distance traveled from home ports but catching only one-third of the historical amount per kilometer traveled. Catch per unit area has declined by 22% since the mid-1990s, as fleets approach the limits of geographical expansion. Allowing these trends to continue threatens the bioeconomic sustainability of fisheries globally.

INTRODUCTION

Distant-water fishing, that is, fishing in areas far removed from a country's domestic waters, existed well before the 19th century industrialization with, for example, Europeans fishing for Atlantic cod (*Gadus morhua*) off Newfoundland from the early 16th century (*1*) and Indonesians first fishing for *trepang* (sea cucumber) in northern Australia in the late 17th century (*2*). However, the practice accelerated with the deployment of the first steam trawlers around the British Isles in the 1880s (*3*). The increased fishing capacity of engine-powered trawlers led to greatly improved catches, but their introduction was soon followed by signs of depletion in coastal fish stocks and conflict with smaller inshore fishers (*4*). Vessels capable of moving further offshore did so, targeting less heavily exploited fishing grounds and beginning a process of progressive spatial expansion, first into the open North Sea, then south to the coasts of Spain and Portugal, and north into the North Atlantic waters around Iceland (*4*). The latter move ultimately led to a series of Cod Wars between 1958 and 1976, which culminated in the expulsion of British fishers from Icelandic waters (*5*). The industrial fleets of other developed countries followed similar patterns of expansion, interrupted only by wars and other crises (*6*, *7*). Increasing competition between domestic and foreign fishing vessels for national fisheries resources was one of the motivations behind the series of international negotiations in the 1970s and 1980s, leading to the adoption of the United Nations Convention on the Law of the Sea (UNCLOS) in 1982 (*8*). Key to UNCLOS was its permission for maritime countries to declare 200–nautical mile exclusive economic zones (EEZs), within which they have exclusive responsibility and control over resource exploitation, management, and conservation. Although UNCLOS did not come into force until 1995, countries began asserting their sovereign rights to fisheries resources in unilaterally declared EEZs or exclusive fisheries zones after the early rounds of UNCLOS III discussions began in 1973, and EEZ declarations accelerated in the 1980s. The expansion of sovereign claims to fisheries marked the beginning of the end of unrestricted and uncontrolled open-access fishing for distant-water fleets (*9*). However, this formalization of resource ownership and control affected the activities of the distant-water fishing fleets of major industrialized countries only briefly, as countries quickly moved to negotiate extensive access agreements for their fishing vessels, particularly in the waters of developing countries (*10*–*12*).

While a long history of expansion is well documented (*3*, *6*), the second half of the 20th century saw an unprecedented increase in catching power, as industrial fisheries reaped a peace dividend from wartime technologies such as LORAN [long-range navigation; a precursor to Global Positioning System (GPS)], radar, and sonar (*13*–*15*). The postwar period also marked the start, in 1950, of detailed record collection at the global scale by the Food and Agriculture Organization (FAO) of the United Nations (*16*). However, while a huge and laudable undertaking, the FAO data ultimately derive from the annual reports of flag states, which have differed greatly in quality and scope of the data submitted, both between countries and years. These data are characterized by poor spatial resolution.

The Sea Around Us addresses several shortcomings in the data reported by FAO on behalf of flag states by reconstructing unreported catches using complementary data sources and in-country expertise to extend and harmonize official reported data. This catch data reconstruction process also allows Sea Around Us data to separate wider-ranging industrial from relatively local artisanal, subsistence, and recreational fisheries (*17*–*19*). Furthermore, the sector-specific reconstructed catches have been spatially allocated to a half-degree latitude-longitude resolution spatial grid system, using both biological probability distributions for each taxon in the catch data sets and detailed information on EEZ fishing access agreements and available spatial catch information (*20*). These high-resolution spatial and temporal reconstructed catch data have allowed the geographical expansion of industrial fisheries over time to be quantified and visualized. Here, we have examined, for the first time, the trends since 1950 in the mean distances traveled to fish by the industrial fleets of the 20 largest fishing countries, collectively accounting for 80% of global industrial catches, and the trend in total industrial catch relative to the growth in the total area fished.

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RESULTS

Analysis of the mean distance traveled by the industrial fleets of the world's 20 largest fishing countries between their home countries and the locations where catches were taken illustrates three distinct patterns: rapid and largely continuous expansion (Fig. 1A), early expansion followed by stabilization or retrenchment (Fig. 1B), and limited or no expansion (Fig. 1C). The fishing fleets of Taiwan, South Korea, Spain, and China have continuously expanded their mean distance to fishing grounds by at least 2000 km since the 1950s, with the first three of these now fishing, on average, more than 3000 km from their home ports (Fig. 1A). These are globally operating distant-water fleets and flag states, accounting for nearly 20% of the global industrial catch over the last decade (Fig. 1A). Spain was already fishing, on average, nearly 1500 km from home at the start of global data records in 1950 (Fig. 1A), largely driven by the country's long history of fishing for Atlantic cod off the Canadian east coast. Five countries or former countries that currently account for about 27% of global industrial catches showed expansion during the early postwar decades but appear to have curtailed or consolidated their distant-water operations since then (Fig. 1B). This includes the former USSR, which had a large distant-water fleet during the 1950s and 1960s, operating, on average, more than 2000 km from home. In scale and early timing of expansion, the former USSR is only exceeded by Spain, South Korea, and Japan (Fig. 1, A and B). However, while Spain and South Korea have continued a fairly monotonic expansion, the countries of the former USSR began to retrench in the 1970s. Japan, after rapid postwar industrial expansion, also consolidated its fishing effort within the Indo-Pacific region starting in the 1970s (Fig. 1B). The remaining 11 of the 20 largest fishing countries, accounting for 33% of global industrial catches, have shown little or no expansionist efforts over the last 65 years (Fig. 1C). Norway has begun to fish relatively further afield in recent years, likely driven by the rapid growth in contribution of its Antarctic krill (*Euphausia superba*) fishery from <1% of the national total catch in 2006 to 7% in 2014 (www.seaaroundus.org). For the top 20 fishing countries, catches caught on the high seas or in the EEZs of other countries grew by more than 600% between 1950 and 2014, increasing their contribution to global catches from 16 to 23% over this period (www.seaaroundus.org). Catches by distant-water or "foreign" vessels have therefore grown faster than catches by countries within their own waters, illustrating the increasing importance of distant-water fishing among the countries that supply most of the world's wild-caught seafood.

Driven strongly by the trends in fishing distance among the 20 largest fishing countries, the net effect since 1950 is a global doubling of the mean distance fished from port (fig. S1). However, this net expansion has been associated with a strong decline in the catch obtained per kilometer traveled over the 65-year time period. Catches declined from more than 25 metric tons per 1000 km traveled in the early 1950s to approximately 7 metric tons per 1000 km traveled by 2014 (Fig. 2). The global industrial fishing catch increased fivefold between 1950 and its peak of 100 million metric tons in 1996 but has declined steadily by around 18% over the two decades since (Fig. 3A). In contrast, the percentage of total ice-free ocean area used for industrial fishing increased rapidly from 60 to 90% during the 1950s and 1960s, plateaued through the mid-1990s, and has expanded by less than 5% in the last two decades (Fig. 3B). The combination of these two patterns suggests that industrial catch per unit area of ocean fished expanded through peak catch in 1996 but has since declined by 22% (Fig. 3C).

A comparison of the spatial distribution of industrial catches between the 1950s and the 2000s illustrates and confirms the predominance of continental shelf waters as the source of most fish (Fig. 4, A and B). Expansions were most pronounced along the coasts and archipelagic waters of Southeast Asia, Africa, South America, and the South Asian subcontinent (Fig. 4, A and B). However, offshore and high seas waters have also become increasingly exploited in the past 65 years, with essentially no waters other than those at extreme high latitudes presently unfished to some degree (Fig. 4B).

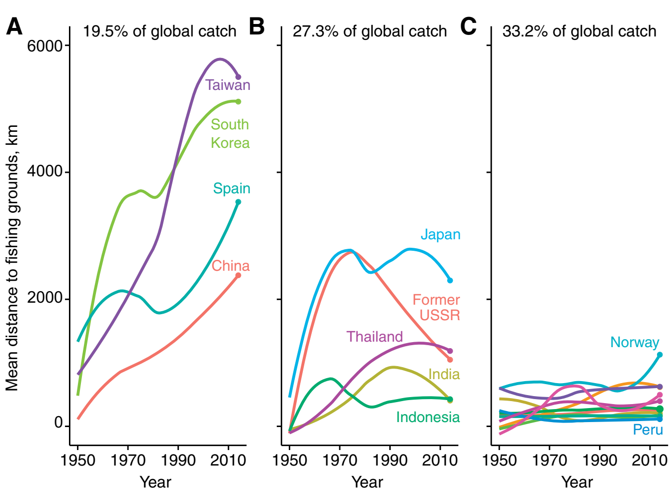

Fig. 1. Trends in the distance traveled to fish from 1950 to 2014. Mean distance to fishing grounds for the world's 20 largest industrial fishing countries (by tonnage) grouped by expansion history: (**A**) rapid and continuous expansion, (**B**) expansion followed by retrenchment, and (**C**) limited expansion. Percentage of global catch over the past decade is shown at the top of each panel. Countries not labeled in (C) are Argentina, Chile, Iceland, Malaysia, Mexico, Morocco, Philippines, and United States.

DISCUSSION

The trends in the spatial expansion of industrial fisheries and their overall catch together indicate that we may be approaching the physical limits of expansion in capture fisheries (Figs. 3B and 4). Similar concerns have been raised by work showing the rapidly growing proportion of marine primary productivity being redirected to human consumption (*6*).

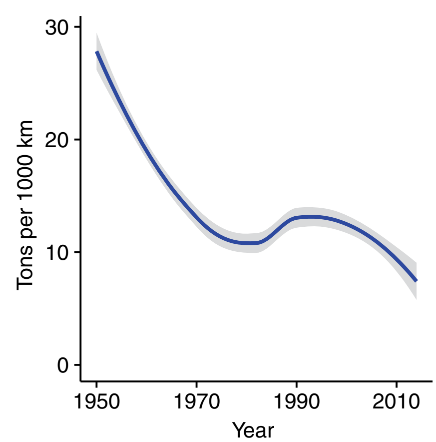

Fig. 2. Trend in mean global industrial catch per 1000 km traveled from 1950 to 2014. Gray band indicates ±95% confidence interval of LOWESS smoothed time series.

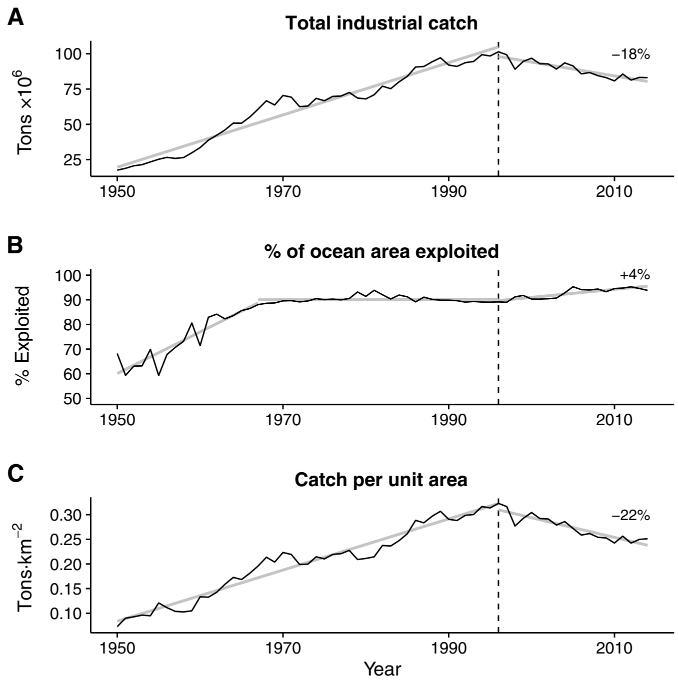

Fig. 3. Trends in total catch and area fished by global industrial fisheries, 1950–2014. (**A**) Global industrial fisheries catch (*8*), (**B**) percentage of ice-free ocean area exploited, and (**C**) industrial catch per unit ocean area. Dashed line indicates year of peak global catch in 1996, with percentage growth/decline since 1996 labeled on each time series.

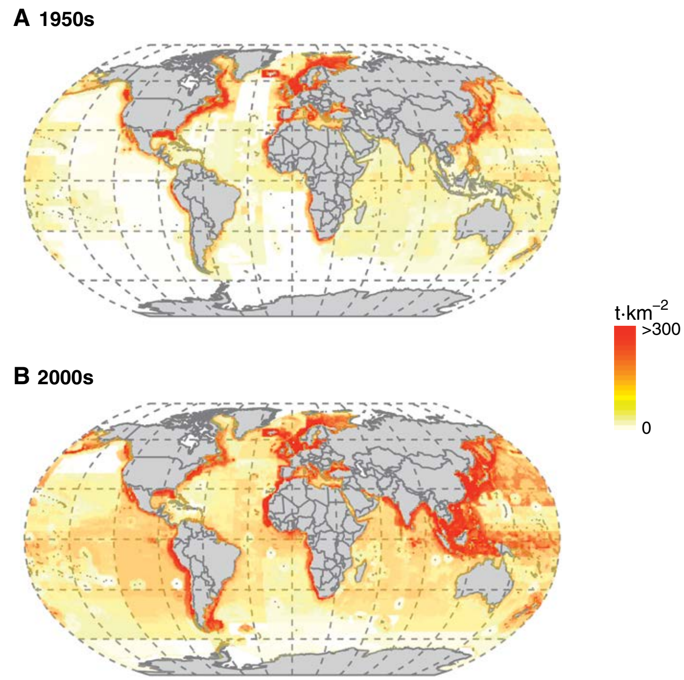

Fig. 4. Spatial mapping of the distribution and intensity of industrial fishing catch. Mean industrial fisheries catch in metric tons per square kilometer by catch location during the (**A**) 1950s and (**B**) 2000s.

The trends in catch and effort data presented here suggest that the continuous increase in global catches to peak catch in 1996 (*17*) resulted from a combination of intensifying fishing effort and geographical expansion, which together masked underlying declines in the stocks being targeted (*21*). Between 1950 and 1970, the fraction of the global ocean exploited by fisheries grew by half and catches increased strongly. We suggest that this continued expansion and the concurrent intensification of fishing effort sequentially depleted new areas of the ocean such that catches peaked in 1996 when the rate at which new stocks were discovered could no longer keep up with the declines in existing stocks (*17*, *18*, *22*). This mechanism of serial discovery and depletion of fishing grounds is exemplified by the correlation between time series of fishing pressure and ecosystem regime change in large marine ecosystems (*23*) and the "boom and bust" trends documented in deep sea trawl fisheries over the last 65 years (*24*). By our measure, total industrial catch per unit ocean area has declined by 22% since 1996, despite spatial expansion having continued, albeit slowly. Further expansion into the remaining accessible areas of the polar seas, even if it were ecologically justifiable, seems unlikely to reverse this trend (Figs. 3B and 4).

Distance trends observed here imply that most of the fishing countries concentrate their effort in relatively local waters, with Peru, for example, largely focusing on its domestic fishery for Peruvian anchoveta (*Engraulis ringens*) (*25*). In addition, several former distant-water fishing fleets either have retrenched to domestic or regional waters near home countries or have been reduced or abolished (Fig. 1, B and C). For example, the countries of the former USSR fished extensively in the waters of the southwest Atlantic and the EEZs of Argentina, Uruguay, and Brazil before the collapse of the Soviet Union with its state support of distant-water fisheries. They have since reduced their distant-water activities to concentrate on northeast Atlantic, European, and western Pacific waters closer to domestic ports (*23*). Japan, after rapid postwar expansion aimed at improving domestic food supply, began consolidating its distant-water fishing effort from the mid-1970s, as access to many of its traditional fishing grounds became increasingly restricted with the emergence of the EEZ regime and increasing competition from low-cost fishing countries. Rising domestic labor costs and growing wealth also shifted Japanese food supply policy toward imports, paving the way for fleet reductions and spatial retrenchments that have helped remaining Japanese distant-water fishing to be relatively profitable (*26*, *27*). For the few countries seemingly locked into the expansionist strategy, such as China and South Korea, distant-water fleets have become the mainstay of their industrial fisheries, with catches from outside their EEZs contributing 39 and 45%, respectively, of national total catches (www.seaaroundus.org). However, returns from this activity, in terms of catch per unit distance traveled, appear to have declined sharply, likely a combined result of declining fish stocks and the greater distances required to access them (Fig. 2). Long-haul distant-water fishing also incurs significantly higher fuel and crew costs (*28*) due to the long travel times to fishing grounds [for example, (*29*)]. To keep vessels fishing, fuel costs may be partly offset by generous government subsidies (*30*–*32*), and there is a good correlation between the distance a country fishes from home and the level of subsidies paid for fuel, vessel, and fleet support. In the case of Taiwan, these payments amount to more than 80% of the landed value of the industrial fishing catch (fig. S2). The relationship between subsidies and fishing distance suggests that expansion has been driven, in large part, by national policies that actively promote distant-water fishing through the provision of fuel and vessel subsidies. A recent analysis of the economics of high seas fishing found that profits from these activities for the major distant-water fishing countries would be greatly reduced, or even disappear completely, if fleets were not subsidized (*33*). While governments continue to subsidize fleet expansion, the labor costs of these operations can typically only be reduced by cutting back on crew numbers, pay, or working conditions, which may be contributing to the growing tally of human rights and labor abuses that have been recorded on fishing vessels (*28*, *34*). Illegal fishing and the use of flags of convenience can also serve to reduce the cost component for vessels suffering diminishing returns (*35*).

Continuing distant-water fishing activities are also increasingly viable only due to the growing number of refrigerated transshipment and resupply vessels (or "reefers") that allow individual fishing vessels to remain at sea for extended periods and avoid the fuel expenditure and lengthy breaks in fishing required to return to port or their home countries (*34*, *36*). However, by transshipping and aggregating catches, and thus allowing fishing vessels to avoid port visits, reefers may also facilitate the "laundering" of illegally caught fish and permit other crimes at sea to remain undetected (*37*, *38*). Transshipment also denies developing countries that host distant-water fleets (for example, in West Africa) the revenue from port activities and the processing and exporting of seafood associated with foreign fleets (*36*).

Our findings on the spatial expansion of industrial fishing are consistent with previous estimates by the Sea Around Us using only the FAO reported landings data (*6*). The spatial allocation of reconstructed fisheries data reported here assumes that fish are caught wherever a species' spatial distribution overlaps the operating sphere of a fishery targeting it, in proportion to its habitat preference–driven probability distribution (*20*). Therefore, this approach likely constitutes an upper bound to the current spatial coverage of fisheries, with some locations at the fringes of a taxon's distributional range likely not commercially viable for fisheries. For comparison, a recent analysis of vessel automatic identification system (AIS) data by Global Fishing Watch (GFW) and partners estimated that up to 73% of the oceans was fished in 2016, based on identifying gear-specific vessel movements assumed to indicate fishing activity and after taking into account spatial variations in AIS satellite coverage (*34*). Given that not all vessels carry or consistently use AIS transponders, for example, turning them off to preserve commercial secrecy around fishing grounds or during illicit activities, it is likely that the GFW figure is a lower-bound estimate of the area currently in use by industrial fisheries. Our analysis is able to provide historical context to the more precise but incomplete and temporally limited AIS data, showing how different countries have risen and fallen as distant-water fishing powers. The GFW study found that China, Spain, Taiwan, Japan, and South Korea dominate global industrial fishing effort; our results confirm that these five are also the world's most important distant-water fishing countries in terms of distance traveled (*34*). Collaborative research efforts combining AIS data and catch reconstructions will further refine our understanding of the spatial distribution of catch and effort in these fisheries.

Global catch per unit of effort has halved since FAO records began in 1950, despite a steady improvement in fishing power and technology (*39*). Our analysis corroborates this evidence of diminishing returns, showing that, while fisheries have extended their reach into all but the polar extremes of the global oceans, catch per unit area and per kilometer traveled have declined continuously for over two decades. Considered alongside the well-documented increase in the number of overfished stocks (*21*), these trends warrant an urgent reduction in fishing effort if declines in fisheries productivity are to be halted and reversed. Reducing the high levels of fuel and capacity-enhancing subsidies paid by fishing countries, in particular by the very small number of countries that fish the furthest from home (Fig. 1, A and B), would be a powerful first step in addressing our global overfishing problem and returning an element of economic rationality to commercial fisheries (*33*). Reducing the subsidies that enable unprofitable fishing on the high seas would also reduce income inequality among maritime countries (*40*). Fish are a vital component of global food and economic security, and further degrading the productive capacity of the oceans puts both at risk for hundreds of millions, if not billions, of people and increases the risk of fisheries conflict (*41*). As with other spheres of human endeavor, recognizing that there are physical limits to growth on a finite planet is vital to humanity's long-term well-being. The oceans, once thought boundless and inexhaustible, may at last now also be proving a barrier to our quest for endless growth.

MATERIALS AND METHODS

The data were extracted from the global reconstructed fisheries catch database of the Sea Around Us (*18*). All Sea Around Us data and associated documentation and descriptions are freely accessible and downloadable at www.seaaroundus.org. Data can also be accessed through an R package via the Sea Around Us GitHub site at https://github.com/seaaroundus/. These data consist of more than 270 country-level catch reconstructions that currently cover 1950–2014 and that account for all fishing sectors (industrial, artisanal, subsistence, and recreational) as well as landed and discarded catches (*42*). These reconstructed data include best estimates of all unreported catches by year, fishing sector, and taxon for each country, following the established and well-documented catch reconstruction methodology (*20*, *43*). It should also be noted that the baseline data for the Sea Around Us catch reconstructions are the data reported by member states to the FAO. Hence, all catches are assigned to a flag state (country) rather than that of the country of beneficial ownership. Thus, catch by vessels flagged to Togo but owned by a South Korean company, for example, will be assigned to Togo in both the original FAO data and the Sea Around Us reconstructed catch data. Had we been able to assign flag of convenience and open registry catches to beneficial owners, the average fishing distance of countries with significant numbers of foreign flagged vessels, such as Taiwan, Spain, and South Korea, would likely increase because, in many cases, those catches are treated as "local" catches of the flag state in our analysis rather than distant-water fishing by the beneficial owner country.

These reconstructed catch data sets were mapped onto a grid of $^1/_2° \times {}^1/_2°$ latitude and longitude cells overlaid over the global oceans to generate data for more than 150,000 oceanic grid cells. Allocations of catch data to individual cells take into account spatial variation in species' abundance, as well as political and historical accessibility of EEZ waters by the fleets of each fishing country (*20*). For the current analyses, only industrial sector data were used, as these represent the catches of fleets, including distant-water fleets, that fish domestically and internationally, that is, also outside of national EEZ waters. The nonindustrial catches from the small-scale artisanal, subsistence, and recreational sectors are excluded here as they are assumed to be spatially restricted to the inshore fishing areas within each home country's EEZ (*20*). Larger "artisanal" operators capable of operating further out to sea would be included as "industrial" vessels under the Sea Around Us classification [for example, the large semi-industrial pirogue fleets of Senegal that fish throughout many West African countries (*44*)]. Filtering for industrial fishing only, >62 million cell/fishing entity/catch/year allocation records were extracted from the Sea Around Us database, together with grid cell metadata (latitude and longitude of cell centroid and total water area). These data formed the basis for all spatial analyses. Catch locations were deemed to be spatially represented by the cell centroids.

Distances to fishing grounds were calculated from each relevant cell centroid to the nearest major port of each fishing country. Port locations were obtained from the World Ports Index (WPI) (https://msi.nga.mil/MSISiteContent/StaticFiles/NAV_PUBS/WPI/WPI_Shapefile.zip). For a small number of island fishing countries without port listings in the WPI, the geographical center of their landmass was used instead of port locations. Geographical centers for the relevant island entities were downloaded from the Center for International Development at Harvard University (https://sites.hks.harvard.edu/cid/ciddata/geographydata.htm).

The catch-weighted average distance between the major ports of each fishing country and fishing grounds (cells with catch taken by each country in question) was calculated for each fishing country and year as follows (fig. S3):

1) Catches were summed within each $^1/_2° \times {}^1/_2°$ grid cell (Catch in cell). The great circle distance from each grid cell centroid to the fishing country's nearest domestic port (Distance to cell) was then calculated using the function distGeo() in the R package geosphere.

2) The catch-weighted mean distance traveled to fish, for each country and year (1950–2014), was calculated as the weighted mean of all catch distances as follows

$$\frac{\sum_{i=1}^{180,000}(\text{Distance to cell}_i \times \text{Catch in cell}_i)}{\text{Total catch}}$$

The purpose of the calculation was to generate a measure that captured relative changes over time in geographic reach of the fisheries of the major fishing countries, and the distance measure derived here is therefore a simplification of the actual distances traveled by industrial fishing vessels. In particular, the great circle distance used here is the shortest straight-line distance between a country's major ports and the location of allocated fishing catches. This calculated distance thus ignored realities affecting actual vessel travel distances, including landmasses, shipping routes, and other navigational complexities. In addition, distances moved within a given $^1/_2°$ cell to achieve the catch within that cell (that is, smaller-scale "searching" and fishing operation patterns) were not included here. We also omitted factors that would likely reduce an individual vessel's actual distance to fish, such as temporary or seasonal "home-porting" in ports outside a vessel's flag country, or the use of support vessels for catch transshipment and refueling at sea.

The mean distance traveled to fish was visualized for the 20 largest fishing countries, as ranked by total catch. The fishing countries of the former USSR (Estonia, Georgia, Latvia, Lithuania, Russia, and Ukraine) were treated as a single fishing entity to capture the expansion history of the Soviet Union, given its significant role in postwar industrial fisheries. Distance trends for each country were plotted as smoothed time series using locally weighted regression (LOWESS) (*45*) with a span coefficient of 0.75, implemented in the stat_smooth() function in the R package ggplot2. Plots were grouped according to three distance trends over the 65-year time period: steady and rapid increase, initial increase followed by stagnation or decline, or little or no increase.

The mean fishing distance for the global industrial fleet in each year was calculated as the catch-weighted mean of all individual country fishing distances, as calculated above. A smoothed time series (±95% confidence interval) was plotted as per the method above. Tons of fish caught per 1000 km traveled were calculated by year for all countries' industrial fisheries by dividing the global industrial catch by the total distance traveled to fish by all countries, with individual country's fishing distances calculated using the methodology described above.

Total industrial catch and total area fished were calculated by summing total catch and total cell area with industrial catch by year for the entire data set. Only the water area of each cell was used, where cells crossed coastlines. The trend in total area fished was presented as a percentage of the total ice-free ocean area. This was taken to be the total ocean area, 361.9 million km^2, minus the combined mean summer minimum ice coverage for the Arctic and Southern Oceans of 9.6 million km^2 (https://nsidc.org/cryosphere/seaice/index.html). Total ice-free ocean area available to fish was therefore estimated to be 352.3 million km^2. Industrial catch per unit area (metric tons per square kilometer) was calculated as the total industrial catch divided by the total area fished in each year. The data were plotted as line charts overlaid with broken stick regression lines showing points of inflection in the trend lines, notably the point of peak fish in 1996.

The global geographical distribution of industrial catch was mapped for the first and last decades of the time series (1950–1959 and 2005–2014) by averaging total industrial catch in each cell for each 10-year period and plotting the resulting values as a spatially defined raster superimposed on the world map. Since the distribution of cell catch values was highly skewed, catch per unit area in each cell was color-coded using a logarithmic scale, to give greater visual resolution among the smaller values.

To examine the relationship between fishing distance and government subsidies, mean distance to fish was plotted against harmful (fuel and capacity-enhancing) subsidies as a percent of landings. Subsidies were taken from Sumaila *et al.* (*31*). The relationship was tested using linear regression, and the line of best fit (±95% confidence interval) was added to the scatterplot. All analyses were performed using the R Statistical Language and packages in RStudio.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/8/eaar3279/DC1

Fig. S1. Mean distance traveled to fishing grounds by the world's industrial fisheries.

Fig. S2. Mean distance traveled to fishing grounds versus harmful subsidies.

Fig. S3. Schematic of methodology used for great circle distance calculations.

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Acknowledgments: We appreciate the detailed and constructive reviews we received, which greatly improved the text. **Funding:** The authors acknowledge the support of the Sea Around Us and the Sea Around Us–Indian Ocean. All Sea Around Us activities are supported by the Oak Foundation, the Marisla Foundation, Oceana, the MAVA Foundation, the David and Lucile Packard Foundation, and the Paul M. Angell Family Foundation. **Author contributions:** D.P., D.Z., and J.J.M. conceived the analysis. D.T. analyzed the data, with support from M.-L.P., and produced the figures. D.P., D.Z., and D.T. wrote the manuscript, with reviews and edits by M.-L.P. and J.J.M. **Competing interests:** D.Z. is a member of the scientific advisory board of Denver (USA)–based NGO Secure Fisheries but receives no compensation or funding in this capacity. The other authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Data used in the analyses reported above are available upon request from the Sea Around Us (www.seaaroundus.org). Additional data related to this paper may be requested from the authors.

Submitted 26 October 2017
Accepted 10 July 2018
Published 1 August 2018
10.1126/sciadv.aar3279

Citation: D. Tickler, J. J. Meeuwig, M.-L. Palomares, D. Pauly, D. Zeller, Far from home: Distance patterns of global fishing fleets. *Sci. Adv.* **4**, eaar3279 (2018).

ENVIRONMENTAL STUDIES

Wealthy countries dominate industrial fishing

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The patterns by which different nations share global fisheries influence outcomes for food security, trajectories of economic development, and competition between industrial and small-scale fishing. We report patterns of industrial fishing effort for vessels flagged to higher- and lower-income nations, in marine areas within and beyond national jurisdiction, using analyses of high-resolution fishing vessel activity data. These analyses reveal global dominance of industrial fishing by wealthy nations. Vessels flagged to higher-income nations, for example, are responsible for 97% of the trackable industrial fishing on the high seas and 78% of such effort within the national waters of lower-income countries. These publicly accessible vessel tracking data have important limitations. However, insights from these new analyses can begin to strategically inform important international- and national-level efforts underway now to ensure equitable and sustainable sharing of fisheries.

INTRODUCTION

How nations share access to fish in the oceans significantly influences global food security, wealth distribution, competition between industrial and small-scale fisheries, and even international conflict. Globally, approximately 110 million metric tons of marine wild fish are caught annually, with an estimated annual value of over 171 billion USD for reported and unreported catch (*1*). Approximately 3 billion people receive 20% of their average intake of animal protein from aquatic animals, and in certain countries the per capita intake can be >50% (*2*). Contributions to human health from seafood-derived nutrients other than protein may be even more important. It has been estimated, for example, that 845 million people are currently at risk of experiencing deficiencies of essential micronutrients including zinc, iron, and vitamin A, a number expected to increase if projected declines in fisheries catch potential and per capita fish supply continue into 2050 (*3*). Conflict over fishery resource sharing has also shaped historical patterns of regional stability and promises to continue to do so in the near future (*4*, *5*). The dynamics by which we divide up global fisheries resources also shape competition between large-scale, capital-intense industrial fisheries and small-scale fisheries, with cascading effects upon the health, prosperity, and well-being of the communities that depend on small-scale fisheries (*6*–*8*).

Describing fishing patterns in comprehensive and quantitative terms, both in national waters and on the high seas, is challenging due to the lack of open access to detailed records on the behavior of fishing vessels. However, advances in machine learning technologies and big data capacity now offer us access to high-resolution fishing vessel activity from 22 billion automatic identification systems (AIS) points, processed by the Global Fishing Watch platform using convolutional neural network models (*9*, *10*). We analyzed these data to generate a global, fishery-independent assessment of the amount of industrial fishing effort conducted by vessels flagged to higher-income nations (that is, World Bank categories "high income" and "upper middle income" combined) and lower-income nations (that is, World Bank categories "lower middle income" and "low income" combined). We concentrate this analysis solely on industrial fishing (defined here as all vessels >24 m) (*11*) because industrial fishing is the dominant fishery on the high seas, it is much more readily visible via AIS data than small-scale fishing, and it globally accounts for an estimated 84 million metric tons and 119 billion USD [3.1 times more biomass and 2.3 times more revenue than smaller-scale artisanal fishing (*1*)].

Analyzing and communicating patterns of the distribution of fishing effort by different nations on the high seas are especially timely and important given the immediate opportunity to use these data to shape progress toward a United Nations treaty being developed for biodiversity on the high seas (*12*). Resources on the high seas are unique with respect to their governance, as they have been designated as international resources that are to be cooperatively managed. Currently, fisheries are overseen by regional fishery management organizations, but both geographic and taxonomic gaps in coverage exist (*13*, *14*). New insight derived from these big data analyses of high seas fisheries can help decision makers at the United Nations identify how different policy interventions may affect high seas stakeholders and can highlight which states have the most opportunity and responsibility for the development of this emerging treaty (*14*).

Understanding the distribution of fishing effort in a nation's marine Exclusive Economic Zone (EEZ) is also useful for policy-making, especially in the context of access agreements that allow foreign fishing in a nation's waters. Existing research has highlighted the fact that fleets from higher-income nations travel farther to fish after they deplete their own fish populations, increase their per capita fish intake, or otherwise experience increases in seafood demand (*15*). The increased capacity and improved technology characteristic of higher-income nations have also enabled these countries to build and operate their own distant water fishing fleets, and often to subsidize those fleets heavily (*16*, *17*). Lower-income countries usually lack the same capacity to industrially catch their fish populations and thus frequently enter into fishing access agreements with these wealthier countries, sanctioning foreign fishing within their national waters. There are numerous challenges

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that have been raised concerning the sustainability and equitability of these arrangements. For example, the benefits projected to accrue from these partnerships, such as revenue and investment in local technology and infrastructure, have not always lived up to their promise (*18*–*22*). In addition, lower-income nations have in some cases failed to adequately assess and manage their fisheries, including foreign exploitation (*17*). Addressing any shortcomings in these fishing access agreements has become even more pressing as concerns about food security have increased in the many areas of the world where people are nutritionally dependent on seafood and the sustainability of seafood supply is threatened by overfishing and climate change (*3*, *23*). It is now imperative to have a clear view of who is controlling access to fish within a nation's EEZ and whether fish as food are making it to the food insecure. Quantitative and open assessments of the degree to which foreign fishing occurs, particularly within the waters of lower-income nations, can help diverse stakeholders more thoughtfully engage in national-level conversations about fishery resource sharing.

The AIS-derived measures of fishing effort have proven uniquely insightful. They have been used for marine protected area surveillance (*9*), to examine how environmental variability shapes fishing behavior (*10*), to quantify the overlap between marine wildlife and fisheries (*24*), and to assess the economic costs and benefits of high seas fishing (*25*). However, AIS presently does not detect all industrial fishing effort and has a number of limitations. As a means of quantitatively evaluating these potential biases and gaps, we (i) directly compared differences between fishing activity detected using AIS and traditional national-level published registries of industrial fishing vessels; (ii) compared patterns of fishing effort detected using the open AIS data and closed access proprietary vessel monitoring system (VMS) data voluntarily shared by a lower-income nation, Indonesia, which hosts the largest industrial fishing fleet of all lower-income nations; and (iii) compared our AIS-estimated fishing effort outputs against measures of fishing catch drawn from the Sea Around Us database (including newly updated high seas catch estimates) (*1*, *25*). Our examination of biases using these methods provides a first means to constructively contextualize and cautiously interpret these AIS-derived patterns.

The outputs from our analyses reveal profound heterogeneities in the distribution of AIS-detectable industrial fishing effort. Overall, these results present a valuable quantitative and open opportunity for diverse stakeholders to reexamine a number of important questions surrounding how marine fisheries resources are globally shared. Results such as this may assist in constructively designing policies for marine areas both within and beyond boundaries of national jurisdiction that promote responsible and equitable sharing of the wealth, food, and biodiversity found in our oceans.

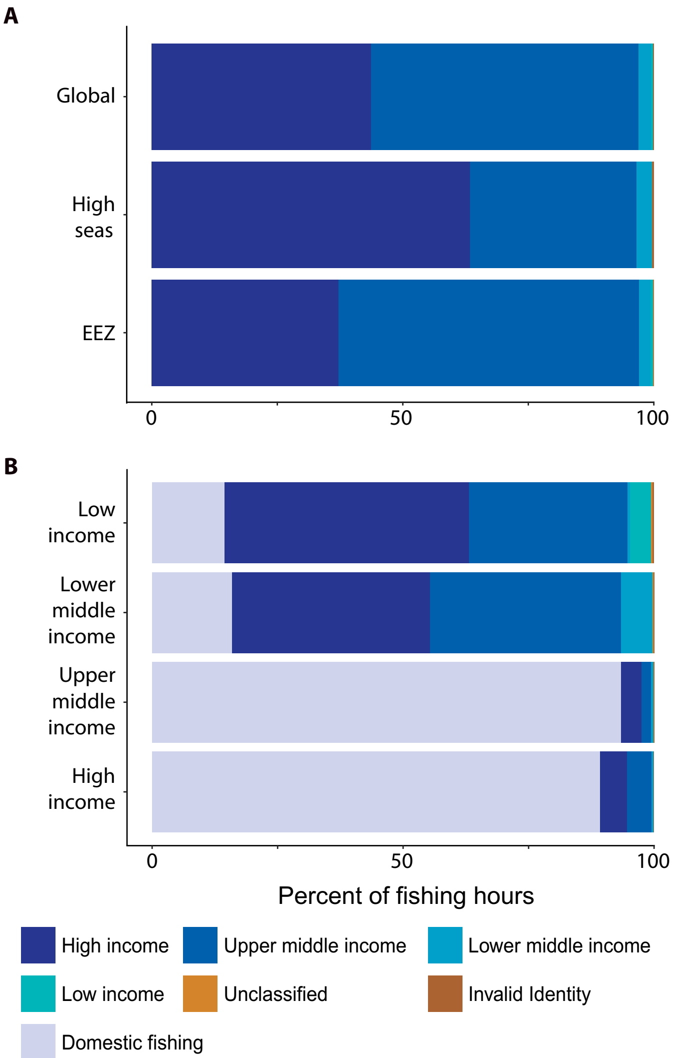

Fig. 1. Distribution of industrial fishing effort by vessels flagged to nations from different income classes as measured using AIS data and convolutional neural network models. (**A**) The percent of fishing effort (measured in fishing hours) detected globally on the high seas and in all EEZs for vessels flagged to nations from four different World Bank income groups. (**B**) The percent of AIS-detected industrial fishing effort in all EEZs, grouped by the World Bank income groups of the EEZs. Here, the category Domestic fishing is included, which refers to instances when a fishing country was fishing in its own EEZ. Other categories represent foreign fishing effort conducted within an EEZ by a nation flagged to one of the four World Bank income classes. "Invalid identity" refers to vessels with a Maritime Mobile Service Identity (MMSI) number that did not accurately refer to an individual country. "Unclassified" refers to fishing entities that were fishing in an EEZ but did not have a World Bank income group. All data presented here are summarized from the year 2016.

RESULTS

High seas

An analysis of all AIS-detectable fishing effort identified on the high seas using convolutional neural networks during the years 2015–2016 revealed that industrial fishing effort was dominated by vessels flagged to higher-income nations, with less than 3% of effort attributed to vessels flagged to lower-income nations (Figs. 1A and 2 and fig. S1A). These patterns remain consistent when each of these years is analyzed individually and when measuring AIS-detectable fishing effort in terms of fishing days rather than fishing hours for 2016 (Fig. 1 and figs. S1 and S2). The spatial distribution of this industrial fishing effort in 2016 was summarized at the global level (Fig. 2) and by ocean basin (fig. S3) and reiterates the spatial dominance of vessels flagged to higher-income countries across the high seas. The majority of all AIS-detectable high seas industrial fishing effort was detected in the Pacific Ocean (61%), followed by the Atlantic Ocean (24%) and the Indian Ocean (14%; fig. S3).

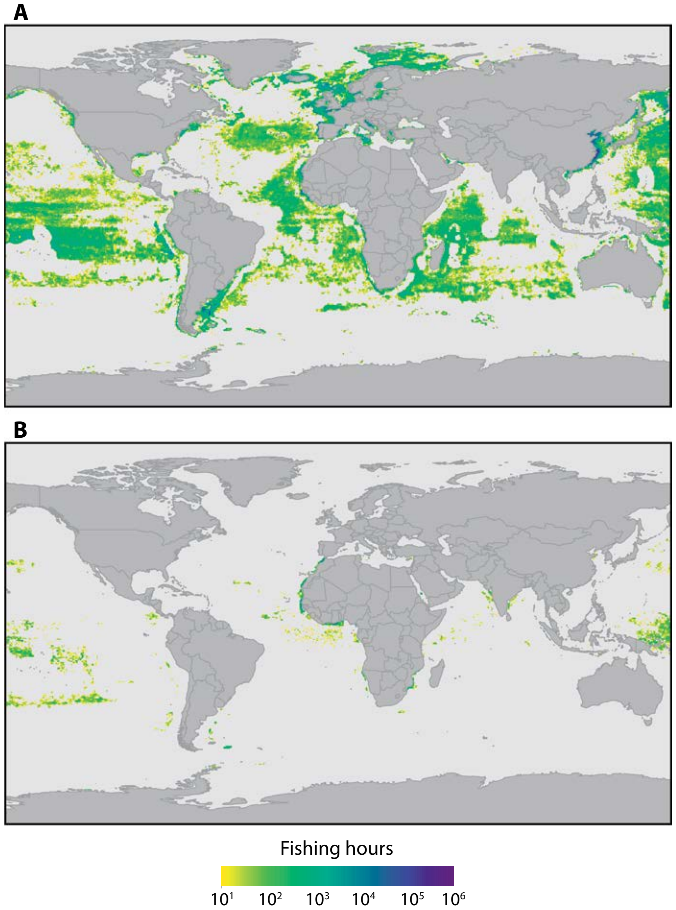

Fig. 2. Density distribution of global industrial fishing effort, derived using AIS data. (**A**) Vessels flagged to higher-income countries and (**B**) vessels flagged to lower-income countries. Industrial fishing effort is estimated using convolutional neural network models and plotted as the $\log_{10}$ number of fishing hours.

National waters

Globally, vessels flagged to higher-income nations made up the vast majority (97%) of all industrial fishing effort detected in EEZs for 2016 (Fig. 1A). In the EEZs of higher-income nations, fishing effort was predominantly attributed to each nation's domestic fishing fleet, making up 89% of fishing effort in high-income EEZs and 93% of fishing effort in upper middle–income EEZs. Conversely, domestic fishing made up very little of the overall fishing effort in lower-income nations. Eighty-four percent of the industrial fishing effort in lower-income EEZs was conducted by foreign countries, with the majority of this industrial fishing effort (78%) from vessels flagged to high- and upper middle–income nations. Most AIS-detectable industrial fishing effort that was observed within all EEZs was detected in the Pacific Ocean and the Atlantic Ocean (60 and 35% of total fishing effort observed in all EEZs respectively; fig. S4). Patterns were consistent across the 2 years studied with nearly identical patterns recorded in 2015 (fig. S1B).

Evaluating gaps and sensitivity of AIS coverage

In an effort to begin to evaluate the level of vessel coverage afforded by the above reported AIS-derived measures of fishing effort, we compared the number of unique industrial fishing vessels categorized as actively fishing in the Global Fishing Watch vessel database to the total number of industrial fishing vessels recorded in the Food and Agriculture Organization of the United Nations (FAO) vessel registry (*10*). During the period of our study, we detected a global total of 30,469 active vessels matching our definition of industrial fishing (that is, >24 m in length). This figure represented 59% of the global total number of fishing vessels >24 m logged in the FAO registry (fig. S5). Alignment of vessel counts between these two data sets was stronger for vessels flagged to higher-income nations than lower-income nations.

When we conducted the same AIS-based analyses including smaller-sized vessels (industrial fishing threshold defined at >12 m instead of vessels >24 m), our conclusion that higher-income vessels dominate industrial fishing on the high seas and within EEZs was only further confirmed (fig. S6). As a means of assessing and potentially adjusting for possible lower AIS detection rates of industrial fishing vessels in lower-income nations, we compared AIS-derived estimates of industrial fishing during 2016 to closed access VMS-derived estimates of industrial fishing from data shared voluntarily by Indonesia. Both the number of individual industrial fishing vessels and the amount of estimated fishing effort were found to be lower in AIS estimates than in VMS estimates for Indonesia (fig. S7). When these calculated AIS/VMS differences for Indonesia were used to create correction factors for lack of AIS vessel visibility for other lower-income nations (see Supplementary Materials and Methods), this increases the amount of projected lower-income fishing effort on the high seas and within the waters of lower-income EEZs (fig. S8). However, even when these VMS-informed corrections are included, these results do not qualitatively change the directionality or bulk conclusions of the patterns reported in the AIS-only results, namely, that vessels flagged to higher-income nations dominate industrial fishing effort on the high seas, within EEZs globally, within low-income EEZs (64%), and nearly dominate within lower middle–income EEZs (48%).

Comparison of AIS-derived fishing effort and reconstructed catch data

When comparing 2016 AIS-derived industrial fishing effort for all vessels >24 m and catch reconstructions from 2014 (most recent year available), we found moderate and variable congruence. In the case of the high seas, the same five top-ranked flag states were listed for both AIS-derived estimates of fishing effort and the newly updated reconstructed catch. The combined activity of these five states on the high seas made up 86.3% of all AIS-derived industrial fishing effort (fishing hours) and 59% of all of the reconstructed catch (metric tons).

In the case of EEZs, we again compared overlap between the vessel flag states on the top five lists for both AIS-measured fishing effort and reconstructed catch data. In 53 such comparisons (table S1), we observed a mean of 2.2 flag states that were present on both lists (that is, 2.2 of 5 possible flag states in common between AIS-measured effort and catch reconstruction top five lists) and a median of two flag states on both lists. In addition to these comparisons, we compared the proportional contribution with respect to amount of AIS-measured fishing effort and reconstructed catch data for flag states that matched on both top five lists. The strength of these matches varied by EEZ income category. In the case of high-income EEZs, flag states appearing on both the top five lists for AIS effort and catch reconstruction data contributed an average of 81% of AIS-detected fishing effort and 85% of the reconstructed catch. In contrast, in low-income countries, these flag states on both top five lists contributed on average 35% of AIS-detected fishing effort and 50% of the reconstructed catch.

DISCUSSION

The new view afforded from this open AIS-based analysis of global fishing activity reveals stark levels of unevenness with respect to wealth class for industrial fishing effort. Globally, 97% of all industrial fishing effort detectable using AIS (on the high seas and within EEZs) comes from vessels flagged to higher-income nations—or 23 million total hours of industrial fishing effort in 2016. This same pattern of dominance by higher-income nations repeats itself on the high seas, within the EEZs of higher-income nations, and within the EEZs of lower-income nations.

On the high seas, 97% of all such fishing effort detectable by AIS is conducted by vessels flagged to higher-income nations. Dominance of this high seas industrial fishing effort at the level of flag nation was highly uneven. The vast majority (86%) of this effort can be attributed to only five higher-income countries/entities, in rank order (high to low; table S2): China, Taiwan, Japan, South Korea, and Spain. When China and Taiwan are analyzed together, they account for approximately 52% of the industrial fishing effort we detected on the high seas, which, by reference, is an amount approximately 12 and 27 times greater than the high seas fishing effort detected for the United States and Russia (two other large nations), respectively. The only two lower-income nations that ranked among the top 20 nations with the highest amount of AIS detectable industrial fishing effort on the high seas were Vanuatu and Ukraine (both lower middle–income nations). Vanuatu is a nation with an open vessel registry (colloquially known as a "flag of convenience") that has been reported to include many vessels owned and controlled by higher-income foreign nations (*26*). The majority of the Ukraine fleet is owned by the Ukrainian government.

We observed strong dominance of vessels flagged to higher-income nations with respect to industrial fishing effort on the high seas in all ocean basins (fig. S2). The majority of the industrial fishing effort we identified on the high seas was observed in the Pacific Ocean, a pattern likely reflecting the intensity of tuna fisheries in the Pacific. Overall, these AIS-derived estimates for the distribution of industrial fishing effort on the high seas are qualitatively similar to other estimations created by key actors tracking industrial fishing on the high seas. For example, quantitative assessments of fisheries landings and estimations of the value of these landings likewise suggest that wealthy nations dominate fisheries resources on the high seas (*27*).

Very similar dominance patterns were reported in our analysis of the world's EEZs, where the majority of AIS-detectable industrial fishing effort within national waters was executed by vessels flagged to higher-income nations. We emphasize, however, that a strongly divergent pattern emerges from our analyses of fishing effort density within the EEZs of higher- and lower-income nations. The vast majority of AIS-detected fishing effort within the EEZs of higher-income countries came from their own fishing fleets (Fig. 1). Nearly the inverse was true for lower-income nations, where foreign fishing vessels (mostly flagged to high- and upper middle–income countries) dominated the industrial fishing effort in their EEZs. Most of the industrial fishing effort in lower-income EEZs was conducted by foreign countries, with the majority of this effort from vessels flagged to high- and upper middle–income nations. As an example of this dichotomy, the vast majority of the AIS-detected industrial fishing in high-income Spain's EEZ (96%) was recorded from vessels flagged to Spain. In contrast, in low-income Guinea-Bissau, the vast majority of the industrial fishing effort we detected came from foreign flagged vessels (95%), including 45% from Spain (table S1). Globally, the three countries showing the greatest fishing activity in other nations' EEZs were (from high to low) China, Taiwan, and South Korea. China and Taiwan together accounted for 44% of this global foreign fishing (table S3). We detected fishing effort from China alone in the marine waters of approximately 40% of all non-landlocked nations (n = 60 distinct EEZs). China, Taiwan, and South Korea (from high to low) also carried out the highest amounts of foreign fishing effort recorded globally in lower-income EEZs, or approximately 63% of all such effort detected (table S4). There are certainly exceptions to the bulk pattern of higher-income dominance of fishing effort in lower-income EEZs. In some lower-income nations, such as India, there was virtually no detectable higher-income fishing within their EEZs. These patterns may be explained in part by national legislation prohibiting or limiting foreign fishing within such EEZs, but could also result from joint fishing regimes occurring within these EEZs.

The patterns of industrial fishing effort within EEZs derived using these AIS-based techniques reinforce and extend conclusions drawn elsewhere using other methodologies and data sources. For example, analyses of fisheries production and trade data reveal a persistent trend whereby wealthy nations fish in the waters of less wealthy nations, but not vice versa (*28*, *29*). The relatively recent emergence of the capacity to track industrial fishing effort using AIS prevents examination of the history of this buildup. Elsewhere, however, it has been suggested that the ascendancy in dominance of more wealthy nations fishing within the waters of less wealthy nations (for example, Europe in Northwest Africa) has occurred within the last several decades (*28*).

Our AIS-derived estimates of industrial fishing effort agree, in some but not all instances (table S1), with published catch reconstruction data (*1*). Differences in governance appear to explain some of the deviation between these two data sources. For example, in high-income nations in the European Union, where laws and enforcement of AIS regulation in national waters are strong and compliance is expected to be high, we see high congruence among the top five countries in AIS and catch reconstruction estimates of fishing activity, and these top-ranked countries often contributed the vast majority of the overall effort (table S1) (*10*). However, in lower-income nations where enforcement of AIS regulations is sometimes, but not always, lacking, there were many examples of poor alignment. In Sierra Leone's EEZ, for example, vessels from Italy and China were the top rank–ordered fishing entities recorded using AIS, making up 90% of this fishing effort, while reconstructed catch data estimated that the two most active nations, Sierra Leone (domestic fishing) and Russia, caught 93% of the total catch. Explanations for this discrepancy include the following: that industrial fishing vessels flagged to Russia and Sierra Leone were not transmitting AIS; that cancellation of a World Bank project in the region that occurred during this period may have reduced capacity for monitoring, control, and surveillance (MCS) activities (*30*); an increase in illegal fishing displaced from Guinea's EEZ to the north due to increased MCS there (*31*); that top nations observed fishing using AIS (for example, Italy and China) were not reporting catch; or that there is extreme year-to-year volatility in the players involved in industrial fishing in Sierra Leone, which complicates comparisons of the 2014 catch data to the 2016 AIS-derived effort data. The difficulty of interpreting year-to-year volatility in Sierra Leone fishing activity was further increased by the Ebola outbreak that occurred in the region during this period, which necessarily diverted attention from traditional fisheries reporting and enforcement efforts and may have accelerated levels of foreign fishing (*30*). Another general explanation for some of the observed deviations between the AIS and catch reconstruction measures of industrial fishing in other contexts may derive from the fact that the catch reconstruction data will, in some cases, reassign catch from vessels flagged to a particular country to the nation of origin or ownership for the vessel. In the Seychelles, for example, catch from Seychelles-flagged, foreign-owned vessels was assigned in the catch reconstruction data to these foreign countries or to the category "unknown fishing country." A large portion of the catch in the unknown countries category is likely to be from Spain, as large Spanish fishing companies own Seychelles-flagged fishing vessels or otherwise operate in the Seychelles under access agreements. Although three of the five top fishing nations were listed in both the AIS and catch reconstructed measures for the Seychelles, the amount of effort attributed to each nation varied. In the AIS measure of fishing effort within the Seychelles EEZ, Taiwan was responsible for 64% of the observed fishing effort followed by the Seychelles-flagged fleet with 25% of the observed fishing effort. Meanwhile, the catch reconstruction data listed "unknown fishing country" for 68.8% of all catch in the Seychelles, followed by Taiwan at 20%; the Seychelles-flagged fleet was listed in fourth place, responsible for 0.4% of all catch in their own EEZ.

In these AIS-based analyses of fishing effort, we did not attempt to differentiate between legal and illegal fishing effort. We wish, however, to directly call attention to the fact that illegal and unreported fishing constitutes an important fraction of the global industrial fishing effort that occurs worldwide. For example, by some estimates, IUU (illegal, unreported, and unregulated) fishing has historically accounted for, on average, 18% of global catch (*32*). Determining, however, which of the vessels that we tracked in this analysis using AIS were legally permitted to fish in any given domain of ocean is hampered by a lack of transparency and disclosure for many fishing access agreements (*19*). Furthermore, while some illegal fishing is detectable using AIS data (*14*), certainly much illegal and unreported industrial fishing is conducted by vessels lacking or improperly using AIS [often in contravention of International Maritime Organization (IMO) and national maritime regulations] and cannot be tracked. It is difficult to predict exactly if and how inclusion of illegal and unreported fishing behavior would affect the patterns we report. Many high-profile cases have been noted of higher-income nations illegally fishing in lower-income EEZs (for example, European and other more wealthy states illegally fishing in West Africa) (*30*). However, illegal fishing is perpetrated by vessels flagged to both higher- and lower-income nations.

Given our direct focus on industrial fishing, this analysis wholly omits any consideration for patterns of catch by artisanal or other small-scale fishing fleets. The focus on industrial fishing in this analysis should not be meant in any way to discount the importance of small-scale fisheries, particularly the vital role they play in coastal community health and food security. For example, it has been estimated that small-scale fisheries may contribute between 25 and 30% of global catch (*33*) and are the source of a large fraction of fish that make it into the diets of local and regional communities. The patterns that we highlight of extensive industrial fishing from vessels flagged to foreign wealthy nations in the EEZs of less wealthy nations are likely to directly affect the future of many artisanal fisheries. It is known in many regions that industrial fisheries can outcompete smaller-scale artisanal fishing, a potentially undesirable outcome in areas where small-scale fisheries use less fuel, are less ecologically damaging, and provide more food and jobs to local communities (*6*–*8*).

Our analysis also does not differentiate between gear types used by industrial fishing vessels. Self-reporting of gear type in AIS data suggests that our pooled analysis of global industrial fishing is dominated numerically (that is, proportion of unique vessels) by trawlers, purse seiners, and longline vessels. Certainly different gear types fish in different ways, which may complicate our estimations of fishing effort made using fishing hours; for example, the extreme time efficiency of purse seiners setting rapidly upon fish aggregating devices is not comparable to more time-intensive fishing methods, such as longline fishing. To investigate the sensitivity of our conclusions to this choice of fishing hours as our currency of measure for fishing effort, we reanalyzed our data measuring fishing effort in the time currency of fishing days. Effort analyses made using fishing days did not change the direction or pattern of our major conclusions for the high seas or within national waters (fig. S2).

We highlight here three major shortcomings of using AIS. First, international and national regulations for the use of AIS and enforcement of these regulations are insufficient in many parts of the high seas and in many EEZs. Many countries adhere to IMO requirements on AIS usage; however, the specifics by which these regulations are codified into national law vary widely, with examples of strict and lax regulation found among both higher- and lower-income nations (see table S5) (*9*). Second, industrial fishing vessels in lower-income nations may be less likely to carry and use AIS for reasons unrelated to AIS policy. We note that we detected fewer vessels using AIS than are represented on FAO vessel registries and that there is less AIS visibility for vessels registered to lower-income nations (fig. S5). There are a variety of explanations for these discrepancies. For example, some vessels listed by the FAO may have been inactive during our study or regional officials may have overreported fleet sizes to emphasize local growth. By using VMS data derived from Indonesia, we were able to conservatively estimate upper bound corrections for AIS underreporting in lower-income nations (figs. S7 and S8). This correction, however, only increases the global contribution of lower-income fishing on the high seas by approximately 6% and within the EEZs of lower-income nations by 29%. A third potential weakness of AIS stems from reliance on a vessel's reported maritime identification digits (MID) to identify flag state. These MID are typically self-reported and may be entered incorrectly. This also relates to the larger, well-known problem of flag states not always corresponding to the state of vessel control or owner residence [rates estimated at 22.4% based on one analysis (*26*)], as many vessels operate with flags of convenience to take advantage of lower operational costs, less regulation, and reduced tax liability (*26*, *34*). Consequently, many vessels that we class in this analysis as flagged to lower middle– or low-income nations may actually have economic ties that are more closely aligned with higher-income nations. A related important nuance not treated in our analysis is that we do not track the actual firms or companies that own or fund the vessels observed through AIS, despite the influence that these firms have over vessel behavior.

Collectively, some of these uncertainties and potential biases inherent to AIS data may act to overestimate fishing effort from higher-income nations (for example, reduced visibility of smaller vessels from lower-income nations), and some may act to underestimate higher-income nation fishing effort (for example, a large number of vessels originating from higher-income nations flagged to lower-income nations known as flags of convenience). Our general conclusion that vessels flagged to higher-income nations dominate industrial fishing on the high seas and within EEZs largely persisted when we aggregated effort by day instead of fishing hour (fig. S2), retested our conclusions using a smaller size threshold (that is, >12 m) for defining industrial fishing vessels (fig. S6), and added a VMS-informed correction for undetected fishing effort in lower-income nations (figs. S7 and S8). Nevertheless, responsible interpretation of the new patterns we report using AIS requires direct consideration of all the aforementioned potential weaknesses and uncertainties.

These AIS-based analyses find that vessels flagged to higher-income nations dominate industrial fishing within the EEZs of lower-income nations. This observation requires explicit consideration in the analysis of development policy and strategy where fisheries governance intersects with food and nutrition policy, trade policy (export promotion, import substitution), wealth creation and economic growth, job creation, and technological innovation. There has been considerable productive and healthy debate concerning how the dominance of higher-income fishing in lower-income nations EEZs shapes these agendas (*19*, *21*, *28*, *35*). These perspectives are diverse and sometimes conflicting.

On one side, many researchers and managers have expressed unease concerning the potential vulnerabilities that may be created by concentrating dominance over fisheries in the hands of a few wealthy nations. These groups sometimes refer to this skew in control over marine resources as "ocean grabbing" or "marine colonialism" and connect the potential risks involved to those often associated with the practices of land or resource grabbing that occurs when wealthy foreign nations or foreign companies take control of terrestrial or agricultural resources or infrastructure in less-wealthy nations (*36*). Concerns in these discussions about food sovereignty relate to the rights of local people to control their own food systems, including the ecological dynamics, production pathways, and markets underpinning these systems (*37*). These issues are particularly pronounced in nutritionally sensitive areas like West Africa. Guinea, a low-income nation that is heavily reliant nutritionally on seafood, presents an apt example. Approximately 75% of Guinea's population (an estimated 10.1 million people) may be vulnerable to micronutrient deficiencies in future scenarios with reduced access to seafood, making it one of the most nutritionally vulnerable countries in the world to losses of seafood (*3*). In this analysis, we estimate that over 80% of the industrial fishing effort we detected in Guinea's EEZ came from China (table S1), a situation that presents potential challenges. Many argue that a rights-based approach focusing on the human right to adequate food would lead to greater retention of important nutritional resources in lower-income nations, ensuring healthier diets, reduced rates of malnutrition, and increased access to foods of cultural importance (*38*). Significant concern has also been raised about how corruption in some lower-income nations may facilitate misuse of fisheries access payments that prevent such cash from constructively aiding health, development, and growth goals of these nations (*17*, *19*–*21*). Policy options for meeting rising demand for fish in the Pacific region include actions such as diverting some of the tuna currently exported (and captured mostly by foreign fishing vessels) onto domestic markets of lower-income states (*39*). Another possible opportunity for intervention for stakeholders concerned about foreign dominance of industrial fishing in their national waters derives from the open nature of the data we report and the transparency it fosters. Access to these publicly accessible data feeds creates opportunities for all citizens in lower-income nations to put meaningful questions to their local leaders regarding sanctioned and unsanctioned foreign industrial fishing in their home waters.

Others have argued that allowing higher-income nations to dominate fisheries presents a desirable and efficient pathway for developing nations to turn their natural capital (for example, fish resources) into financial capital (for example, access fees, license fees, taxes, foreign exchange earnings). Building up a domestic industrial fishing fleet, maintaining it, and servicing it require port infrastructure, a trained workforce, processing and handling capacity, and considerable financial capital—all of which can be challenging to mobilize or lacking in many fish-rich lower-income countries. Kiribati provides an example of a country where arguments have been made for the efficiency of translating fish into cash. Kiribati is a lower middle–income nation for which we determined that 99% of the industrial fishing effort within its EEZs was delivered by foreign flagged vessels, with the majority of this effort (91%) coming from higher-income nations. Kiribati reported generating 121.8 million USD in 2016 by selling access to fishing rights in its EEZs, with similarly substantial revenues collected in surrounding years (*39*, *40*). Generally, it is not entirely clear that allowing industrial fisheries from wealthier countries to dominate offshore fisheries within less-wealthy nations' EEZs always has negative food security impacts. The efficiencies of industrialized fisheries allow them to put large quantities of lower-cost fish onto the global market, and this results in a net import of lower-priced processed fish from wealthier nations to poorer nations that, in terms of overall per-capita supply, may help counterbalance the net movement of higher-priced fish from poorer to richer countries (*35*, *41*). Much of the lower-value fish that is eventually exported back to lower-income nations are small pelagic fish that are particularly nutrient rich (for example, canned anchovetas, sardines, herrings, and mackerels), and while there is concern that an increasing proportion of these fish are going toward aquaculture and livestock feeds (*42*), this may represent an important nutritional benefit to developing countries. The global industrial fishing fleet thus plays a part in maintaining and enhancing the contribution of fish to meeting micronutrient requirements in lower-income populations in developing economies (*35*).

The capacity to view and analyze large portions of publicly accessible data that reveal how the world divides up a major global resource, like marine fish, is unique. Analogous sources of detailed insight are not, unfortunately, available for other environmentally, socially, and economically important large transnational resource harvest domains, such as logging or mining. The results presented in this analysis represent data-driven hypotheses surrounding distributions of industrial fishing effort that can be thoughtfully considered during the ongoing high seas biodiversity treaty proceedings at the United Nations and by regional fishing management organizations. This information can help these leaders more effectively pursue shared goals for maximizing equity, food security, and sustainability on the high seas in the near future. These patterns also help to clearly identify which states may stand to win or lose from alterations to the current order of high seas biodiversity management and highlight how the hegemonic powers in high seas fishing can constructively assume more responsibility in leading toward this improved future. Observations of the apparent dominance of wealthy foreign nations in the EEZs of less-wealthy nations can similarly empower and inspire both citizens and leaders in these regions to have more constructive discussion about best pathways toward securing sustainable and equitable futures for their domestic fisheries. These data also provide an improved understanding of the scope for potential competition between foreign industrial fleets flagged to wealthy nations and domestic small-scale fisheries—competition that is known to create numerous challenges for affected small-scale fisheries and the stakeholder communities linked to these fisheries (*6*, *7*, *42*). The extent and lopsided nature of the dominance of higher-income flag states in industrial fishing can and should also inform ongoing conversations about how fisheries subsidies reform can potentially curb socioecological abuses associated with distant water fishing (*25*). Addressing all of these issues is a time-sensitive matter. Significant stresses are likely to be placed very soon upon the food future and political stability of many of the marine regions where we highlight greatest levels of imbalance in regimes of industrial fishing (*3*–*5*). Success in meeting these challenges on the high seas and within EEZs will matter both for the future of fisheries and the many stakeholders whose economic bottom lines, nutrition, and well-being depend on sustained long-term use of these resources.

MATERIALS AND METHODS

AIS-based characterization of fishing effort

To increase the transparency surrounding control over global fisheries and the benefits that can be derived from fishery resource sharing agreements, we used a big data approach to undertake a global fishery-independent assessment of industrial fishing effort by vessels flagged to higher- and lower-income countries. Use of AIS is required by the IMO for all passenger vessels, all cargo ships greater than 500 gross tonnage, and all vessels greater than 300 gross tonnage engaged in an international voyage. Many fishing vessels are, however, below the IMO's 300 gross tonnage size threshold, and adoption (and enforcement) of these regulations into national legislation varies, with some nations modifying the regulations to be more or less strict as to the size of vessels required to carry AIS (*9*). AIS receivers aboard a vessel transmit information about the vessel's current speed, position, and course along with other vessel identification information (for example, vessel name, MMSI number).

Satellite and terrestrial processed AIS data from January 2015 to December 2016 were provided by Global Fishing Watch (www.globalfishingwatch.org). The Global Fishing Watch data set makes use of convolutional neural networks to identify fishing effort in this global data repository (*10*, *43*). To identify fishing vessels, a convolutional neural network model was trained on tracks of 45,000 marine fishing vessels that had been identified through registries as fishing vessels or nonfishing vessels. Using AIS tracks that have been labeled by experts as fishing or nonfishing for 500 vessels, another convolutional neural network model was trained to identify when a specific AIS point was most likely fishing.

Here, we summarize only the data for industrial fishing, defined here as all fishing effort from vessels >24 m in length [lengths of vessels were compiled from registry records and when not available, estimated by the convolutional neural network, as described in Kroodsma *et al.* (*10*)]. Although no absolute threshold exists for what defines an industrial fishing vessel with respect to length, by including only vessels >24 m in length, most artisanal fishing vessels will be excluded (*11*). By conservatively focusing on vessels >24 m in length, we also confine this analysis to industrial fishing vessels for which AIS coverage is strong. A total of 30,469 vessels >24 m in length were active during the study period and included in the analysis. To examine how the selection of this vessel size threshold affected the analysis, an additional 29,988 vessels that were between 12 and 24 m in length were also included in a separate analysis to examine patterns of fishing effort for vessels >12 m in length for 2016. We used comparisons between AIS and VMS data from Indonesia to create corrections to adjust for any potential underreporting bias in AIS-only analyses of fishing effort in lower-income countries (all methods and results reported in Supplementary Materials). We do not differentiate in any of these analyses between different gear types of industrial fishing. The time between each consecutive AIS point labeled as fishing was calculated and included in the data set as fishing hours. All analyses in this report consider industrial fishing effort that can be detected using AIS and aggregated by fishing hours, referred to throughout as "fishing effort." As an alternative measure of fishing effort, fishing days for each vessel were also calculated, where each fishing day is defined as any calendar day a vessel was determined to be engaged in fishing behavior. We contribute these algorithm-based identifications of fishing effort purely for research purposes and make no legal claims, expressed or implied, about the reported patterns.

The MMSI assigned to each vessel was used to identify unique vessels. Each MMSI number was assumed to correspond to one vessel throughout the study period. The flag state for each vessel was determined using the registered flag state in vessel registries when available, alternatively by the first three digits of the MMSI (the marine identification digits, which correspond to a particular flag state), and finally by a manual review of vessels whose marine identification digits did not correspond to a flag state. Because of a lack of data tracking vessel ownership, vessels that may have had a flag of convenience or were otherwise registered to a flag state other than the vessel owner's state were not identified and were considered part of the fleet of whatever state to which they were flagged. Further description of the methods used for processing the AIS data to determine fishing vessels and fishing effort can be found in Kroodsma *et al.* (*10*).

World Bank country classification and status of fishing entities

All unique vessels were assigned to one of four World Bank income group country categories: high income, upper middle income, lower middle income, or low income (www.worldbank.org; using 2016 classifications). Throughout, we refer to "higher-income nations" to collectively indicate nations classed as either high income or upper middle income. Likewise, we refer to "lower-income" nations when collectively indicating nations classed as lower middle income or low income. We adopt here World Bank practices of using the term "country" (interchangeably with nation and state) to refer to a statistically relevant economic data reporting entity, without any implication of political independence. The proportion of industrial fishing effort attributed to nations from different income categories was compared at the global level, and analyses were then subdivided between the high seas, EEZs, and ocean basins. Fishing effort observed on the high seas and each EEZ was aggregated by the flag state of vessels involved in fishing activity. EEZs without a designated World Bank income classification (high/upper middle/lower middle/low) were excluded from the analysis. The EEZs of state territories were not included because fishing agreements and policies vary widely between territory entities and their sovereign state (table S6). Any fishing vessel whose MMSI marine identification digits indicated that it was flagged to a territory was listed as an unclassified entity in this analysis. When a vessel's flag state was the same as the EEZ it was fishing in, it was classified as domestic fishing. When the MMSI marine identification digits of a vessel did not correspond to a specific flag state or the MMSI number was incompletely reported, the vessel was classified as invalid identity. Ocean basin delineations were based on those of the International Hydrographic Organization; fishing activity that took place outside of these ocean basins (that is, the Red Sea) was not included when comparing fishing activity by ocean basin. The boundaries for both oceanic basins and EEZs were obtained from www.marineregions.org, a project of the Flanders Marine Institute. Mapping of higher- and lower-income fishing effort in Fig. 2 used an equal area 0.5° grid, following past estimates of fishing effort (*1*, *10*).

Comparison of AIS-derived measures of fishing effort to catch reconstruction data

We compared estimations of AIS-derived industrial fishing effort for 2016 generated using the methods described above against reconstructed catch estimates for global marine fisheries generated by the Sea Around Us from 2014 (the most recent year available) (*1*) for all EEZs of countries categorized as high income or low income by the World Bank (upper and lower middle income classifications were not included). More recent data were available and were used for the high seas reconstructed catch estimates, found and described in Sala *et al.* (*25*). For the catch reconstruction estimates, catch is defined as metric tons fished per fishing entity using only industrial fishing catch (this includes both estimated landings and discards). Fishing effort for the AIS data is defined as total fishing hours for each entity. The top five fishing entities for each country's EEZ according to the catch reconstructions and AIS fishing effort data were identified. These top five fishing entities of both lists were compared to assess the rank order consistency of the top fishing entities on the high seas and in each EEZ.

As with AIS data and associated analyses, data on catch reconstructions come with their own set of advantages and challenges (*44*, *45*). While effort and catch are very different measures, they are fundamentally related and often positively correlated (*46*). Consequently, any alignment observed in these comparisons between patterns of AIS-measured effort data and catch reconstruction data provides a potentially valuable first opportunity to validate the efficacy of the AIS fishing effort measures we report and a means to begin building hypotheses that explain congruities and incongruities in pattern match.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/8/eaau2161/DC1

Supplementary Materials and Methods

Fig. S1. Distribution of 2015 industrial fishing effort by vessels flagged to nations from different income classes as measured using AIS data and convolutional neural network models.

Fig. S2. Distribution of 2016 industrial fishing effort (measured in fishing days) by vessels flagged to nations from different income classes as measured using AIS data and convolutional neural network models.

Fig. S3. Distribution of 2016 industrial fishing effort from vessels flagged to higher- and lower-income nations by high seas ocean basin derived via AIS.

Fig. S4. Geographic distribution of industrial fishing effort from vessels flagged to higher- and lower-income nations for 2016 derived via the AIS in all countries' EEZ.

Fig. S5. Number of vessels for each World Bank income group in FAO registry compared to number of vessels detected through AIS in Global Fishing Watch's vessel database for vessels >24 m in length.

Fig. S6. Distribution of 2016 industrial fishing effort (measured in fishing hours) by vessels flagged to nations from different income classes as measured using AIS data and convolutional neural network models for vessels >12 m in length.

Fig. S7. Distribution of 2016 industrial fishing effort (measured in fishing hours) by vessels flagged to nations from different income classes using both AIS data and Indonesian VMS data for vessels >24 m.

Fig. S8. Distribution of 2016 industrial fishing effort (measured in fishing hours) by vessels flagged to nations from different income classes using AIS data, Indonesian VMS data, and corrected low-income and lower middle–income fishing effort for vessels >24 m.

Table S1. Comparison of top 5 fishing flag states for the high seas, and all high- and low-income EEZs based on AIS-derived effort (total fish hours per fishing state) in 2016 and reconstructed catch (total metric ton caught per fishing state) in 2014 (most recent year of available data).

Table S2. Top 20 most active fishing flag states on the high seas in 2016.

Table S3. Top 20 most active fishing states across all EEZs for the year 2016 based on AIS-derived estimates of industrial fishing effort.

Table S4. Top 20 most active fishing states across all lower-income (lower middle income and low income) EEZs for the year 2016 based on AIS-derived estimates of industrial fishing effort.

Table S5. Breakdown of countries that have variably codified IMO ratified standards for use of the AIS.

Table S6. List of countries and other entities used in the analysis and their World Bank income group country classifications (2016).

Table S7. Amount of fishing effort by Indonesian vessels >24 m from Indonesian VMS data.

Table S8. Number of vessels >24 m in the FAO registry and detected via AIS for each lower-income country.

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Acknowledgments

Funding: This work was supported by Benioff Ocean Initiative (to D.J.M., C.J., and F.H.J.), Alfred P. Sloan Foundation (FR-2015-65479) (to D.J.M.), the SESYNC (National Socio-Environmental Synthesis Center) National Science Foundation (DBI-1052875) (to D.J.M., C.D.G., and E.H.A.), the Wellcome Trust Our Planet, Our Health (grant no. 106864MA) (to C.D.G. and E.H.A), and the National Geographic Society's Pristine Seas project and E. Sala (to J.M.). **Author contributions:** Conceptualization: D.J.M., C.J., and F.H.J. Data analysis and interpretation: D.J.M., C.J., D.K., and J.M. Writing: D.J.M., C.J., F.H.J., C.D.G., and E.H.A. with input and feedback by all the other authors. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Rasters of daily fishing effort, gridded at 0.1° by flag state, are available at globalfishingwatch.io, as are the results of the neural net vessel classification algorithm. Additional data related to this paper may be requested from the authors.

Submitted 18 May 2018
Accepted 9 July 2018
Published 1 August 2018
10.1126/sciadv.aau2161

Citation: D. J. McCauley, C. Jablonicky, E. H. Allison, C. D. Golden, F. H. Joyce, J. Mayorga, D. Kroodsma, Wealthy countries dominate industrial fishing. *Sci. Adv.* **4**, eaau2161 (2018).

ENVIRONMENTAL STUDIES

The economics of fishing the high seas

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While the ecological impacts of fishing the waters beyond national jurisdiction (the "high seas") have been widely studied, the economic rationale is more difficult to ascertain because of scarce data on the costs and revenues of the fleets that fish there. Newly compiled satellite data and machine learning now allow us to track individual fishing vessels on the high seas in near real time. These technological advances help us quantify high-seas fishing effort, costs, and benefits, and assess whether, where, and when high-seas fishing makes economic sense. We characterize the global high-seas fishing fleet and report the economic benefits of fishing the high seas globally, nationally, and at the scale of individual fleets. Our results suggest that fishing at the current scale is enabled by large government subsidies, without which as much as 54% of the present high-seas fishing grounds would be unprofitable at current fishing rates. The patterns of fishing profitability vary widely between countries, types of fishing, and distance to port. Deep-sea bottom trawling often produces net economic benefits only thanks to subsidies, and much fishing by the world's largest fishing fleets would largely be unprofitable without subsidies and low labor costs. These results support recent calls for subsidy and fishery management reforms on the high seas.

INTRODUCTION

Fishing in the marine waters beyond national jurisdiction (the "high seas" covering 64% of the ocean's surface) is dominated by a small number of fishing countries, which reap most of the benefits of fishing this internationally shared area (*1*). The rationality of widespread high-seas fishing has been questioned because of its environmental impacts and uncertain economic profitability (*2*). Deep-sea bottom trawling can damage fragile habitats containing unique biodiversity including millenary deep-sea corals (*3*). Highly migratory species such as tuna and sharks that move between the high seas and countries' jurisdictional waters [exclusive economic zones (EEZs)] tend to be intensely fished and overexploited (*4*). Although the International Seafood Sustainability Foundation indicates that 57% of managed tuna stocks are considered to be at a healthy level of abundance, 13% are overfished (*5*), and even those that are not overfished show slight declines in biomass over time (*6*) and may benefit from increases in biomass. Oceanic sharks, of which 44% are threatened (*7*), spend a great deal of time in the high seas, where shark fishing is largely unregulated and unmonitored (*8*).

Although the environmental impacts of fishing on the high seas are well studied, the lack of transparency and data has precluded reliable estimates of the economic costs and benefits of high-seas fishing. Fisheries data suggest that fish catch in this vast area amounted to around 6% of global catch and 8% of the global fishing revenue in 2014 (see www.seaaroundus.org/data/#/global). However, the high level of secrecy around distant-water fishing has impeded the calculation of fishing effort and associated costs. Nevertheless, recent technological developments in machine learning and satellite data now allow us to obtain a far more accurate picture of fishing effort across the globe at the level of individual vessels (*9*). This capability provides a more transparent and novel method to examine high-seas fisheries and answer key questions such as whether fishing in the high seas is profitable and whether government subsidies enable current levels of fishing.

Here, we characterize the global high-seas fleet in detail and estimate the net economic benefit of high-seas fishing using (i) reconstructed estimates of the global fishing catch and its landed value, (ii) the costs of fishing based on satellite-inferred fishing effort and vessel characteristics, and (iii) estimates of government subsidies per country. We report high-seas fishing profits by fishing gear type, flag state, and Food and Agriculture Organization of the United Nations (FAO) region, with the goal of understanding whether fishing the high seas is economically rational.

RESULTS

Global patterns

Until very recently, the composition of the high-seas fishing fleet has been largely unknown, and this lack of transparency has prevented any serious analysis of the economic rationality of fishing in that vast swath of Earth's surface. New technologies are now shedding light on this previously dark corner of Earth. Using the Global Fishing Watch (GFW) database, which uses automatic identification systems (AIS) and vessel monitoring systems (VMS) to track individual vessel behavior, fishing activity, and other characteristics in near real time, we identified a minimum of 3620 unique fishing vessels operating in the high seas in 2016 (Fig. 1). In addition to the actual fishing vessels, we tracked 35 bunkers (tankers that refuel fishing vessels) and 154 reefers (refrigerated cargo ships onto which fishing vessels transfer their catch at sea, a process called transshipment), vital to the operation of the high-seas fishing fleet (fig. S2 and table S6). Only six countries (China, Taiwan, Japan, Indonesia, Spain, and South Korea) accounted for 77% of the global high-seas fishing fleet and 80% of all AIS/VMS-inferred fishing effort (measured in kilowatt-hours; table S1). Fifty-nine percent of the vessels active in the high seas used drifting longlines and represented 68% of all fishing days. The top four fishing gears operating in the high seas are drifting longliners, purse seiners, squid jiggers, and trawlers (Fig. 1 and table S2).

The global high-seas fishing fleet identified here spent an aggregate 510,000 days at sea in 2016; 77% of these days were spent fishing, with an average of 141 days at sea per vessel (table S1). The time spent by vessels fishing in the high seas versus fishing in EEZs varied according to the type of fishing they conduct (fig. S1).

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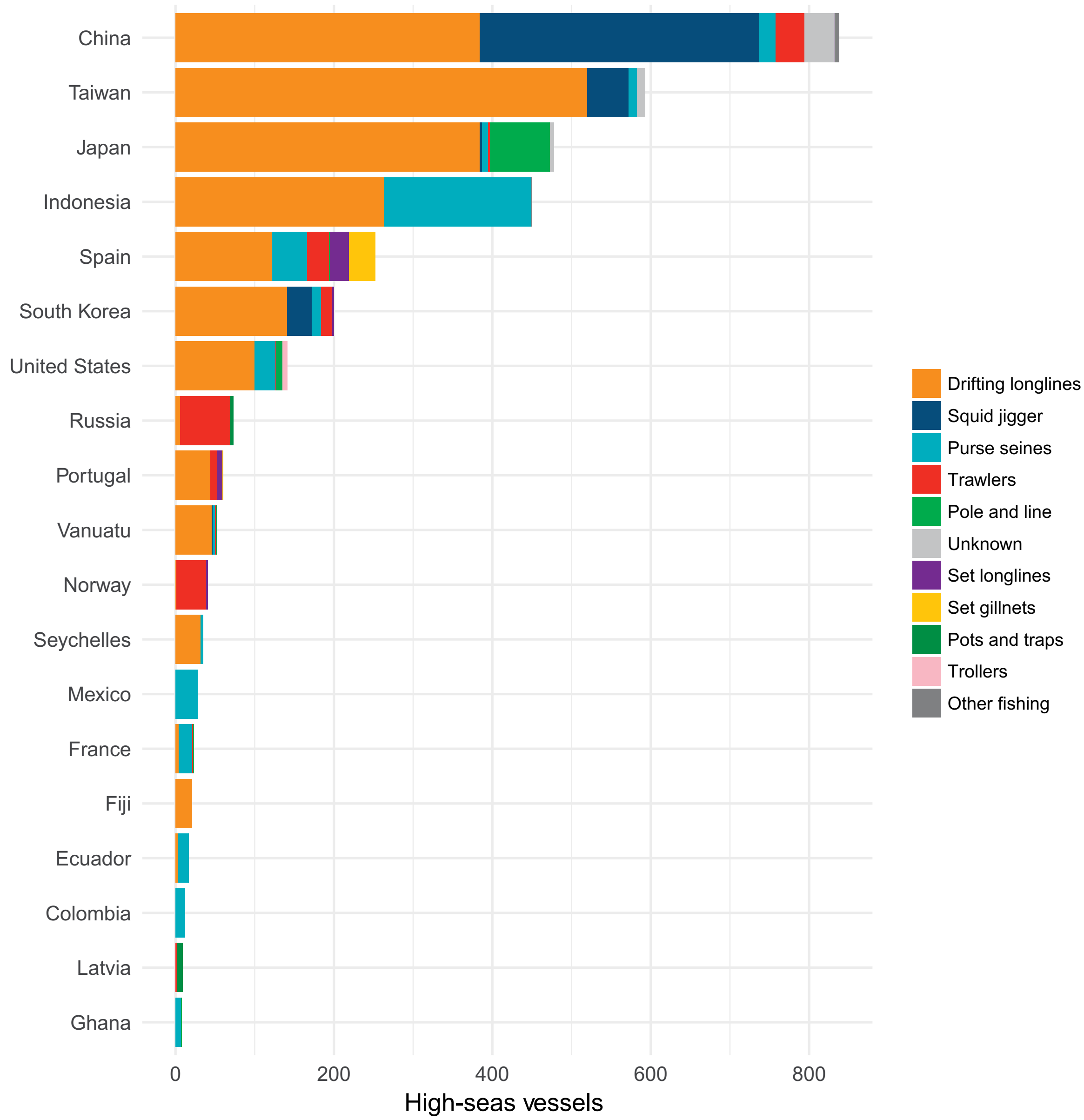

Fig. 1. The high-seas fishing fleet. High-seas vessels by flag state and gear type, as detected by GFW in 2016.

This characterization of the global high-seas fleet enables a detailed estimation of the total cost of fishing the high seas. Using vessel-level data on ship length, tonnage, engine power, gear, flag state, trip-level fishing and transit tracks, speed, and other factors that affect the costs of fishing, we estimate that total costs of fishing in the high seas in 2014 (the most recent year for which spatially allocated global reconstructed catch data are available) ranged between \$6.2 billion and \$8.0 billion (Table 1). The uncertainty around total costs was driven mainly by labor costs, particularly for China and Taiwan, which exhibited the highest total costs, but for which fisheries data are often scarce.

The total fisheries catch from the high seas in 2014 was 4.4 million metric tons, with an aggregate revenue (landed value of the catch in US\$) of \$7.6 billion (Table 1). Five countries alone accounted for 64% of the global high-seas fishing revenue: China (21%), Taiwan (13%), Japan (11%), South Korea (11%), and Spain (8%). High-seas catch by country and FAO region significantly and positively increased with rising fishing effort ($R^2 = 0.46$, $P < 0.001$) (fig. S4). Subtracting our estimated costs from the landed value of catch provides the first empirically based estimates of the net economic profit of fishing the high seas.

Globally, our estimates of high-seas fishing profits (without accounting for subsidies) ranged between −\$364 million and +\$1.4 billion (Table 1). We estimated that governments subsidized high-seas fishing with \$4.2 billion in 2014, far exceeding the net economic benefit of fishing in the high seas. This result suggests that without subsidies, high-seas fishing at the global scale that we currently witness would be unlikely (at the aggregate level), and that most of the negative returns accrue from China, Taiwan, and Russia (Table 1). Coupling our estimates of profits with country-level subsidies suggests that subsidy-distorted high-seas profits range between \$3.8 billion and \$5.6 billion.

Table 1. The economics of fishing in the high seas. Catch (in thousand metric tons), revenue, costs, subsidies, and profits without subsidies (π) and with subsidies (π^*) for each country. All monetary values reported in million US dollars. These 14 countries accounted for 90% of the high-seas catch.

	Catch	Revenue	Costs		π		Subsidies	π^*	
			Lower bound	Upper bound	Lower bound	Upper bound		Lower bound	Upper bound
Global	4391	7656	6228	8020	−364	1428	4185	3821	5613
China	1523	1624	1563	2041	−418	60	418	1	479
Taiwan	545	983	1048	1220	−237	−65	244	6	179
South Korea	403	807	553	605	202	254	409	612	664
Spain	248	637	434	492	145	203	603	749	807
Japan	213	816	639	639	177	177	841	1018	1018
Ecuador	194	271	95	186	85	176	22	107	198
Indonesia	192	384	178	260	123	206	102	226	308
Russia	188	195	153	309	−114	42	12	−102	54
Mexico	107	252	81	184	68	170	32	100	202
United States	93	377	100	162	216	278	256	471	533
Norway	86	107	77	88	19	30	14	33	43
France	58	235	78	86	148	157	195	344	352
Seychelles	55	50	26	50	−1	24	10	9	33
Panama	55	104	32	66	38	72	25	63	98

We conducted these calculations spatially, revealing that, even with subsidies and our lowest estimate of labor costs, 19% of the currently fished high seas cannot be exploited profitably at current rates (Fig. 2). Assuming higher labor costs, and the fact that companies still receive subsidies, the area of unprofitability jumps from 19 to 30%. Finally, without subsidies and low wages to labor, the area of unprofitability shoots to 54%, implying that without subsidies and/or low labor compensation, more than half of the currently fished high-seas fishing grounds would be unprofitable at present exploitation rates.

The countries that provided the largest subsidies to their high-seas fishing fleets are Japan (20% of the global subsidies) and Spain (14%), followed by China, South Korea, and the United States (Table 1). It is remarkable that in these cases, the subsidies far exceed fishing profits, with the extreme being Japan, where subsidies represent more than four times our estimate of their high-seas profits. For 17 countries, contributing 53% of the total high-seas catch, current extraction rates would not be profitable without government subsidies (Table S5). Among these countries, China and Taiwan alone account for 47% of the total high-seas catch, which is significant. Whether subsidies enable profitability or not, the magnitude of subsidies and the fact that many of these subsidies lower the marginal cost of fishing suggest that high-seas fishing activity could be markedly altered in their absence.

In what fisheries do these high-seas dynamics play out? We find that drifting longliners and purse seiners, targeting mainly large mobile, high-value fishes such as tuna and sharks, are the most profitable high-seas fisheries (Fig. 3). All other fisheries are either barely profitable or unprofitable. We estimate that deep-sea bottom trawling would not be globally profitable at current rates without government subsidies, with maximum annual losses of $230 million before subsidies. Similarly, squid jiggers would be, on average, very unprofitable without subsidies, with maximum annual losses estimated at $345 million, but when we look at the spatial economic patterns per country, type of gear, and fishing grounds, the picture becomes much more complex.

Spatial fishing patterns and profitability

While fishing is geographically extensive on the high seas, it is perhaps less so than previously assumed. Using a spatial grid with 0.5° resolution, we estimate that fishing occurred in 132 million km^2 or 57% of the high seas in 2016; this number reduces to 48% with a grid of 0.25° resolution. Fishing effort in the high seas occurs mostly between latitudes 45°N and 35°S (Fig. 2). Hot spots of fishing effort were detected at the EEZ boundaries of Peru, Argentina, and Japan, dominated by the Chinese, Taiwanese, and South Korean squid jiggers; deep-sea bottom trawling off Georges Bank and in the Northeast Atlantic; and to a lesser extent in the Central and Western Pacific, associated mostly with tuna longline/purse seine fleets. The spatial footprint of high-seas fishing was most extensive for longliners; purse seiners were restricted to the equatorial zone; squid jiggers operated mostly on the EEZ boundaries of Peru, Argentina, and Japan; and deep-sea bottom trawlers were restricted to the continental shelf edge and seamounts (fig. S3).

China and Taiwan had the largest spatial footprints, followed by Japan, Spain, and South Korea (Fig. 4). A global pattern emerged in which unprofitable high-seas fishing (without subsidies) transformed into profitable fishing (with subsidies) in most areas for Japan, Spain, and South Korea. However, the global map of profits after subsidies still showed many areas with an apparent economic loss for China and

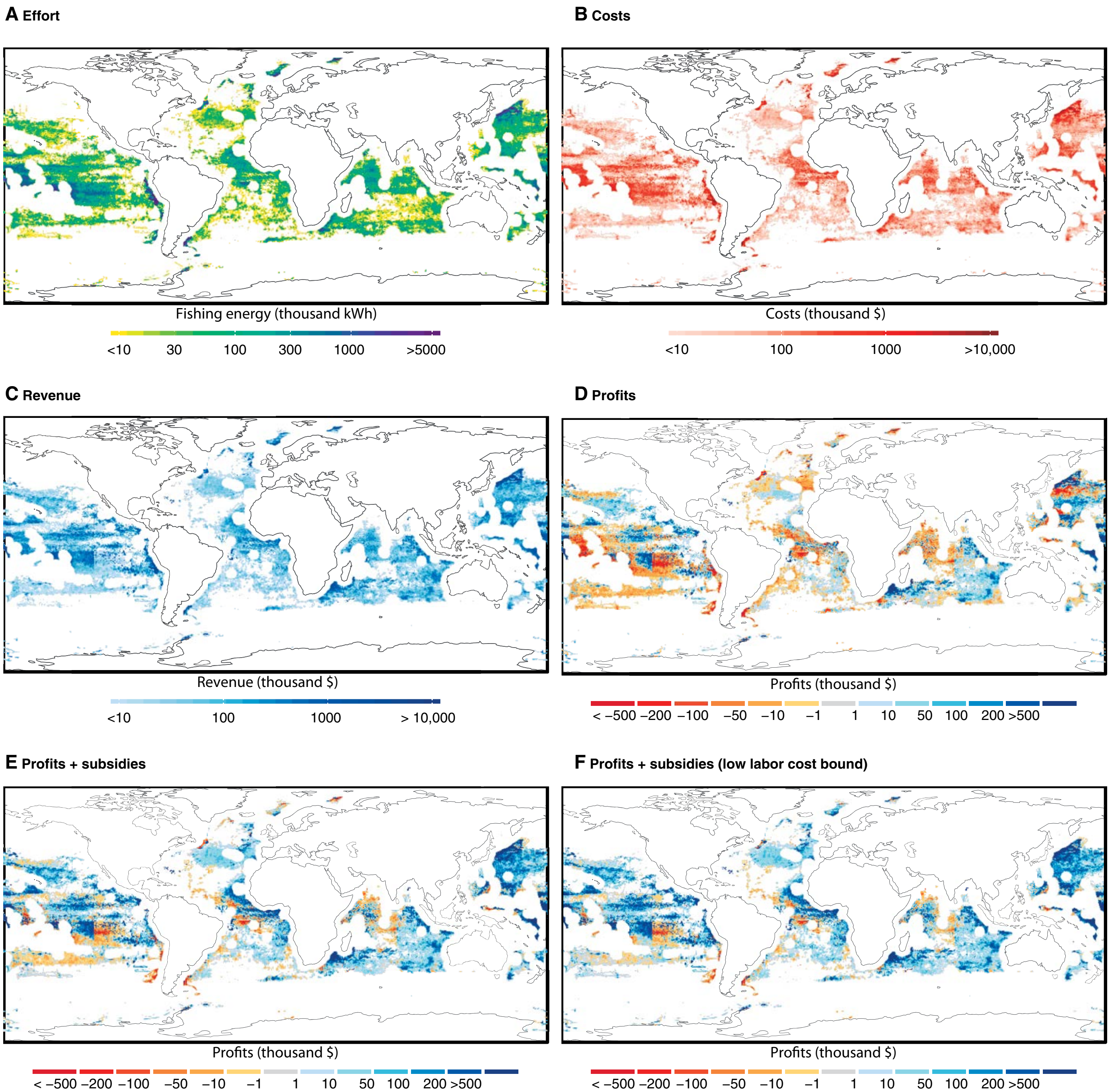

Fig. 2. Global patterns of fishing in the high seas. (**A**) Fishing effort, (**B**) economic costs, (**C**) revenue (landed value of the catch), (**D**) profits before subsidies, (**E**) profits after subsidies, and (**F**) profits after subsidies and low labor costs. Values for costs and profits are scaled averages between lower and upper bound estimates.

Taiwan, such as the Western Indian Ocean. Fishing by China and Taiwan became profitable at many locations only after assuming low labor costs, that is, by lowering average labor costs from these countries by 30 and 53%, respectively (table S5).

Economic profitability also varied markedly between countries, fisheries, and FAO regions (Fig. 5). The analysis at this level is most important for understanding the economics of individual fisheries, with direct management implications. The following are the results for the most important high-seas fishing countries.

China

China shows the highest economic contrasts of fishing in the high seas, as it deploys some of the most and least profitable fisheries (Fig. 5 and table S7). The most profitable of the high-seas operations by China and globally were in the Northwest Pacific, where we estimate that fuel expenditures are only a fraction of those elsewhere because of the proximity to mainland China. Longlining and bottom trawling in the Northwest Pacific showed an estimated average profit (before subsidies) of $325 million and $111 million, respectively. Most other

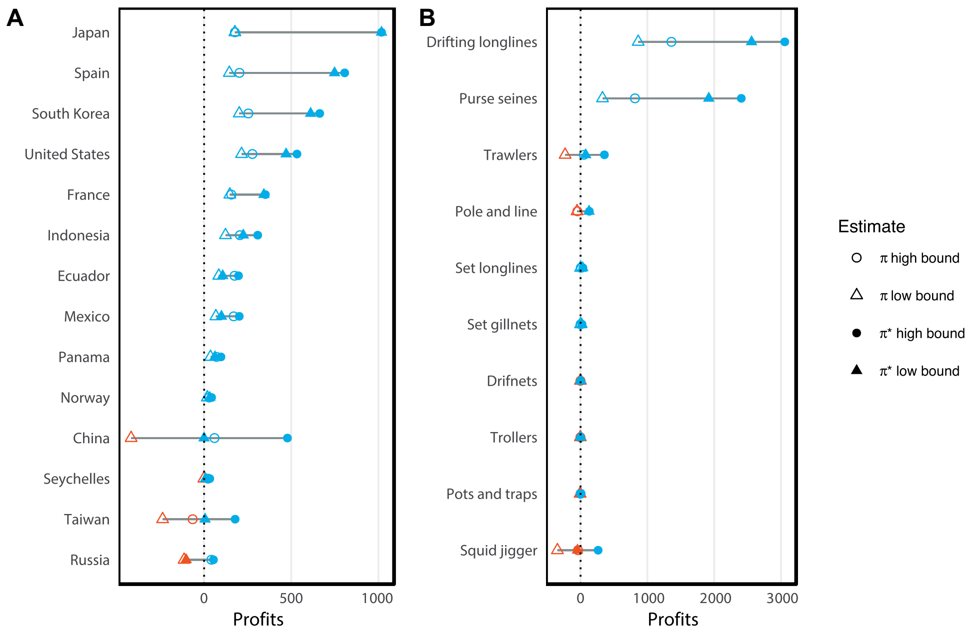

Fig. 3. Net economic benefit of high-seas fishing. Range of estimates of fishing profits (US$ millions) before (π) and after (π*) subsidies for (**A**) major fishing countries and (**B**) gear types.

Chinese fisheries appeared to be unprofitable, and the worst were in the Southwest Atlantic, where estimated fishing costs are four times greater than near mainland China. The most unprofitable of all Chinese fisheries was bottom trawling in the Southwest Atlantic, which exhibited an average net loss (even after subsidies are taken into account) of $98 million. China's squid fishing was consistently unprofitable, and subsidies made it profitable only off Peru's EEZ.

Taiwan

Similar to mainland China, Taiwan's high-seas fisheries in the Northwest Pacific are its most profitable (Fig. 5 and table S7). Taiwanese longlining and squid jigging in the Northwest Pacific are among the most profitable high-seas fisheries globally without subsidies (average profit $193 million and $63 million, respectively). Taiwanese longlining elsewhere appears to be unprofitable. We estimate that in the Western Central Pacific and Eastern Central Pacific, longlining results in average annual losses of $65 million and $63 million, respectively. Similar to China, only after assuming low labor costs does Taiwanese high-seas fishing produce profits (table S7).

Japan

In contrast to China and Taiwan, Japanese fishing in the high seas was mostly profitable, especially in the Eastern Central and Western Central Pacific (Fig. 5 and table S7), with longlining profits before subsidies estimated at $205 million and $113 million, respectively. Japanese pole and line fishing in the Western Central Pacific and longlining in the South Atlantic and Eastern Indian Ocean were also profitable even without subsidies. Surprisingly, the least profitable Japanese tuna fishing occurs in the Northwest Pacific, close to Japan, with net economic losses unless subsidies make that fishery profitable.

South Korea

South Korea's most profitable high-seas fishing was longlining in the Western Central Pacific ($173 million on average before subsidies), followed by bottom trawling in Atlantic Antarctic waters ($129 million) (Fig. 5 and table S7). Korean squid jigging off the EEZ of Argentina and off the Falkland Islands (Malvinas) is also profitable ($91 million on average before subsidies). The least profitable South Korean high-seas fishery was bottom trawling in the Southeast Atlantic, where costs exceeded revenue even after subsidies were subtracted. Longlining in the Southeast Pacific was the second most unprofitable of South Korean fisheries.

Spain

Spain's most profitable fishery was longlining in the Western Indian Ocean, followed by longlining in the Southeast Pacific, off West Africa, and the Southwest Pacific (Fig. 5 and table S7). However, Spain's purse seining in the Eastern Central Pacific, the Western Indian Ocean, and the Eastern Central Atlantic (West Africa) would not be profitable at current rates without subsidies. Purse seining in the Southeast Pacific was not profitable even with subsidies, and current bottom trawling effort everywhere in the high seas was unprofitable without subsidies.

Other countries and fisheries

Deep-sea bottom trawling on the high seas showed a broad pattern of unprofitability worldwide (table S7). Sixty-four percent of all national bottom trawling operations in FAO regions were unprofitable without subsidies, and a remarkable 32% of these operations appear to have been unprofitable even with subsidies, which raises obvious questions about the incentives to fish there.

Indonesia, the only flag state that publicly provides VMS data, fished only in the high seas of the Indian Ocean. Tuna fishing using purse seines and longlines in the Eastern Indian Ocean was profitable even without subsidies because of the relatively low costs of fishing off the western edge of their EEZ and the characteristics of the fleet, that is, small vessels with small engines (Fig. 5 and table S7). However, Indonesian fishing in the Western Indian Ocean was unprofitable, as we estimate that costs are 15 times greater than the landed value of the catch. This result may be due to the sharp differences in reported catch across FAO regions of the Indian Ocean.

DISCUSSION

Our results show that, by and large, fishing the high seas is artificially propped up by an estimated $4.2 billion in government subsidies (more

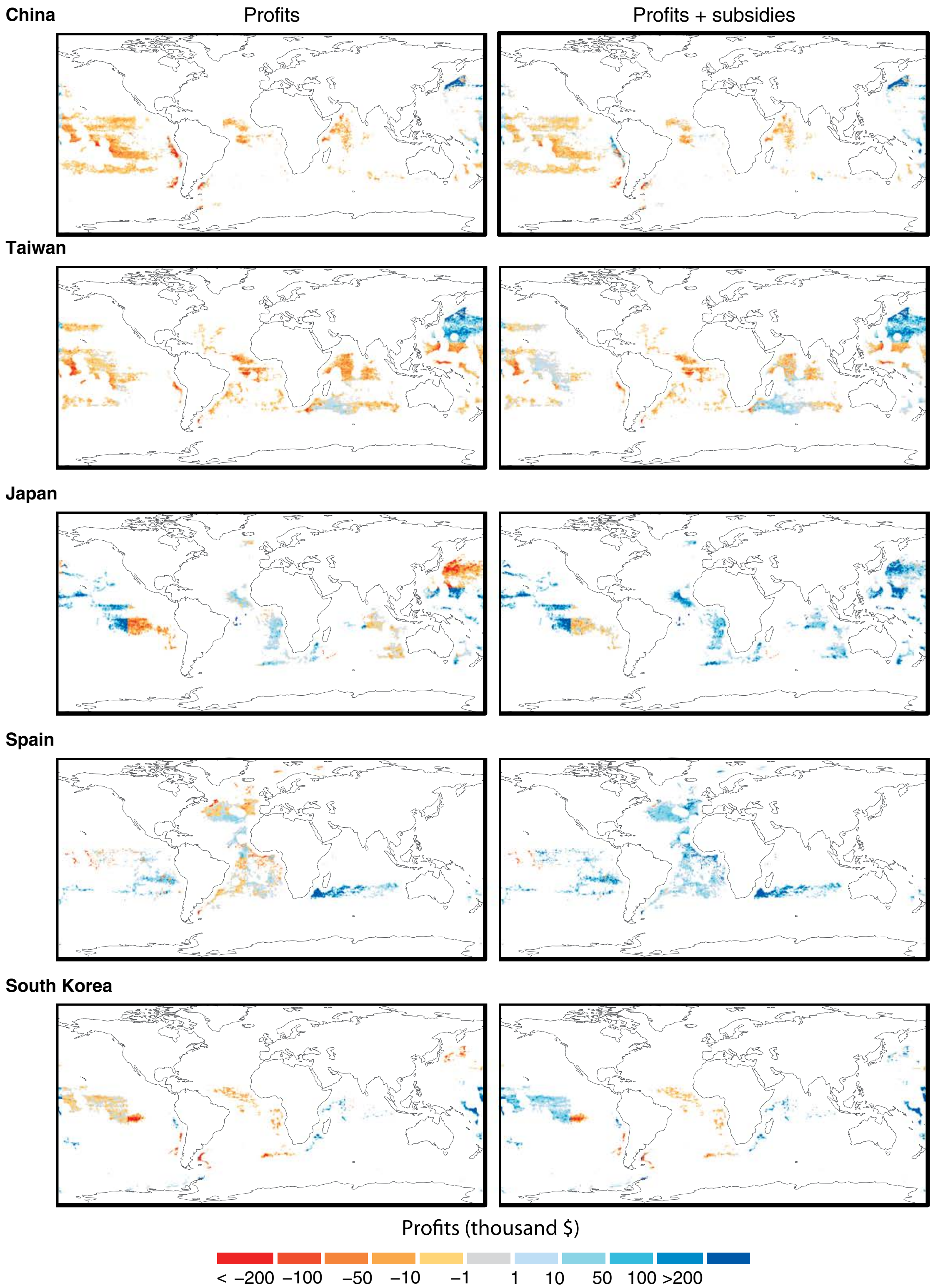

Fig. 4. National patterns of fishing in the high seas. Average high-seas fishing profits with and without subsidies for the five main fishing flag states.

than twice the value of the most optimistic estimate of economic profit before subsidies are taken into account). The economic benefits vary enormously between fisheries, countries, and distance from port. On aggregate, current high-seas fishing by vessels from China, Taiwan, and Russia would not be profitable without subsidies. This is globally significant since these three countries alone account for 51% of the total high-seas catch. Other countries exhibit annual profits ranging from negligible to $250 million, which were increased substantially by subsidies (for

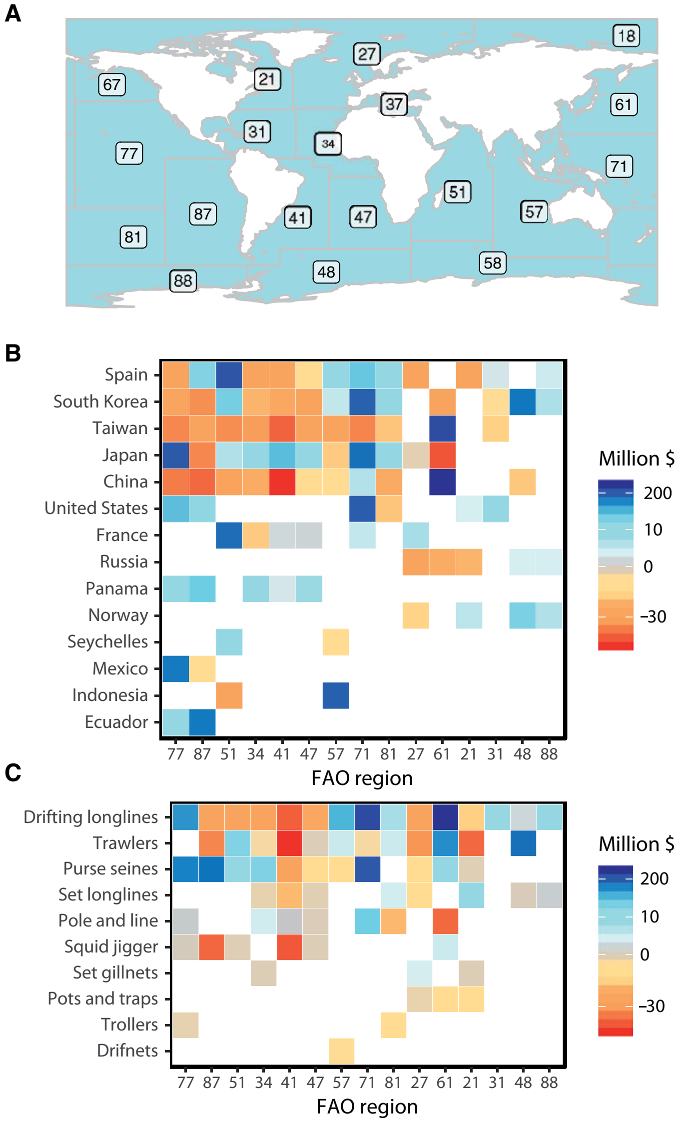

Fig. 5. Spatial patterns of high-seas fishing profits. (**A**) FAO regions, (**B**) profits before subsidies by country, and (**C**) fishing gear.

example, Japan, Korea, Spain, and the United States). Surface fisheries for pelagic species such as tuna were profitable, whereas most other fisheries barely broke even, and squid jigging (mostly concerning Chinese and Taiwanese fleets) and deep-sea bottom trawling were generally unprofitable without subsidies. Some national fisheries in specific regions were unprofitable even after government subsidies are taken into account.

The lack of profitability for China and Taiwan may be related to massive overcapacity. After realizing the declining returns from their domestic fishing, China embarked on a vessel construction program in the 1990s destined to "distant-water fishing," which continued through the 2000s, when China declared its interest in developing high-seas fisheries (*10*), although GFW data suggest a recent sharp decline in its fishing fleet. Japan, on the other hand, has undertaken well-documented vessel-scrapping programs to decrease the overcapacity of its large-scale tuna longline fleet (*11*). Scrapping means that vessels are decommissioned and dismantled, which results in effective reduction of the fleet.

How is it possible that some countries continue to fish in certain high-seas regions while exhibiting an apparent economic loss? For this behavior to be incentive-compatible, there must be a net benefit for individual companies to continue operating in the high seas. The most obvious reason is underreporting the catch, which would result in an underestimate of fishing revenue and profits. The data used in our analysis are reconstructed catch data that attempt to correct for underreporting (*12*, *13*). Some analysts have criticized catch reconstructions on a methodological basis, suggesting high uncertainty about the reliability of the reconstructions and claiming that FAO's annual catch reports are "the only validated source of global fisheries landings" (*14*), but see (*15*). Reconstructed data suggest catches perhaps 30% larger than those reported by FAO (*13*), which makes our estimates of fishing revenue and profits larger than they would be had we used FAO's raw data. However, global catch reconstructions mainly address unreported catches within countries' EEZs. The data for industrially caught tuna and other large pelagic fishes were largely on the basis of officially reported data provided by the various tuna Regional Fisheries Management Organizations to which major discards were added before spatial allocation (*16*). Therefore, catches for some high-seas areas may still be underreported.

Overall, we conjecture that fishing the high seas could become rational for the most unprofitable fisheries due to a combination of factors including the following: (i) currently available catch data continue to underrepresent real catches, (ii) vessels fish only part of the time in the high seas and make most of the economic benefit from fishing in EEZs, (iii) government subsidies not accounted for in this analysis, (iv) reduced costs because of unfair wages or forced labor, and (v) reduced costs because of transshipment at sea. There may be additional market factors that are fishery-specific, that is, squid fishing by Chinese vessels in South America. Our results suggest that this fishery is unprofitable, but over 100 Chinese squid jiggers amass in January at the limit of Argentina's EEZ to catch small *Illex* squid, before Argentina opens the season inside its EEZ. The low stock size and high demand for squid may allow Chinese companies fishing early in the season to charge higher prices than those used in our analysis (*17*). To these factors, we could add geostrategic reasons, where countries may fish in some regions as part of their long-term foreign policy strategy, regardless of the economic benefit. Examples of this strategy have been documented for Chinese and Russian fleets fishing in Antarctica (*18*, *19*).

Previous studies showed that total government subsidies equaled 30 to 40% of the global landed value of catch (*20*), but this study allows us to compare subsidies to the actual profits in the absence of subsidies, specifically for fishing in the high seas. Even under the lowest estimates of high-seas fishing costs, subsidies more than double the net economic benefit of fishing in the high seas. For some fishing fleets, subsidies make the difference between negative and positive profits, but for a few countries, subsidies are extremely large (especially Japan and Spain) and appear to play a central role in economic outcomes. Some of the Japanese and Spanish fishing fleets do not appear to require subsidies to be profitable, yet they collect the highest sums globally. To the extent that government subsidies enhance fishing activity (for example, through fuel or other subsidies that affect the marginal cost of fishing) (*20*, *21*), they artificially boost the bottom line of fishing companies, perhaps at the expense of sustainability of the underlying resource stocks.

Forced labor or modern slavery is a key cost-reducing factor in long-distance fishing, which manifests itself both at sea (using forced labor) and on land (using child slavery) (*22*–*24*). In some countries, high-seas fisheries are profitable only after assuming government subsidies and low labor costs (mainly for China and Taiwan). Thus, it seems possible that unfair labor compensation, or no compensation at all, allows seemingly unprofitable fisheries to be economically viable. High-seas fishing has also been linked to illegal activities (that is, smuggling of drugs, weapons, and wildlife) by transnational organized criminal groups that use flags and ports of convenience, poor regulation of transshipments, and offshore shell companies and tax havens (*25*, *26*). These illegal activities may also justify the rationality of some of the fishing in the high seas.

Refueling and transshipment at sea also reduces the costs of fishing in the high seas because it allows fishing vessels to continue fishing for months or years without having to return to port (*27*). Without bunkers and reefers, fishing in the high seas would be far less profitable, especially for China, which showed the largest number of encounters with reefers for transshipment. These results also show how chronically unprofitable some fisheries are, such as Chinese squid jigging, which appears to be profitable only through the provision of subsidies, the use of transshipment, and low compensation for labor.

A caveat of our analysis is that GFW data are not able to detect all fishing vessels because some of them do not carry or will simply deactivate AIS or VMS. However, including more vessels in our analyses would only further increase the estimated costs of fishing the high seas and reduce the per-vessel subsidies. Comparing our data with the best available estimates of the number of active vessels per country, gear type, and Regional Fisheries Management Organization, we estimated the proportion of the fleet detected by satellites, and calculated scaling factors to correct for underobserved fishing effort (see the Supplementary Materials). This calculation assumes that the vessels not in the GFW data are as active as and behave similarly to those in the data set. If this assumption does not hold, and undetected vessels are less active and/or fish more inside EEZs than on the high seas, then our scaled estimates may overestimate high-seas effort. For many of the major fleets, including China's longline and purse seine fleet in the Western Central Pacific, we observed >90% of the active fishing vessels, resulting in small correction factors to account for vessels we could not track (table S3). However, a number of fleets have notably bad coverage, including Taiwan's small-scale longline fleet in the Western Central Pacific (40%) and China's squid fleet operating in the South Atlantic (48%). In aggregate, scaling up for undetected vessels augments effort by 20%.

Labor costs are the largest source of uncertainty in our analysis, accounting for 68% of the uncertainty around our estimate of total profits. Wages and labor compensation schemes are highly variable across fleets and nations, and violations of human rights and modern slave labor have been documented in some high-seas and distant-water fleets. We address this uncertainty by providing conservative upper and lower bound estimates of labor costs for each country. Nevertheless, unfair wages or unpaid labor could further decrease our lower bound of costs and increase profitability for some fleets. For example, if crew wages were 20% lower than our current low bound estimate, our highest estimate of total profits would increase by 26%. Fuel costs account for the remaining uncertainty (32%), which is determined by the assumed fuel consumption factor of each vessel (see Materials and Methods). Last, we used the global average price of fuel, which may not reflect regional price variability. While this may affect our results (for example, a 10% change in fuel price would result in a 7% change in our estimate of total costs), tracing the origin of the fuel each vessel uses and the price it pays for it would require strong assumptions and is further complicated by the common practice of refueling while at sea.

For our calculation of fishing profits, we use the landed value of the reconstructed catch for 2014, which is the latest year for which both global FAO statistics and global reconstructed data are available (*15*, *28*, *29*). To estimate costs, we use effort data from 2016 (the year for which we have the most complete AIS and VMS databases) combined with 2014 global average fuel prices. Using data 2 years apart might result in some discrepancies, but we believe that high-seas fishing effort in 2016 is a good proxy for effort in 2014. Evidence to support this claim is the small short-run price elasticity of fuel demand of the large-scale industrial fishing fleet (*9*). Assuming that the spatial distribution of effort has remained constant, we used the estimate of elasticity (−0.06) to adjust fishing effort in response to higher fuel prices in 2014.

Fishing profits are likely to vary over time as factors such as fuel price, fish price, climate, and fish stocks fluctuate. While our analysis is for a single year, the slight increase in high-seas catch and revenue, coupled with the high and constant price of fuel between 2010 and 2014, suggests that our estimate of profits is likely to be representative of, or slightly higher than, the average state during the first half of this decade. In addition, we have likely underestimated the costs of fishing in the high seas because our calculations do not include capital investments. For example, the capital invested in Japan's distant-water fisheries in 2014 (the only country for which this information is available) corresponds to around 40% of total annual expenditures, which would decrease the country's profits (before subsidies) from $177 million to virtually zero. However, since 2014, fuel prices have decreased by ~50% and we estimate that total profits may have increased (before subsidies) by up to $720 million. If current fuel prices remain stable, the second half of this decade may be considerably more profitable for high-seas fisheries, and their dependency on government subsidies may be reduced. As more recent effort, catch, and costs data become available, we will be able to better assess the temporal dynamics of the economics of fishing the high seas.

Satellite data and machine learning technology have opened up a new era of transparency that allows us to evaluate quantitatively what we previously could only speculate about. This study opens a window into the economic profitability of high seas fishing across spatial scales, countries, and fisheries, which can be updated in near real time going forward. Our results show that, in many locations, the current level of fishing pressure is not economically rational, despite the overall profitability of major pelagic fisheries such as tuna fishing. Potential food security arguments in favor of continued or ramped-up high-seas fishing seem misguided because high-seas fisheries mainly target catches of high-value species such as tuna, squid, and deep-sea fishes, which are primarily destined for markets in high-income countries (*30*).

Our findings provide economic evidence that supports growing calls for substantial reforms of high-seas fisheries to align conservation and economic potential. These reforms could include combinations of better fisheries management including capacity reduction, marine reserves, and innovative financing (*31*), but our most direct finding is that subsidy reform could substantially alter fishing behavior in the high seas. Strong fishery management reform could act as a kind of substitute, even in the presence of subsidies, provided strong catch limits were adhered to. In a similar manner, several authors have suggested that closure of large areas, and even all of the high seas, could both achieve conservation goals and increase the economic benefits of fishing migratory species, particularly when they are overfished (*1*, *32*). The uncertainties in our analysis highlight the need for increased monitoring and transparency in fisheries, particularly regarding labor practices. The additional evidence presented here can serve as a starting point for targeting policies in the most efficient manner, as the United Nations starts discussions in 2018 to negotiate a new agreement for conservation of biodiversity in the high seas (*33*).

MATERIALS AND METHODS

High-seas fishing fleet

We defined the global high-seas fleet as fishing vessels that spend more than 5% of their fishing effort in the high seas and that either (i) self-report as fishing vessels in their AIS messages, (ii) were matched to official fishing vessel registries, or (iii) were classified as fishing vessels by the neural net models of the GFW (*9*). In addition, we included bunker and reefer vessels that met at sea with the high-seas fishing fleet based on AIS data. We complemented these data with Indonesian VMS data to incorporate all Indonesian vessels that operate more than 5% of their time in the high seas. For details on vessel characteristics, crews, speed, and fuel consumption, see the Supplementary Materials.

Fishing effort

We estimated and reported vessel activity and fishing effort for 2016 in units of days, hours, kilowatt-days, and kilowatt-hours. Days were calculated by summing the number of days a vessel was actively transmitting AIS or VMS signals. We excluded time at port by filtering out positions where a vessel is closer than 1000 m from shore and traveling at a speed under 0.1 knots. For each vessel, energy in kilowatt-days was estimated by multiplying active days by the vessel's engine power. We estimated the hours at each AIS/VMS position as half the time elapsed between the previous and next position and calculated energy in kilowatt-hours by multiplying hours by the vessel's engine power. Each position was classified as fishing or not fishing using GFW's neural net model, and we used this classification to distinguish active fishing effort from transiting and other activities. We removed noise in AIS/VMS data by filtering out positions that had invalid coordinates (for example, >90°N) and kept only track segments that had over five positions.

The fraction of vessels detected by GFW relative to the total number of vessels varied by country and gear type (see the Supplementary Materials). For example, for China, we likely saw 100% of purse seiners and 95% of longliners in the Western and Central Pacific in 2016, but only 70% of all squid jiggers. We report scaled estimates of high-seas fishing costs and profits for the entire high-seas fishing fleet plus reefers and bunkers (tables S5 and S6).

To calculate fishing costs in 2014, we adjusted total fishing effort using a published estimate of the short-run price elasticity of fuel demand of the global large-scale industrial fleet (*9*). This resulted in an estimated 5.8% reduction of the total high-seas effort in 2016.

Fishing costs

We built an activity-based model of the cost of fishing that takes into account individual vessel behavior and characteristics to estimate the total fuel and labor costs per vessel per year. To estimate total costs, we then used estimates of the fraction of the total costs that fuel and labor costs represent and scaled them up accordingly. The total costs for each vessel were apportioned spatially in proportion to the energy spent fishing in each 0.5° cell.

Fuel costs

For each vessel (i) and AIS/VMS position (j), we calculated fuel cost (FC) for the main and auxiliary engines by multiplying the time in each position (T) by an estimated fuel consumption (C) and the global average quarterly price of fuel (p).

$$\mathrm{FC}_{i,j} = T_{i,j} \times C_{i,j} \times p$$

The time associated to each position (T) was estimated as the average between time to next position and time from last position.

$$T_{i,j} = \frac{t_{j+1} - t_{j-1}}{2}$$

Fuel consumption (C) was estimated on the basis of the methodology used by the European Environmental Agency (EEA) to estimate emissions from the shipping industry (*34*). The general formula to estimate fuel consumption for the main and auxiliary engine is

$$C_{i,j} = P_i \times \mathrm{SFC}_i \times \mathrm{LF}_{i,j}$$

where P is engine power (in kilowatts), SFC is the specific fuel consumption (in grams per kilowatt-hour), and LF (in percentage) is known as the load factor, which represents the engine loading relative to its maximum continuous rate.

Main engine power was obtained from official vessel registries and inferred from the neural net. Data on the auxiliary engine power of 1156 European Union (EU) fishing vessels were used to train conditional inference random forests and fill in gaps for the remainder of the high-seas fleet.

The SFC parameter measures the efficiency of an engine and varies with engine type (for example, medium speed versus high speed), type of fuel [for example, marine diesel oil (MDO) versus bunker oil], engine age, vessel size, and type of activity (for example, maneuvering and cruising) (*35*). It has been estimated that 96% of the world's fishing fleet installed engine power uses MDO and 84% uses medium-speed diesel engines (*35*). For this type of engine and fuel, SFC factors range from 203 to 280 g/kWh (*36*).

Given this information, we estimated upper and lower bound estimates of fuel costs using (i) country-specific estimates of SFC when available and the size-specific SFC for remaining countries (high bound) and (ii) only the size-specific SFC (low bound). In both cases, we used a constant SFC of 217 for auxiliary engines and used the difference in SFC between cruising and maneuvering (9% higher SFC when maneuvering) as a proxy of SFC when fishing versus transiting (*35*).

The load factor (LF) is calculated from the cubed ratio of a vessel's instantaneous speed (v) and its design speed (d). This is bounded between a minimum load (20%) when engines are idling to a maximum load assumed when vessels operate at design speed (90%) (*37*). For trawlers, we need to account for high LFs at relatively low speeds when vessels are towing gear in the water, so we used a LF of 0.75 to all trawlers during fishing activities as suggested by Coello *et al.* (*37*).

$$\mathrm{LF}_{i,j} = L_{\max} \times \frac{\frac{v_{i,j}3}{d_i} + \frac{L_{\min}}{L_{\max} - L_{\min}}}{1 + \frac{L_{\min}}{L_{\max} - L_{\min}}}$$

Instantaneous vessel speed (v) was obtained from AIS/VMS messages and also inferred using time and distance from AIS/VMS data. The design speed of each vessel was estimated using a linear regression of engine power versus design speed using vessel characteristics of

23,000 fishing vessels from the IHS Fairplay database (N. Olmer, International Council on Clean Transportation, personal correspondence, April 2017; see eq. S1). For auxiliary engines, we used the average LF reported by the EEA for cruising (0.3) and maneuvering (0.5) (*34*). Last, annual averages of global fuel prices were calculated with daily data of the price of MDO ($/metric ton) obtained from the Bunker Index for 2010–2016 (www.bunkerindex.com/prices/bixfree.php?priceindex_id=5).

To account for gaps in AIS transmission, we applied the average fuel consumption per hour of each vessel to the total time it spends in the gaps. The costs associated with gaps represented ~16% of total fuel cost. This same methodology was used to estimate the fuel costs of reefers and bunkers that support the high-seas fishing fleet (table S6).

Labor costs

We built a database of labor costs using different sources such as government reports, gray literature, and estimates of mean wages for fishers and similarly skilled workers reported by the International Labor Organization (ILO). This search often yielded two different metrics of labor cost: (i) labor cost per day and (ii) labor cost per crew member per day. We used these to estimate total labor cost for each vessel (LC_i) with the following two equations

$$\mathrm{LC}_i = N_i \times W_i$$

or

$$\mathrm{LC}_i = N_i \times w_i \times C_i$$

where N_i is the total number of days at sea for vessel *i*, W_i is the estimated labor cost per day assigned to that vessel, w_i is the labor cost per day per crew member, and C_i is the estimated crew size of vessel *i*.

For a subset of countries, representing 25% of total high-seas fishing effort—the EU, Japan, South Korea, and Chile—we were able to obtain reliable estimates of labor costs per day. For China, we obtained information on the average labor costs per month of crew members onboard the country's squid jigger fleets (J. Ho, Maritima Oceánica S.A.C., personal communication, December 2017). For Taiwan, we used the country's minimum wage. Given that fleets often use labor from similar nationalities (for example, Philippines and Indonesia), and assuming that labor costs are mostly determined by a vessel's gear type and size, we used the average labor costs from these countries to estimate the labor costs of the remaining high-seas fleet. We considered this our high bound estimate.

Realizing that fleets often use the cheapest labor available and that it is not uncommon for human rights violations to take place on board high seas and distant-water vessels [for example, (*22*–*24*)], we searched for additional—often less reliable—information on labor costs to estimate a lower bound. For China, Taiwan, the United States, and Vanuatu, we obtained gray literature estimates of labor cost, and for several other countries, we used the mean wages for fishers or similarly skilled workers as reported by the ILO. For the remaining countries, we filled in data gaps with regional, gear type, and size-specific averages. All monetary values have been converted to US dollars.

Total fishing costs

The EU Annual Economic Report and Japan's Fisheries Yearbook provide detailed information on the cost structure of distant-water fleets by vessel size class. Using these data, we estimated the fractions that fuel and labor cost represent from the total costs (f). These costs include depreciation, opportunity costs of capital, repair, maintenance, rights, other variable costs, and other nonvariable costs.

$$\mathrm{TC}_i = \frac{\mathrm{FC}_i + \mathrm{LC}_i}{f}$$

After estimating the total fishing costs of each vessel, we distributed it spatially proportionally to the fishing energy spent at each position

$$\mathrm{TC}_{i,j} = \frac{\mathrm{TC}_i \times E_{i,j}}{\sum_j E_{i,j}}$$

where TC_i is the total cost of vessel *i*, and $E_{i,j}$ is the fishing energy by vessel *i* on position *j* defined as

$$E_{i,j} = h_{i,j} \times P_i \times F_{i,j}$$

where $h_{i,j}$ is the time associated with each position, P_i is the vessel's engine power, and $F_{i,f}$ is a binary variable that represents whether or not a vessel is fishing at a particular position (that is, 0, not fishing; 1, fishing). This methodology allows us to determine the fraction of total fishing costs associated with fishing activity on the high seas.

Reefers and bunkers

We used the same methodology as above, with slight modifications, to estimate the costs of the reefers (transshipment vessels and fish carriers) and bunkers (fuel replenishment vessels) that support the high-seas fishing fleet. To estimate fuel costs, we used the same formula as for fishing vessels, excluding the rules that increase engine LFs during fishing behavior (that is, 0.75 LF for trawlers, 9% increase in LF during fishing behavior for other gears, and 0.5 LF for auxiliary engines). This approach likely results in an underestimate of the fuel costs of these vessels because it does not account for the potential increase in power needed during rendezvous events. For labor costs, we used the same average upper and lower bounds of labor costs per day by vessel size class used to fill in gaps as described in the Labor costs section above (see also the Supplementary Materials). Similarly, we used the same fractions of total cost by vessel size class to estimate total costs. The main difference in methodology is apportioning high-seas costs from total cost. To do this, we calculated the fraction of total encounters that involved vessels from the high-seas fleet and used this estimate as the fraction of total costs associated with the high seas (C_{hs_i})

$$C_{\mathrm{hs}_i} = \frac{\mathrm{TC}_i \times R_{\mathrm{hs}_i}}{\mathrm{TR}_i}$$

where TC_i is the total costs of vessel *i*, TR_i is the total number of rendezvous of vessel *i*, and R_{hs_i} is the number of rendevouz of vessel *i* with fishing vessels of the high-seas fleet.

Catch and revenue

We used high-seas catch and landed value data from the Sea Around Us research initiative for 2014, aggregated by fishing country and FAO region. Global catch data were reconstructed separately for every maritime country and its territory by the Sea Around Us or by over 300 colleagues around the world, following a general catch reconstruction approach (*38*). In principle, this approach evaluates and reviews a country's official reported catch data to ascertain what fisheries components are missing from official reported data. These identified gaps are then filled in using all available data and information sources to derive time series of unreported catches. This may include the use of assumption-derived estimates [see (*12*) and references therein]. Thus, the Sea Around Us reconstructed catch data complement official reported data as presented by the FAO on behalf of countries with best estimates of unreported catches and major discards. The Sea Around Us reconstructed catch database contains three layers of catch data: layer 1, domestic catches within the home EEZ; layer 2, non-tuna catches taken by fleets outside of home (domestic) waters (that is, foreign catch); and layer 3, industrial tuna and other large pelagic fisheries catches. The domestic data in layer 1 was the major focus for reconstructions, and thus data within EEZs have the most comprehensive coverage for unreported catches. These data, while of no direct relevance in the present context of high-seas areas, suggest that around 30% of total EEZ catches are unreported (*13*). Layer 2 (foreign non-tuna catches) and layer 3 (industrial tuna and other large pelagic catches) have so far received less attention on unreported catches, although discards have been added to all data. Thus, the catch data used here for high-seas areas, although reconstructed, need to be considered as minimal estimates of the likely actual high-seas catches.

Catch reconstructions are now widely documented in the peer-reviewed literature [for example, (*39*–*43*)] and increasingly used, for example, as part of the Environmental Performance Index (*44*) or in global studies on human nutrition and health (*45*). The landed value of catches was derived by multiplying the reconstructed catches by the global ex-vessel price database first derived by Sumaila *et al.* (*46*), and since updated by Swartz *et al.* (*47*) and Tai *et al.* (*48*).

The reconstructed catch data for high-seas areas were combined with effort data to estimate ratios of landed value per fishing energy (in dollars per kilowatt-hour)

$$\mathrm{RR}_{k,f} = \frac{\mathrm{LV}_{k,f}}{E_{k,f}}$$

where $\mathrm{RR}_{k,f}$ represents the revenue per unit of energy spent fishing by country k on FAO region f, $\mathrm{LV}_{k,f}$ is the total landed value of high-seas catch by country k on FAO region f, and $E_{k,f}$ is the total energy spent fishing by country k on FAO region f.

We then used these ratios to apportion fishing revenue across high-seas positions

$$R_{i,j,k,f} = \mathrm{RR}_{k,f} \times E_{i,k,f,j}$$

where $\mathrm{RR}_{k,f}$ represents the revenue per unit of energy spent fishing by country k on FAO region f, and $E_{i,k,f,j}$ is the fishing energy spent by vessel i on position j. This process was species-agnostic for all gear types except for squid jiggers, for whom mapping species to gear type is a direct link. Of the total landed value of \$8.5 billion for the 2014 reconstructed catch by the Sea Around Us, we were able to match \$7.6 billion (that is, 89%) to GFW effort by country and FAO region.

Fishing profits

We estimated fishing profits on the high seas without (π) and with (π^*) subsidies by combining costs, revenues, and subsidies at each position

$$\pi_{i,j} = R_{i,j} - \mathrm{TC}_{i,j}$$
$$\pi^*_{i,j} = R_{i,j} - \mathrm{TC}_{i,j} + S_{i,j}$$

where $R_{i,j}$ represents high-seas revenue, $\mathrm{TC}_{i,j}$ denotes cost, and $S_{i,j}$ indicates subsidies from vessel i at position j.

We present two scenarios, with and without scaling for unseen vessels, and for each we estimated upper and lower bounds of profits with and without subsidies. The principal driver of the uncertainty that makes the upper and lower bounds is labor costs (especially for Chinese and Taiwanese vessels). In the upper bound, we assumed that labor costs from the EU, Japan, South Korea, and Chile are representative of the average labor cost per day across all fleets. In the lower bound, we used gray literature estimates of average labor costs of crew on Chinese and Taiwanese distant-water fleets, as well as estimates of mean wage of fishers or similarly skilled workers from the ILO.

Government subsidies

We made the reasonable assumption that high-seas fisheries are large scale and used this to estimate high-seas fisheries subsidies for each country that is known to have vessels operating in the high seas. We applied two steps. First, we computed the amount of fisheries subsidies to large-scale fisheries (LSF) per landed value (LV) they generate for countries identified to be fishing in the high seas. In other words, we calculated subsidy per landed value, $x_n = y_n/z_n$, where y is subsidies to LSF and z is LV generated by LSF of high-seas fishing country, n. Second, we estimated the amount of subsidies provided by each high-seas fishing country, s_n, to its fleet operating in this area of the ocean by multiplying subsidy per landed value, x_n, to the estimated landed value generated in the high seas (l_n): $s_n = x_n{*}l_n$.

To accomplish the first step, we needed data on the total landed values and the proportion thereof that was generated by LSF versus small-scale fisheries (SSF) by each high-seas fishing country (n), and the total amount of fisheries subsidies and the proportion thereof that was received by SSF compared to LSF. To implement the first step, we needed data on the total landed values and the proportion thereof that was generated in the high-seas versus within-country EEZs.

Subsidies to LSF (that is, y_n) were taken from Sumaila *et al.* (*20*, *49*) and Schuhbauer *et al.* (*50*), while LVs generated by LSF (that is, z_n) by high-seas fishing countries were taken from the Sea Around Us and Fisheries Economics Research Unit databases (*46*–*48*) (www.seaaroundus.org). The estimated landed values generated in the high seas (l_n) were obtained from the same database.

For each country, we then apportioned total high-seas subsidies across high-seas vessels ($S_{i,k}$) proportionally to a vessel's fraction of the country's installed capacity (engine power)

$$S_i = \frac{S_k \times P_{i,k}}{\sum_i P_{i,k}}$$

where $S_{i,k}$ is the high-seas subsidies of vessel i from country k, S_k is the total high-seas subsidies of country k, and $P_{i,k}$ is the engine power of vessel i from country k.

Last, similarly to the method used to apportion costs spatially, we apportioned subsidies proportionally to the energy spent fishing at each AIS/VMS position on the high seas

$$S_{i,j} = \frac{S_i \times E_{i,j}}{\Sigma_j E_{i,j}};\ \text{for } j \text{ on high seas}$$

where $S_{i,j}$ represents the subsidies from vessel i allocated to high-seas position j, S_i is the total subsidies allocated to vessel i, and $E_{i,j}$ is the energy spent fishing by vessel i on high-sea position j.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/6/eaat2504/DC1
Supplementary Materials and methods
fig. S1. Distributions of vessel characteristics, high-seas fishing effort relative to total fishing effort, and nonlinear relationships between length, tonnage, and engine power.
fig. S2. Vessel encounters on the high seas (2016).
fig. S3. Fishing effort by gear type.
fig. S4. Effort versus catch.
table S1. High-seas fishing fleets and effort by country (2016).
table S2. High-seas fishing fleets and fishing effort by gear type.
table S3. AIS coverage of high-seas fleet and scale factors by country, Regional Fisheries Management Organization, gear type, and vessel size in 2016.
table S4. Average labor costs per day by country, gear type, and vessel size class.
table S5. High-seas costs, catch, revenue, subsidies, and profits by country.
table S6. High-seas fishing costs by reefers and bunker vessels per flag state.
table S7. Summary of high-seas economics by country, gear type, and FAO region (scaled results).
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Acknowledgments: We thank GFW and SkyTruth for their continued support and for facilitating the use of their satellite database, Google for their ongoing technical guidance and substantial in-kind contribution of Google Cloud Platform that enables GFW and our analysis, and B. Liu for assistance with Chinese fishery data. Many thanks to two anonymous reviewers for their comments, which greatly improved an earlier version of the manuscript. **Funding:** This study was funded by National Geographic Pristine Seas (see pristineseas.org for a list of funders). D.P., D.Z., and M.L.D.P. acknowledge support from the Oak Foundation, the Marisla Foundation, the Paul M. Angell Family Foundation, and the MAVA Foundation. C.C. acknowledges support from the Waitt Foundation. U.R.S. acknowledges support from OceanCanada Partnership and the Social Sciences Research Council of Canada. **Author contributions:** E.S., J.M., C.C., and U.R.S. designed the study. J.M., D.K., M.L.D.P., D.P., U.R.S., and D.Z. provided data. E.S., J.M., C.C., D.K., and U.R.S. performed the analysis. E.S., J.M., C.C., D.K., M.L.D.P., D.P., U.R.S., and D.Z. wrote the paper. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 12 February 2018
Accepted 10 May 2018
Published 6 June 2018
10.1126/sciadv.aat2504

Citation: E. Sala, J. Mayorga, C. Costello, D. Kroodsma, M. L. D. Palomares, D. Pauly, U. R. Sumaila, D. Zeller, The economics of fishing the high seas. *Sci. Adv.* **4**, eaat2504 (2018).

APPLIED ECOLOGY

The environmental niche of the global high seas pelagic longline fleet

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International interest in the protection and sustainable use of high seas biodiversity has grown in recent years. There is an opportunity for new technologies to enable improvements in management of these areas beyond national jurisdiction. We explore the spatial ecology and drivers of the global distribution of the high seas longline fishing fleet by creating predictive models of the distribution of fishing effort from newly available automatic identification system (AIS) data. Our results show how longline fishing effort can be predicted using environmental variables, many related to the expected distribution of the species targeted by longliners. We also find that the longline fleet has seasonal environmental preferences (for example, increased importance of cooler surface waters during boreal summer) and may only be using 38 to 64% of the available environmentally suitable fishing habitat. Possible explanations include misclassification of fishing effort, incomplete AIS coverage, or how potential range contractions of pelagic species may have reduced the abundance of fishing habitats in the open ocean.

INTRODUCTION

The high seas [or areas beyond national jurisdiction (ABNJ)] encompass more than 45% of the world's surface area and 90% of the ocean's volume. Before the 1950s, limitations in fisheries technologies predominantly restricted global marine fisheries to coastal and shelf waters. However, technological advancements after World War II, such as improved refrigeration, increased engine power, and acoustic sonars, prompted a rapid expansion of marine fisheries into ever more remote high seas waters (*1*). Consequently, high seas fisheries catch increased by 10-fold, from 450,000 metric tons (MT) in 1950 to about 6,000,000 MT by 2014 (*2*). As of 2015, high seas fisheries represented 6% of the global annual marine fisheries catch by mass and 8% by fishing revenue (*3*). Tuna and billfish make up the majority of the reported high seas catch by longliners and purse seiners and, by 2012, represented 9.3% of global annual marine fisheries catch (*4*, *5*). This expansion also entailed novel impacts on oceanic and deep-sea systems (*6*, *7*). While the importance of the high seas for the global seafood industry has continued to grow, the regulatory frameworks and monitoring mechanisms necessary to support their sustainable use have lagged (*7*).

The current governance frameworks for management of marine life in ABNJ were established in 1982 by the third United Nations Convention on the Law of the Sea and were further developed by the 1995 UN Fish Stocks Agreement (UNFSA) through the establishment and consolidation of regional fisheries management organizations (RFMOs). RFMOs have the legal responsibility to manage high seas fish stocks, but also nonfish species [UNFSA Article 5(g)], and biodiversity [UNFSA Article 5(f)]. The performance of these bodies in protecting biodiversity beyond their target commercial species has been questioned recently (*8*, *9*). According to the UN Food and Agriculture Organization, migratory and straddling stocks harvested in ABNJ are overfished or are experiencing overfishing at twice the rate of stocks found within national waters (64% versus 28.8%)(*4*). A separate assessment of the status of the stocks managed by the world's RFMOs concluded that 67% of these were either overfished or depleted (*8*) and that several of these have experienced range contractions due to overharvesting (*10*).

Some of the existing concerns about RFMO management include insufficient monitoring and weak implementation of ecosystem-based management measures due to the consensus-based RFMO governance process (*9*). As an example, the fisheries observer coverage of some pelagic longline fleets is as low ~5%, and can be even lower (*11*), which means that most longline fishing remains unmonitored. Novel forms of electronic monitoring help to address challenges related to the monitoring of catch and bycatch, reporting of fishing effort, and vessel distribution (*12*). These new technologies include vessel tracking systems such as the vessel monitoring system (VMS) or the automatic identification system (AIS), which can help with the surveillance and monitoring of marine fisheries (*13*, *14*) even in remote waters. Not all vessels are required to carry AIS devices onboard, and regulations change between vessel type, size, and nationality as well as where vessels are fishing. For example, the United States requires that all self-propelled fishing vessels of 20 m or more in length must carry an AIS device onboard, but only while fishing in nearshore waters (Code of Federal Regulations, § 164.46). The International Maritime Organization (IMO) requires all passenger vessels or those larger than 300 gross MT to carry AIS devices. A growing number of programs have recently emerged using satellite-based AIS geolocation data to track and monitor fishing at sea. Some monitoring programs such as the Pew Charitable Trusts' Eyes on the Sea project or the FISH-i Africa project (www.fish-i-africa.org) focus on identifying illegal and unreported fishing, while other programs such as Global Fishing Watch (GFW; www.globalfishingwatch.org) classify the behaviors of fishing vessels, providing open access data on the global distribution of fishing effort across the main gear types, and are continuously improving their ability to detect, classify, and quantify fishing effort estimates (*12*, *15*).

Ecosystem-based fisheries management must address the impacts of fishing, such as habitat destruction and alterations of biological

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communities, via techniques that can monitor current activities and predict and manage future ones. Many of the management and conservation conflicts addressed by the ecosystem-based fisheries management framework are the result of a lack of information on the spatiotemporal distribution of resources and resource users. One mechanism to understand existing impacts on high seas biodiversity is to compare the distribution of fishing effort with bycatch species such as sharks (*16*) or seabirds (*17*). While these studies are very useful for gaining an initial understanding of the overlap of fisheries and their associated species (which RFMOs are required to manage), they are retrospective and do not capture the underlying dynamic oceanographic processes that result in the spatiotemporal overlap. To understand potential future interactions, mechanistic or correlative statistical models that explore the distribution or density of species in relation to environmental predictors are necessary [for example, (*18*–*20*)]. These studies have been conducted on many marine vertebrate species, yet very few studies (*21*) have analyzed the environmental correlates of human (for example, fisheries) distribution and attempted to understand their impacts through this lens. One example of such a study accurately predicted the distribution of fishing effort a year in advance (*21*). Fisheries managers can use information regarding the predicted distribution of fishing effort and bycatch species to provide information on the likely location of bycatch [for example, (*22*)], targeted observer coverage or enforcement (*23*), and partial closures or zoning (*24*). Further, models of the distribution of fishing effort can be run under different climate scenarios to help understand how fishing effort may shift in the future and affect fishing communities (*25*).

For instance, Kroodsma *et al.* (*26*) explore the influence of primary productivity and surface temperature estimates on the intensity of global fishing effort across multiple types of gear and flag States derived from AIS data. They conclude that other socioeconomic factors are much more influential in explaining the intensity of fishing effort than either environmental variable; however, they also note that longline fishing effort in the Indian Ocean was correlated with surface temperature (*26*). We consider that the lack of a global response of fishing intensity across gear types to either environmental variable is to be expected given the wide range of fishing strategies that were assessed jointly. We find that their conclusions of a correlation between longline fishing and temperature are evidence that, when assessed individually, individual gear types may show well-delineated responses to certain environmental predictors.

Here, we explore the spatial ecology and drivers of the global distribution of the pelagic longline fishing fleet in the high seas by creating environmental predictive models of fishing distribution from satellite-based AIS data from GFW. We build environmental niche models using a boosted regression tree (BRT) modeling approach that relates the location of fishing events to different environmental conditions and compares them to a set of pseudoabsence points (areas of no observed fishing). By comparing the conditions where fishing was observed to locations where fishing was not observed, we hope to decipher which environmental conditions seem to be preferred by longliners. Our model used 14 environmental variables: sea surface temperature (SST), temperature at 400 m (T400), turbulent kinetic energy (TKE), particulate organic carbon (POC), net primary productivity (NPP), mixed-layer depth (MLD), surface oxygen concentration (SOC), oxygen concentration at 400 m (O400), sea surface salinity (SSS), salinity at 400 m (S400), euphotic depth (ZEU), bathymetry (BATH), distance to continental shelf (DCS), and distance to seamount (DSM). By applying concepts that were originally developed to explore the ecological niches of terrestrial and marine animals, we aim to better understand the environmental preferences of longline fishing fleets in ABNJ and to shed light on the factors shaping their distributions at large scales, which opens new avenues for predictive forecasting of future spatial patterns of global longline fishing effort and concomitant stresses on the high seas. We are aware that other socioeconomic factors play important roles in the decision-making process of marine fishing activities and hope that our analysis informs future work that also includes these variables.

RESULTS

High seas longline fleet composition and distribution

After analyzing all satellite-based AIS fishing effort data from GFW, we found that longline fishing effort in the high seas accounted for 84 to 87% of the fishing effort (by hour) across gears during the study period (fig. S1). While longline fishing effort is lower in ABNJ, it represents a major top-down pressure on oceanic ecosystems (*27*). Of the high seas longline fishing effort, 88.9% (2015) and 80.4% (2016) were attributable to five fishing States or territories: China, Japan, South Korea, Spain, and Taiwan (fig. S2). Taiwan dominates global longline fishing effort (by hour) in the high seas, followed by Japan, Spain, China, and South Korea. Our analysis focuses on these top-five fishing States or territories. AIS-derived fishing effort data show that the distribution of longline fishing effort in the high seas changes across space (Fig. 1) and time (Fig. 2). During 2015 and 2016, the tropical (23.5°N to −23.5°S) and temperate (66.5°N to 24.5°N and −24.5°S to −66.5°S) regions contained 64.6 and 35.3% of the global fishing effort, respectively. On average, the intensity of fishing effort in the high seas is higher during the boreal summers and peaks in July and August during 2015 and 2016, respectively (Fig. 2). The overall increase in fishing effort data between years is likely driven by an increase in the number of orbiting satellites capable of detecting AIS signals, as well as an increase in the capability of detecting and classifying longline fishing effort by the GFW group. Despite the increase in fishing effort intensity, the seasonal pattern where global longline fishing effort increases during the boreal summer months seems to be preserved between the two years. Untangling the drivers of the observed seasonal patterns of fishing effort requires a regional, fleet-specific approach that includes information about target species, fishing seasons, and quotas. All fishing effort data needed to evaluate the conclusions in this paper are available from GFW.

Model performance and prediction

We assessed the accuracy of our models using various metrics that measured the degree to which we can predict the raw fishing effort observations using our environmental suitability models. Our results demonstrate how the global distribution of longline fishing effort in the high seas can be predicted with high levels of accuracy across months and years using BRTs to explore the environmental conditions in which fishing observations occurred. By comparing four different model performance metrics across years and threshold types (n = 16), we were able to determine that predictions from monthly models outperformed the temporally averaged model that used the data across all months. Using a Wilcoxon signed-rank test, we found statistically significant differences in the distribution of the accuracy metrics in 14 of the 16 model performance comparisons (table S5), and the average performance scores were superior for the

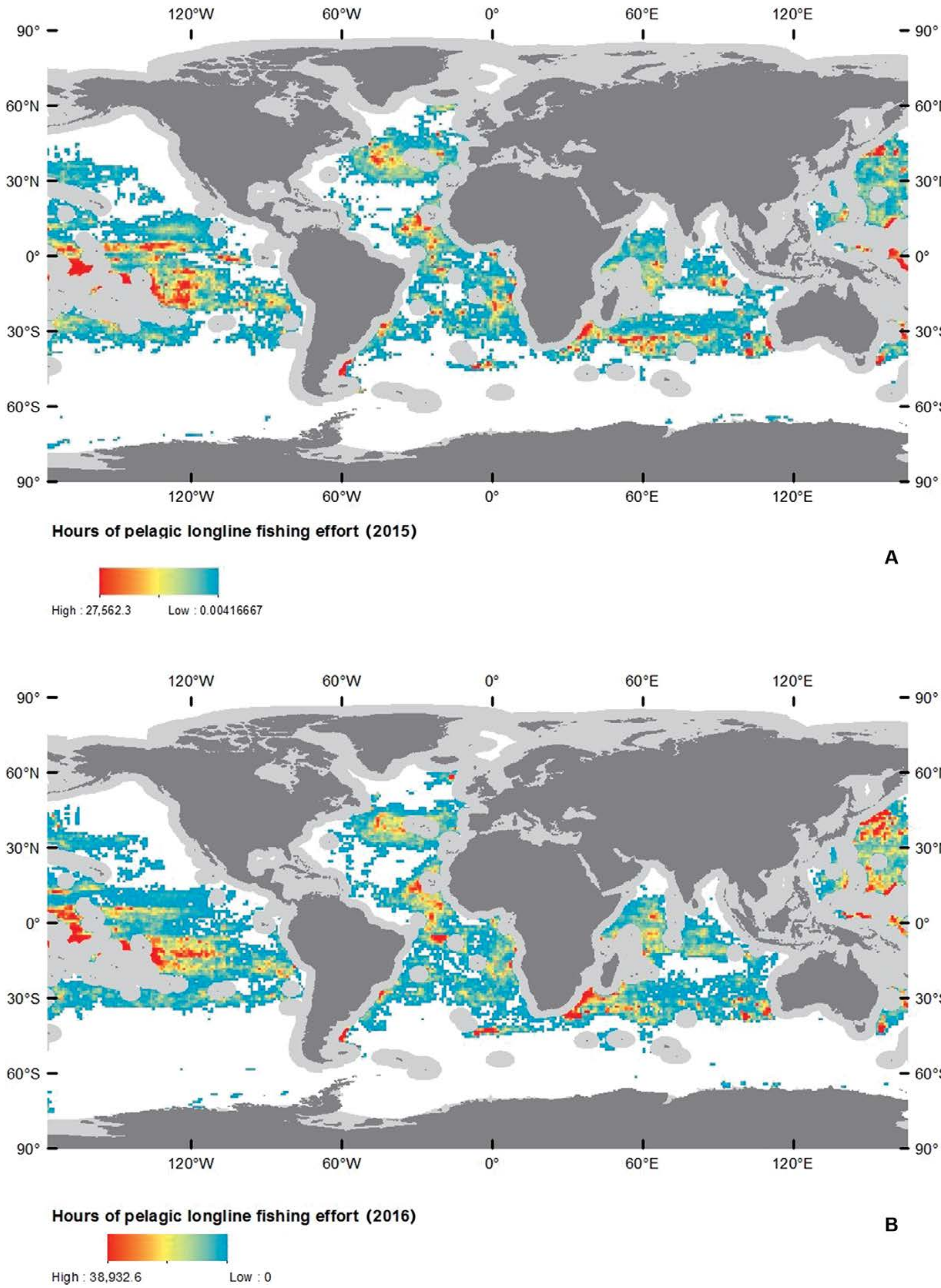

Fig. 1. Distribution of global pelagic drifting longline fishing in ABNJ in 2015 and 2016. (**A**) 2015. (**B**) 2016. Light gray areas depict exclusive economic zones (EEZs) that were excluded from this study. Fishing effort (hours) as calculated by GFW using satellite-based AIS data. Given the differences in quantified fishing effort between 2015 and 2016, the scales were maintained separate to showcase how, despite changes in intensity, the main trends in longline fishing effort are maintained. Gray areas around coastlines depict EEZs excluded from this study. Data are from GFW.

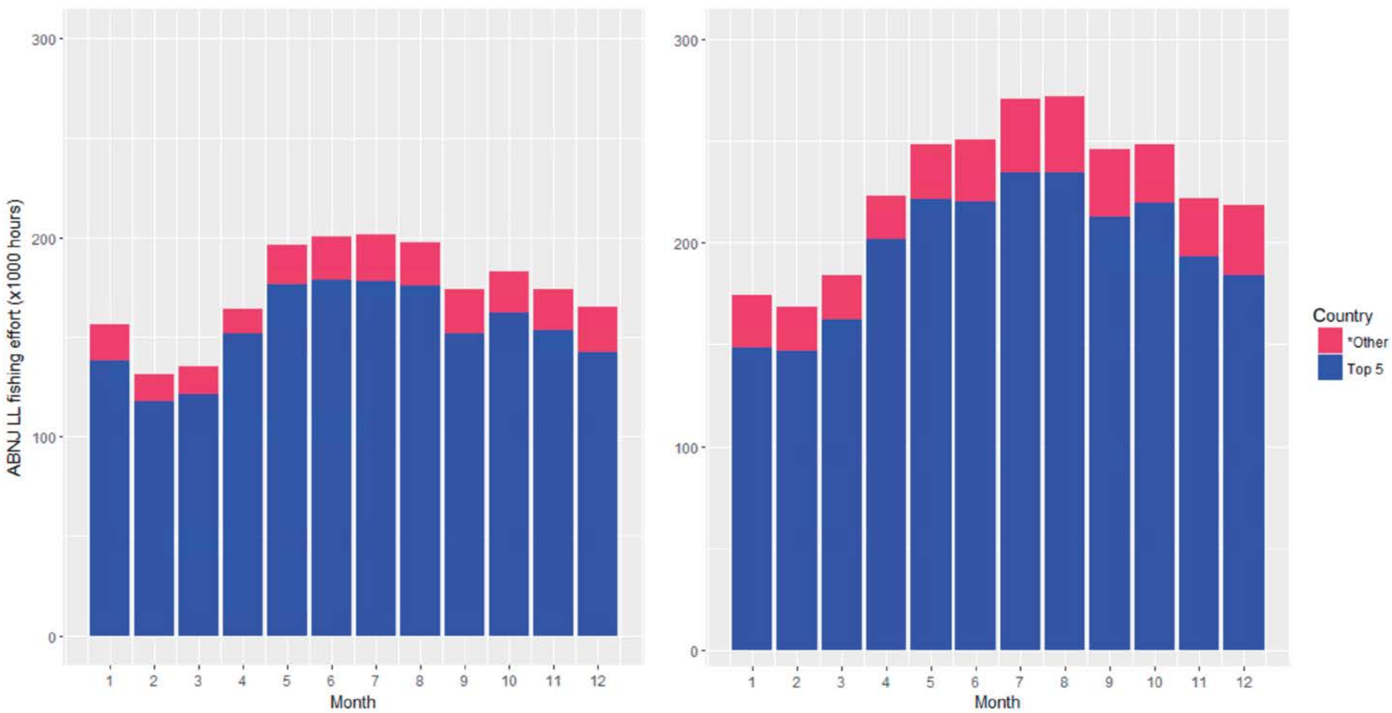

Fig. 2. Monthly distribution of pelagic longline fishing effort in ABNJ by the top five fishing States or territories, and all other countries combined. The total calculated fishing effort between the years increases between 2015 and 2016, with China and Taiwan experiencing the largest increases in quantified fishing effort. "*Other" represents a total of 45 other fishing nations deployed longline (LL) gear in ABNJ between 2015 and 2016.

monthly model in 15 of the 16 cases. The predictive accuracy and correct classification scores were high throughout the entire period studied (figs. S3 and S4 and tables S1 and S2) and support the use of environmental modeling for understanding the spatial patterns and environmental drivers of the human fisheries footprint in the ABNJ. We found that the predictive accuracy of the monthly environmental niche models after projecting them onto future environments (1, 6, and 12 months in advance) remained high. The mean predictive accuracy was lowest for the 6-month prediction (~74%), and both the 1- and 12-month predictions showed similar mean accuracy rates at ~82% (fig. S5).

The model outputs were projected onto geographic surfaces, where the likelihoods of observing longline fishing effort were displayed as probability estimates between 0 and 1. Post-processing of the model outputs required a definition of "suitable fishing habitat," which was done by selecting a probability cutoff value threshold for each map. Lower thresholds will classify more areas of the study region as suitable, while higher thresholds will be more restrictive. Here, we assessed the implications of applying two different types of threshold on our model outputs: receiver operator characteristic (ROC) curve and mean probability distribution (MPD) thresholds. Our results show how the choice of threshold provides slightly different estimates of longline suitable fishing habitat, although the differences in model performance are small (tables S1 and S2 and figs. S3 and S4). The thresholds derived from the ROC curve resulted in higher cutoff values, while the MPD thresholds were lower on average. Higher thresholds minimized the overprediction of suitable fishing grounds, while lower thresholds resulted in higher classification rates of observed fishing effort; this is reflected in the specificity and sensitivity values presented in the Supplementary Materials (tables S1 and S2).

Monthly persistence maps provide a visual representation of the global changes of fishing habitat suitability throughout the year (Figs. 3 and 4) and help identify areas of the high seas where favorable environmental conditions for longline fishing are most stable. The monthly persistence maps also help identify areas of the high seas that are not classified as environmentally suitable for longline fishing throughout the year, which provides valuable information about which areas may be experiencing less longline fishing pressure. The variability of environmental suitability to fishing in the high seas was assessed by mapping the average coefficient of variation of predicted high seas fishing suitability for each year (Fig. 5), which combines the 24 monthly predictions and identifies the areas where we can expect the highest changes in suitability. Tropical latitudes were found to be the most stable year-round fishing grounds after assessing both persistence maps and estimates of variability.

We used the binary estimates of suitable fishing habitat to calculate the proportion of the predicted fishing grounds where longliners were observed to obtain estimates of the global suitable fishing habitat that is occupied (table S6). These estimates are important to understand the realized niche of global longliners, that is, the amount of suitable fishing habitat that is actually fished. Results show how the global fleet is not occupying large proportions of the fishing grounds that our models classify as potentially environmentally suitable for fishing. In 2015, the average proportion of occupied suitable fishing habitat was estimated to be 38 to 55%, whereas estimates were slightly higher for 2016 at 47 to 64%; the differences within each year were partly related to the choice of threshold. We briefly explored the distribution of false-negative and false-positive classification for two months (January and July) in 2015 to explore potential seasonal effects or patterns and the influence of using different cutoff thresholds (fig. S6).

We consider that, while there might be a slight seasonal effect on the distribution of unfished areas that were classified as suitable—higher latitudes earlier in the year and lower latitudes in the boreal summer months—the distribution of false negatives (unsuitable fished habitat) did not seem to follow any patterns associated with latitude, longitude, or environmental gradients when these areas were overlaid with various environmental predictors, including SST, T400, O400, and DCS.

Environmental predictors of fleet distribution

The relative explanatory variable importance (VI) of the environmental variables used in the BRT models fluctuates on a monthly and interannual basis (Fig. 6 and tables S7 and S8), with different environmental variables explaining the distribution of fishing effort during different times of the year. The VI scores obtained from the monthly models (Fig. 6) show (i) how the environmental preferences of the high seas longline fleet can be characterized by a few environmental variables, namely, SST, DCS, T400 and O400; and (ii) how the correlates of fishing effort distribution show both intra- and interannual variability. The four variables shown to be consistently important throughout the year had annual average VI scores >10. Our results also showed how other environmental predictors with lower average VI scores (that is, NPP, SOC, POC, MLD, and S000) gain importance during certain times of the year (figs. S3 and S4), although these may be difficult to interpret given their weak signals.

We further explored the explanatory power of static and dynamic predictors by comparing various iterations of the 2016 monthly models by using (i) only static predictors, (ii) only dynamic predictors, and (iii) a combination of the two. The model performance metrics (table S9) demonstrate how the model that included both static and dynamic predictors outperformed both the static and dynamic models.

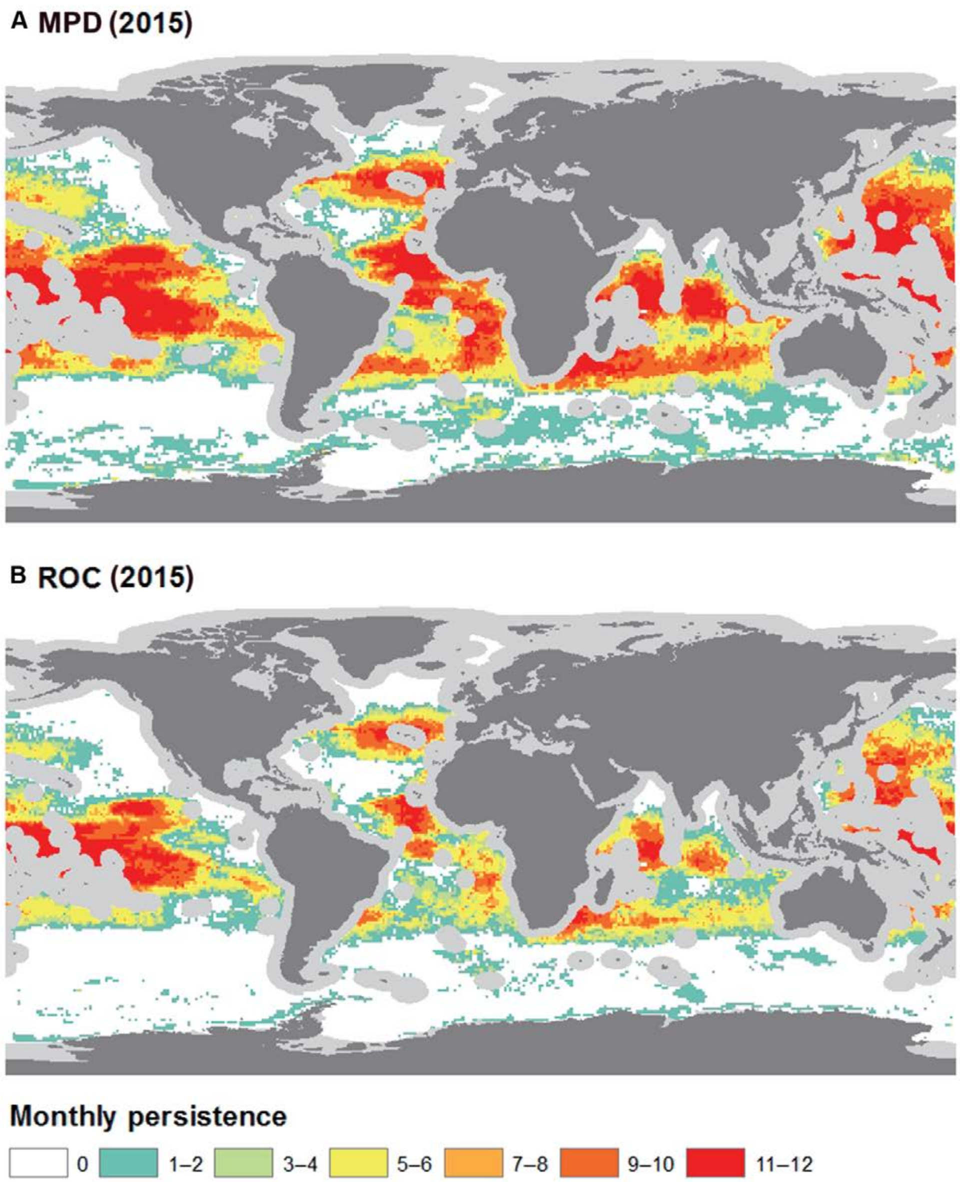

Fig. 3. The monthly persistence of suitable habitat in ABNJ for 2015. These persistence estimates were calculated using two different probability distribution cutoff thresholds: (**A**) MPD and (**B**) ROC. Gray areas around coastlines depict EEZs excluded from this study. Data are from GFW.

The performance of the model with static predictors was worse than that of the other two.

We explored the preferences of the longline fishing fleet further by assessing graphical visualizations of how increases or decreases in an environmental variable (for example, higher or lower temperatures) affect the probability of longline fishing; these figures are termed partial dependence plots (figs. S7 and S11). For instance, the relationship between longline fishing and SST, which was the most important environmental predictor in both years, shows a two-state response, where higher temperatures lead to higher suitability between January and February, and then progressively transitions to a response favoring a broader range of temperatures (including ~15° to 20°C surface waters). This second temperature state is most apparent in the months of June and July. We assessed the partial dependence plots for the environmental predictors that appeared to be persistently important throughout 2015 and 2016: SST, O400, T400, and DCS.

DISCUSSION

Here, we demonstrate how environmental niche models can be used to explain and predict the distribution of longline fishing effort in the high seas. What ecological niches do these new "fisheries apex predators" occupy in the high seas? Studying fisheries using analyses similar to those used to study marine animals has been suggested previously (*28*) and may provide opportunities to understand and predict the dynamics of fishing fleets. We suggest that models like the ones presented here be used in management to (i) identify likely areas of interaction between fisheries and bycatch species, allowing for spatial management approaches to be used to mitigate interactions; (ii) anticipate changes in the distribution of fishing effort by using the existing model output to predict fishing effort 12 months out or by running this type of model under various climate scenarios as has been done for many species (*18*); and (iii) better focus monitoring and surveillance efforts of longlining in open-ocean pelagic

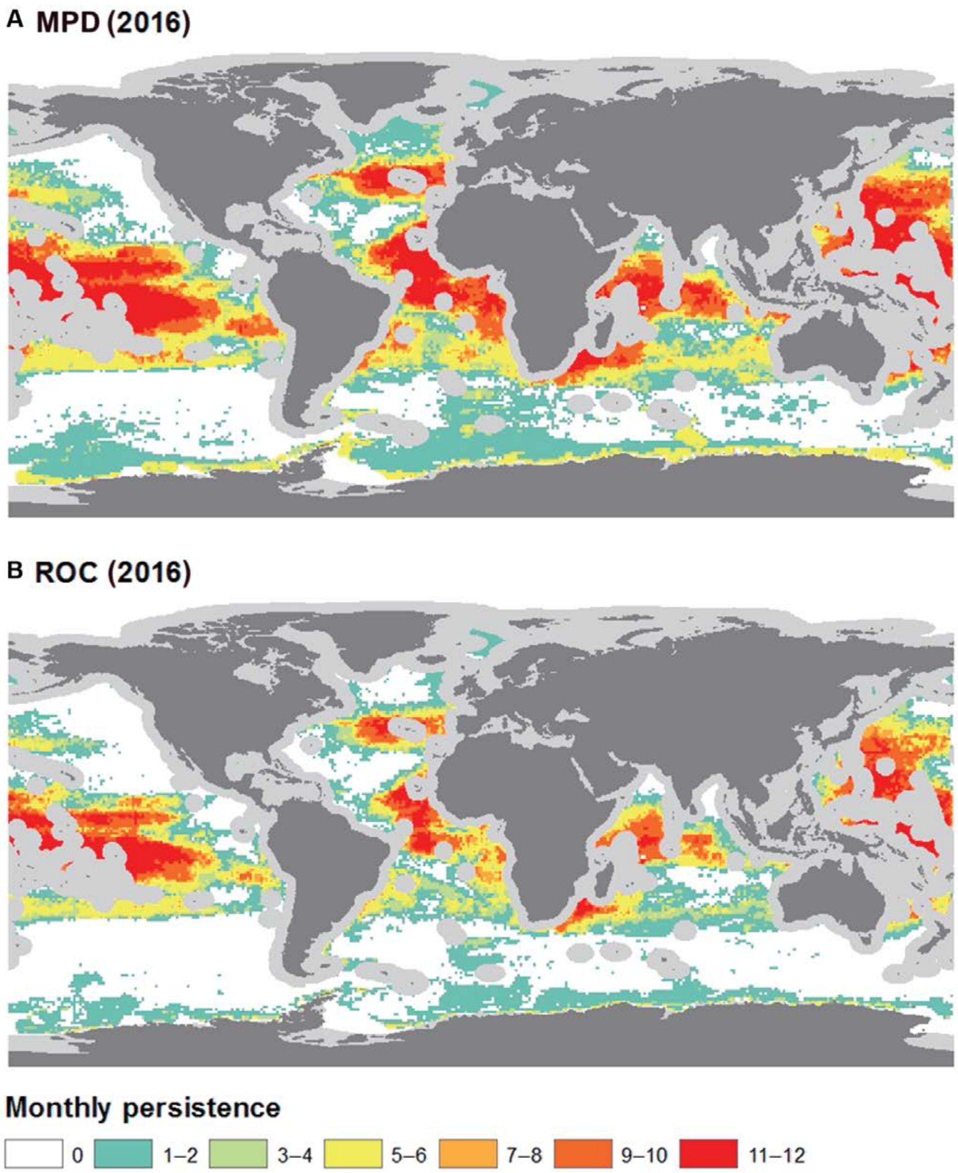

Fig. 4. The monthly persistence of suitable habitat in ABNJ for 2016. These persistence estimates were calculated using two different probability distribution cutoff thresholds: (**A**) MPD and (**B**) ROC. Gray areas around coastlines depict EEZs excluded from this study. Data are from GFW.

environments within EEZs by directing authorities to areas of likely fishing (*23*), and should be applicable to similar management of living marine resources in the high seas.

Model accuracy

The high model performance metrics (figs. S3 and S4 and tables S1 and S2) demonstrate how the distribution of pelagic longline fishing effort in the high seas is environmentally structured and can be explained and projected using predictive models combined with information on the environment surrounding fishing observations. The mean accuracy values (0.84) and area under the curve (AUC) scores (0.86) throughout the study period were high and exhibited slight average increases in 2016. Improvements in the availability of fishing effort data due to increased numbers of AIS-capable satellites launched over the past years as well as increased accuracy of the neural net detecting and classifying longline fishing effort due to more data available may have contributed to this slight improvement. The average correct classification (sensitivity) scores for both years were also high (0.93) and showed slight increases (6 to 11%) in correct classification when applying an MPD threshold. Conversely, the average false-positive classification (specificity) values were lower, suggesting that our model can correctly classify most of the observed fishing effort observations but slightly overpredicts fishing in some areas where no fishing effort was observed. The small differences in sensitivity and specificity scores between cutoff thresholds were expected as the MPD thresholds were, on average, lower than the thresholds derived from ROC curves. Lower probability distribution thresholds translate to larger areas of the high seas being classified as suitable for longline fishing effort, thus capturing more observed presence points (explaining the higher sensitivity scores) and including more areas with no fishing observations (which explains the higher overprediction of fishing or false positives). Regardless of the choice of threshold, our BRT models were able to explain most of the high seas longline fishing effort observations, which we consider to be a meaningful step toward understanding the current and future human use of the high seas. Potential explanations for the overprediction of the models into areas where no fishing effort was observed follow later in the discussion.

Variability and persistence of suitable fishing habitat

Through mapping the habitat suitability of the longline fleet in ABNJ across months, we identify areas of the ocean with higher intra-annual variability of environmental suitability for fishing; these predominantly occur in the peripheries of the more stable year-round fishing grounds. These areas of high intra-annual variability may correspond to waters where oceanographic conditions show strong seasonal variability throughout the year, such as boundary currents in the peripheries of oceanic gyres. The latitudinal poleward spread of some variables—such as surface temperature or dissolved oxygen, which decreases and increases, respectively, as you move away from the equator—during the boreal and austral summers likely causes the temporary increase in suitability of areas within the temperate and subpolar latitudinal bands. As previously mentioned, some target species show stable north-south seasonal movements, which correspond well to the seasonal increases in habitat suitability in those waters.

Persistent suitable habitat for longline fishing (that is, areas suitable for 6 to 12 months) is contained within the tropical and temperate latitudes, though there are longitudinal differences (Figs. 3 to 5) and the lower latitudes are the most stable and hold most of the persistent suitable habitat. These areas seem consistent with the global latitudinal habitat preferences displayed by the top-six tuna target species (*29*, *30*), which are among the main target species of longliners in ABNJ. However, further work is required to assess the degree of overlap by longline fisheries and target, both in geographic space and in

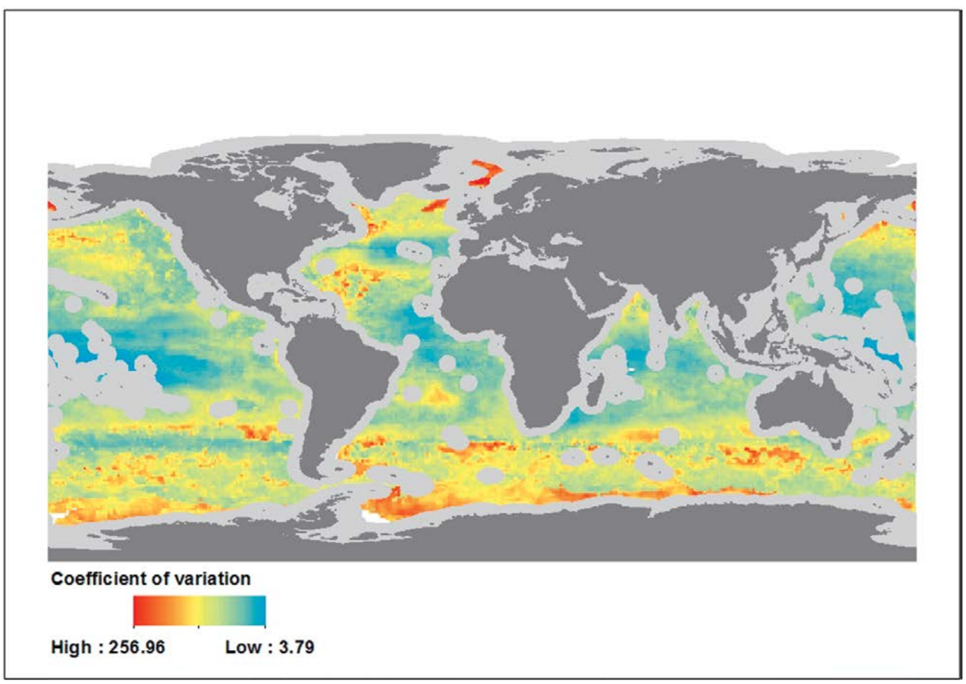

Fig. 5. The average coefficient of variation of predicted high seas fishing suitability for 2015 and 2016. Tropical latitudes show, on average, more predictive stability throughout the study period, whereas temperate and subpolar waters show higher degrees of variability of suitable habitat. Gray areas around coastlines depict EEZs excluded from this study. Data are from GFW.

environmental space; this may help better understand the areas of high persistence of fishing suitability seen in Figs. 3 and 4.

Environmental predictors of fleet distribution

Tuna and billfish species comprise 81.2% of the global longline landing estimates in ABNJ between 1950 and 2014 (*2*). While there seems to be a clear geographic overlap between the preferred habitat of the main tuna species and suitable fishing habitat for pelagic longliners in the high seas, our models also offer the opportunity to compare their environmental preferences. Our results suggest that longliners in the high seas show similar preferences to those of the species they are targeting. In 2015, the fleet showed strong preference for areas where the temperature at 400-m depth was between 8° and 18°C (fig. S8); this preference was stable throughout the year and consistent with the temperature preferences of some commercially exploited tunas (*31*). The response of fishing to different oxygen concentrations at 400-m depth (fig. S10) shows that longline fishing effort in ABNJ is more commonly found in waters where the dissolved

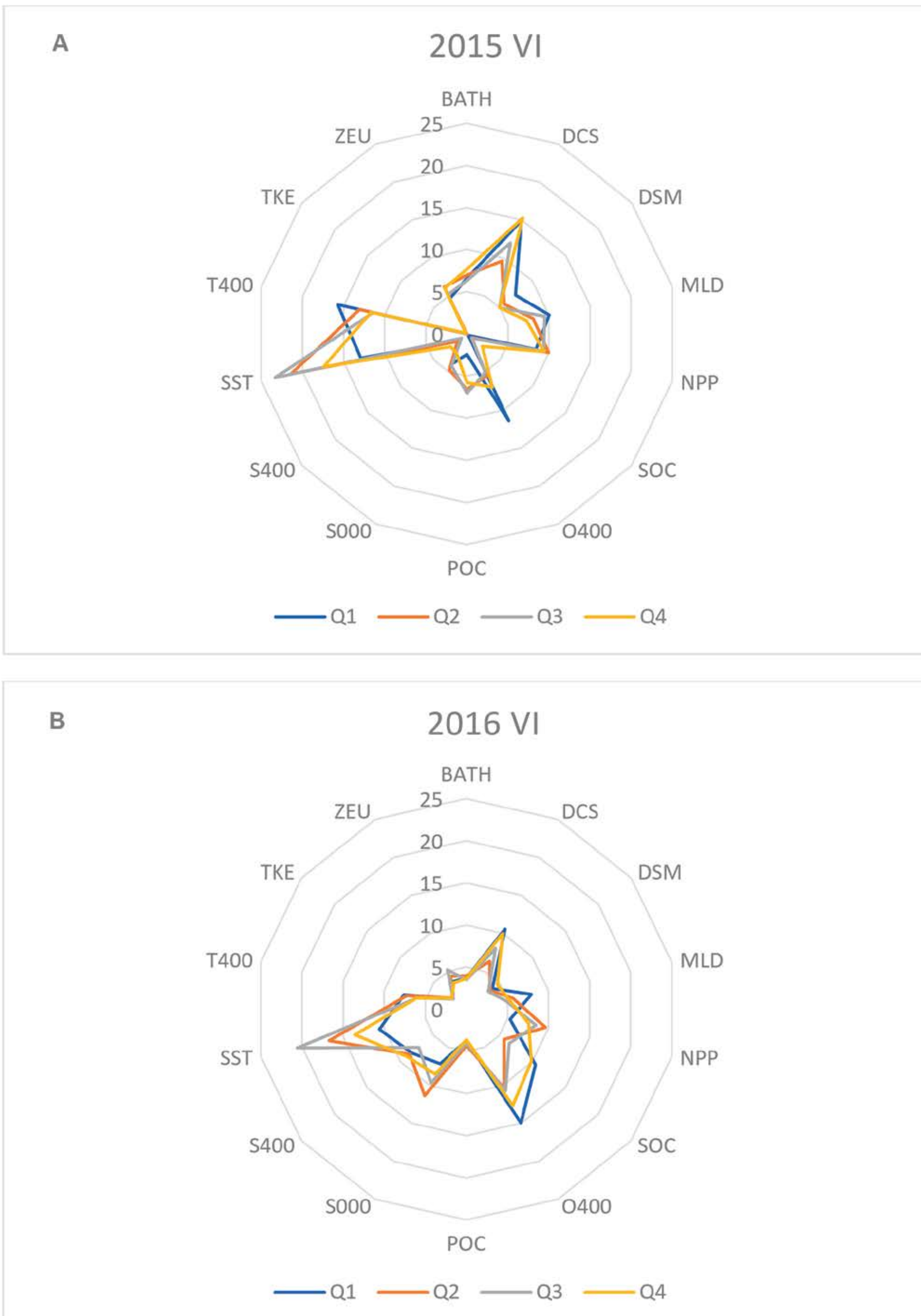

Fig. 6. Radar plots of the average quarterly VI scores in 2015 and 2016. (**A**) 2015. (**B**) 2016. The monthly VI scores for each of the two years assessed were averaged by quarter (Q) to capture the seasonal changes in the importance of each of the environmental predictors: Q1, January–March; Q2, April–June; Q3, July–September; Q4, October–December.

oxygen concentration at that depth is between 1 and 5 ml O_2 liter^{-1}; this is also consistent with findings on the physiological preferences and thresholds of tuna. For instance, studies have found oxygen concentration tolerances as low as 3.5 ml O_2 liter^{-1} for skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) and 1.5 ml O_2 liter^{-1} for bigeye tuna (*Thunnus obesus*) (*32*). We consider that the response to the DCS variable is partially masked by the 200-nm jurisdictional buffer that was used to exclude any within-EEZ fishing in this study; a separate analysis including coastal fishing may be required to interpret the true influence of this variable on longline fishing effort distribution. From the DCS partial dependence plot (fig. S9), we can infer that the probability of fishing in the high seas increases with DCS during some months of the year, which is likely driven by the high amounts of longline fishing in the central Pacific Ocean. The overall preference for warmer waters described by the model likely results from the fact that many of the species targeted by the global pelagic longline fleet year-round are tropical or subtropical (for example, *T. albacares* or *T. obesus*). These results (figs. S7 and S11) agree with those of Kroodsma *et al.* (*26*), who found that longline fishing effort intensity was highest between the 16° and 19°C isotherms. The bimodal response to SST that can be observed during the boreal summer months may be caused by the northward movement of some targeted species into more temperate waters during these months, as seen in swordfish (*Xiphias gladius*) (*33*) or Atlantic bluefin tuna (*Thunnus thynnus*) (*34*). These findings are aligned with the conclusions of the study by Arrizabalaga *et al.* (*30*), where sea temperature and dissolved oxygen were the variables that explained the most deviance when modeling tuna logarithmic catch per unit effort. Despite differences in the extents between our studies, as well as some variations in the environmental variables, the similarities in the environmental preferences of tunas and those displayed by longliners suggest that the high seas longline fleet is tracking many of the same environmental cues as their main target species. Given the wide range of species targeted by the global pelagic longline fleet, the environmental preferences of the fleet are not expected to bear exact resemblance with any one given taxon. Further, the high seas longline fleet may not have a static environmental niche but instead may adapt its distribution and "environmental preferences" to maximize overlap with its multiple target species throughout the year, in a potentially consistent and predictable manner.

Given the global scale of our analysis, the spatial and temporal resolution of our predictors was coarse, which limited our ability to capture the influence of mesoscale oceanographic features, such as oceanic frontal zones and eddies, on the distribution of fishing effort. However, given the spatial scale of our study, we consider that our models successfully explain the broad environmental patterns that shape the distribution of the global longline fishing fleet in the high seas. We also see great promise in the use of environmental niche models for predicting the distribution of future fishing effort, which could bring us a step closer to designing and implementing precautionary spatiotemporal management measures based on future oceanographic conditions. While these efforts would have to be tailored for specific regional fleets, the promising predictive accuracy estimates that we obtained from our models indicate that estimating the future distribution of fishing pressure based on oceanography is likely feasible.

Interpreting low occupancy rates

Our models predict significantly more area as being suitable for fishing than was observed to have fishing effort. The unfished parts of ABNJ that were classified as suitable fishing grounds are not closed to fishing by RFMOs and are not further away from commercial fishing ports than those areas fished in ABNJ. While these areas could be the result of classification errors in our models, ecological theory provides an alternative explanation: decreased occupancy by target species of their fundamental niche. Multiple factors may influence whether a species occupies its fundamental niche, including limitations to dispersal, predator avoidance, exclusion by interspecific or intraspecific competition, or lack of resources. Our results show that the average proportion of fishing ground occupancy for high seas longliners fluctuated by year and threshold method, with a maximum of 55 and 64% in 2015 and 2016, respectively. Just as an animal would avoid habitats with limited resources, unfished areas with appropriate environmental conditions may be avoided by the high seas pelagic longline fleet due to reduced overlap with target species or insufficient abundances despite environmentally suitable conditions. A recent study demonstrated how several pelagic target species have experienced contractions in their ecological range because of decreasing abundance (*10*). It is therefore conceivable that environmentally suitable fishing areas are avoided by longliners given changes in the distribution and abundance of pelagic target species, such as the range loss in the South Atlantic seen for bluefin tuna (*10*). Have the last six decades of pelagic fishing led to the overfishing of a significant proportion of the suitable fishing grounds in ABNJ? Or are longline fleets just following changes of prey abundance influenced by other factors such as decadal oscillations or climate change? Limitations in fleet capacity or fuel cost seem unlikely reasons to explain the absence of fishing effort in 36 to 62% of suitable fishable habitat in ABNJ, as the high seas fishing fleet is supported by subsidies and the extent of their distribution suggests that no region of the ocean is too distant to be fished. We run a linear regression between the intensity of longline fishing effort and DCS and found no correlation between the two (fig. S12); this suggests that any lack of fishing is not due to the remoteness of those areas despite the high fuel costs. The suite of explanatory variables used in our models is limited to the biophysical and physiographic dimensions, and therefore, do not take into consideration socioeconomic factors that may be crucial for explaining observed patterns of fleet distribution. Fishermen are not subject to the same physiological and dispersal limitations as are marine species; their limitations are more likely to be political and economic ones. The distribution of high seas longliners is therefore likely to also be influenced by socioeconomic factors, including, but not limited to, catch quotas, market prices of commercial species, fleet communication, or selection of landing sites. Regional bioeconomic models of the distribution of fishing effort could be used to understand differences in the drivers of distributions of fishers and nontarget species and allow for the development of dynamic management measures based on the environmental and economic correlates (*33*); we believe that our models could represent a meaningful component of these wider frameworks.

Additional factors may explain the lack of observed occurrence of fishing activities in areas predicted to be suitable for fishing, including (i) misclassification and thus missed observations of longline vessels or fishing effort, (ii) poor spatiotemporal satellite coverage, (iii) intentionally switching AIS transponders off, and (iv) fishing events by fishing States or territories not included in our analysis. We addressed the last factor by assessing how much of the unfished suitable habitat may have been fished by longliners from the 26 States or territories not included in our analysis. We found that none of these countries fished the unoccupied suitable fishing areas; most (65%) of the 1267 fishing events by these fleets were predicted by our model. We think that a more detailed understanding of the behavior of fishing vessels out at sea may help us identify the general areas of expected fishing vessel activity, thus bringing us one step closer to abating illegal fishing by designating enforcement resources more strategically.

Reflections on the use of predictive models of fishing effort

While the distribution of some sectoral activities, such as deep-sea mining or oil and gas exploration, is well mapped and static, the dynamism of open-ocean fisheries makes understanding their spatiotemporal distribution difficult and, consequently, monitoring, control, and surveillance a challenge. The models we present could become a useful tool for managers to focus their efforts on areas of likely fishing activity. As high-resolution satellite imagery is increasingly being used to look for fishing vessels, narrowing the areas of the ocean where there is a high portability of fishing activities may help streamline the process of detecting legal or illegal fishing vessel activity. The spatial and temporal resolution of our predictors was coarse, which limited our ability to capture the influence of mesoscale oceanographic features, such as oceanic frontal zones and eddies, on the distribution of fishing effort. However, given the global scale of our analysis, we consider that our models successfully explain the broad environmental patterns that shape the distribution of the global longline fishing fleet in the high seas.

We see great potential in improving the predictive ability of global longline fishing effort models through the development of future region-specific models that capture the regional relationships between fishing effort and environment, and predator-prey dynamics in more detail. Additionally, partitioning the niche models by fishing State may also be required to tease apart distinct environmental correlations and behaviors, leading to more accurate predictions. As the spatiotemporal coverage of satellites capable of recording AIS signals improves and fishing effort classification algorithms become more accurate, so will the estimates of fishing effort between years, and behavior classification errors will decrease. Furthermore, with more years of data and improving spatiotemporal satellite coverage, the differences in environmental preferences between years will be attributable more to changes in fleet behavior than to biases in fishing effort observations.

CONCLUSIONS

As we combine an improved understanding of open-ocean fleet behavior with knowledge of the drivers of distribution of target and nontarget marine taxa, our ability to predict the co-occurrence of fishing with sensitive species or ecosystems will improve, as will the efficacy of related management measures. As the intensity and overlap of human uses of ABNJ continue to grow, ocean governance structures will have to rely more heavily on different forms of dynamic spatial management to accommodate all users and activities (*35*), which, in turn, rely on open-access remote sensing data and collaborations between researchers, fishers, and the management community (*36*). Our research demonstrates how the global pelagic longline fleet exhibits predictable environmental preferences for various biophysical and physiographic predictors, which can be used to explore the current and future distributions of fishing fleets. Improvements in remote sensing and oceanographic forecasting for variables (for example, SST) open new opportunities for the implementation of adaptable ocean management measures that match the dynamics and distributions of ocean biological resources and resource users. As we grapple with rapidly changing oceans and ocean uses, advancements in predictive modeling, aided by new technologies, will help us move away from reliance on retrospective tactics in area-based management and toward more dynamic approaches capable of delivering ecosystem-based management.

MATERIALS AND METHODS

Here, we used a form of classification model known as BRT to characterize the distribution of longline fishing in the high seas (as reported by GFW) from environmental variables primarily obtained from increasingly available remote sensing sources (*36*). We used the processed AIS geolocation data from GFW in the form of gridded fishing hour estimates for 2015 and 2016 as observations to fit the environmental niche models.

AIS fishing effort data

GFW analyzes and provides online interactive maps of the behavior of fishing vessels from global AIS and VMS data. AIS was originally designed as a tool to avoid collisions at sea as part of the IMO Safety of Life At Sea Treaty [SOLAS Treaty, Chapter V; (*37*)]. Vessels equipped with an AIS transponder signal their position and vessel identification data such as IMO number, maritime mobile security information number, call sign, ship type, speed and course over ground, and other information to ships nearby carrying the transponders as well as to receiving ground stations and low-orbit satellites. Signal transmission frequencies vary with speeds between a few seconds and a few minutes. These high-resolution tracking data are then analyzed by GFW to assess ship movements and behavior, using neural network algorithms and logistic models to classify different fishing gear types as well as the points in space and time where individual vessels deploy their fishing gear (*16*). Data used for this study were derived from the logistic regression model 1.1 (http://globalfishingwatch.io/fishing__logistic_1_1.html). It is worth noting, however, that GFW only uses satellite-based AIS data, which have limitations such as a maximum number of individual signals that can be detected simultaneously, heterogenous satellite spatiotemporal coverage, or gaps near coastlines, where shore-based stations receive the signal that the satellite can no longer detect. It is unlikely for areas in the high seas to experience satellite channel saturation, and vessel AIS signals are also unlikely to be detected by shore-based stations. Fishing effort is detected and calculated, as hours of fishing, for individual fishing gear types: (i) pelagic longlines, (ii) trawls, (iii) purse seines, (iv) fixed gear, and (v) other types of fishing gear. However, each of these is subject to behavior classification errors. For this study, estimates of global pelagic fishing effort for the years 2015 and 2016 were extracted from the GFW database, including vessels from 114 countries and territories.

We filtered the GFW fishing effort estimates spatially to only include longlining events in the high seas. Within the high seas, fishing effort by pelagic longliners accounted for 88.9 and 80.4% of the quantified fishing effort (hours) in ABNJ across all gear groups in 2015 and 2016, respectively (fig. S1). The dominance of longline fishing effort in ABNJ and its known negative impacts on multiple nontarget species (*38*) underscore the importance of understanding the potential drivers of its global distribution (Fig. 1). Hence, we focused on longlines only in our modeling efforts, particularly the distribution of fishing events rather than fishing intensity.

According to GFW fishing effort estimates, 45 to 50 fishing States and territories deployed longlines in ABNJ throughout 2015 and 2016.

We refined the list of countries to only include those that accounted for the >80% of the observed fishing effort; this reduced the list of fishing States and territories to five (fig. S2). We further selected the fishing effort data used to build the environmental niche models by only including these five major fishing States and territories. The fishing effort applied by these countries was aggregated spatially to 1° by 1° cells for 2015 and 2016 (Fig. 1) given the global extent of the analysis (*39*) and then partitioned temporally into 24 months (Fig. 2). Environmental data layers specific to each month were then used to run each of the 24 monthly environmental niche models. The use of monthly averages and monthly climatologies for certain environmental variables inevitably resulted in the loss of some fine-scale environmental features (for example, mesoscale oceanic eddies and frontal zones) that may influence the distribution of fishing effort at submonthly time steps. Future analysis at finer spatiotemporal resolution may allow the inclusion of more information on dynamic oceanographic features. For the purpose of this study, we focused on the monthly environmental variability on the distribution of fishing effort.

Environmental predictor variables

The environmental variables selected for modeling the ecological niche of global longline fishing effort in ABNJ included both static (physiographic) and dynamic predictors (biophysical). Various habitat-modeling studies support the inclusion of biophysical and physiographic predictors across spatial and temporal scales for studying the ecology of species of commercial interest (*30*, *33*). The dynamic variables were extracted by month and consisted of SST, T400, TKE, POC, NPP, MLD, SOC, O400, SSS, S400, and ZEU. The static physiographic variables included BATH, DCS, and DSM. All variables were extracted at 1° by 1° spatial resolution cells or aggregated as necessary and had different temporal resolutions; some are monthly estimates while others are climatological (that is, averages for the month across many years; see table S9).

Environmental niche model fitting, validation, and projection

All BRTs were fitted to the fishing effort data using RStudio, a development environment for the open-access statistical software R. The models were fitted to the number of monthly fishing effort presence points derived from GFW estimates and double the number background (pseudoabsence) points from the high seas region; a low number of points is recommended for modeling approaches such as BRTs (*40*). Background points were created on a monthly basis by randomly selecting from the unfished areas of ABNJ (tables S11 and S12). Randomly selecting background pseudoabsence points from anywhere in the high seas, including polar and subpolar regions, where almost no longline fishing effort occurs, biased the results and exaggerated the importance of latitudinally structured variables such as SST and SOC (fig. S13). The distribution of background pseudoabsence points was therefore constrained to areas that had SST values within the observed temperature range of observed fishing. In addition to the 24 monthly models, we computed a temporally averaged model that included the data from all 24 months to assess which of the two approaches performed better. After fitting the classification models, model outputs were mapped onto geographic space by projecting them using layers of the same environmental predictors. The resulting two-dimensional map represents a probability distribution surface where each grid cell in ABNJ was assigned a value between 0 and 1. Confusion matrices were then computed to assess how well each of the monthly models could predict the distribution of longline fishing effort. Various model performance indices were calculated, including the AUC, κ statistic (a measure of categorical agreement describing the difference between the observed and chance agreements), sensitivity (the proportion of actual presence that is accurately predicted), specificity (the proportion of actual absences that are accurately predicted), and accuracy values (tables S1 to S4 and figs. S3 and S4). We then used a nonparametric Wilcoxon signed-rank test to assess whether the performance metrics of the monthly models are statistically dissimilar from those of the temporally averaged model (table S5).

We also explored the explanatory accuracy of the monthly models at predicting the distribution of future fishing effort by projecting monthly models onto the oceanographic conditions 1 ($n = 23$), 6 ($n = 180$), and 12 ($n = 12$) months in advance and assessing how accurately we could predict the distribution of observed longline fishing effort in those months (fig. S5). We further explored the influence of the environmental variables by running two additional monthly models for all the months of 2016, one of which only included static ($n = 3$) variables and the other was run using only dynamic variables ($n = 11$) (table S10).

There are multiple possible approaches for selecting a probability distribution threshold to convert probability maps into binary maps. Here, we explored the influence of two separate methods of selecting thresholds for obtaining binary habitat suitability maps. Areas with a monthly probability distribution above the set threshold were considered as suitable habitat for the studied organism. First, we calculated monthly thresholds based on ROC curves, which show the relationship between the true-positive (sensitivity) and false-positive (specificity) rates. The second type of threshold that we calculated was based on the MPD of the monthly models. While both methods are widely accepted procedures (*41*) for establishing cutoff threshold values, the resulting binary habitat suitability landscapes can differ, and results must not be interpreted as final, but instead as different scenarios of pelagic longline fishing suitability in the high seas. Additional information about how BRTs were fitted and projected is available in Supplementary Materials and Methods.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/8/eaat3681/DC1

Supplementary Materials and Methods

Fig. S1. The proportion of 2015 and 2016 fishing effort (hours) in ABNJ by gear.

Fig. S2. The proportion of pelagic longline fishing effort attributed to the main fishing States or territories.

Fig. S3. Accuracy values obtained for the 2015 and 2016 monthly boosted regression tree models after applying an ROC threshold.

Fig. S4. Accuracy values obtained for the 2015 and 2016 monthly boosted regression tree models after applying an MPD threshold.

Fig. S5. The predictive accuracy of the monthly BRTs after projecting them onto future environments.

Fig. S6. Distribution of predicted and observed fishing effort in January and July of 2015 using different thresholds: ROC and MPD.

Fig. S7. The SST partial dependence plots from the monthly 2015 models.

Fig. S8. The temperature at 400-m partial dependence plots from the monthly 2015 models.

Fig. S9. The DCS partial dependence plots from the monthly 2015 models.

Fig. S10. The oxygen at 400-m partial dependence plots from the monthly 2016 models.

Fig. S11. The SST partial dependence plots from the monthly 2015 models.

Fig. S12. The distribution of fishing effort intensity as a function of the Euclidean distance (kilometers) to the continental shelf.

Fig. S13. Monthly variable importance scores for boosted regression trees using background pseudoabsence points from the entire high seas areas for 2015 and 2016.

Table S1. Various model performance indices of the monthly BRTs for 2015 and 2016.

Table S2. Various model performance indices of the monthly BRTs for 2015 and 2016.
Table S3. Various model performance indices of the temporally averaged BRT model.
Table S4. Various model performance indices of the temporally averaged BRT model.
Table S5. Results from the Wilcoxon signed-rank test comparing the performance of monthly models to the temporally averaged model.
Table S6. Amount of fundamental niche occupied by pelagic longliners.
Table S7. The 2015 VI scores.
Table S8. The 2016 VI scores.
Table S9. Average 2016 model performance metrics using different environmental variables.
Table S10. Description of the variable type and source for each of the 14 biophysical and physiographic predictors.
Table S11. The number of presence and pseudoabsence points in 2015.
Table S12. The number of presence and pseudoabsence points in 2016.

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Acknowledgments: This study is a product of the Nippon Foundation Nereus Program. We thank the GFW partnership for their technical support and for providing the global fishing effort estimates that we used in this study. They were an indispensable asset to this study. We also thank Dalhousie University, in cooperation with B.W., D.P.T., and K.B., for hosting a workshop in May 2017 that helped shape some of the ideas and analyses presented here. **Funding:** G.O.C., D.C.D., and P.N.H. received financial support from the Nippon Foundation Nereus Program to lead this research. K.B., D.P.T., and B.W. acknowledge support from the Google Earth Engine Research Award for the funding opportunity to convene a workshop that was instrumental for structuring the study. **Author contributions:** All authors were engaged in the intellectual design of the project, and all participated in editing the manuscript. G.O.C., D.C.D., and P.N.H. coordinated the research effort. G.R. and K.B. helped with the analysis and pre-processing of the GFW data. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data and code related to this paper may be requested from the authors or the GFW portal (www.globalfishingwatch.org).

Submitted 21 February 2018
Accepted 14 July 2018
Published 8 August 2018
10.1126/sciadv.aat3681

Citation: G. O. Crespo, D. C. Dunn, G. Reygondeau, K. Boerder, B. Worm, W. Cheung, D. P. Tittensor, P. N. Halpin, The environmental niche of the global high seas pelagic longline fleet. *Sci. Adv.* **4**, eaat3681 (2018).

APPLIED ECOLOGY

Global hot spots of transshipment of fish catch at sea

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A major challenge in global fisheries is posed by transshipment of catch at sea from fishing vessels to refrigerated cargo vessels, which can obscure the origin of the catch and mask illicit practices. Transshipment remains poorly quantified at a global scale, as much of it is thought to occur outside of national waters. We used Automatic Identification System (AIS) vessel tracking data to quantify spatial patterns of transshipment for major fisheries and gear types. From 2012 to 2017, we observed 10,510 likely transshipment events, with trawlers (53%) and longliners (21%) involved in a majority of cases. Trawlers tended to transship in national waters, whereas longliners did so predominantly on the high seas. Spatial hot spots were seen off the coasts of Russia and West Africa, in the South Indian Ocean, and in the equatorial Pacific Ocean. Our study highlights novel ways to trace seafood supply chains and identifies priority areas for improved trade regulation and fisheries management at the global scale.

INTRODUCTION

Seafood is the world's most traded food commodity, with global exports worth more than US$148 billion in 2014 (*1*). The vast majority of fish and shellfish (78%) is processed and traded internationally through complex supply chains that connect fishing vessels with individual consumers (*1*). Most of the global catch estimated at 100 million metric tons year^{-1} (*2*) is landed directly by fishing vessels in port, particularly from vessels that operate closer to the coast and in national waters. However, larger fishing vessels and those fishing further offshore and on the high seas often offload catch to refrigerated cargo vessels ("reefers") instead while often also being resupplied with food, water, bait, crew, and fuel; this common practice is known as transshipment of catch at sea (hereafter referred to as "transshipment").

It has been previously reported that most of the species subject to transshipment are high seas–related species such as tuna, sharks, and billfishes (*3*), but other species including groundfish, salmon, and crustaceans also get transshipped in both national and international waters (*4*). Transshipment increases the efficiency of fishing by eliminating trips back to port for fishing vessels while maintaining product quality, but it can also obscure the origin of the catch and may or may not be legal, depending on local regulations (*5*). Thus, transshipment can be problematic from a regulatory, business, or consumer perspective because it decreases transparency; it may also facilitate human-rights abuses and has been implicated in other crimes such as weapon and drug trafficking (*4*, *6*). The situation is further complicated by the fact that transshipment often occurs in regions of unclear jurisdiction where policy-makers and enforcement agencies may be slow to act against a challenge that they cannot see.

Transshipment is also thought to be a factor in enabling illegal, unreported, and unregulated (IUU) fishing, which is a global problem, extracting an estimated 11 to 26 million metric tons from the oceans each year (*2*, *7*). In addition to incurring an annual revenue loss of US$10 billion to US$23.5 billion for legal fisheries, IUU fishing undermines fisheries management and conservation efforts and contributes to global overfishing (*7*). It has been estimated that about a quarter to a third of all wild-caught seafood imports into major markets, such as the United States and Japan, could have been caught illegally (*8*, *9*). Vessels transshipping part of their catch at sea or the mixing of catches from several fishing vessels from different regions can obscure the traceability of seafood through the supply chain and introduce IUU catch into the global market under false labeling. The United Nation's Food and Agriculture Organization (FAO) acknowledged this possible link between transshipment and IUU and developed guidelines and procedures for transshipment at sea to minimize illegal activities (*10*). In addition, FAO launched an international plan of action to prevent, deter, and eliminate IUU fishing, calling on flag states to improve monitoring and control of transshipments or to prohibit it entirely (*11*). To date, transshipment is individually regulated by coastal and flag states and by Regional Fisheries Management Organizations (RFMOs). Some RFMOs, especially concerned about the laundering of high-value species such as tuna, restrict transshipment to ports (*12*), prohibit certain fishing vessels from transshipping, or require onboard observers to be present (*13*).

With increasing global demand for better seafood supply chain transparency and traceability, transshipment has become an important yet poorly quantified focal point in the international trade of seafood. This can be addressed and resolved if each transshipment event is monitored and documented appropriately. New tools have emerged lately with the application of machine learning technology to analyze vessel tracks on the basis of satellite-based Automatic Identification System (AIS) data, tracking the behavior of fishing vessels at a global scale and even in remote waters (*14*, *15*). Recently, researchers at Global Fishing Watch have expanded these methods to analyze the behavior of reefers, making it possible to detect and monitor transshipment at sea (*16*, *17*).

Here, we build and extend on this method to map and better understand the extent, spatial distribution, and role of transshipment for different fleets, gear types, and supply chains at a global scale. Using AIS data, we ask where and when transshipment occurs, which fisheries and fleets are most involved in this practice, and what proportion of high-seas catch is transshipped versus landed directly. We also apply this methodology to trace detailed seafood supply chains for tuna fisheries in the Indo-Pacific.

RESULTS

Likely transshipment events (fishing vessel–reefer encounters at sea detected from AIS positions of vessels within 500 m of each other and lasting longer than 2 hours, traveling at less than 2 knots while at least 10 km from shore, hereafter called "encounters") were identified from

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22 billion individual AIS position signals where AIS data were available for both the reefer and fishing vessel engaged in the encounter (Fig. 1). AIS messages provide detailed information on vessel identity and behavior and have become more widely available since 2012 (*14*, *15*). Novel machine learning algorithms allowed us to automatically detect and map encounters between fishing and refrigerated cargo vessels at sea. Using a subset of the global database developed by Global Fishing Watch (*17*) including AIS tracks from both reefers and fishing vessels, we quantified the spatial distribution of encounters between fishing vessels (focusing on four major gear types) and refrigerated cargo vessels and estimated the fishing effort (in hours spent fishing) as a proxy for the catch that was accumulated between encounters or port calls (see Materials and Methods below for more details). Between 2012 and the end of 2017, we observed 501 reefers meeting up with 1856 fishing vessels in 10,510 likely transshipment events worldwide. The refrigerated cargo vessels involved comprise a variety of types, including fish carriers, fish processors, and a small number of fish tenders.

Together, 35% of all observed transshipment encounters occurred on the high seas, while 65% took place within exclusive economic zones (EEZs) where most global fishing occurs (*15*). A large fraction (39%) of all detected encounters occurred in the Russian EEZ, with the remainder (61%) spread over 41 other nations' EEZs. Excluding Russia, 57% of likely encounters took place on the high seas.

Fishing vessels engaged in transshipping were mostly trawlers (53%) and longliners (21%), the former being more active in shallow continental shelf waters, the latter concentrating on the high seas. Squid jiggers (13%), fishing vessels using pots and traps (7%), and purse seiners (1.2%) contributed less to global transshipment events detected from AIS data.

Transshipping from trawlers was most common in EEZs in the Northern Hemisphere, most notably in Russian waters, whereas most

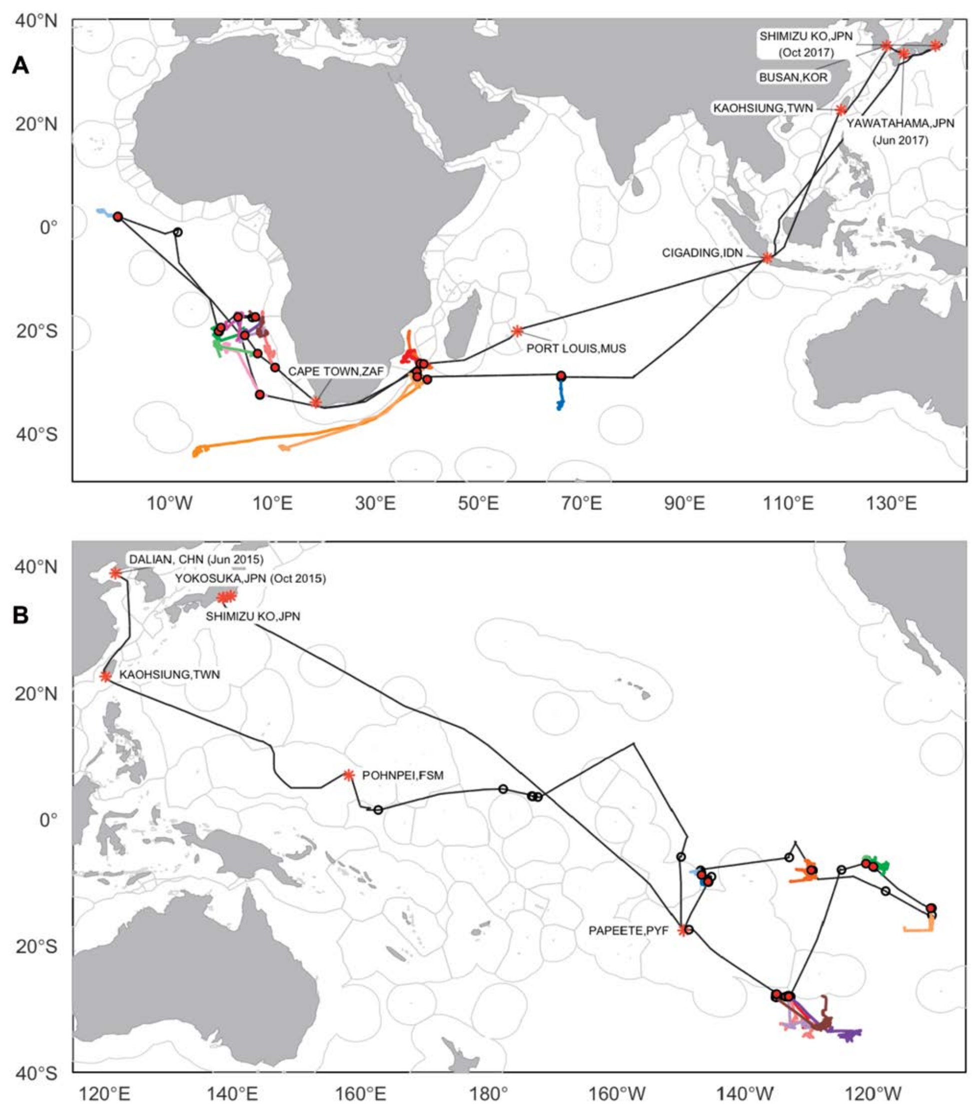

Fig. 1. Transshipment of catch at sea. Example AIS tracks of reefer (black) and fishing vessels (colors), port calls (asterisks), likely transshipment encounters (red circles), and potential encounters (white circle) in the (**A**) Atlantic and (**B**) Pacific are shown. EEZs are outlined in light gray. Note that tracking data for fishing vessels are missing for some likely encounters, but reefers exhibited behavior consistent to an encounter.

of the transshipments from longliners, purse seiners, and squid jiggers occurred on the high seas, with hot spots off West Africa, in the South Indian Ocean, and the equatorial Pacific (Fig. 2).

The average duration of likely transshipment events identified in the AIS data was 11.6 hours (median, 7.3 hours), which is close to the 9.5 hours reported in transshipment documentation (see below). Fishing vessels transshipped their catch to a reefer roughly once a month. Most reefers traveled to meet the fishing vessels at or close to the fishing grounds (Fig. 1), whereas fishing vessels only traveled relatively short distances (mean distance, 122 km; median distance, 42 km) to meet a reefer.

For most of the time vessels spent fishing before meeting a reefer, they were located in EEZs (Fig. 3, A and B). Catch from more than three-quarters of all observed fishing in EEZs (86%) was landed directly, whereas only 14% was transshipped. Transshipment was much more prevalent on the high seas, with nearly half (45%) of catch from observed fishing effort on the high seas being transshipped (Fig. 3). In EEZs, trawlers predominated landings and transshipment events, whereas on the high seas, longline fishing dominated both in terms of landed and transshipped catch, followed by squid jiggers (Table 1 and Fig. 4). Trawlers predominantly fished and transshipped in Northern Hemisphere temperate waters, whereas longliners operated globally in tropical and subtropical waters, and squid jiggers were observed in international waters along the EEZs of South American countries both in the Pacific and Atlantic (Fig. 2).

A fishing vessel's voyage may be broken into three segment types of varying durations. For short daily fishing trips, the entire voyage might be characterized by the segment of time between two anchorages (docking in port or anchoring nearby). Longer trips, which include likely transshipment encounters, can be divided into additional segments such as the time between an anchorage and an encounter at sea or the time between two sequential encounters. Excluding the upper and lower 5% of the data to eliminate implausible outliers caused by data gaps (fig. S1), we found that fishing vessels that undertook voyages characterized solely by an anchorage exit and a return (no transshipment involved) spent about 18 days at sea (median, 6 days) and fished about 46 hours (median, 23.5 hours). Short coastal fishing trips with vessels returning to port every day influence this estimate. For fishing vessels engaging in transshipment, we found that the time between an anchorage exit and a fishing vessel's first likely transshipment encounter was about 50 days (median, 37 days), during which time the vessel fished for an average of 100 hours (median, 74 hours). Between transshipment encounters, we found that fishing vessels met with a reefer about every 31 days (median, 19.5 days) and fished about 132 hours (median, 135.5 hours). The longer time between anchorages and first transshipment encounters is likely due to the time fishing vessels spent traveling to their fishing grounds and the fact that some encounters are not identified because of missing AIS signals (lack of satellite coverage and/or switching off of AIS transponder).

Of 33 flag states observed to operate reefers, Russia accounted for almost a third (32%), followed by Panama (20%) and Liberia (7%), the latter two representing so-called flags of convenience (FoCs), flags of states characterized by loose regulation and limited oversight (fig. S2A). About 41% of all reefers were flagged to FoCs,

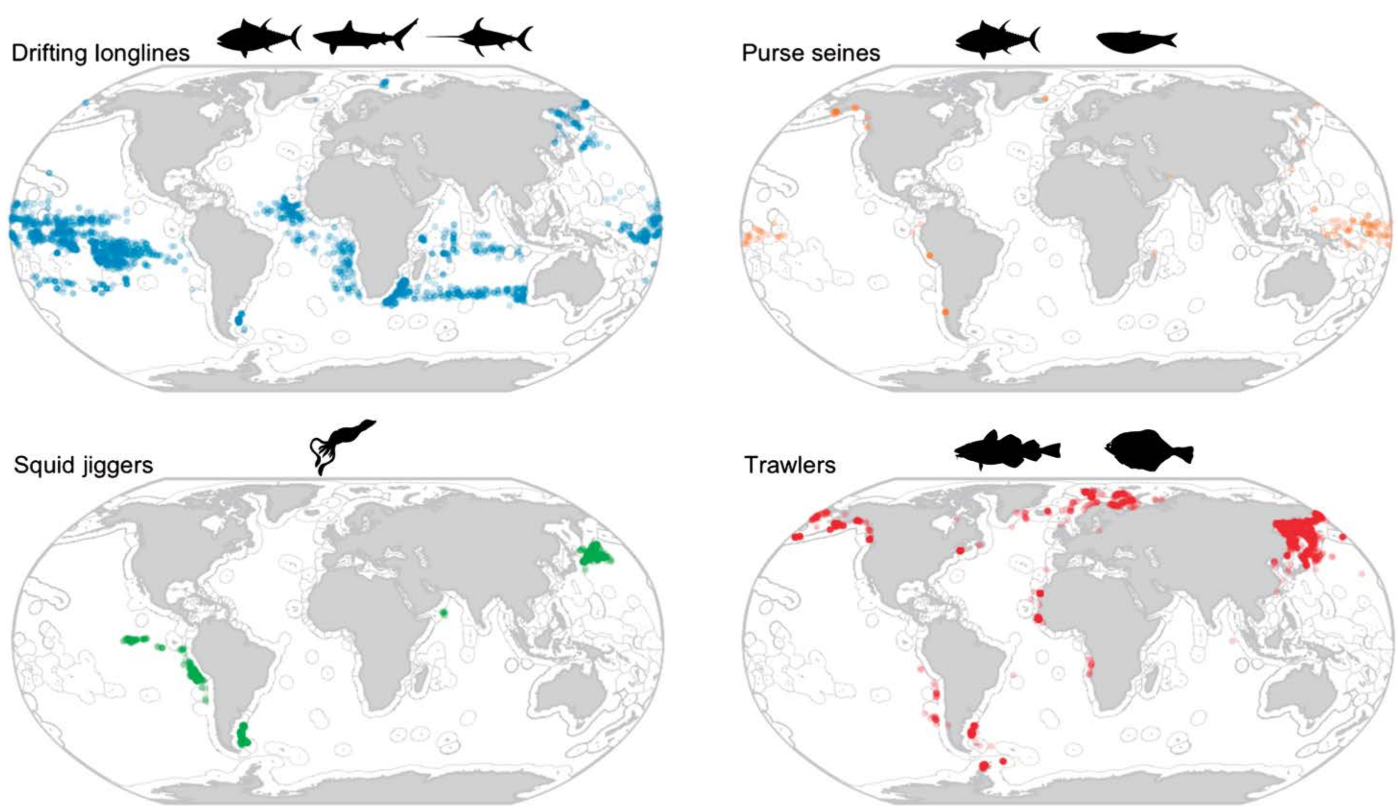

Fig. 2. Global patterns of transshipment for different fishing gears. All likely encounters (colored dots) between reefers and fishing vessels as identified from AIS data spanning 2012 to 2017 and separated by fishing gear type are shown. EEZs are outlined in light gray, and pictograms illustrate major target species.

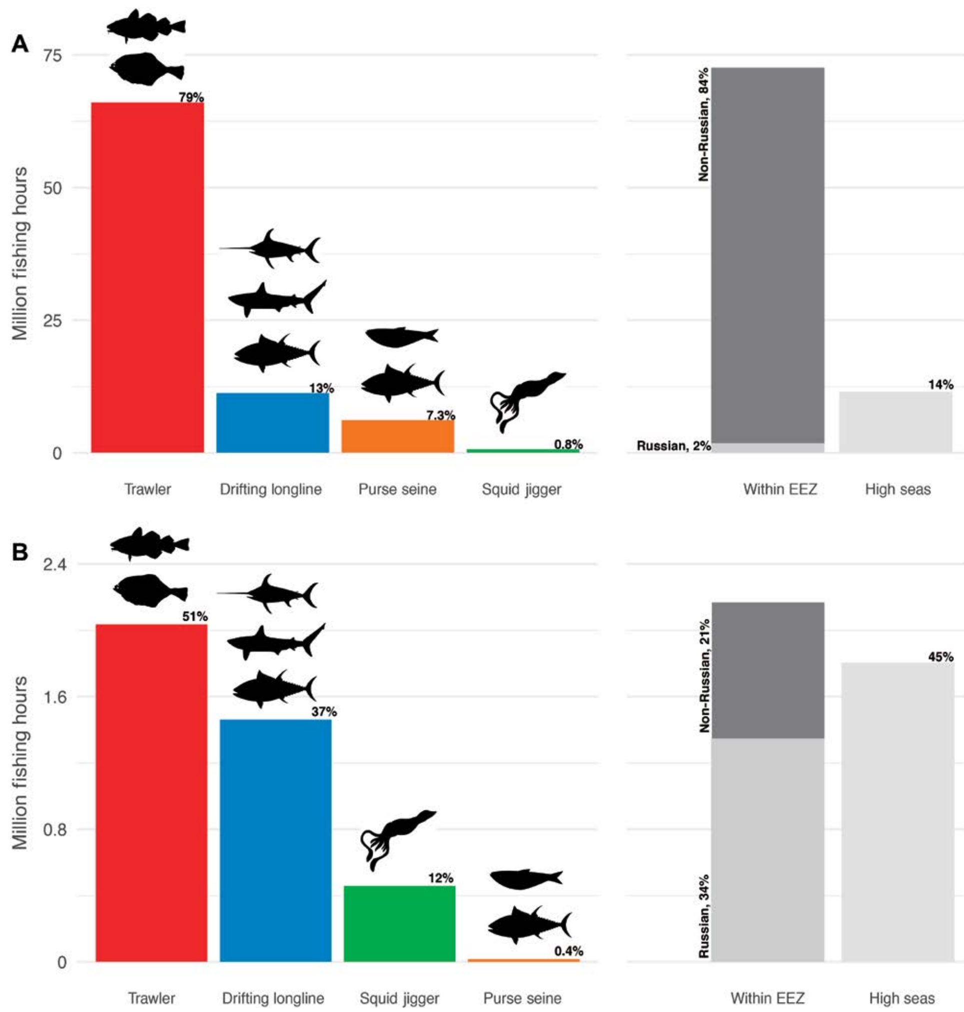

Fig. 3. Relative extent of transshipment for different types of fishing gear. The fishing effort (estimated fishing hours) that is (**A**) landed directly in port versus (**B**) transshipped and brought to port by reefer is shown. Data are separated by fishing gear type (left) and for EEZs versus the high seas. Data include fishing vessels that, at least once, have met up with a reefer. Gears represent more common gears used by fishing vessels involved in encounters. Pictograms denote major target species by gear type.

Table 1. Direct landing or transshipment of catch in EEZs versus the high seas. The percentages of fishing hours landed directly in port by fishing vessel or transshipped at sea and landed by reefer are shown. Data are separated by fishing gear and for EEZs and the high seas (HS; bold). Percentages are given for fishing in all EEZs and for the Russian EEZ separately because of outstanding importance of transshipment for Russian fleets.

	In EEZ				In HS	
	Landed directly (%)	Landed directly from Russian EEZ (%)	Transshipped (%)	Transshipped from Russian EEZ (%)	Landed directly (%)	Transshipped (%)
Trawler	84.3	97.9	81.2	97.2	**41.8**	**15.3**
Longliner	8.1	1.2	13.7	1.8	**47.0**	**64.5**
Purse seiner	7.1	0.5	0.6	0.06	**8.3**	**0.1**
Squid jigger	0.5	0.4	4.4	0.9	**2.9**	**20.1**

or 60% when excluding Russia. Fishing vessels from 47 nations were found to encounter those reefers and engage in a likely transshipment, again, a majority from Russia (26%), followed by China (20%) and Taiwan (15%) (fig. S2B). Encounters of fishing vessels with reefers flying FoCs were more prevalent on the high seas than in EEZs for all gear types, especially for squid jiggers (78% of all high-sea encounters compared to 27% within EEZs) and longliners (62% to 25%, respectively).

Testing for a correlation between the number of likely transshipment encounters and regional extent of IUU estimated for each FAO area (*7*), we found a weak positive but nonsignificant relationship ($P = 0.1626$) (fig. S3). FAO area 61 (Northwest Pacific) emerged as

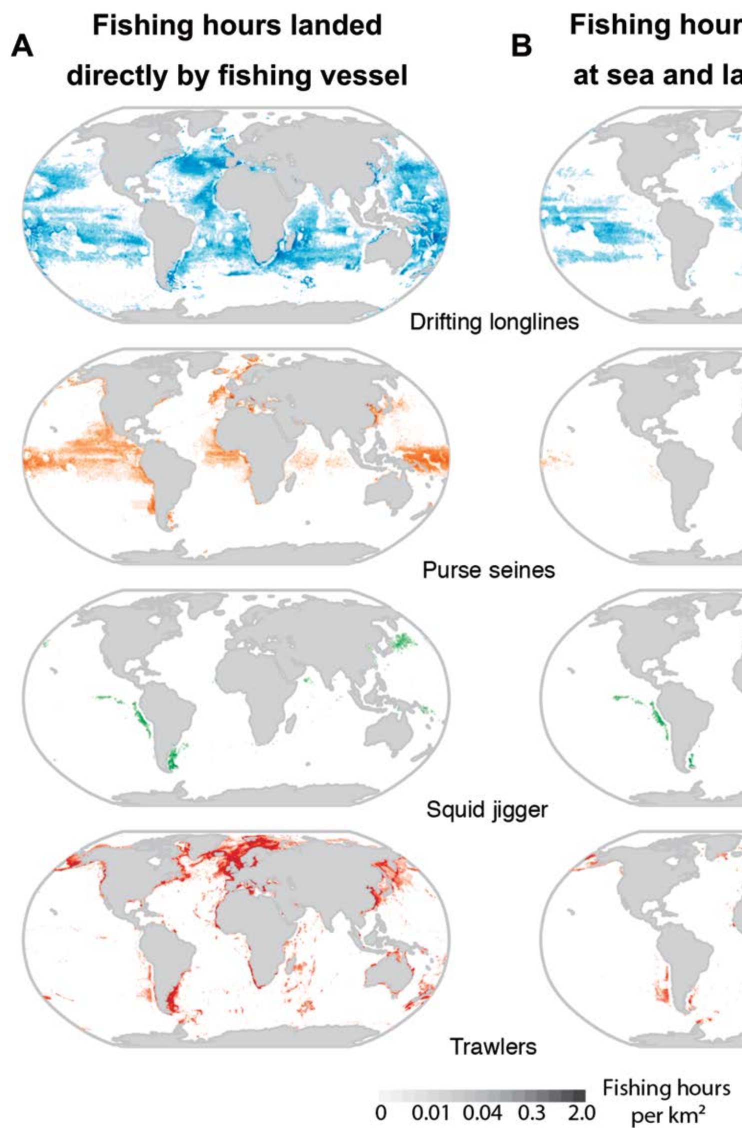

Fig. 4. Spatial patterns of landed versus transshipped fishing effort. The spatial distribution and intensity (fishing hours per square kilometer) of fishing effort for each gear type landed directly (**A**) by fishing vessel or (**B**) by reefer after transshipment at sea between 2012 and 2017 are shown.

a notable outlier of this analysis, with both a high percentage of IUU (33%) and by far the highest number of likely transshipment events (44% of total).

Tuna case study

On the basis of information provided from a tuna processor and retailer, we were able to reconstruct detailed supply chains for tuna transshipped to and landed by three reefers flagged to China, Taiwan, and Panama and operating in two of the global hot spots that we identified here: the south Indian Ocean and the equatorial Pacific (Fig. 5). These three vessels spent an average of 8 days (1 to 23 days) in port and about 50 days at sea (23 to 96 days, excluding short transits from port to port) and received an average amount of 57,500 kg of catch [mostly albacore tuna (*Thunnus alalunga*)] per transshipment from 16 fishing vessels flagged to either China or Taiwan. Of these fishing vessels, AIS data were available for 13 (Fig. 5). Using the transshipment location as noted in the reefer's documentation, we were able to match 7 of the 13 documented transshipment events to the AIS data used in this paper. For six events, it was not possible to identify a likely transshipment event (within a 100-km radius) from the AIS data.

On the basis of AIS tracks and industry documentation, we estimate that tracked tuna fishing vessels fished for about 2 to 3 weeks before meeting with a reefer to offload their catch. The reefer returned to port to land the transshipped catch about once a month, depending on the distance from port and the number of fishing vessels encountered. In processing facilities in or close to the port of landing, the whole fish was processed into loins and shipped in sealed containers to canning facilities, in this case located in the United States. This takes 4 to 8 weeks, depending on the location of the port. Reprocessing and canning happen over another 4 weeks with a subsequent distribution to retail within 2 to 12 weeks. It thus takes about half a year on average (18 to 35 weeks) from the catch of albacore tuna to the canned final product on the shelf. Along the entire supply chain, the fish have traveled an average 17,000 km (13,000 to 20,000 km, excluding traveling on the fishing boat and transport to final retail)

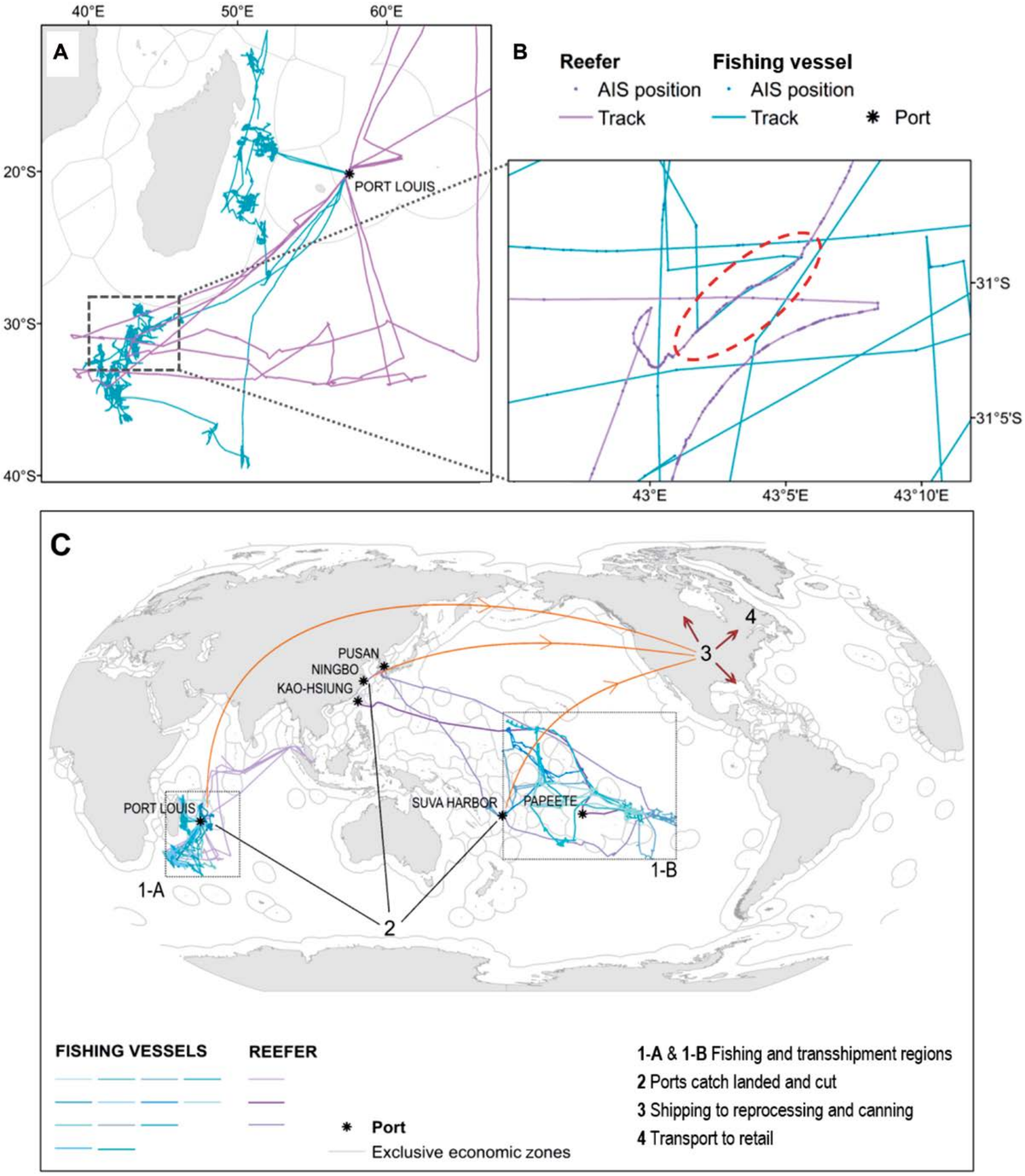

Fig. 5. Tuna case study. The path of albacore tuna from fishing location to retail shelf is shown. Reefer and fishing vessel tracks are in purple and blue, respectively, the area of fishing and transshipment is denoted by a dashed black rectangle, and EEZ boundaries are in light gray. (**A**) Fishing and transshipment off Mauritius, port call into Port Louis, (**B**) close-up of transshipment event (dashed red circle). (**C**) Tracks of three reefers and 13 fishing vessels from January 2017 to February 2018. (1-A) and (1-B) (dashed rectangles) denote fishing and transshipment areas, (2) ports (asterisks) where reefers landed whole fish and fish is cut, (3) transport to reprocessing and canning facilities, and (4) transport of final product to retail.

with about five discrete steps involved, including postproduction steps such as shipment of cans (Fig. 5).

DISCUSSION

In the last decade, transshipment of catch at sea has become a focal point in the international discussion surrounding seafood supply chain transparency, especially for fisheries operating in distant waters and featuring complex supply chains. Fish commonly pass from producers (individuals/companies operating fishing vessels) to fish brokers, who aggregate catches upon landing or transshipment to a reefer and arrange for sale to processors and distributors. Unsurprisingly, traceability of products becomes more complicated with increasing supply chain length, complexity, and levels of aggregation of catch. While fish landed directly in port by fishing vessels is usually documented by vessel before aggregation of catches from multiple sources, this documentation is less precise for catches transshipped at sea.

Here, we build on a global database of transshipment encounters developed by Global Fishing Watch (*16*, *17*), mapping empirical observations of transshipment at sea by gear and region and connecting it to supply chains to highlight the role, scale, and importance of transshipment in the global seafood trade. We found that, while transshipment is occurring in all oceans and across 42 EEZs (*16*), it is more common in distinct hot spot areas on the high seas (for example, south Indian Ocean and equatorial Pacific), in some EEZs (for example, off Russia and West Africa), for some gear types (trawlers and longliners), and involving few dominant states that flag a majority of reefers (Russia, Panama, and Liberia).

Transshipment is mostly seen close to fishing grounds (Fig. 2), as it is common practice for fish traders to arrange for the reefer to meet the fishing vessels. The distribution of transshipment activity and the types of fishing vessels transshipping catch depend on the nature, value, and volume of target species and can be useful indicators for fisheries managers to pinpoint areas and fisheries where monitoring and documentation should be enhanced.

Observed transshipment events within EEZs largely involved trawlers, likely fishing on the continental shelves for demersal- or coastal-pelagic species. As these fisheries generate high-volume catches, transshipment enables vessels with limited hold capacities to continue fishing. On the high seas, more than half (excluding Russia) likely transshipment events involved longline fishing vessels, presumably transshipping highly migratory species such as tuna, sharks, and billfishes (swordfish and marlins) (*3*, *18*). Few longline vessels have adequate deep-freezing facilities; thus, quick transshipment to reefers is essential to maintain high quality and market prices (*5*). This suggests that the type of catch (high volume or high value) and its location shape the infrastructure of the supply chain involved and thus can be an indicator which fisheries and supply chains might be the most susceptible to illicit activities surrounding transshipment, thus warranting closer monitoring, control, and surveillance.

Some fishing fleets rely heavily on the use of reefers regardless of the type of fishing. More than a third of all observed transshipments were conducted between Russian-flagged reefers and fishing vessels in the Russian EEZ and the Bering Sea, which are areas with poor monitoring of transshipment (*4*) and a history of illegal fishing. Russia's fishing fleet largely dates back to the Union of Soviet Socialist Republics, and struggling to meet targets set to close a gap in food supply after World War II, Soviet fishing fleets were restructured in the 1950s and 1960s to increase operation time and range (*19*, *20*). Fishing operations were centered around mother ships and fish carriers to supply the fishing fleet and process their catch (*20*); these historical developments may, in part, explain the importance of transshipment and the central role of reefers in Russian fisheries today (*16*). In addition, a strong link to the nearby Chinese market (57% of all fish imports to China come from Russia) further favors transshipment in Russian waters and under Russian flag (*9*). Relatively poor monitoring, low compliance, weak enforcement, and high levels of transshipment enable IUU fishing for Russian pollock, crab, and salmon, which are imported to the United States and Europe following reprocessing in China (*9*). These fisheries are contributing to high estimated prevalence of IUU (33%) in the Northwest Pacific (FAO area 61) (fig. S3) (*7*, *9*). However, the overall correlation between AIS-detected transshipment and estimated IUU fishing is weak (fig. S3), possibly owing to large uncertainties in quantifying both processes and a scale mismatch between localized transshipment observations and FAO-area IUU estimates. For improved analysis, more regional knowledge on IUU fishing is required.

No comprehensive global regulations or codes of conduct for transshipment exist. Next to regulations by RFMOs for their convention areas (see below), it is up to individual states to regulate transshipment within their own EEZ and for vessels flying their flag. Following FAO recommendations (*11*), some nations, such as Thailand, Nauru, and Indonesia, have temporarily or permanently banned transshipment in their waters or for vessels flying their flags (*4*). Some flags feature weaker regulations and enforcement and less oversight, particularly so-called FoCs [following definition by (*21*)]. The high prevalence of FoC-flagged reefers found in this study (41% of total observed, 60% if excluding Russia) and the fact that they primarily engage in transshipments in areas beyond national jurisdiction might compromise transparent documentation of seafood supply chains and warrants further consideration.

In the international waters of the high seas, responsibility for fisheries management lies with the RFMOs. While some RFMOs have developed measures to document and regulate transshipment such as required onboard observers and an electronic vessel monitoring system (VMS) (*14*), this is not globally coordinated (*4*). A recent study found that, of the 17 RFMOs active on the high seas, 5 have mandated a partial and only 1 has a total ban of transshipment at sea (*4*). Thirteen RFMOs mandate some form of vessel tracking in relation to transshipment such as VMS, and 10 require an onboard observer. For example, the Western and Central Pacific Fisheries Commission requires observer coverage and a notice of planned transshipments at least 36 hours prior (*13*), while the Indian Ocean Tuna Commission allows transshipments from large tuna longliners only (*22*). Fishing vessels using certain gear types, such as purse seines, are prohibited to transship in some areas, which is likely one reason why only 1.2% of all fishing vessels involved in encounters seen in this study are purse seiners.

How these mandates and regulations are enforced on the water, however, remains questionable, and documentation by authorities is hard to access. For instance, more than 100 likely encounters between fishing vessels and reefers were observed between 2012 and 2017 in the convention area of the South East Atlantic Fisheries Organization (SEAFO) where all transshipment of fishery resources covered by the Convention is banned (Fig. 1) (*23*). One such instance involving a likely encounter between a Japanese longline vessel and a Liberian reefer is highlighted in fig. S4. It remains unclear whether the likely encounters observed within the convention area are transshipping fish from resources covered by the SEAFO convention and resources covered by another convention with overlapping area (in this case, the International Commission for the Conservation of Atlantic Tunas and the Commission for the Conservation of Southern Bluefin Tuna, both regulating tuna and tuna-like species) or whether the encounter constitutes a mere resupplying of the fishing vessel by the reefer (which, however, appears not to be exempt from the term transshipment by SEAFO). This highlights the importance of proper monitoring and transparent documentation of all encounters at sea, whether they are to transship catch or to resupply.

Monitoring of remote waters and the high seas can be facilitated through the use of AIS data, complementing existing monitoring, control, and surveillance tools (*24*). This combination of various tools is useful to create a complete picture of global fisheries and seafood supply chains. Looking at tuna fisheries in two global hot spot areas (south Indian Ocean and equatorial Pacific; see below) and tracking known transshipment events using AIS data, we found that only 7 of 13 (or 54%) documented transshipment events could be reconstructed using AIS. This is likely due to a combination of gaps in the AIS data and poorly recorded transshipment locations. Hence, our estimates of the global prevalence of transshipment should be seen as very conservative; the true extent is evidently much higher.

As discussed in detail elsewhere (*15*, *25*, *26*), some important caveats and limitations apply to the use of AIS data in general: While coverage by AIS-capable satellites is continuously increasing, some areas may not be covered 100% of the time, and transshipment events in these areas might go unnoticed some of the time. Furthermore, AIS transponders can be manually switched off, or location data can be manipulated (*15*). For the detection and subsequent classification of a likely transshipment event in this study, AIS data of both the reefer and the fishing vessel need to be available and correspond to the chosen characteristics of an encounter. Where no AIS data for fishing vessels involved in encounters are available, "loitering" behavior of the reefer may still be indicative of likely transshipment events (*16*). However, because of the missing AIS data for fishing vessels involved in those events, we excluded these from our data. This reduces the numbers of encounters analyzed and may bias results toward transshipment events including large, AIS-equipped vessels operating offshore. However, global patterns of other potential transshipments events are largely similar to those shown here and discussed in (*16*). Last, gaps in the AIS data might also influence the calculations of fishing hours landed versus transshipped. If an encounter or port call is not included because of missing data, then fishing hours might be overestimated or wrongly allocated to the following transshipment or encounter.

Tuna case study

On the basis of a fully documented industry supply chain, we illustrated the voyage of albacore tuna from the hook to a retailer's shelf. In this case, individual fish travel roughly 17,000 km after catch, over a time span of about half a year, changing boats, owners, and processing facilities several times (Fig. 5). Ideally, every step of this complex supply chain is documented and recorded electronically, at sea and in port, and the documentation that we received from industry illustrates how this can be done. At-sea documentation includes fishing location, gear used, and amounts caught by species (ideally also recording bycatch), time, date, and location of all transshipment events during that trip, as well as identity of vessels involved, catch already transported by the reefer, and all ports visited. Some of this information was not included in the transshipment documentation used in this study: Fishing locations were recorded only by RFMO or ocean area, and overall information on the origin of all catches transshipped by reefers servicing fishing vessels for more than one buyer appears to be generally not available.

The entry of fish to the market via port is a key point in supply chains to require and verify documentation and preclude IUU catch from landing, as included in the recent Port State Measures Agreement (*27*). On land, further documentation includes the method of delivery (fishing vessel direct, by reefer, containerized via another port) and the production code or lot numbers specific to the fishing vessel trip the fish was caught. Following landing, catches ideally are binned in sealed containers corresponding to these codes and lot numbers, which are carried through all levels of processing to maintain traceability of the fish to the final product.

As we presented here, satellite-based AIS enables independent verification of vessel activities, including transshipment (*14*), expanding and complementing existing monitoring and documentation tools. Ultimately, improved legislation and transboundary management may want to include mandatory AIS to ensure increased traceability and transparency in supply chains (*5*, *24*).

CONCLUSIONS

In this analysis, we have highlighted global hot spots of transshipments such as the Russian EEZ and the high seas, especially off West Africa, in the southern Indian Ocean, and (most prominently) in the tropical Pacific where high-value species such as tuna are fished. Trawlers in territorial waters and longliners on the high seas contributed a large majority of likely transshipment events. To reduce the probable introduction of IUU catch into the supply chain, strict monitoring and documentation of each transshipment event are needed, especially if it takes place in international waters. AIS data are ideally suited for long-range monitoring and surveillance of vessel movements, and new methods are available to independently detect and document likely transshipment events, in addition to documentation provided by vessels and observers. Therefore, AIS-based monitoring of transshipment, coupled with improved regulation and oversight, holds promise for improving fisheries management and trade practices on the high seas and elsewhere.

MATERIALS AND METHODS

Likely encounters and fishing effort

Likely transshipment events (encounters) were detected using satellite and tower-based AIS data between 2012 and 2017, as described by (*17*). AIS was designed as a tool of maritime safety to avoid ship collisions. Transponders installed aboard vessels send position and vessel identification messages to receivers on other ships, land, and satellites every few seconds. These messages can be used to reconstruct vessel tracks with high precision and allowed us to analyze their activity on the basis of an automated analysis of movement patterns.

Likely encounters were identified by Global Fishing Watch as locations where two vessels remained within 500 m of each other for longer than 2 hours, traveling at less than 2 knots while at least 10 km from an anchorage (including ports). These parameters balance the need to detect vessel pairs in close proximity while recognizing our ability to identify long periods in which vessels are in immediate contact is limited by satellite coverage and inconsistent AIS transmission rates. Some vessels are known to tranship within ports, but these events are more likely to be subject to surveillance, and therefore, we focused on events that do not occur within the vicinity of port and the accompanying oversight. Here, we used a subset of the data analyzed by (*16*), only including encounters where AIS data are available for both the reefer and the fishing vessel engaged in the encounter.

To exclude vessel meetings that occur within port, encounters were filtered to be more than 10 km from an anchorage (defined as docking in port or anchoring close by) by using a global anchorage data set developed by Global Fishing Watch and made publicly available at http://globalfishingwatch.org/datasets-and-code/anchorages/. Briefly, the anchorage data set was developed by applying an approximately 0.5-km grid to the globe using S2 grid cells (level 14) (http://s2geometry.io/). Using AIS messages from 2012 to 2016 from all vessel types, those grid cells where at least 20 vessels remained stationary for at least 48 hours were identified. For each grid cell, the mean location of the stationary periods was calculated, and this point was labeled as an anchorage. This method identified 102,974 anchorages, and the mean location of an encounter was required to be at least 10 km from any anchorage.

A maximum encounter duration of 3 days was chosen to exclude encounters too short to offload catch and encounters that significantly exceed expected catch offload durations. These events likely represent vessels meeting for other reasons, such as repairs. This upper bound resulted in the removal of 97 events, representing less than 1% of the identified encounters.

Fishing vessels, refrigerated cargo vessels, fish carriers, and fish tender vessels were identified using vessel lists from the International Telecommunications Union and major RFMO fleet registries. Additional vessels were identified by a vessel classification neural network developed by Global Fishing Watch to predict vessel types based on movement patterns. Vessels that were identified as likely reefers by this neural network were manually reviewed through web searches and national, as well as RFMO registries. We do not expect that this list includes all vessels capable of receiving catch at sea, but it likely includes a majority of large specialized reefers that transport fishing for much of the offshore fishing fleet. Of the 641 refrigerated vessels identified in this manner (*17*), 501 were involved in likely transshipment events with AIS-tracked fishing vessels.

Fishing vessels included in this study were cross-checked for gear types through web searches using fleet registries and other reliable sources such as fishing company websites. To estimate the amount of catch landed directly by a fishing vessel versus catch brought to port via a reefer, we identified encounters and port/anchorage visits longer than 24 hours for each fishing vessel. For this analysis, a vessel was not considered to have "visited" a port or anchorage if it did not remain for longer than 24 hours to avoid assigning fishing effort to a port where a vessel was not present long enough to offload significant catch. For reefers, we identified the port visited following an encounter and the hours of fishing per fishing vessel that took place between events (the hours of fishing since the previous encounter or port visit). The fishing that preceded a port visit was assumed to have been landed in that port. Fishing hours that preceded an encounter were assumed to have been transferred from the fishing vessel to the reefer and offloaded in the next port that the reefer visited. The total fishing hours were aggregated by gear and attributed accordingly to ports (Russia considered separately from Asia and Europe).

Fishing activity and vessel gear type were classified following the methods described by (*15*). Briefly, two convolutional neural networks were trained on data from fleet registries, logbooks, and data labeled by experts to identify vessel types and classify their behavior (transiting and fishing) based on movement characteristics as seen in the AIS data.

Tuna supply chain

Data on supply chains for three reefers and 16 fishing vessels transshipping catch at sea were supplied by industry and consisted of official transshipment documentation and captain's statements. On the basis of the vessel identification numbers and details on date, location, and vessels involved in the transshipment given, AIS tracks were reconstructed for the three reefers and 13 of the 16 fishing vessels from raw AIS data supplied by Global Fishing Watch. Industry-recorded encounters were compared against the AIS-based detection method for transshipments, as described above.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/7/eaat7159/DC1

Fig. S1. Activity profiles of fishing vessels at sea.

Fig. S2. Reefers and fishing vessels involved in likely encounters between 2012 and 2017 worldwide by flag.

Fig. S3. Correlation between the number of rendezvous from 2012 to 2017 and IUU fishing by FAO region ($P = 0.1626$).

Fig. S4. Likely encounter between reefer flagged to Liberia (orange) and a Japanese longline fishing vessel (blue) off the west coast of Southern Africa.

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Acknowledgments: Global Fishing Watch provided the AIS data, vessel information, and support. We are grateful to H. Packer, Bumble Bee Foods, and Anova Food for industry information and J. Charbonneau for the help with vessel identification. **Funding:** K.B. has been funded by a Google Earth Engine Research Award to B.W. with additional support from Natural Sciences and Engineering Research Council of Canada. **Author contributions:** N.A.M. performed the data preprocessing. K.B. and N.A.M. conducted the data analyses. K.B., N.A.M., and B.W. contributed to the discussion and writing of the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors. Data and materials are also available through Global Fishing Watch and upon request to research@globalfishingwatch.org.

Submitted 28 March 2018
Accepted 2 July 2018
Published 25 July 2018
10.1126/sciadv.aat7159

Citation: K. Boerder, N. A. Miller, B. Worm, Global hot spots of transshipment of fish catch at sea. *Sci. Adv*. **4**, eaat7159 (2018).

ENVIRONMENTAL STUDIES

High seas fisheries play a negligible role in addressing global food security

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Recent international negotiations have highlighted the need to protect marine diversity on the high seas—the ocean area beyond national jurisdiction. However, restricting fishing access on the high seas raises many concerns, including how such restrictions would affect food security. We analyze high seas catches and trade data to determine the contribution of the high seas catch to global seafood production, the main species caught on the high seas, and the primary markets where these species are sold. By volume, the total catch from the high seas accounts for 4.2% of annual marine capture fisheries production and 2.4% of total seafood production, including freshwater fisheries and aquaculture. Thirty-nine fish and invertebrate species account for 99.5% of the high seas targeted catch, but only one species, Antarctic toothfish, is caught exclusively on the high seas. The remaining catch, which is caught both on the high seas and in national jurisdictions, is made up primarily of tunas, billfishes, small pelagic fishes, pelagic squids, toothfish, and krill. Most high seas species are destined for upscale food and supplement markets in developed, food-secure countries, such as Japan, the European Union, and the United States, suggesting that, in aggregate, high seas fisheries play a negligible role in ensuring global food security.

INTRODUCTION

To address high seas conservation and governance issues, the United Nations (UN) will start negotiations on a legally binding instrument to protect biodiversity in marine waters beyond national jurisdiction in September 2018 (*1*). Among the proposed conservation suggestions is the use of area-based management tools, in which fishing and other extractive activities could be prohibited. The prospect of closing any ocean area to fishing can raise many concerns, including negative impacts on food security. To understand potential trade-offs between conservation actions on the high seas and food security outcomes, it is necessary to assess the contribution of high seas fisheries to global food security.

The UN defines food security as "the condition in which all people, at all times, have physical, social, and economic access to sufficient, safe, and nutritious food that meets their dietary needs and food preferences for an active and healthy life" (*2*). Currently, more than 800 million people remain affected by severe food insecurity, and recent increases in the prevalence of civil conflicts and the severity of natural disasters due to climate change have exacerbated this problem in certain parts of the world (*3*). Seafood (defined here as both marine and freshwater species) provides more than a third of the global population with 20% of their animal protein intake (*4*); many researchers and nongovernmental organizations suggest that it is especially important for assuring food security in less developed countries (*5*–*7*) and in coastal indigenous communities (*8*). Marine fish and invertebrates from both wild capture fisheries and aquaculture are predicted to be increasingly important protein sources as the global population grows to 9 billion by 2050 (*5*, *9*, *10*).

Between one-quarter and one-third of the world's marine catch is caught by small-scale coastal fisheries (*11*), which play a role in addressing food security at a local level. However, fisheries are not just contained to the coasts. As inshore fish populations have been sequentially overfished and depleted, the development of industrial and technologically advanced fishing gears, storage, and processing capabilities has enabled vessels to travel farther offshore in pursuit of fish (*12*), and industrial fishing currently occurs in more than half of the global ocean (*13*). As fisheries have industrialized and markets have become globalized, those who rely most on fish for food are often marginalized through lack of capital and restrictions on accessing fishing grounds or purchasing fish (*14*). However, markets may allow the fish caught far offshore by industrialized fleets to feed those who are food-insecure, and so it is often assumed that high seas fisheries make an essential contribution to global food security [for example, (*15*)]. But is it true?

The "high seas" are the area beyond national jurisdiction as defined by the 1982 UN Convention on the Law of the Sea and represent almost two-thirds of the ocean surface. Areas of ocean adjacent to shore—that is, the 200 nautical miles that extend from the coastline—are the exclusive economic zones (EEZs) of countries. While the pelagic environment is lower in biological productivity compared to nearshore areas, the high seas are habitat for migratory, high-trophic fish species, such as tuna and some sharks, and long-lived species, such as orange roughy and toothfish. Thus, high seas fisheries can exert a high degree of top-down control in the open ocean at both the species and community level (*16*).

To assess the contribution of the high seas catch to global food security, we determined (i) the contribution of the high seas catch relative to other sectors of seafood production, (ii) the main high seas fishing countries, (iii) the species composition of the high seas catch, and (iv) the primary importing countries and associated markets for those species. We used annual catch statistics from the Sea Around Us reconstructed fisheries database (v. 47), aquaculture and freshwater production estimates from the UN and Food and Agriculture Organization (FAO) (*4*), and import and export data from the FAO FishStat database (v. 3.01).

RESULTS

High seas catch by volume

Between 2009 and 2014, the total landed catch on the high seas was an average of 4.32 million metric tons annually. This volume represents

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4.2% of the annual marine catch (102 million metric tons) and 2.4% of all seafood production, including freshwater fisheries and aquaculture (178 million metric tons; Fig. 1).

High seas catch by species

Thirty-nine fish and invertebrate species accounted for 99.5% of the high seas catch identifiable to the species level during the time period sampled (Table 1). Only one of those species, Antarctic toothfish, was caught exclusively on the high seas (3700 metric tons annually) and represented 0.11% of the total high seas catch. The remaining species are "straddling" and/or highly migratory species (that is, caught both on the high seas and within EEZs). The top three species caught on the high seas were all tunas: skipjack (967,000 metric tons annually), yellowfin (563,000 metric tons annually), and bigeye (336,000 metric tons annually). The tunas (these species plus albacore and the three bluefins) collectively accounted for 61% of the total high seas catch by volume. Other main species groups were non-tuna pelagic fishes (26%), pelagic squids (7%), billfishes (3%), demersal fishes and invertebrates (2%), and krill (1%) (Table 1).

High seas catch by producers and consumers

Ten fishing countries were responsible for 72% of the total high seas catch between 2002 and 2011 (Table 2). China and Taiwan alone accounted for one-third of the world's total high seas catch, while Chile and Indonesia had the third and fourth largest catches, followed by Spain. Despite having the largest high seas catch by volume, fish from the high seas account for only 5% of China's total domestic catch. Catch from the high seas contributed to ≤6% of the total national catch for half of the top 10 fleets: China, Japan, India, Indonesia, and the Philippines; only for Ecuador and Taiwan did high seas catches account for more than one-third of their domestic landings (Table 2).

Current traceability standards do not allow disaggregation of imported seafood into spatial jurisdictions (that is, caught on the high seas versus in an EEZ). However, imports of species caught on the high seas are available, and Japan was the top importer of all three globally traded bluefins (93% for southern, 58% for Atlantic and Pacific), as well as bigeye (75%), and the secondary importer of yellowfin (20%) and both toothfishes (22%). Thailand was the top importer of skipjack (63%), yellowfin (21%), and albacore (30%), and Spain was the secondary importer of albacore (19%). The United States imported the majority of both toothfishes (48%) and all of the krill and was the secondary importer of southern bluefin (2%). With the exception of South Korea importing almost all of the globally exported chub mackerel and Pacific saury, all other primary importers of species caught on the high seas were from the European Union (EU) (for example, Denmark, France, Italy, Spain, and the Netherlands). Further details of these trade flows—and additional trade of affiliated processed products—are available in Fig. 2 and table S2 and are discussed below.

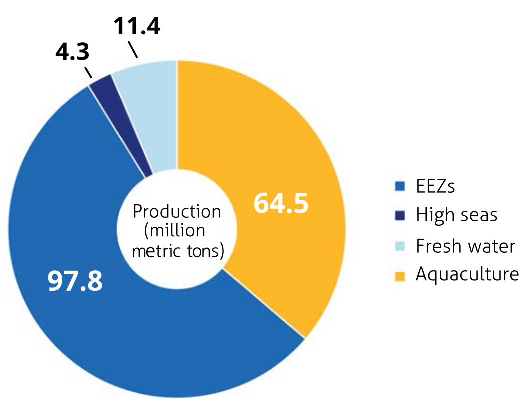

Fig. 1. Average contribution (million metric tons) of seafood-producing sectors, 2009–2014. The high seas catch represents 2.4% of total global production. Data: FAO 2016 and Sea Around Us.

DISCUSSION

High seas fish catch and global food security

High seas fisheries contribute an estimated 4.3 million metric tons (2.4%) to the global seafood supply. In 2014, these fisheries were valued $7.6 billion, yet they are enabled by an estimated $4.2 billion in annual government subsidies (*17*). We found that only one species, Antarctic toothfish, is caught on the high seas and nowhere else; the remaining species are also caught in EEZs.

Antarctic toothfish, along with its close relative, Patagonian toothfish, is usually consumed under the pseudonym "Chilean sea bass." Our results indicated that citizens in the United States are the main consumers of these fish, which is consistent with other work that found that the Unites States imported roughly 70,000 metric tons of toothfish between 2007 and 2012 (four times as much as the secondary importer Japan) (*18*). Some toothfish are certified by the Marine Stewardship Council eco-certification program, which notes that "this fish's fine quality meat means it is considered to be luxury seafood" (*19*). A 5-lb (2.3-kg) frozen portion currently retails through New York City's Fulton Fish Market website for $170 (*20*)—an equivalent portion of fresh chicken costs $7.35.

The remaining species caught on the high seas are also caught within national waters. Japan catches Pacific bluefin tuna within its EEZ and on the high seas and imports most of all three bluefin species caught by other countries [fish that were recently selling for $33/kg at Tokyo's Tsukiji Market (*21*)]. Japan is also the primary importer of bigeye tuna, which is used as an alternative to bluefin in sashimi (the fresh/frozen tuna market). Similar to the large tunas, the billfishes have relatively fatty and oily flesh and are usually sold as steaks. Italy is the world's top importer of billfish species, followed by Spain and Japan. From March 2017 to 2018, the average price for frozen swordfish at the Mercamadrid fish market in Madrid, Spain was $11/kg, while fresh swordfish fetched nearly triple at $31/kg (*22*).

Dwarfing the fresh/frozen market, however, is canned tuna. Two-thirds of all tuna caught globally is canned; almost all of this is skipjack, although yellowfin and albacore also contribute to this supply (*23*). As our analysis showed, Thailand is the main importer of these species, which is unsurprising given that Thailand processes many types of seafood and is the top global exporter of canned tuna, supplying about one-quarter of all products to the market (*23*, *24*). Canned tuna is the least expensive form of tuna available and is heavily consumed in the EU and North America (30 and 19%, respectively), while African and eastern European nations consume the least (3 and 1.6%) (*23*). Egypt, Australia, Japan, and Canada are the top importers after the EU and the United States, but current microtrends in the global tuna market suggest stagnation or decline in the import of canned tuna in all places, except the EU, where imports by five of the top six canned tuna–consuming countries (that is, Spain, Italy, France, UK, Germany, and the Netherlands) increased in 2017 (*25*).

Table 1. Species caught on the high seas, 2002–2011. Data: Sea Around Us.

Species	Family	Average annual high seas catch (10^3 metric tons)	Proportion of total catch from the high seas (%)
Skipjack tuna	Scombridae	966.6	35
Yellowfin tuna	Scombridae	562.5	34
Bigeye tuna	Scombridae	335.7	64
Chilean jack mackerel	Carangidae	307	22
Argentine shortfin squid	Ommastrephidae	149.5	25
Blue whiting	Gadidae	130.8	10
Chub mackerel	Scombridae	113.1	10
Albacore tuna	Scombridae	104.5	42
Japanese anchovy	Engraulidae	96.6	6
Jumbo flying squid	Ommastrephidae	83.8	7
Pacific saury	Scomberesocidae	81.7	9
Swordfish	Xiphiidae	64.7	52
Antarctic krill	Euphausiidae	37.4	24
Japanese jack mackerel	Carangidae	28.9	9
Northern prawn	Pandalidae	27.8	8
Flathead grey mullet	Mugilidae	23.3	13
Frigate tuna	Scombridae	17.1	7
Narrowbarred Spanish mackerel	Scombridae	14.6	3
Atlantic cod	Gadidae	11.3	1
Southern bluefin tuna	Scombridae	11.1	48
Kawakawa	Scombridae	10.6	4
Greenland halibut	Pleuronectidae	7.6	7
Shortfin mako shark	Lamnidae	7.6	18
Striped marlin	Istiophoridae	6.5	53
Pacific bluefin tuna	Scombridae	5.3	21
Patagonian toothfish	Nototheniidae	4.8	17
European anchovy	Engraulidae	4.5	0
Black marlin	Istiophoridae	4	24
Indo-Pacific sailfish	Istiophoridae	4	11
Antarctic toothfish	Nototheniidae	3.7	100
Wellington flying squid	Ommastrephidae	3	39
Patagonian grenadier	Merlucciidae	2.4	1
Indo-Pacific king mackerel	Scombridae	2.1	1
Atlantic bluefin tuna	Scombridae	2	5
Silver seabream	Sparidae	2	7
Blue marlin	Istiophoridae	1.4	27
Atlantic sailfish	Istiophoridae	1.3	24
Roundnose grenadier	Macrouridae	1.2	17
Bullet tuna	Scombridae	1.1	5

Although canned tuna is not considered a staple item in food-insecure countries, its price is comparable to other animal proteins (that is, canned tuna and canned chicken both retail for as little as \$1.50 per 5-oz tin online through Walmart), which suggests that it probably does help meet the nutritional and caloric needs of some low-income households in countries where it is sold. Nearly two-thirds of the world's tuna is caught in the western and central Pacific Ocean, where fishing predominately occurs in the EEZs of Pacific Island countries (*26*). In this region, the skipjack population is currently believed to be at

Table 2. Top high seas fishing fleets based on retained catch volume, 2002–2011. Data: Sea Around Us and FishStat (see table S3). Y, yes; N, no; NA, not applicable.

Fishing country	Average annual high seas catch (10^3 metric tons)	Contribution to global high seas catch (%)	High seas fleet contribution to total domestic catch (%)	Prevalence of severe food insecurity (% of population)*	Primary or secondary exporter of high seas species?	High seas species exported
China	714	17.0	5.3	<0.5 ± 0.07	N	NA
Taiwan	503	12.0	42.7	0.8 ± 0.62	Y	Skipjack, albacore, southern bluefin, bigeye, yellowfin, Pacific saury, marlins, and swordfish
Chile	340	8.1	7.4	3.7 ± 1.22	Y	Patagonian and Antarctic toothfish and jack mackerels
Indonesia	277	6.6	5.8	3.3 ± 1.86	Y	Frigate tunas and kawakawa
Spain	260	6.2	17.9	1.5 ± 1.12	Y	Pacific and Atlantic bluefin and swordfish
South Korea	254	6.1	11.9	0.9 ± 0.82	Y	Chub mackerel, skipjack, bigeye, squids, and seabream
Japan	231	5.5	5.1	0.6 ± 0.57	Y	Albacore and Pacific saury
Ecuador	185	4.4	32.3	8.7 ± 2.50	N	NA
India	128	3.0	3.6	12.4 ± 2.43	Y	Spanish and king mackerel
Philippines	119	2.8	5.3	12.0 ± 2.11	N	NA
Total	**3011**	**71.7**	**—**	**—**		

*Values from (*46*). These estimates were determined using a new method for estimating national food insecurity [FIES (Food Insecurity Experience Scale)] and are for 2014. For reference, the highest rate of severe food insecurity is 63.9% (Liberia) and the lowest is ≤0.5% (Azerbaijan, Bhutan, China, Israel, Switzerland, Sweden, and Thailand).

a healthy level of abundance, and the catch is considered sustainable (*27*); however, climate change is predicted to shift the distribution of this species (*28*, *29*). Furthermore, there are uncertainties around yellowfin population structure in this ocean (*30*). With these uncertainties in mind, ensuring the long-term health of these populations through effective management is of paramount importance not only because of the amount of food they provide but also because EEZ-caught tuna plays a vital role in assuring the economic and nutritional well-being of small island developing states in the Pacific Ocean (*31*).

Not all species caught on the high seas are destined for direct human consumption. Chilean jack mackerel, blue whiting, and anchovies are common targets of directed "reduction fisheries" (that is, used for fishmeal), of which almost all is used in aquaculture. About 70% of all farmed fish species require fish-based feed (*32*), although reduction species are also used in the production of feeds for terrestrial livestock and domestic pets, as well as fish oils and nutritional supplements. Trade data pointed to the Netherlands as the primary global importer of blue whiting, jack, and horse mackerels, although they likely re-export these fish to other EU countries (such as, Denmark, Norway, and Iceland) to turn into fishmeal (*33*). Norway is the world's leading producer of farmed salmon (about 1.2 million metric tons annually) (*34*), followed by Chile (*25*), a nation that is also a top producer of fishmeal for aquaculture (*35*). Most of the fish caught by Chile are likely retained domestically for the fishmeal industry. In 2017, the United States imported 24% of the fresh and frozen Atlantic salmon fillets produced by Norway (Japan and France were secondary and tertiary markets with 10 and 8%, respectively) and 30% of the fresh and frozen fillets produced by Chile (followed by Brazil and Japan, 17 and 16% each) (*25*). Advances in feeds, including more plant-based proteins, may eventually reduce the reliance on fishmeal for livestock and aquaculture (*36*).

Norway operates the biggest fishery for Antarctic krill in the Southern Ocean (*37*). The primary destination of these invertebrates has typically been the fishmeal industry, but because of the high fatty acids in krill oil, the past decade has seen an increase in the krill supplements marketed as "essential oils" that improve brain function (*38*). Globally, there are three main manufacturers of krill oil products: Neptune (Canada), Aker Biomarine (Norway), and Enzymotec (Israel). Krill supplements are not food but "nutraceuticals" and are another product sold in developed countries (*39*), and a 1-month supply retails online for $20 to $40 in the United States.

Additional high seas fisheries

The results presented have focused solely on catches and seafood reported in global catch and trade databases. However, some fish catches and discards may be illegal, unregulated, and/or unreported,

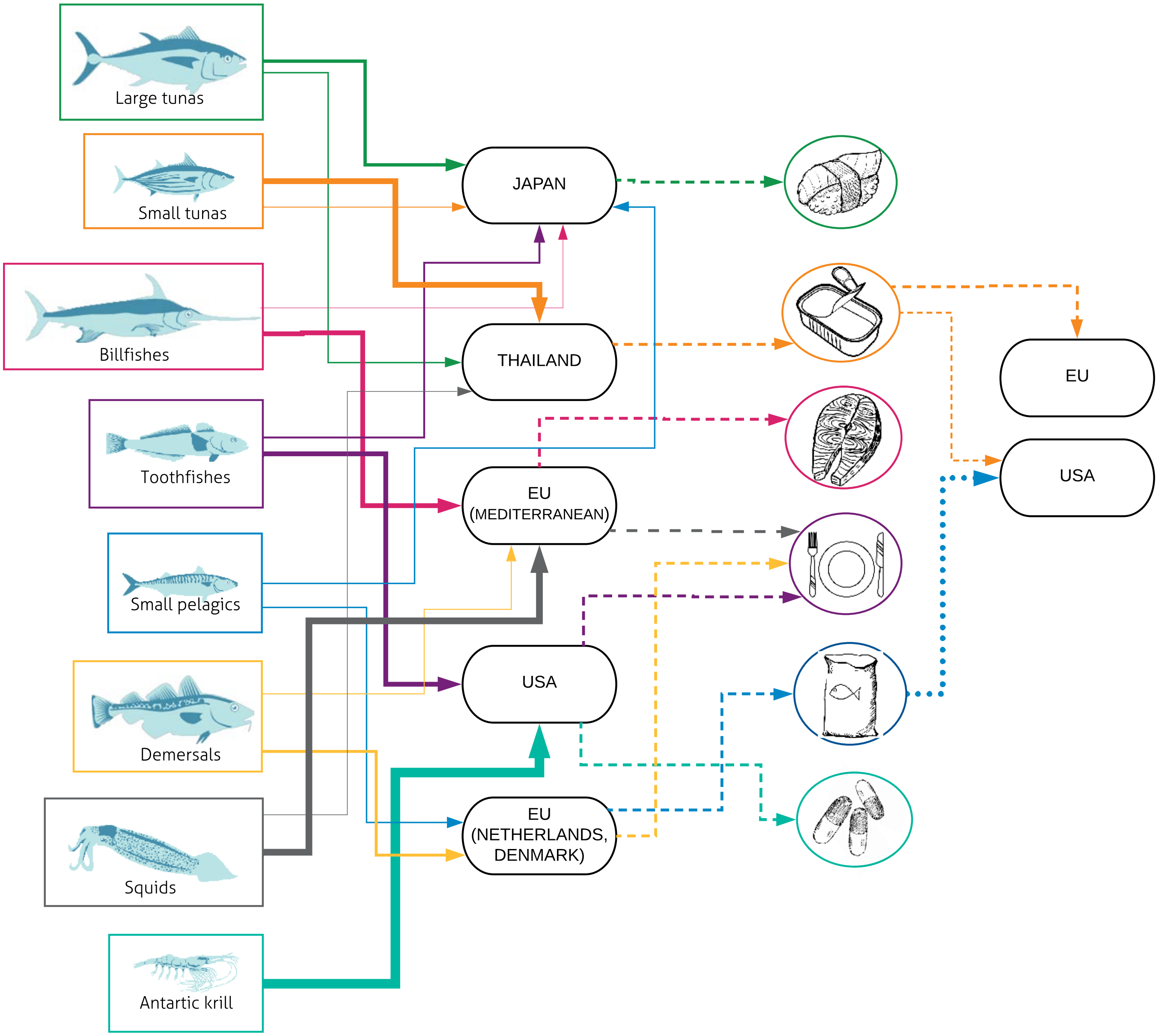

Fig. 2. Imports of species caught on the high seas. Solid arrow width proportional to destination's share of total global imports for each species group (fresh, frozen, unprocessed form), and dashed arrows indicate likely form of consumption in primary importing country or, if applicable, processed product produced. Primary and secondary importers of processed products indicated by weighted dashed lines based on market share of imports (based on information in the literature). Data: FishStat (see table S2).

such as documented cases in previous decades of undocumented toothfish and southern bluefin (*40*, *41*). Sharks were not considered target species in this analysis (see Materials and Methods), and they are routinely discarded at sea to make space for higher-value species often after removing their fins. While shark meat is of low commercial value, shark fins are one of the world's most expensive animal products but are consumed for status, not for calories (*42*). Spain, Taiwan, Indonesia, the United Arab Emirates, Singapore, and Japan are the biggest producers, while Hong Kong has traditionally been the world's primary importer and, along with the Chinese market, the largest consumer (*43*). After a series of conservation measures, a recent review suggested that Hong Kong's imports of shark products declined by 50% since 2007 (*44*), although loopholes in trade legislation and under-reported exports have potentially allowed the shark fin trade to continue (*45*).

Heterogeneity of consumption within countries, indirect contributions to food security, and food waste

Most of the top countries fishing on the high seas are food-secure (95% or more of their citizens are considered food-secure), with the exception of Ecuador, India, and the Philippines (Table 2). In addition, the top importers of high seas–related species (in no particular order: the Netherlands, United States, Japan, Spain, France, Denmark, and Thailand; see table S2) all have a low prevalence of severe food insecurity at the national level (that is, less than 2% of the population) (*46*). However, data are not available to analyze the role of seafood at the household level. Even within a food-secure country, access to food is not uniform, and many people may struggle to meet their caloric and nutritional needs. For example, the United States is one of the top importers of multiple species in this analysis, and the second most food-secure country in the world by some metrics (for example, https://foodsecurityindex.eiu.com/Index). However, more than 3 million Americans (1.2% of the population) are severely food-insecure because they cannot access food that meets their nutritional and caloric requirements and/or food preferences (*46*). Thus, although products derived from species caught on the high seas may be on the market, the prices of these products suggest that they are not financially accessible to these Americans, in the same way that bluefin tuna is likely not accessible to the 612,000 people in Japan (0.5% of the population) considered severely food-insecure (*46*).

There is also the notion that the high seas contribution to food security may be indirect—that sales of a relatively small quantity of high-value seafood by developing countries can generate revenue to allow those countries to import lower-value seafood to alleviate national food insecurity (*47*) or purchase replacement foods (*48*). While we do not have the data to support or refute the notion of "trickle down" food security, we know that the countries catching most of the fish on the high seas are not considered food-insecure (Table 2), although the relatively few people doing the actual fishing on high seas fishing vessels very well might be (*49*).

In addition, the export of high seas–related species for trade revenue may have unanticipated consequences. Evidence from Pacific Island countries, which caught tuna in nearshore waters for local consumption for centuries (*50*, *51*), shows that, as tuna has become a primary export commodity (*51*), there has been a decline in the consumption of local plants and fish in favor of less nutritious imported foods (for example, canned meat and fish, cereal, instant noodles, and soda); these nations now have some of the highest rates of obesity in the world (*52*). Recent local initiatives are focused on improving access to tuna for direct consumption, not only ensuring its continued supply for export (*53*). The global problem of food insecurity is more a problem of food availability given that one-third of all food produced globally is lost or wasted, including seafood (*54*). Putting this in perspective, retaining less than one-fifth of the seafood currently wasted as discards, in postharvest handling, or in poor supply chain practices would be the equivalent of the high seas catch.

CONCLUSIONS

The discussion of access to the high seas will inevitably lead to concerns about how closing areas to fishing could affect global food security. Here, we show that only one species of toothfish is caught exclusively on the high seas, that the high seas catch contributes less than 3% to the global seafood supply, and the vast majority of the marine life caught on the high seas is destined for upscale markets in food-secure countries. On the basis of the available data, high seas fisheries do not make a direct or crucial contribution to global food security.

MATERIALS AND METHODS

Study design

Two large global data sets were used for these analyses: the Sea Around Us fisheries database (v.47, obtained 13 December 2017) and the FAO FishStat database (v.3.01, obtained 11 January 2017). The Sea Around Us database includes reported and reconstructed marine fisheries catch over time since 1950 [for database rationale and methodology, see (*55*)]. FishStat is a global fisheries landings and trade database based on nationally reported figures since 1950, and it is the most comprehensive publicly available set of this kind. Data for aquaculture production and freshwater capture fisheries were obtained from the 2016 FAO State of World Fisheries and Aquaculture report (*4*). We defined "seafood" as all fish and invertebrates consumed by humans, regardless of whether they originate in fresh or salt water or are caught or farmed. See table S1 for an overview of data sources and analyses.

Data analysis

We analyzed the relative contribution of the world's four primary seafood sectors: (i) capture fisheries in national waters (EEZs), (ii) capture fisheries in the high seas, (iii) capture fisheries in fresh water, and (iv) aquaculture (both marine and fresh water combined). Sea Around Us data of capture fisheries landings in EEZs and the high seas and FAO data (*37*) were used for freshwater landings and aquaculture production values. To get a sense of the most recent trends, we used the period of 2009–2014.

Our second analysis determined (i) the primary high seas fishing countries and (ii) key species caught on the high seas. We identified the top fishing fleets (by catch volume) and the key species caught between 2002 and 2011 using the Sea Around Us database. This time frame was chosen as these were the most recent years with trade information in FishStat (v. 3.01, obtained 11 January 2017). On the basis of these data, a total of 395 different species (for example, "bigeye tuna" and "Atlantic cod") and taxonomic groups (for example, "unidentified marine fishes," "deep-sea crabs," and "unidentified pelagic fishes") were caught on the high seas during this time. From this, we extracted the 243 species-specific entries for fish and invertebrates. Because the reconstructed Sea Around Us data used in this analysis include all forms of catch (including nontargeted species that are caught as bycatch), we assumed that not every one of the 243 species were targeted catch and that some would have been caught incidentally as bycatch in certain fisheries. To account for this, we refined this list into "targeted species" by (i) removing any species with an average annual catch of ≤1000 metric tons and (ii) removing any species with a discard/total catch of ≥10%. From these filters, 39 species remained for the subsequent analysis of trade (table S2). As the Sea Around Us data also include estimates of capture fisheries catch within EEZs, these values were used to compute the proportion of a species' total catch that is from the high seas.

Our third analysis used the FishStat database to determine the primary importing and exporting nations of the high seas species identified in the preceding analysis. Here, we defined "primary" importers as those nations with the highest percentage (by volume) of a given species as an imported product. "Secondary" importers are those with the second highest. Unless otherwise specified, import statistics for fresh and frozen, unprocessed product forms (that is, "salted," "dried," "processed," and "prepared" products were not included) for each species were obtained from this database. We also identified which high seas fishing countries had exports of the high seas species identified in the preceding analysis. Trade data were not disaggregated between EEZs and the high seas. Therefore, it was not possible to determine what proportion of a traded species or product was originally caught on the high seas. For the purpose of this study, the assumption was no difference in the importers of EEZ or high seas products of a given species, and the data presented represent imports of the total reported catch for those species. This assumption was made on the premise that the international seafood market predominantly differentiates products based on flag state (fishing country) rather than the geographic location of the catch.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/8/eaat8351/DC1

Table S1. Data sources and associated analyses.

Table S2. Species caught on the high seas and associated primary and secondary importers from 2002 to 2011.

Table S3. Species caught on the high seas and associated primary and secondary exporters from 2002 to 2011.

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Acknowledgments: We acknowledge the Sea Around Us (www.seaaroundus.org) team for their assistance with global catch data acquisition and associated inquiries. Additional thanks to Fish Choice (www.fishchoice.com) for the species graphics used in the trade flow figure and to K. Boerder, W. Swartz, and five anonymous reviewers for their comments on earlier versions of the manuscript. **Funding:** This work was funded by National Geographic Pristine Seas. J.J. is also supported by a Pew Marine Conservation Fellowship. **Author contributions:** Conceived and designed the topic: L.S., M.B., J.J., and E.S. Analyzed the data: L.S. Wrote the paper: L.S., M.B., J.J., and E.S. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 9 April 2018
Accepted 13 July 2018
Published 8 August 2018
10.1126/sciadv.aat8351

Citation: L. Schiller, M. Bailey, J. Jacquet, E. Sala, High seas fisheries play a negligible role in addressing global food security. *Sci. Adv.* **4**, eaat8351 (2018).


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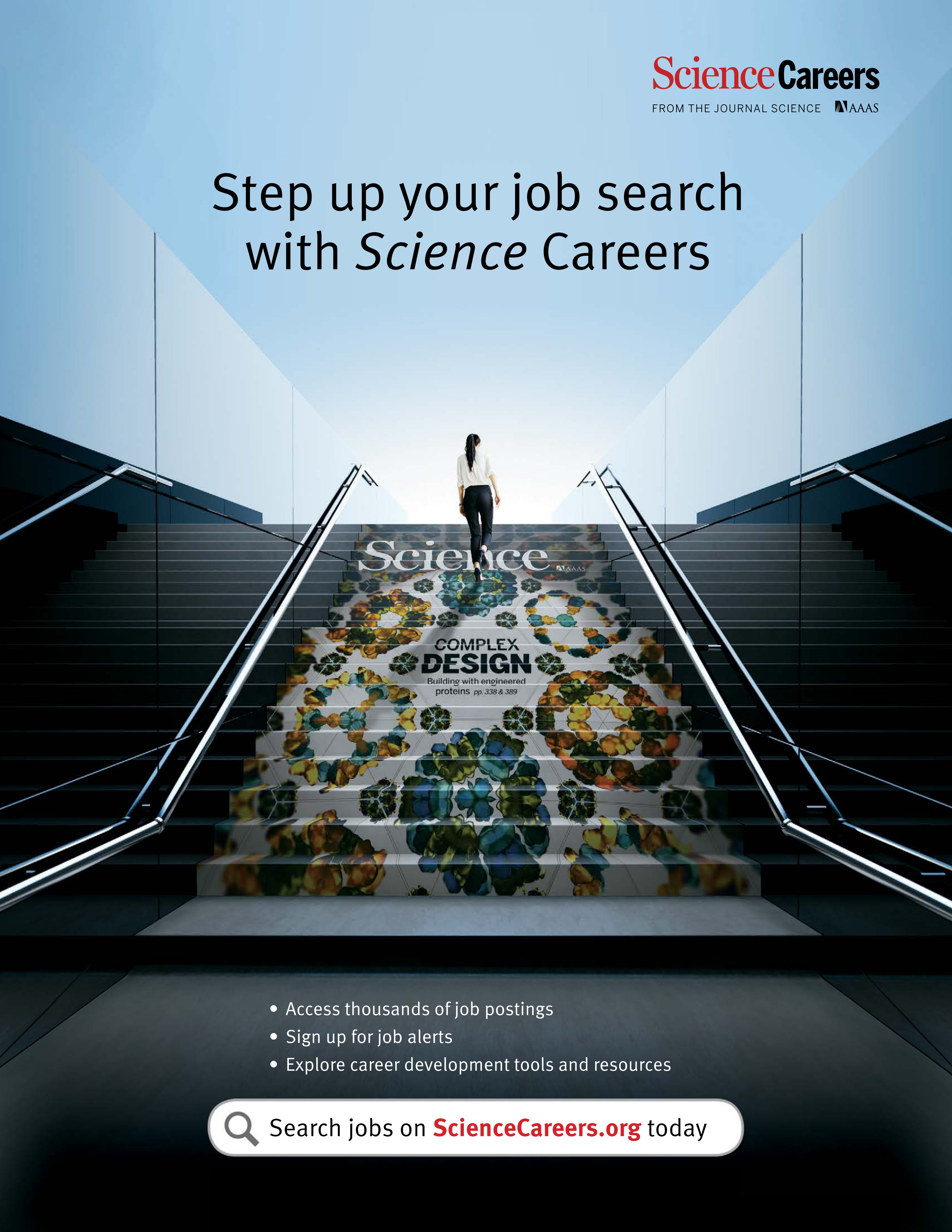
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