FISHERIES

The small world of global marine fisheries: The cross-boundary consequences of larval dispersal

Nandini Ramesh1*, James A. Rising2, Kimberly L. Oremus3

Fish stocks are managed within national boundaries and by regional organizations, but the interdependence of stocks between these jurisdictions, especially as a result of larval dispersal, remains poorly explored. We examined the international connectivity of 747 commercially fished taxonomic groups by building a global network of fish larval dispersal. We found that the world’s fisheries are highly interconnected, forming a small-world network, emphasizing the need for international cooperation. We quantify each country’s dependence on its neighbors in terms of landed value, food security, and jobs. We estimate that more than $10 billion in annual catch from 2005 to 2014 is attributable to these international flows of larvae. The economic risks associated with these dependencies is greatest in the tropics.

Marine fisheries supply food and livelihoods to millions of people around the world (1). Though fisheries are typically managed at the scale of national exclusive economic zones (EEZs), many fish populations are connected beyond EEZ boundaries (2–6). Whereas pelagic species can be tracked across international borders as adults (7), nonpelagic populations connect primarily via the dispersal of fish eggs and larvae, forms that cannot yet swim by ocean currents (2, 8).

Larval connectivity patterns have been analyzed at both the regional (6, 9–12) and global (4, 13, 14) levels and have been used to suggest changes for spatial management and conservation (12, 15). However, the impact on fisheries of larval connectivity across EEZs is not well understood, even though more than 90% of the world’s fish are caught within EEZs (10).

On the scale of a single species or region, this connectivity can be analyzed empirically through genetic testing (9, 10). For analyses on larger scales, dispersal patterns can be estimated using biophysical models that combine oceanographic data with an understanding of the biology of the stocks (4, 14, 17). Such efforts can be challenging, because species vary widely in larval timing and duration and currents vary with the seasons; therefore, generalizations can be misleading. More realistic inputs can be achieved by using life history traits for each species, including time and place of spawning and larval duration. Sensitivity analyses can help to ensure that results are robust to changes in key assumptions (14), while empirical bounding can safeguard against predicting unrealistic dispersion outcomes (6).

Network analysis has previously been applied to marine systems to describe the connectivity of plankton communities (18), local fishing communities (19, 20), and marine reserves (14). Networks of larval flows have been used to identify “hub” subpopulations for protection on a regional scale (12).

In this study, we combined oceanographic and life history data for 706 species and 434 genera of commercially harvested fish to estimate their connectivity across 249 EEZs and constructed a network representing the larval flows between

---

1Department of Earth and Planetary Science, University of California, Berkeley, Berkeley, CA 94720, USA. 2Grantham Research Institute, London School of Economics, London, UK. 3School of Marine Science and Policy, University of Delaware, Newark, DE 19716, USA.

*Corresponding author. Email: nandiniramesh@berkeley.edu

---

Fig. 1. The network of spawn-attributed catch flows between EEZs. Each EEZ is a node (circle) of the network and its color represents its network community. The connectors or edges in this network flow clockwise from source to sink, with their thicknesses representing the magnitude of the net flow of caught biomass between the EEZs. Only the edges in the upper tercile of edge weights are shown, for clarity (see SM 3.2 for the full network). The size of each node represents its out-degree, i.e., the number of other EEZs for which it acts as a source of fish larvae, including connections not shown in this image.
RESEARCH | REPORT

nations. Nations that depend heavily upon their neighbors for recruitment risk losing part of their catch if the fisheries in the source EEZs outside their jurisdiction are poorly managed. We quantified these risks in economic terms and identified regional “hotspots” of risk for catch, fishery employment, and food security.

We used a particle-tracking system (21) with time-varying ocean currents (22) and species-specific life histories (23) to simulate the dispersal of eggs and larvae through a dynamic ocean. We placed multiple simulated particles for each species based on the timing and location of that species’ spawning and let them drift for their larval duration to obtain a probabilistic estimate of species-specific larval trajectories. We used a random-walk parameterization (21) that adds a small velocity at every time step to account for turbulent motion at small scales [see section 3.1.2 in the supplementary materials (SM 3.1.2)].

We empirically bounded our results by discarding particles that arrived in regions where the species is not present in observed catch data (16). For a given EEZ, catch is attributed based on the proportion of particles arriving there from each spawning country (see SM 1.1). This proportionality forms the core assumption of our model. We tested our main results with a series of analyses of sensitivity to this assumption. These included reducing spawn floating duration to account for uncertainties in spawning mortality (2, 24), introducing return adult spawning migration (25) (see SM 3.6), and distinguishing different levels of recruitment limitation.

We estimated how much of each country’s observed catch comes from its neighbors by constructing for each species a transition matrix that describes the probability of its offspring dispersing from one EEZ to another. This transfer of biomass between nations’ EEZs is represented as a network in Fig. 1.

Each connector of the network represents net flows of fish from one country to another. Countries that depend on inflows of juvenile fish to maintain their local populations require international cooperation to ensure sustainable fisheries. Our analysis of these flows revealed that a large proportion of marine fisheries within EEZs form a single, global network (Fig. 1).

We found that the global network of marine fisheries is a scale-free, small-world network. The scale-free network property, common in natural systems (26), is characterized by an exponential distribution of the number of connections from each node (see SM 3.2). This exponential degree distribution results in a “hub-and-spoke” structure that is resilient to random disturbances because of the large number of less-connected countries from which disturbances do not easily propagate to other parts of the network. However, a disturbance to any of the highly connected hubs in a scale-free network can affect numerous surrounding nodes. In this context, habitat destruction, overfishing, or environmental change in a hub EEZ could have impacts that spread beyond its own bounds.

Conversely, targeted efforts to manage fisheries within these hub EEZs could benefit many nations.

To demonstrate the relationship between currents and the network of larval dispersal, we focused more closely on four regions (Fig. 2). The differences between the regional networks and average current speed arise from the details of current speeds during spawning, larval duration, and empirical observations of species presence or catch. The influence of the Guinea Current on the connectivity of West Africa’s fisheries can be seen in the large number of EEZs that act as sources to their eastward neighbors, especially between Guinea-Bissau and Nigeria. While the strongest connections are typically

Fig. 2. Regional currents and community networks. (A to D) The speed (shown in colors, in centimeters per second) and direction (arrows) of ocean surface currents in four regions with interconnected fisheries (West Africa, Baltic Sea, the Caribbean, and Western Pacific) during the month of maximum spawning activity in each (August, May, June, and May, respectively). (E to H) The corresponding subset of the global network encompassed by the four regions. Colors, node sizing, and connector directions are as for Fig. 1. Nodes are arranged to approximately correspond to geographic locations of the EEZs.
between adjacent EEZs, many connections also extend over longer distances. In contrast, the Baltic Sea has substantially weaker currents. There, the largest outward flows originate from Sweden and Norway, which have the region’s longest coastlines. In the Caribbean, the North Brazil Current flows northwestward along the South American coast, and consequently many of the EEZs lying along this current act as sources for the Lesser Antilles. Within the Lesser Antilles, the density of small EEZs gives rise to a highly interconnected, complex network structure. The effect of the northward flow along this island chain can be inferred from the larger node sizes among the EEZs lying in its southern portion. In the Western Pacific, strong currents dominate in the equatorial ocean, with weaker currents at higher latitudes. The large areas encompassed by this region’s EEZs mean that, unlike the other regions, most connections are between immediate neighbors. The small-world property implies that it is possible to traverse the global network in a small number of steps, on average. Within this network, there exist smaller clusters or communities that are tightly connected. Most of these clusters internally exhibit the small-world property. In theory, this property of the global fisheries network suggests that disturbances to a large hub could propagate via cascading effects on the surrounding spokes. A key question is whether disruptions to a given EEZ actually propagate in this manner. A stock's response to external shocks depends on both its population dynamics and mortality from fishing, which can be affected by management.
Some fish stocks are biologically capable of replenishing themselves when their numbers dwindle, provided that fishing pressure is relieved, reducing the likelihood that disturbances will propagate. However, “recruitment-limited” stocks are vulnerable to a decline in spawning population, making it more likely that disturbances will spread across the network even if the receiving fisheries are managed. We adopted FishBase’s classification of stock resilience as a proxy for this type of density dependence. For high-resilience stocks, which are generally not recruitment limited, our measure of stock dependence overestimates the extent to which stocks will be reduced if recruitment inflows fail. For those stocks classified as having medium or low resilience, however, we found a strong correlation between our simulation’s predictions and observed variances in stock levels (see SM 3.5). Even for countries whose fisheries mostly comprise non-density-dependent stocks, these larval inflows serve as a buffer against fishery collapse within their waters.

To contextualize our results, we estimated the economic significance of the network’s international connections. First, we considered the amount and value of catch that flows in and out of each EEZ (Fig. 3). Japan, China, and Alaska are responsible for the greatest outflows, reflecting their productive waters. However, having fewer neighbors makes them smaller hubs (Fig. 1). Indonesia has the most landed value attributable to other countries, due to its high-value catch and many neighbors. The countries with the greatest catch inflows are generally those with the largest fisheries.

Next, we identified nations that are potentially most vulnerable, in socioeconomic terms, to the management of neighboring waters (see table S5). In Fig. 4, we highlight countries that depend the most on the spawning grounds of neighbors in terms of their total catch, gross domestic product (GDP), number of jobs in the fishery industry, and a fishery food security dependence index (29). The most vulnerable nations are concentrated in the hotspot regions of the Caribbean, West Africa, Northern Europe, and Oceania. The risks to national GDP and labor force are generally highest in the tropics. However, our measure of food security risk also identified a few European nations.

Our analysis showed that about $10 billion worth of annual marine catch may rely on transnational exchanges of fish offspring. These dependencies form a single global network, indicating that marine fisheries, even within national boundaries, constitute an interconnected, globally shared resource.

This network’s scale-free and small-world properties imply that fish stocks from a small number of EEZs provide benefits to a large number of “downstream” countries. The most vulnerable nations are clustered in a few hotspot regions (Fig. 4). This pattern lends further support to the use of international frameworks, such as large marine ecosystems and marine protected area networks (29, 30).

Further research is needed to understand how small-scale coastal processes, larval behavior, and fisheries management affect this connectivity. Beyond the spawning connections studied here, national fisheries are interdependent through the movement of adult fish, population shifts under climate change, and international fishing treaties. In particular, the role of adult fish migration in driving international connectivity remains an important question. While a more detailed analysis is required to accurately describe dispersal pathways of individual species, this study highlights the role of larval connectivity across international boundaries and the need for multilateral cooperation for sustainable management of these shared resources.

REFERENCES AND NOTES

1. FAO. “The state of world fisheries and aquaculture: Contributing to food security and nutrition for all.” (Food and Agriculture Organization of the United Nations, 2016).

ACKNOWLEDGMENTS

The authors thank D. Dookey, M. Burgess, M. A. Cane, A. Chaintreau, A. Carlisle, J. Cohen, C. Costello, R. Defries, S. Gaines, S. Hisari, C. Moffat, and C. Szuwalski for comments, suggestions, and references. This work was initiated and partly conducted at Columbia University in the City of New York, which provided computing resources. Funding: N.R. was partially supported by the National Aeronautics and Space Administration (NASA) Headquarters under the NASA Earth and Space Science Fellowship Program, grant NNX09AI56H. Author contributions: N.R. performed the network analysis and Lagrangian modeling. J.A.R. performed the country-level risk analysis. N.R., J.A.R., and K.L.O. designed the study, collected data, and wrote the paper. Competing interests: The authors declare no competing interests.

Data and materials availability: All newly organized data used in this study and the intermediate and final results data are publicly available at Zenodo (32). Analysis reproduction code is available at https://github.com/openmodels/small-world-fisheries.

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/364/6446/1192/suppl/DC1

Materials and Methods Figs. S1 to S13 Tables S1 to S8 References (32–44)

6 September 2018; accepted 23 May 2019 10.1126/science.aav3409
The small world of global marine fisheries: The cross-boundary consequences of larval dispersal

Nandini Ramesh, James A. Rising and Kimberly L. Oremus

Science 364 (6446), 1192-1196.
DOI: 10.1126/science.aav3409

A small, interconnected world
Countries manage their fisheries as if they were a local resource. To some degree, this may reflect reality, but marine fish, perhaps more than any other vertebrate group, are connected across large distances through ocean currents. Ramesh et al. model how these currents distribute the fish larvae of more than 700 species. They used network analysis to assess the degree to which populations found in one part of the world may have come from another. It seems that global fish populations represent a small-world network where connections across populations are tight and particular hubs of productivity are widely important. Such connectivity has wide-ranging implications for conservation, management, and food supplies globally.

Science, this issue p. 1192

ARTICLE TOOLS
http://science.sciencemag.org/content/364/6446/1192

SUPPLEMENTARY MATERIALS
http://science.sciencemag.org/content/suppl/2019/06/19/364.6446.1192.DC1

REFERENCES
This article cites 33 articles, 7 of which you can access for free
http://science.sciencemag.org/content/364/6446/1192#BIBL

PERMISSIONS
http://www.sciencemag.org/help/reprints-and-permissions

Use of this article is subject to the Terms of Service