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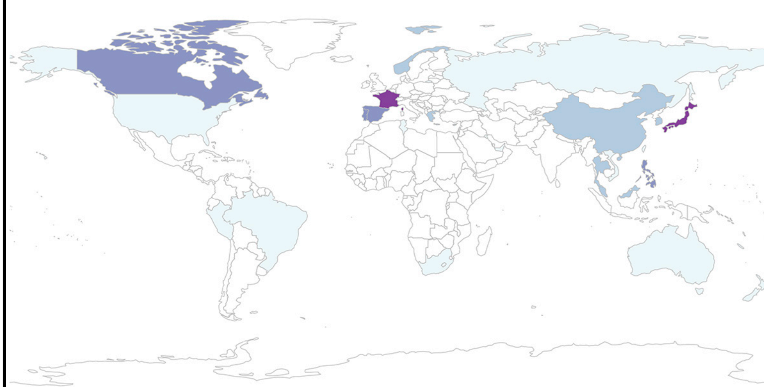
Global pathways of innovation and spread of marine aquaculture species

Graphical abstract



Highlights

- A few key countries developed many of the now commonly farmed mariculture species
- Certain countries seem to be important conduits in the spread of new mariculture species
- Innovation in mariculture is related to a country's governance and economic climate

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In brief

Mariculture, or farming seafood in the ocean, is an increasingly important part of global food production. One way that the mariculture industry innovates and expands is through the domestication of new species that can be successfully farmed in multiple countries. Examining which countries lead the way on new species innovation and the characteristics that these countries have in common sheds light on the patterns of mariculture's path into the future.

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Article

Global pathways of innovation and spread of marine aquaculture species

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SCIENCE FOR SOCIETY As the global human population grows and climate change accelerates, increasing pressure is placed on our food systems. Achieving resilient, equitable, and sustainable food production requires continued research, development, and widespread uptake of new innovations. Mariculture (the farming of seafood in the ocean) has received attention for its potential to expand to meet growing demand, in some cases with low environmental impacts. Developing new mariculture species is important for diversifying production and helping the industry expand sustainably into new geographies. Our research focuses on understanding which countries are global leaders for new species development and for spreading cultivated species, and how country characteristics (e.g., strong governance) may facilitate innovation. Building on this foundation, future work could provide more specific guidance on how to foster innovation and spread in mariculture or for other types of food production.

SUMMARY

Mariculture—the farming of marine species—is a growing industry that could support and diversify food systems, but its sustainable expansion requires innovations to improve yields, profitability, resilience, and environmental performance. However, there is limited knowledge regarding where and why industry innovations spread. Here, we examine one key aspect of innovation, the development of new mariculture species, and evaluate a global network of countries developing, spreading, and adopting new farmed species. We found that countries with long histories of aquaculture innovation (e.g., Japan, France) have had success developing widely produced species. Network analysis revealed that other countries (e.g., Singapore) may play an important role in the subsequent spread of new species. Strong governance and economic conditions seem to play small but significant roles in facilitating the development and spread of mariculture species. Better understanding pathbreaking countries and characteristics of innovation can foster a sustainable trajectory for this burgeoning industry.

INTRODUCTION

The development and expansion of marine aquaculture, or mariculture, has implications for food systems, environmental health, and economic development. As such, there is an increasing focus on the role of mariculture production in current and future food systems and the potential for sustainable development of mariculture to increase and diversify food supplies, while reducing the environmental burdens of food production.[1–5] This is because mariculture can be very space efficient[6] and relatively low in resource use and pollution production.[7,8] However, mariculture can also have considerable environmental concerns, including sustainability of feeds, pollution, spread of invasive species, and impacts on native biodiversity.[9] This combination of mariculture's existing environmental challenges alongside its economic and environmental promises creates an urgent need to explore its future potential and pathways for improvement. And yet, despite the growing attention on mariculture expansion, there is a dearth of information about the factors that drive innovation, growth and diversification of the sector.

Mariculture has been practiced at a small scale for at least hundreds of years but has only been a significant and widespread commercial activity since the middle of the 20th century. Recently, the industry has been growing rapidly; over the past 30 years, the production of mariculture has increased nearly 5-fold, with recent annual production of more than 30 million metric tons.[10] Despite its relative newness, the mariculture industry is diverse, with approximately 249 different species farmed. While more than 90% of terrestrial meat production comes from just pigs, poultry, and cattle,[11] the top 18 farmed marine species would be required to account for a similar fraction of mariculture production. Mariculture species range from fish, such as salmon, to invertebrates like mussels and shrimp, to algae such as kelp. Although there is currently active commercial mariculture production in 102 countries and on every continent except Antarctica, it is heavily concentrated in a smaller number of countries, with China alone accounting for more than one-third of all production.

Research and development of rearing techniques for new species suitable for mariculture is ongoing in areas throughout the world and is one important way that the industry innovates and expands.[12] Certain species have become particularly successful and are farmed in multiple countries; for example, the most widely farmed marine species, the Pacific cupped oyster (*Crassostrea gigas*), has been farmed in 27 countries.[10] How widely species are cultivated, particularly the extent to which cultivation spreads beyond the originating country, has important repercussions for the spatial distribution of mariculture along with the economic and social effects of this production. An example from freshwater aquaculture is the development and spread of genetically improved farmed tilapia (GIFT), a farmed type with a significantly higher growth rate, that resulted from selective breeding of a genetically diverse base population with broodfish from Africa and Asia.[13] The GIFT breed was developed in the Philippines in the mid-1990s and has subsequently been spread substantially across Asia, Africa, and Central and South America.[14] Although tilapia is a high-value species for domestic urban markets (e.g., Brazil, Egypt), it is also a popular subsistence crop in many developing countries. The spread of the GIFT breed, which has contributed to increased growth rates and improved disease resistance, offers both economic and social benefits to these areas.[14,15] However the farming of new or altered species presents inherent risks, such as invasive species introduction or genetic pollution of wild populations, that need to be carefully managed.[16,17] Indeed, in this case the risks to native populations have limited the utility of this new technology in Africa, the region where tilapia were first farmed.[14]

For the case of marine aquaculture, continued development and adoption of new marine species has significant implications for the ability of the industry to continue innovating and adapting in the face of changing environmental, social and market conditions.[18] Growing more species can add resilience to a country's seafood portfolio, and greater investment in species innovation increases the chances that a country will farm a species that could become important economically and/or for food production.

Several studies have provided insight into the social, economic, and political forces that may influence mariculture development and innovation within a country or region.[19–22] Collectively, this work has shown that institutional support, strong economic and governance conditions, and existing infrastructure can help facilitate the growth and expansion of mariculture in an area. Furthermore, research and management institutions that integrate different sectors and span regions, stakeholders, and disciplinary perspectives can help advance aquaculture innovation and sustainability.[23–25] In addition, there is evidence that in some instances, declining fishery catches can lead to increased reliance on farmed seafood, including expansion of marine aquaculture.[26] Looking more broadly at food systems, research on freshwater aquaculture and agriculture also provide a deeper understanding of the conditions that can support innovation development and adoption[27–29]; for example, nodes of innovation for agriculture have provided a foundation for the spread of more environmentally friendly farming methods.[30] Indeed, the institutions, frameworks, and incentives developed by both governments and private industry have been shown to have an important impact on the type and volume of agricultural research and development that occurs within a country.[27]

Although innovation is clearly important to the success and expansion of mariculture, there is limited research documenting patterns of mariculture innovation worldwide. Here, we investigate one key component of mariculture innovation, focusing specifically on new species development and the subsequent geographic expansion of their cultivation. Developing a new species for successful culture can be time and resource intensive and may require considerable technical expertise in areas such as breeding and husbandry, nutrition, genetics, animal health, and economics.[31,32] The appearance of a new species in production data is thus evidence of an underlying suite of innovations, and the spread of a species to new countries shows that the innovations have been disseminated across space. Given the relatively recent appearance of mariculture as a global commodity, it is particularly well suited to this type of analysis. Indeed, widely available annual data can be used to track which species have been farmed in each country over time,[10] making species development a particularly measurable proxy of mariculture innovation and knowledge transfer.

Here, we use several analyses to better understand nodes of innovation and spread in marine aquaculture development (see experimental procedures). We identify which countries most often develop new species and which countries are particularly central in the subsequent spread of new species. We focus the majority of our analysis on 54 marine species that are widely farmed (produced in at least four countries), taking the spread of these species as examples of successful innovation. Furthermore, we examine the characteristics of innovating countries to see if there are certain geographic, economic, industrial, cultural, and governance characteristics that are associated with developing and producing widely farmed mariculture species. We also use network analysis, examining countries that produce the same mariculture species, to investigate if there are certain countries that feature prominently in the dispersion of new species across the world. Our findings demonstrate that certain countries play outsized roles in the development and/or spread of new aquaculture species, and that countries with strong governance and economic conditions may be better able to innovate and spread new species. Understanding the characteristics of countries serving as nodes of innovation and uncovering wider patterns of mariculture adoption are relevant to identifying

Table 1. The taxonomy of the 54 widely produced species included in this analysis

Taxonomic group	Number of widely farmed species (% of widely farmed species)
Crustaceans	6 (11%) (5 shrimp/prawn, 1 crab)
Mollusks	11 (20%) (all bivalves: 4 cockle/clam, 3 mussel, 2 oyster, 2 scallop)
Algae	7 (13%) (3 brown seaweeds; 4 red seaweeds)
Finfish	28 (52%) (see Table S1 for details)
Echinoderms	2 (4%) (2 sea cucumbers)

global mariculture hotspots and how innovation in one region can affect production across the globe. By examining the networks through which mariculture develops and spreads, we can help inform the industry's growth and sustainable development.

RESULTS

Patterns of mariculture adoption

Using Food and Agriculture Organization (FAO) global aquaculture production data,[10] we identified 249 mariculture species that have been produced since 1950; 54 of these (~22%) have been widely produced, which we define as farmed by four or more countries. These widely produced species represent a diverse collection: 6 species of crustaceans, 11 species of mollusks, 2 species of echinoderms, 7 species of algae, and 28 species of finfish, including fish with a range of trophic levels and economic values (Table 1; Table S1). A total of 102 different countries have farmed any mariculture species, with 95 having farmed at least one widely produced species, according to our definition (Table S2).

We found that certain countries frequently developed new species (i.e., are "first producers"), whereas other countries tended to adopt a species only after it had been produced elsewhere. Specifically, Japan, Tonga, Hong Kong, the Cook Islands, and New Zealand have farmed multiple mariculture species and are first producers of the species they farm at least 75% of the time (Figure 1). Conversely, Italy, Saudi Arabia, and Namibia have each farmed at least six mariculture species but were not the first producer of any of these species (Figure 1). Spain is notable for the sheer number of species farmed—46 total species, including 24 widely produced species—and that nation features prominently as both a first producer (19 total species; 4 widely produced species) and a subsequent adopter of species that have been developed elsewhere.

Of countries that first produced a mariculture species, some have disproportionate success in developing species that go on to become widely produced. For example, Japan and France have developed the highest number of species that became widely produced (seven and six species, respectively). Both countries have had particular success developing low trophic level species; between the two countries, they have been first producers for nine widely produced mollusk and algae species. By contrast, Canada has been most successful at developing widely produced finfish species (four total). At least two-thirds of all species first produced in Norway, France, Cyprus, and Canada go on to be widely produced, whereas South Korea and Singapore are more likely to develop new species than to spread them. The latter two countries were both first producers on more than 20 mariculture species but have had less than 20% of these species go on to become widely produced (Table S2).

Looking in more depth at widely produced species, we found that the time it took for new species to spread beyond the first country varied substantially, both by species and by adopting country. Specifically, we found that the mean elapsed time between first production (by another country) and subsequent adoption (by the named country) ranged from a low of 3 years for Madagascar up to 57 years for Senegal (Figure 2). We also examined the mean interval between first production and subsequent adoption broken down by four major species groupings—crustaceans, mollusks, fish, and algae—and found that the mean interval between first production and significant spread (defined as being produced in four countries) was significantly higher ($p < 0.01$) for algae (26.1 years) than for crustaceans, mollusks, or fish (12.4, 10.1, and 11.8 years, respectively).

Using network analysis, we mapped connections between countries on the basis of each widely produced species each pair of countries farms in common (Figure 3). Overall, we found that Singapore, followed by Ecuador and Taiwan, are most central to the network (as measured by betweenness centrality). In terms of breadth of connections, Singapore, Spain, and the United Arab Emirates are all connected to at least 60 other countries by farming the same widely produced species. Spain, France, and the United Kingdom have the most total connections (if two countries farm more than one of the same species, they will have multiple connections) with a total of 230, 203, and 167 connections, respectively. Spain and France have the greatest number of connections, as the two countries farm 14 of the same widely produced species. The network analysis also revealed the clustering of countries from the same continents, suggesting countries within the same continent often farm the same widely produced species. Finally, the countries with the highest centrality scores may be important links between regions, as they are often connected to countries outside of their continent (Figure 3; Table S3).

Characteristics of innovative mariculture countries

We hypothesized several factors that could be related to a country's proclivity to develop, spread, or adopt widely produced species, including indicators relevant to governance, economics, business environment, and seafood production (Tables S4 and S5). Many of our proposed indicators were highly correlated, representing different ways of measuring governance or economic conditions in the country (e.g., regulatory quality and business dynamism). Therefore, we used principal-component analysis to combine these eight highly correlated indicators into two composite variables. Although both composite variables contain information from all the indicators, PC axis 1 (PC1) pulls more evenly from across the variables so can be seen as a more general indication of governance and economic climate, and PC axis 2 (PC2) is influenced most strongly by the "starting a business" and "trading across borders" indicators, and therefore could be seen as reflecting business facilitation (see Table S6; experimental procedures). Our base models examined how these two composite variables affected different

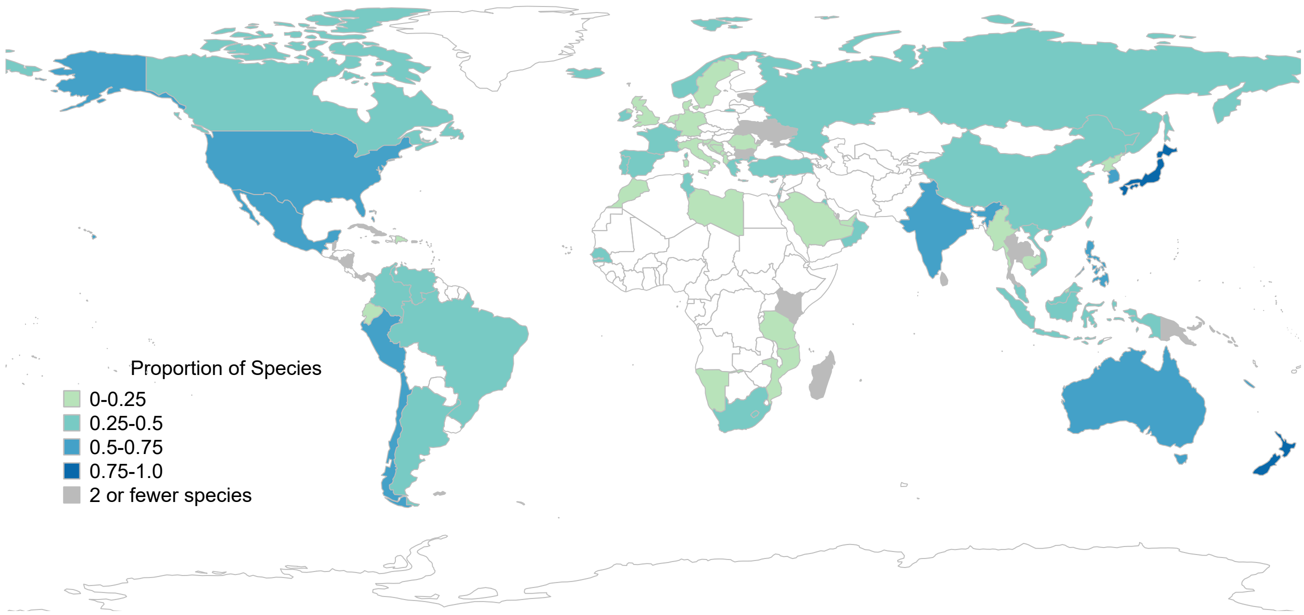

Figure 1. The proportion of mariculture species produced in each country that were first produced domestically
Countries that produce fewer than two species are shaded gray, and countries shaded white do not produce any mariculture species or have no production data.

aspects of innovation spread (centrality, number of countries connected, total connections, and new species produced). The remaining seven variables were added to these base models (see methods), and we found that log-transformed gross domestic product (GDP) improved upon the fit of all four base models. The other variables, including freshwater aquaculture production, wild fishery stock status, and per capita seafood consumption, generally did not add additional explanatory value, either in isolation (Table S7) or with GDP (Table S8).

Overall, we found that strong economic conditions and governance were associated with a country's tendency to innovate and spread mariculture species. Specifically, linear regressions revealed that the number of species first produced in a country was positively and significantly associated with PC1 ($p < 0.05$) and was positively associated with log(GDP) ($p < 0.01$) (Table 2). Similarly, our network analysis revealed that countries scoring higher on our primary governance and economic climate index (PC1) and those with higher economic activity (GDP) had more species-country connections ($p < 0.01$ for both PC1 and log[GDP]) and were connected to more countries ($p < 0.05$ and $p < 0.01$ for PC1 and log[GDP], respectively). The adjusted R^2 value for these regression models were similar, ranging between 0.26 and 0.28. Neither PC1 nor PC2 had a significant relationship with the centrality of a country in the network, and although log(GDP) was significantly associated with centrality ($p < 0.05$), the relationship had little explanatory power (adjusted $R^2 = 0.03$). PC2 was not significant in any of our models.

DISCUSSION

Patterns of mariculture adoption

Mariculture innovation occurs heterogeneously across the globe, as is evident from patterns in the cultivation of new species and the spread of these species to new countries. We found that certain countries, including Japan and France, serve as centers of mariculture innovation, repeatedly developing species that become widely produced across the globe. Additional countries play an important role in the spread of innovation by adopting new species quickly after development (e.g., Madagascar and the Bahamas) and/or by farming many widely produced species (e.g., Spain). Perhaps surprisingly, countries that are innovators (i.e., first producers) for the most species do not mirror the highest producing mariculture countries in terms of seafood volume; for example, the top five mariculture producing countries (China, Indonesia, South Korea, the Philippines, and Norway) account for nearly 90% of total mariculture by weight but have been first producers for only 16% of total species. Conversely, Japan and France alone have been first producers for more than 20% of species that went on to be widely produced and yet only contribute to 2% of total mariculture production. Although this analysis does not focus on diversity of production per se, these results may reflect that some higher producing countries, such as Norway and Chile, have increased efficiency by optimizing production of a single or select few species rather than by developing numerous new species,[33] which can be an expensive and time-consuming process. This mismatch between countries that have been most successful at species innovation and those that have been most successful at producing those species at the highest levels suggests that factors such as production optimization, technological advances, market development, and the industry's regulatory environment are also important in understanding levels of production. Our finding that advances in species adoption and production volume often happen in different countries has implications for how innovation is incentivized in a global context.

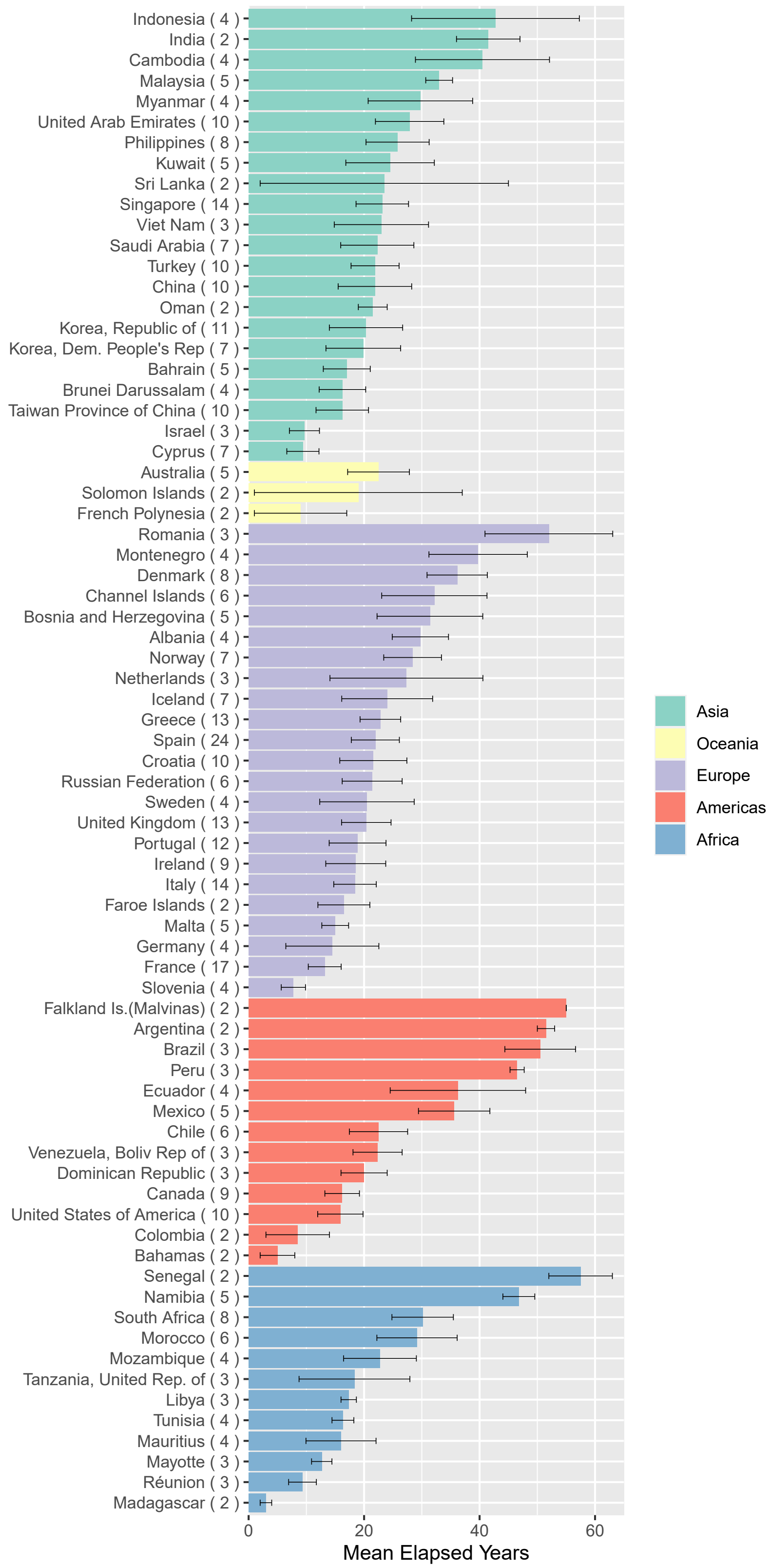

Figure 2. Mean elapsed years between adoption of mariculture species by a country and the first year that species had been produced elsewhere

This plot includes countries that have produced at least two widely adopted species that were first produced elsewhere and excludes species first produced in the country. The number of widely produced species farmed in each country is noted in parentheses following the country name. Error bars indicate ±1 standard error.

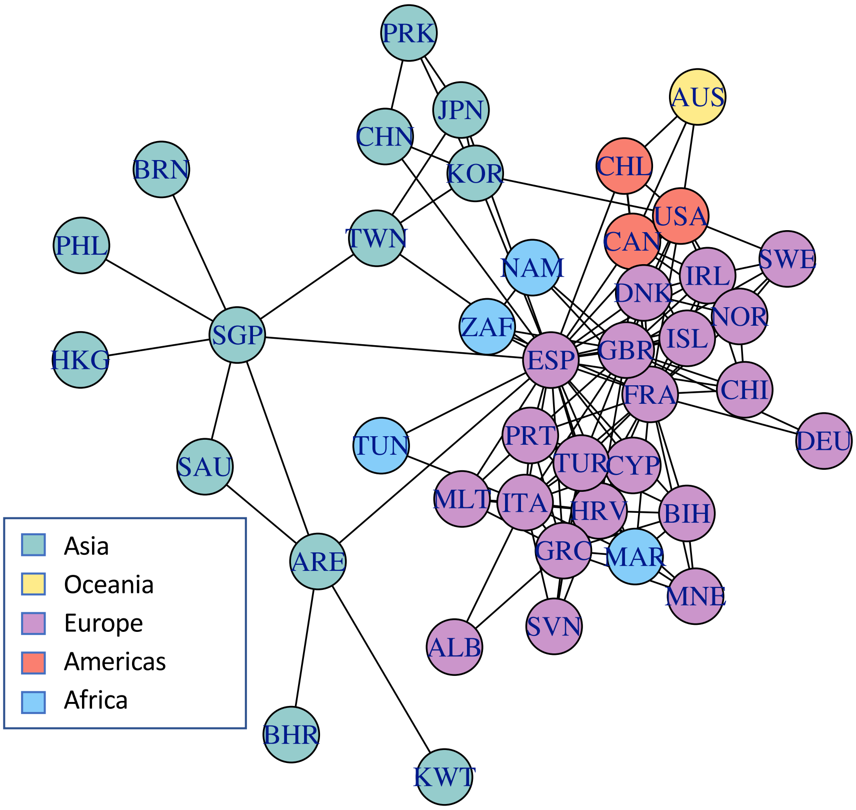

Figure 3. Graphical illustration of the network of countries linked by the production of the same widely produced species

For readability, only countries that are linked by at least four species are shown. The distance between countries indicates the weight of the connection (i.e., shorter distance indicates more species in common). Countries from the same continent are shaded as follows: Asia in aqua, Oceania in yellow, Europe in purple, North and South America in red, and Africa in blue. A key for country name abbreviations can be found in Table S9.

The countries identified as the most successful innovators cultivating new species commonly have a history of successful aquaculture research and development. For example, France and Japan—two of the countries that we found to be most successful in domesticating new species for mariculture—have been farming in the oceans for hundreds of years and have long histories of aquaculture innovation. Japan began cultivating algae as far back at the 17th century and was a leader in developing intensive aquaculture of marine fish in the 1930s. France pioneered closing sea bass and seabream life cycles in the 1970s[34] and has a history of investment in aquaculture research, having built a strong network of research institutes and universities that are involved in many aspects of aquaculture science and husbandry.[35,36] France has explicitly prioritized research partnerships with industry and has strong aquaculture industry organizations that engage with research and innovation. We suggest that long-term investment and prioritization has been a key element for countries that have succeeded with mariculture innovation, but further work is necessary for a more thorough understanding of the role of specific research and development initiatives so that these successes can be replicated more widely.

Although this study does not examine all components of innovation, it does elucidate which countries have been most successful at cultivating new species, including species that become produced in multiple countries around the world, which are critical aspects of mariculture innovation. Identifying these nodes of innovation is important given the role that innovation and supporting research can play in developing a sustainable and resilient industry. For example, evidence from agriculture suggests that the benefits of research are significant, averaging an 81% return per year for dollars spent on research and extension studies.[37] Furthermore, research specifically in areas such as domestication and selective breeding is likely to be increasingly important as we look toward a future of changing oceans and more unpredictable weather patterns.[38,39] In general, research and development in mariculture has played a key role in helping mariculture move toward sustainable practices,[9,16] and a continued emphasis on fostering innovation will be essential into the future.

Although mariculture production is disproportionately concentrated outside the developed world, with countries such as China, Indonesia, and the Philippines among the top producers by volume, many widely produced species, such as the Pacific cupped oyster, European sea bass, and gilthead seabream (the three most widely distributed species in terms of number of countries cultivating), were first produced in the developed world. This raises the issue of spillover, and how research and innovation is valued when the innovation spreads beyond the initial country. Recent research[18] demonstrated that aquaculture specific research and development in the developed world has significant benefits beyond the borders of the innovating country. Considering all the benefits from investment in aquaculture research occurring in the developed world, the vast majority, about 80%, is captured by production outside the innovating country.[18] This has implications in terms of how to target aquaculture research for maximum benefit, while exposing potential drawbacks of country-specific research funding. For example, if much of the benefit of innovation flows away from the country that funded the research and development, there may be underinvestment in research given the overall benefits to the globe.[18] Furthermore, given that most production is in developing countries but much of the new species development research is in the developed world, the substantial time lag between first production of a species and subsequent production by other (potentially higher producing) countries presents a challenge in accelerating growth of the sector into the future.

While some countries are particularly adept at developing new species, others seem to be important in driving further adoption of new mariculture species across the world. For example,

Table 2. Linear regression results for effects of governance and economic indicators on innovation and spread of new mariculture species

Independent variable	β	SE β	Significance
Regression 1: total number of new species produced (adjusted R^2 = 0.28, p < 0.001)			
Intercept	−13.23	5.14	0.012
Governance and economic environment (PC1)	0.510	0.20	0.011
Governance and economic environment (PC 2)	0.61	0.50	0.229
log(GDP)	0.72	0.20	<0.001
Regression 2: centrality of a country in the network analysis (adjusted R^2 = 0.03, p = 0.159)			
Intercept	−147.22	86.77	0.094
Governance and economic environment (PC 1)	−1.71	3.31	0.608
Governance and economic environment (PC 2)	−2.40	8.43	0.776
log(GDP)	7.49	3.38	0.030
Regression 3: number of connections per country in the network analysis (adjusted R^2 = 0.27, p < 0.001)			
Intercept	−106.47	55.14	0.057
Governance and economic environment (PC 1)	6.35	2.10	0.004
Governance and economic environment (PC 2)	9.02	5.36	0.096
log(GDP)	6.37	2.15	0.004
Regression 4: number of other countries connected to a country in the network analysis (adjusted R^2 = 0.26, p < 0.001)			
Intercept	−39.49	18.50	0.036
Governance and economic environment (PC1)	1.43	0.71	0.047
Governance and economic environment (PC 2)	1.79	1.80	0.323
log(GDP)	2.73	0.72	<0.001

Noted in the table are the independent variables, their coefficients, standard errors, and significance values. Coefficients, standard errors, and adjusted R^2 values are rounded to the nearest hundredth. Significance values are rounded to the nearest thousandth.

Singapore, despite its small size and its lack of a record of developing widely produced mariculture species, was the most central country in the network analysis and shared species with the highest number of countries. This suggests that Singapore may play an important role as a key connector in spreading mariculture innovation, which aligns with Singapore's prominence in global trade and historical connections to both Asia and Europe. However, this network analysis is limited to identifying connections between countries and is not able to parse out how the innovation flowed across the network. For example, the third country to farm a species could have acquired cultivation expertise and technology from the first or second producing country, from both countries, or from neither country. Additional research to elucidate the connections and flow of knowledge between the countries within each species network would be valuable in understanding how to facilitate mariculture development and uptake of new innovations. Furthermore, to better understand the environmental impacts of the spread of farmed species, additional analysis could consider how often widely produced species are farmed outside of their native range and the associated effects on local biodiversity. Ultimately, identifying the most important nodes of innovation transfer in mariculture, while accounting for environmental impacts, could help more efficiently target policies and development resources.

Characteristics of innovative mariculture countries

We found that high-quality governance and a strong economic climate and business environment seem to support mariculture innovation. Specifically, our primary governance and economic indicator (PC1), which was significantly related to a country's tendency to innovate and spread mariculture species, included elements such as government effectiveness, regulatory quality, and skills of the workforce, in addition to indicators of innovation and ease of developing new business and trade connections. The additional relationship between GDP and innovation suggests that economic strength can also promote technology generation and adoption. This is in line with recent research[40] that identified economic growth as a strong predictor of national food supply diversification. These conclusions are also supported by research that identifies strong and stable institutions as particularly important for fostering innovation in aquaculture.[23,41] Similarly, our results are consistent with an extensive literature on agriculture innovation systems (AIS), which describe the network of organizations, programs, policies and individuals that advance the development and use of new innovations in agriculture at a national scale.[42] Research on AIS has emphasized that innovation is promoted by coordinated and strong support for research, extension, and training; private sector investment; mechanisms for collective action and knowledge exchange; and incentives for business development and entrepreneurship.[43,44]

Looking at other factors beyond governance and economic/business climate variables, such as existing freshwater production, wild fishery sustainability, and seafood consumption, did not increase the ability of our models to explain a country's mariculture innovation in terms of new species development and spread. The breadth of variables included in the analysis (both as part of the composite indicators and those evaluated individually) and the somewhat low R^2 value associated with our models indicate there are complex interactions driving the innovation of mariculture species and farming methods not easily captured by global datasets. In fact, given these complex and overlapping interactions between the many determinants of new species development—governance, economics, business environment, cultural context, freshwater aquaculture history, and wild fishery status—it is noteworthy that our models were able to explain a quarter of the variation in new species development and spread.

Furthermore, the specific factors that have allowed successful innovation are often local in character and may vary substantially across locations.[20] For example, local demand for a diversity and abundance of seafood has been suggested as one of the drivers for Japan's successful and innovative hatchery operations.[45] However, when we included variables related to local seafood dynamics, specifically per capita seafood consumption and total seafood supply, we did not find that they were significantly associated with any of our dependent variables. Furthermore, although economic and governance indicators were related to how many connections a country had in our network analysis, they did not predict the centrality of a country in the network. "Centrality" refers to how many paths in the network pass through any given country, and high centrality can be interpreted as a country potentially playing an important linking role in the spread of innovation. We suggest that other factors, such as location, colonial history, language, and importance in trading networks would likely be more important than the economic and governance indicators that we were able to include in our analysis. Subsequent research exploring these factors in more detail would add significant contribution to our understanding of innovation spread in mariculture.

Our analyses were somewhat limited by data availability and quality. Although our four dependent variables included 95 countries, missing data across our composite indicators and GDP truncated the sample size for our final models down to 81 countries. Missing data further reduced our sample size for more complex models (ranging from $n = 61$ to $n = 78$), and these data limitations may have affected the regression results. Similarly, many of the global datasets we used might have problems with accuracy or coverage due to the nature of collecting data from a wide variety of sources. Smaller scale or less valuable production can be particularly challenging to capture in this type of dataset and can often be excluded from global statistics.[46] Indeed, other research has suggested that aquaculture data can be incomplete and fraught with errors.[47] Furthermore, many additional factors that may be relevant to innovation spread, such as cultural context and corporate objectives, are not easily quantifiable at the global scale.

Implications and conclusions

Species domestication and development is but one important means of mariculture innovation. Innovation throughout the farming practice, including genetic selection, feed formulation, and growing methods, including those to reduce environmental impacts, improve seafood quality, and ensure profitability, are all essential in the achievement of a sustainable mariculture industry.[16] The development and spread of new mariculture species can be tracked using widely available data and provides important insight into some of the conditions that lead to innovation. However, whether a country produces a species is driven at least partially by the environment and proximity to other countries, which may influence our network in a way that is difficult to account for in this analysis. Also, the initial development and adoption of innovations—what we focus on here—likely captures only a subset of the innovations necessary for a farmed species to be produced successfully at scale. Indeed, the trajectory from initial adoption of marine aquaculture has been shown to take a wide range of different paths, from exponential growth to almost no growth at all.[19] Future research could investigate if the patterns we identified hold for other types of mariculture innovation, such as husbandry practices and farm design. It would also be useful to look at these patterns on a sub-country or regional level, as species development and subsequent production often takes place locally, and thus such research could be more relevant for understanding the earliest stages of species development and expansion. We also suggest that further research would be useful to more deeply explore the connection between innovation, diversity of production, and production output across a variety of scales and time frames.

In summary, we are currently faced with a significant challenge of how to sustainably produce food for a growing population in a changing world. Ultimately, this challenge will need to be met through innovation and cooperation across all food systems, including the potential for seafood to play a significant and growing role in meeting this challenge. For example, aquatic foods—farmed and wild caught—can help address food insecurity and malnutrition, in some cases with lower environmental impacts than terrestrial alternatives.[4,48,49] Mariculture in particular is promising because of its significant scope for growth, diversity of cultivated species, high nutritional quality of many farmed species, some species and farming methods with low environmental footprints, and the ability to produce food where human populations are concentrated. However, many sustainability challenges remain, and continued innovation will be essential to building a productive, sustainable, and resilient mariculture future. Therefore, by taking a global view of mariculture species development and spread across countries, we show the wider effects of innovation and emphasize that a long-term and global lens needs to be used to understand the benefits of aquaculture research.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information should be addressed to and will be provided by the lead contact, Rebecca Gentry (rebecca.gentry@fsu.edu).

Materials availability

This study did not generate new unique materials.

Data and code availability

All data used in these analyses are publicly available from the following sources: the Food and Agriculture Organization of the United Nations,[10,50] the World Bank,[51–53] the World Economic Forum,[54] and published scientific papers.[55,56] All code used in the analysis is available at: https://doi.org/10.5281/zenodo.7443483.

Centers of mariculture innovation

We used marine (excluding brackish) aquaculture production data from 1950 to 2018 from the Food and Agriculture Organization of the United Nations.[10]

The first record of each species produced in each country was selected to create lists of countries that produce each mariculture species and when they first farmed the species. This allowed us to determine the first country to produce each species ("first producer") and to identify all subsequent countries to farm each species ("subsequent adopters"). We excluded all FAO species using the "nei" suffix, meaning "not elsewhere included" (e.g., "marine fishes nei"), as these do not represent single species but rather groups of species. Furthermore, given some changing national boundaries over time (e.g., the dissolution of Yugoslavia), we assigned historical production on the basis of the borders of modern countries. In every case where a formerly unified country split into multiple countries it was possible to extrapolate where pre-dissolution production most likely occurred, as production immediately after dissolution was recorded for only one of the component countries. For species being produced at the start of our dataset (1950), we assume 1950 to be the first year of production. However, when more than one country produced a species in 1950 (N = 6 species), we tried to ascertain the first country that produced the species on the basis of evidence in the literature[34] and designated the first year of production for the originating country as 1949. We could not determine the first country that produced blood cockle, so in that one case we designated all three countries that produced it in 1950 as first producers.

For certain analyses we considered only species that have been produced in at least four countries, which we term "widely produced" species (n = 54; Tables 1 and S1). For all mariculture species and the subset that are widely produced, we identified how many species each country produced and how many times each country was a first producer of species. For widely produced species, we also calculated the time that elapsed between a species first being produced anywhere in the world and being produced in each specific country. In addition, we calculated mean elapsed time across all adoptions for each major taxonomic group included in our analysis: fish, mollusks, crustaceans, and algae.

To assess the networks of countries that commonly produce the same suite of species, we performed a network analysis.[57] We made each country a node and created an edge between each pair of countries that shared a mariculture species. Each edge was multiplied by the number of species shared between the two countries. Using this network, we calculated the betweenness centrality of each country to the overall network using the method described in Brandes.[58] Betweenness centrality detects the influence of each node over the flow of information in a network and is based on the measurement of shortest paths. We also calculated the overall number of connections for each country and the number of different countries each country is connected to.

Characteristics of innovating countries

We used a diversity of country-level data to assess whether innovating countries share certain similarities in terms of geography, economics, culture, and governance. Specifically, we evaluated the business and governance conditions in each country using component scores of three widely cited and publicly available global indices: the World Bank Governance Indicators, the World Bank Doing Business Data, and the World Economic Forum Global Competitive Index.[51,52,54] We used only the elements of each index that we hypothesized are most strongly related to developing and subsequently producing new species (Table S4). As these indicators are strongly correlated and describe related governance and economic aspects of a country, we performed a principal-component analysis (PCA) to identify one or more components that could be used as independent variables in regression analyses. The first component (PC1) captured 69.2% of the variance (eigenvalue = 5.53) and had factor loadings between 8.8% and 14.8% from every indicator. The second factor (PC2) (eigenvalue = 0.89) had its highest loadings for "starting a business" and "trading across borders," the two components with the lowest contributions to the first factor (Figure S1; Table S6). Together PC1 and PC2 captured 80.2% of total variance. Remaining factors had eigenvalues below 0.5 and were not included in subsequent analyses.

Using a series of linear regressions, we examined if these economic and governance indicators (PC1 and PC2) are related to a country's tendency to develop or spread new mariculture species, focusing on four different dependent variables: the total number of new species produced ("NewSpecies"), the centrality of a country in the network analysis ("Centrality"), the number of connections for each country in the network analysis ("Connections"), and the number of other countries each country is connected to in the network ("Countries"). The regression equations took the following forms:

$$\text{NewSpecies} = \beta_0 + \beta_1 \times \text{Factor 1} + \beta_2 \times \text{Factor 2} \qquad \text{(Equation 1)}$$

$$\text{Centrality} = \beta_0 + \beta_1 \times \text{Factor 1} + \beta_2 \times \text{Factor 2} \qquad \text{(Equation 2)}$$

$$\text{Connections} = \beta_0 + \beta_1 \times \text{Factor 1} + \beta_2 \times \text{Factor 2} \qquad \text{(Equation 3)}$$

$$\text{Countries} = \beta_0 + \beta_1 \times \text{Factor 1} + \beta_2 \times \text{Factor 2} \qquad \text{(Equation 4)}$$

In addition to the two PCA components, we also considered the possible influence of additional social, economic, and fishery variables (Table S5).[10,50,53,55,56] These additional variables were selected on the basis of a literature review, our expert knowledge, and the availability of global datasets. Using the same linear regression approach described above, we evaluated the impact of these additional variables on the base models. We tested each variable's statistical contribution to the base models individually by comparing adjusted R^2 values. Because the sample sizes differed depending on which additional variable we were evaluating, we could not use Akaike information criterion to compare models. We found that log(GDP) contributed the greatest explanatory power to the base models (with the exception of centrality) when tested individually, so we also evaluated the performance of the other additional variables within regressions that included the base models and log(GDP). The following is an example of the regression equation for this portion of the analysis:

$$\begin{aligned}\text{NewSpecies} = {} & \beta_0 + \beta_1 \times \text{Factor 1} + \beta_2 \times \text{Factor 2} + \beta 3 \times \log(\text{GDP}) \\ & + \beta 4 \times [\text{additional variable}]\end{aligned} \qquad \text{(Equation 5)}$$

Given that the inclusion of additional variables in the above model generally did not contribute greater explanatory power to the regression, we only - retained log(GDP) in the final models. The few exceptions only captured 1%–5% more variance in the data and tended to be associated with smaller sample sizes because of limited data for some countries (Table S8).

All analyses were performed in R version 3.6.1,[59] and the following packages were used: dplyr, tidyr, igraph, ggplot2, rworldmap, nnet, DescTools, FactoMineR, Factoextra, foreign, reshape2, Hmisc, MuMln, and cor.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2022.12.007.

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AUTHOR CONTRIBUTIONS

R.R.G., A.R., and S.E.L. developed the research. R.R.G. and E.O.R. preformed the analysis with input from S.E.L. and A.R. All authors interpreted the results. R.R.G. wrote the manuscript with input from S.E.L., E.O.R., and A.R.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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