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Marine Aquaculture Development:

Spatial Management, Conservation Opportunities and Production Potential

A dissertation submitted in partial satisfaction of the

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by

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ABSTRACT

Marine Aquaculture Development:

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by

Rebecca Rae Gentry

Aquaculture is currently the fastest growing food sector in the world, and the oceans are seen as one of the most likely areas for expansion. Marine aquaculture holds immense potential for alleviating food security concerns, revitalizing coastal communities, and spearheading blue development initiatives. However, the growth of aquaculture also presents risks to the environment and other uses and goals in the marine environment. Within the context of likely future expansion, the research presented assesses the development trajectories of marine aquaculture and examines opportunities for conservation focused development.

In this dissertation, I present three separate studies focused on different aspects of aquaculture development and conservation. The first chapter develops a framework for marine spatial planning for offshore aquaculture. The second chapter considers the global potential for marine aquaculture development and assesses the areas that have the most favorable physical and biological characteristics for aquaculture growth. The third chapter

investigates when conservation-motivated wildlife farming could be a successful market mechanism to alleviate poaching pressure on threatened species.

I take a multidisciplinary approach to answering these diverse questions, integrating spatial and ecological modeling, ecological and economic theory, and data and literature synthesis.

Key results include that the productivity and environmental impact of aquaculture vary spatially, but that spatial management can be used to maximize value and create synergies with other ocean management objectives (Chapter 1); global scale development potential for marine aquaculture far exceeds the space required to meet foreseeable seafood demand and that suitable space is unlikely to limit marine aquaculture development (Chapter 2); and that aquaculture may be a promising market solution particularly well suited to many threatened aquatic species, especially those that can be farmed relatively cheaply (Chapter 3). Taken together these studies make an important contribution to the field of aquaculture science and provide foundational information on the potential and opportunities for aquaculture development.

I. Offshore Aquaculture

Spatial Planning Principles for Sustainable Development

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A. Introduction

Aquaculture is currently the fastest growing food sector in the world, and the open oceans are seen as one of the most likely areas for large scale expansion (Lovatelli, Aguilar-Manjarrez, and Soto 2013; Rubino 2008). The global demand for seafood is continuing to rise sharply, driven by both population growth and increased per capita consumption (Godfray et al. 2010). Wild-capture fisheries are constrained in their potential to produce more seafood (Costello et al. 2016) making aquaculture growth the most likely scenario to meet the majority of increased demand (Goldburg and Naylor 2005).

Traditionally mariculture has taken place at the land-sea interface – in intertidal areas, estuaries, and sheltered bays. While calm waters and easy access make nearshore seafood farming attractive, some environmental impacts and conflicts with other uses are accentuated in the increasingly crowded coastal zone. Advances in technology and culture methods have made it possible to establish farms further from shore and in rougher open ocean conditions, opening up new expanses to potential aquaculture farming (Bostock et al.

2010; Shainee et al. 2012). Offshore aquaculture offers promise for increasing the supply of seafood and as a source of new economic development.

Ensuring sustainable management of this emerging industry requires an understanding of how marine aquaculture, or ‘mariculture,’ interacts with the surrounding environment and how the location and density of development affects both aquaculture value and the health and productivity of the surrounding ecosystem. Mariculture development has raised many environmental concerns, including habitat destruction (Ottinger, Clauss, and Kuenzer 2016), pollution (Islam 2005), introduction of disease (Lafferty et al. 2015), interbreeding of escapees with wild stocks (Naylor, Williams, and Strong 2001), entanglement of marine mega-fauna (Kemper et al. 2003), and the sustainability of fish-derived feeds (Naylor et al. 2009); many of these impacts have been well studied across a variety of cultures and environments. Although farm practices (e.g., low stocking density, reduced feed waste, preventative veterinary care) can play a major role in ensuring good environmental outcomes (Wu 1995; Cho and Bureau 2001), the choice of farm location also plays a critical role in determining its productivity, environmental impact and interactions with other ecosystem services provided by the ocean.

Scientists and policymakers have recommended spatial planning as an approach to comprehensively consider multiple uses and values of the marine environment (Calado et al. 2010; Obama 2010; Lester et al. 2013). Although ocean planning lags behind terrestrial planning, the spatial complexity and dynamics of the ocean environment make spatial planning particularly important (Crowder and Norse 2008). Most siting for aquaculture, like other uses of marine space, has been undertaken on an ad-hoc basis for a single farm or collection of farms without integrated or broader strategic planning (Douvere 2008) and many “comprehensive” spatial planning processes fail to explicitly plan for offshore aquaculture. However, there is an increasing emphasis on the need for proactive planning and zoning for mariculture in locations across the globe (Aguilar-Manjarrez, Kapetsky, and Soto 2010). A growing number of national and regional authorities are beginning to engage in aquaculture planning processes or wider marine spatial planning processes that involve aquaculture (Sanchez-Jerez et al. 2016), highlighting the need for more comprehensive scientific guidance.

Pro-active spatial planning is essential for successful and sustainable mariculture development because many of the interactions between aquaculture farms and the surrounding ecosystem vary significantly with location. These interactions can have strong impacts on both the mariculture operation and on other uses and values in the marine environment; in some instances, ecosystem effects of mariculture can be seen far beyond the footprint of the farm. Although there are many important aspects of aquaculture sustainability related to supply chains and farm practices, here we focus on spatial planning considerations for aquaculture development. We review the emergence of offshore aquaculture, outline ways in which it interacts with the surrounding environment, and assess which aspects of offshore aquaculture sustainability are important from a spatial planning perspective, at both the scales of individual site selection and regional planning. Finally, we suggest relevant tools and planning approaches for guiding sustainable offshore aquaculture siting.

Although we highlight gaps in current knowledge, our primary goal is to demonstrate the substantial body of knowledge, from across disciplines, that informs our understanding of aquaculture interactions with the surrounding environment, and how this understanding can be used to inform spatial planning. This includes assessment of tools that have primarily been used for aquaculture in shallow sheltered environments, and their relevance for more open-ocean conditions. By synthesizing this knowledge, we are able to clarify key risks and opportunities related to aquaculture planning, even when data are limited. We suggest that the location of marine aquaculture development has a significant effect on its potential environmental effects and suitability within a region, and thus spatial planning can make a large difference in creating positive outcomes. We add to the growing literature on ecosystem-based management of our oceans and create a platform for considering the role of sustainable aquaculture development as a part of healthy and productive seascapes.

B. Spatial Considerations for Offshore Aquaculture Development

Offshore aquaculture has been defined using a variety of criteria, including water depth, distance from shore, wave exposure and jurisdictional boundaries (Holmer 2010; Kapetsky 2013; Rubino 2008); here we use a broad definition that includes all mariculture that is located in open water (i.e., not directly adjacent to land or within a bay or fjord). There is significant diversity in marine aquaculture species, with nearly 200 species currently being farmed (FAO 2015) and many more under development, however all types of mariculture fall into three broad categories: fed (e.g., fish, most crustaceans), unfed (e.g., filter feeding bivalves, some grazers and detritivores), and autotrophic species (kelp and other algae). Each of these culture categories interacts with the environment in fundamentally different ways, both in terms of external inputs to the farm and effects of the farm on its surrounding environment (Fig. 1). As aquaculture moves into new frontiers – both geographically and technologically – there is an important opportunity to determine where to pursue offshore development in the context of the ocean's complex ecological dynamics and the diversity of existing marine activities and benefits that could interact with or be impacted by aquaculture. We examine four categories of spatial interactions between offshore aquaculture, the environment, and other uses: effects of the environment on farms; effects of farms on the environment; cumulative impacts and regional planning issues; and synergies and conflicts with other ocean management goals

1. Effects of the Environment on Farms

An essential consideration for offshore aquaculture planning is determining which areas could be most productive and profitable. The suitability of locations varies widely, even over small distances. Physical factors, such as water temperature, ocean currents, sunlight, and food and nutrient availability have a direct effect on the growth of aquaculture species (Ferreira, Hawkins, and Bricker 2007). Unfed and autotrophic aquaculture species are particularly sensitive to environmental conditions because they rely on the surrounding environment to provide the energy needed for growth. Available oceanographic data can be integrated into species-specific growth functions to compare the suitability of potential sites for maximizing growth. There are also several software applications that can model site-level production for specific aquaculture species, such as the FARM model (Ferreira, Hawkins, and Bricker 2007), ShellSim (Hawkins et al. 2013), Depomod (Cromey, Nickell, and Black 2002) and Aquamodel (Rensel et al. 2007). While these models are designed for modeling site-specific production and impact, they can also be utilized to determine the areas of highest production within a region by running the model across a spectrum of sites. This type of spatial comparison of productivity has been applied to nearshore bivalve aquaculture in Chile and Scotland (Silva et al. 2011; Ferreira et al. 2008) and to offshore aquaculture in the Southern California Bight (S. Lester, personal communication, 2016).

Generally this type of approach requires significant environmental and farm level data, such as currents, primary productivity, temperature, and stocking density, which can limit its broad application in areas with limited environmental information.

Farm location also impacts the quality of seafood produced. Notably, concerns about the accumulation of toxins in seafood are driving efforts to ensure the safety of aquaculture products (Karunasagar 2008; Focardi, Corsi, and Franchi 2005). Existing research on the distribution and impacts of land-based pollutants on marine ecosystems (e.g., Fabricius 2005; Halpern *et al.* 2009) and monitoring of water quality could help inform offshore aquaculture planning. For example, Fabricius *et al.* (2005) detail spatial, physical, and hydrodynamic properties of the environment that are likely to affect the susceptibility of coral reefs to the effects of land-based runoff. Many of the characteristics of susceptible reef areas, such as close proximity to discharge, shallow depths, and slow currents, are also likely to be risk factors for aquaculture operations. In general, moving into offshore environments, which is likely to increase the distance from most pollution sources and to increase water flow, will be beneficial in mitigating food safety concerns. Evidence from bluefin tuna ranching in Australia suggests that moving marine aquaculture into offshore environments may also enhance fish condition, while reducing parasite loads and mortality rates (Kirchhoff, Rough, and Nowak 2011).

Farm productivity and profit can also be impacted by wild predators, such as seals, sea lions, otters, and birds, that are often attracted to mariculture farms. For example, predator presence near farms can generate stress-related fitness reductions in farmed fish, damage to farms, and increased escapement of farmed fish from damaged nets (Nash, Iwamoto, and Mahnken 2000). These interactions can be minimized through cage design and auditory or other deterrents (Quick, Middlemas, and Armstrong 2004), but location of the farm is also important. For example, evidence from both Australia and Chile suggests that predation rates on an aquaculture farm are related to distance from the nearest pinniped colony (Kemper et al. 2003). In general moving farms further offshore and away from coastal concentrations of marine mammals is likely to help minimize interactions and protect the cultured product from predation (Nash, Iwamoto, and Mahnken 2000).

Farm location can also have a significant impact on the cost of farm operations. Factors such as depth, distance from port (and associated infrastructure and processing facilities), wave conditions and storm activity modify transport, labor, construction and maintenance costs (Kaiser, Snyder, and Yu 2011; Klinger and Naylor 2012). Additionally, risks due to climate variability, pollution, disease, and harmful algal blooms can vary spatially (e.g., Husson *et al.* 2016) and may have an effect on the profitability of a farm.

2. Effects of Farms on the Environment

By introducing a high density of additional life into the ocean, mariculture affects the surrounding environment in diverse and complex ways. In some cases this can lead to desirable outcomes; for example algal aquaculture has the potential to improve water quality in regions that have been affected by nutrient pollution through uptake of nitrogen, phosphorous and carbon (Neori et al. 2004). Bivalves have also been promoted for their ability to reduce the standing stock of phytoplankton, and therefore potentially mitigate some of the effects of eutrophication (Cranford, Dowd, and Grant 2003). However, aquaculture can also contribute to nutrient and chemical pollution (Cao et al. 2007). The magnitude of these effects is heavily influenced by operational characteristics, such as the species farmed, stocking density and feeding strategy, but location also plays an important role. Specifically, physical and chemical characteristics of the surrounding environment, such as background nutrient levels, currents, and depth help to determine the fate and impact of pollutants released from a farm.

Both fed and unfed aquaculture operations can release particulate organic matter that is likely to fall to the seafloor, potentially leading to local oxygen depletion in and near the benthos as the organic matter is consumed by microbes (Ferreira, Hawkins, and Bricker 2007; Price and Morris 2013). Generally, deeper water and faster currents result in more diffusion of organic material (Lovatelli, Aguilar-Manjarrez, and Soto 2013; Sarà et al. 2006). For example, a study examining ten aquaculture sites across Europe found that shallower depths and slower current speeds were significant predictors of higher levels of benthic impact; these hydrodynamic variables were second only to the amount and duration of aquaculture production in predictive strength (Borja et al. 2009). In general, while bivalve farms have been shown to have benthic impacts in shallow sheltered areas, there are low risks of significant organic enrichment in well managed marine farms, especially in areas of high current and depth (typical of offshore sites) (Crawford, Macleod, and Mitchell 2003; Crawford 2003). The potential benthic impacts of offshore finfish farming are less clear, and can vary significantly with farm practices (such as stocking density) and site characteristics (Price and Morris 2013). While high levels of nutrient enrichment can cause adverse hypoxic conditions, low levels of nutrient enrichment may only have a minor effect and can actually result in an increase in benthic diversity (Rosenberg et al. 2002).

One possible approach to mitigate pollution from finfish farms is through integrated multi-trophic aquaculture (IMTA), which aims to imitate natural ecological nutrient cycling by pairing different trophic levels of aquaculture in the same area (Neori et al. 2004; Troell et al. 2009). Fed aquaculture produces excess organic matter, which can feed bivalve aquaculture both directly and indirectly (i.e., by encouraging additional phytoplankton growth). In addition, fish and bivalves also produce dissolved nutrients that are necessary, and often limiting, for the growth of autotrophs. Therefore, placing unfed and autotrophic aquaculture in the same location as or adjacent to fed aquaculture could theoretically improve growing conditions for bivalves and kelp while mitigating some of the potential impacts of fed aquaculture. However, commercial operationalization of this idea in the offshore environment is relatively new and faces challenges with efficiency and economic scaling (Troell et al. 2009). The potential effectiveness of IMTA depends on environmental context, particularly background nutrient levels, food availability, and hydrodynamics (Troell *et al.* 2009).

Another environmental concern associated with offshore aquaculture is potential negative interactions with marine mammals, birds, and other wildlife. Wildlife can be attracted to aquaculture farms and then get caught in lines and nets (Kemper et al. 2003). However, the frequency of entanglement is typically quite low, and in general the risk of entanglement in aquaculture gear is less than the risks associated with fishing gear (Young 2015). Conversely, there is also concern that farms may displace whales and dolphins, which could impact their access to foraging grounds or impede movement. Evidence from Western Australia supports this concern by demonstrating that bottlenose dolphins avoid oyster farming areas (Watson-Capps and Mann 2005). Information about home ranges, movements and behaviors of local marine mammals in response to aquaculture farming can help inform aquaculture development and provide better understanding of the risks to wildlife.

3. Cumulative impacts and regional planning issues

As the density of aquaculture within an area increases, additional regional-scale considerations emerge regarding the number of farms that can be supported as part of a healthy ecosystem. These considerations are quite different and conceptually almost opposite for fed and unfed aquaculture: cumulative effects of adding additional organic matter to the ecosystem for fed aquaculture versus cumulative effects of organic removals from the system for unfed aquaculture.

For offshore finfish farms, there is considerable uncertainty about how pollution impacts scale with the concentration of farms, and at what density and in what environments eutrophication is likely to become significant (Cao et al. 2007; Klinger and Naylor 2012). Much of what we know about nutrient enrichment from mariculture comes from studies of farms in sheltered coastal locations (e.g., McKinnon *et al.* 2010; Niklitschek *et al.* 2013), where limited water flow can amplify pollution problems. Since offshore sites tend to be less susceptible to nutrient enrichment due to increased water flow and depth, offshore locations should sustainably support a higher density of production than sheltered near-shore locations, particularly if conservative stocking densities are used. Nonetheless, both the environmental context, in terms of background nutrient concentrations, other sources of organic influx, and the strength of currents, as well as farm management, particularly stocking density and feeding practices, are important in determining whether larger scale nutrient enrichment is likely to be a concern in any given area. If cumulative pollution is considered a risk, aquaculture-specific modeling software, such as Aquamodel (Rensel et al. 2007), can provide further insight on the potential for cumulative nutrient pollution issues by modeling the effluent from several farms within a region.

With unfed, specifically bivalve, aquaculture there is a farm density at which the cultured species will consume so much food from the water column that ecosystem function will be impacted. Potential impacts include reduced wild recruitment due to over consumption of planktonic larvae and reduced food availability for wild populations (Gibbs 2004). Several studies, including by Jiang and Gibbs (2005) in New Zealand and by Byron *et al.* (2011) in Rhode Island, have used Ecopath, an ecosystem modeling software, to assess both the effect of existing bivalve culture on the ecosystem and determine sustainable limits to future production. While this type of study is data intensive, it is a powerful approach for considering ecosystem-level effects and providing an assessment of carrying capacity. In general, food competition between wild and farmed species is more likely to be a concern in regions with low primary productivity (Grant et al. 2007; Gibbs 2004), although those regions are also less likely to experience intense development of unfed aquaculture. In addition, the high water flow typical of open ocean farms makes significant issues with food competition unlikely, except at very high farm densities. Similarly, local nutrient depletion is potentially possible in areas of very high density kelp culture, but this has not generally been an issue in kelp-growing regions (Kraan 2013).

The risk of disease outbreak is also a prominent concern with aquaculture development, particularly in terms of cumulative impacts from multiple farms in a region (Leung and Bates 2013; Holmer 2010). Although site selection is often seen as secondary to management and husbandry practices in reducing disease outbreaks, the spatial distribution of aquaculture farms can play an important role in modifying this risk (Salama and Murray 2011; Murray and Gubbins 2016). The diversity of potential diseases and the constant emergence of new disease threats make spatial planning to reduce disease risk challenging

(Lafferty et al. 2015). Each disease is specific in terms of its biology, how far it is likely to spread, and the specificity of its targeted host. Host specificity is particularly important in determining whether any disease outbreak is a serious environment concern that has potential to spread to wild populations or is likely to remain within aquaculture farms (and is primarily an economic issue). Unfortunately there are still significant unknowns concerning the biology and spread of many emerging diseases that could affect aquaculture species. However, even without disease-specific information, spatial planning can reduce disease risk. For example, reducing the size and density of farms and increasing the distance between farms can mitigate the risk of disease spread; generally, larger farms spaced further apart pose less risk than multiple smaller farms clustered closely together (Salama and Murray 2011). Infectious salmon anemia (ISA) is one disease that has received considerable research attention due to its history of impact on the aquaculture industry. Researchers in Chile and Norway have found that ISA spread among farms is more likely when farms are clustered closely together and recommend a separation distance of at least five kilometers between farms (Mardones, Perez, and Carpenter 2009; Jarp and Karlsen 1997). These simple guidelines are especially useful for diseases that are not shared with wild stocks and could be refined considerably with specific information about both the environment and the disease of concern.

Importantly, it is not precisely the geographic proximity of farms that matters for disease spread, but rather their connectivity – in other words, the likelihood that infectious agents from one farm reach another farm. In addition to physical distance, current speed and direction also determine site connectivity. Oceanographic models, such as Regional Ocean Modeling Systems (ROMS) (e.g., Dong, Idica & McWilliams 2009), can be used to evaluate connectivity by modeling the release of particles at any one location and tracing the likelihood of transport to all other locations (Simons, Siegel, and Brown 2013). Indeed, a recent study demonstrated that water contact via current flow had the strongest explanatory power in describing the dynamics of pancreas disease spread between salmon farms in Norway (Stene et al. 2014). This approach can be useful for forecasting the risks of disease spread (Groner et al. 2016) and informing spatial planning to minimize the connectivity between aquaculture locations. This type of spatial risk assessment for disease spread can be combined with other models to assess overall production and ecological carrying capacity for a region (Ferreira et al. 2014). This approach also has the advantage of using a systems perspective to demonstrate how the location and density of farm development affects both other farms and the surrounding environment across a spectrum of scales and sustainability metrics.

In addition to minimizing connectivity among farms, locating farms away from dense or vulnerable wild populations may reduce the risk of disease exchange between wild stocks and farmed animals (Holmer 2010). Wild populations are well documented as the source of most aquaculture diseases (via water exchange, feed, or broodstock), and even diseases that do not affect wild hosts can be problematic if transferred to an aquaculture setting (Lafferty et al. 2015). However, it is the risk of disease export from aquaculture to the wild that has created the most concern and controversy from an ecological perspective (Johansen et al. 2011). This risk may be heightened when the farmed species is native or related to a native species (Gross 1998). While diseases do pose potentially severe risks to wild populations, the role of aquaculture as a source of these diseases is controversial, and considerable uncertainty around the dynamics of disease spread from farms to wild stocks remains (Lafferty et al. 2015).

4. Synergies and Conflicts ith Other Ocean Management Goals

The location of offshore aquaculture facilities could have significant impacts, both positive and negative, on other ocean management considerations, including shipping, fishing, recreation and conservation. This web of interactions suggests the need to plan for multiple objectives in concert. One planning approach is to avoid siting aquaculture in the most important areas for other ocean uses. However, simply avoiding areas that are already being used for another purpose will not necessarily lead to the best outcomes. Using theory adapted from economics, trade-off analysis can provide guidance on how spatial planning can be used to minimize the inherent conflicts associated with multiple overlapping goals and arrive at a suite of solutions that maximize overall value (Lester et al. 2013).

Spatial tradeoffs between aquaculture, marine fisheries and conservation are highly intertwined and present challenges and opportunities across a spectrum of spatial scales. For one, most aquaculture farms exclude other commercial activities, including fishing, effectively creating a refuge for some marine species. Literature on marine protected area network design has emphasized the importance of connectivity between reserves in ensuring conservation and management objectives (Gaines, Gaylord, and Largier 2003; Gaines et al. 2010). Therefore, if aquaculture farms are well connected to other farms or to a network of protected areas, they could help bolster conservation. However, aquaculture is a leading source of marine invasive species (Molnar et al. 2008), and also potentially introduces risks of pollution and disease. Therefore, locating a farm so that it is highly connected to protected areas could introduce increased environmental risk. One key question is the relative rates of spread of these different biological and chemical entities. While more is known about the dispersal of larvae than the infection patterns of marine diseases, we do know that some larvae have the potential to disperse far longer in the open ocean (Kinlan, Gaines, and Lester 2005) than many viruses (Suttle et al. 1992). This suggests their scales of dispersal may also be much larger and presents interesting spatial planning opportunities to minimize unwanted connectivity over smaller spatial scales, while maximizing desired connectivity over larger distances.

Aquaculture can have both positive and negative impacts on wild fisheries depending on farming methods, species, regulations, and environmental characteristics. Specifically, aquaculture can negatively impact the health of fish stocks by introducing disease and escapees that can interbreed with wild stocks (Tisdell 2003; Hoagland, Jin, and Kite-Powell 2003); affecting food webs (Gibbs 2004); and by degrading water quality and habitats via farm effluent and habitat conversion (Naylor et al. 2000). Avoiding aquaculture development in areas that are known to host high densities of target fish species can potentially reduce some of these risks. Furthermore, aquaculture can also potentially benefit wild fisheries by creating structure that could be utilized as habitat by target species or their prey, and by adding food and nutrients to the ecosystem, which could increase productivity or be consumed directly by target fish (Arechavala-Lopez et al. 2011; Pitta et al. 2009; Hehre and Meeuwig 2016). Several empirical studies in the Mediterranean (Machias et al. 2006; Bacher and Gordoa 2015) have investigated the relationship between aquaculture and wild capture fisheries. Taken together they have found either no impact or a positive effect. However, it is important to note that the Mediterranean is generally nutrient limited, so a modest influx of nutrients is more likely to boost productivity there than in more nutrient-rich oceans. Figure 2, provides an example of how we can apply current knowledge to complex issues, like the effects of offshore aquaculture on fisheries, to evaluate potential risks and use spatial planning strategies to mitigate these risks and maximize positive synergies between objectives.

Siting decisions should vary based on the species being farmed, allowing for spatial plans that maximize potential benefits and minimize risks of aquaculture in any specific area. For example, placing kelp and bivalve farms in areas known to have high nutrient levels from other human sources could provide ideal growing conditions and benefit the surrounding environment. Conversely, finfish farms should likely be avoided in close proximity to particularly sensitive conservation areas, where any risk of pollution may be less acceptable. Further exploration of the ecological relationships between aquaculture, wild fisheries and conservation would be particularly useful for improving spatial planning models.

C. Recommendations and Conclusions

Offshore aquaculture is still an industry in its infancy, which makes it tempting to focus on information gaps and conclude that more research is necessary to understand its interactions with the surrounding environment. And while this is an area ripe with research opportunities, we can make informed siting decisions today about farm location and density. Furthermore, offshore aquaculture development is unlikely to wait for more research, making it essential that planning decisions leverage the best available information. Fig. 3 provides guidance for organizing and distilling the most important ecological questions and analysis for aquaculture spatial planning. We highlight data and analytical tools that would inform a participatory planning process, acknowledging that this type of spatial analysis is only one part of a broader spatial planning process and that stakeholder engagement would be an essential component throughout.

As an initial step, it is important to narrow the focus to the most likely and relevant spatial planning issues for a specific development or region. Given specified environmental conditions, cultured species and production goals, we can identify and assess when particular issues warrant further investigation, and when they are unlikely to be a concern For example, benthic deposition is unlikely to be a concern for a bivalve farm located in deep waters with high current, but should be more closely assessed for a finfish farm in relatively shallow or calm water. Table 1 provides a qualitative assessment of several key environmental risks, along with spatial planning strategies for reducing these risks, and available analytical tools if further evaluation is necessary. It is important to note that aquaculture technology is constantly improving, and new solutions are being introduced that mitigate environmental concerns. Therefore, planning that minimizes the environmental risks we encounter today will likely see even better performance in the future.

Data, analytical models, and planning tools can help guide development, but the final steps of spatial planning rely intrinsically on the values that people place on different outcomes. Using analyses such as trade-off modeling can identify planning solutions that minimize conflict and also provide insight about the strength of unavoidable trade-offs among objectives that cannot be resolved solely by efficient spatial planning(Lester et al. 2013). However, these analytical approaches can only provide guidance on the relative advantages of different development plans; managers and developers will ultimately have to make decisions about the type, location and number of farms in a region based on societal risk tolerances and preferences across different objectives.

In general, we conclude that the profitability of an aquaculture farm and the potential environmental risks and impacts will vary substantially across regions and are influenced by the number and density of farms. In addition, the most important planning considerations depend on the species being farmed and the specific ecology and environmental conditions of the farm location. Since different species react in various, and often complementary ways to their surrounding environment, it is important to consider not just the total amount of aquaculture in an area, but also the diversity of farming methods and species. While grouping of similar farms together or the development of large monoculture farms may appear to be more valuable to the aquaculture industry due to efficiency gains and economies of scale, this tendency towards consolidation may increase environmental impact and disease risks. A large literature, primarily focused on terrestrial systems, has suggested that increased diversity can lower disease risk (e.g., Keesing, Holt & Ostfeld 2006) and reduce the need for chemical inputs in agroecosystems (e.g., Smith, Gross & Robertson 2008). Further, promoting the farming of diverse species not only has the potential to alleviate some environmental concerns, but also to create a more resilient industry (Troell et al. 2014), better placed to remain productive in our changing world.

D. Acknowledgements

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E. Figures

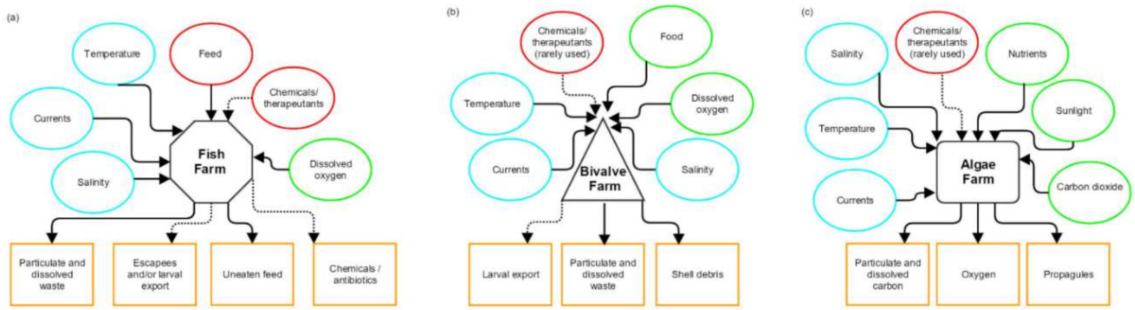

Figure 1. Schematic of key inputs and outputs associated with the three major categories of aquaculture: (a) fed, (b) unfed, and (c) autotrophic. Red indicates external inputs into the farm; green indicates environmental inputs; blue indicates other environmental conditions that affect the farm; and orange indicates outputs from the farm into the environment. Dashed lines indicate inputs and outputs that are only sometimes present.

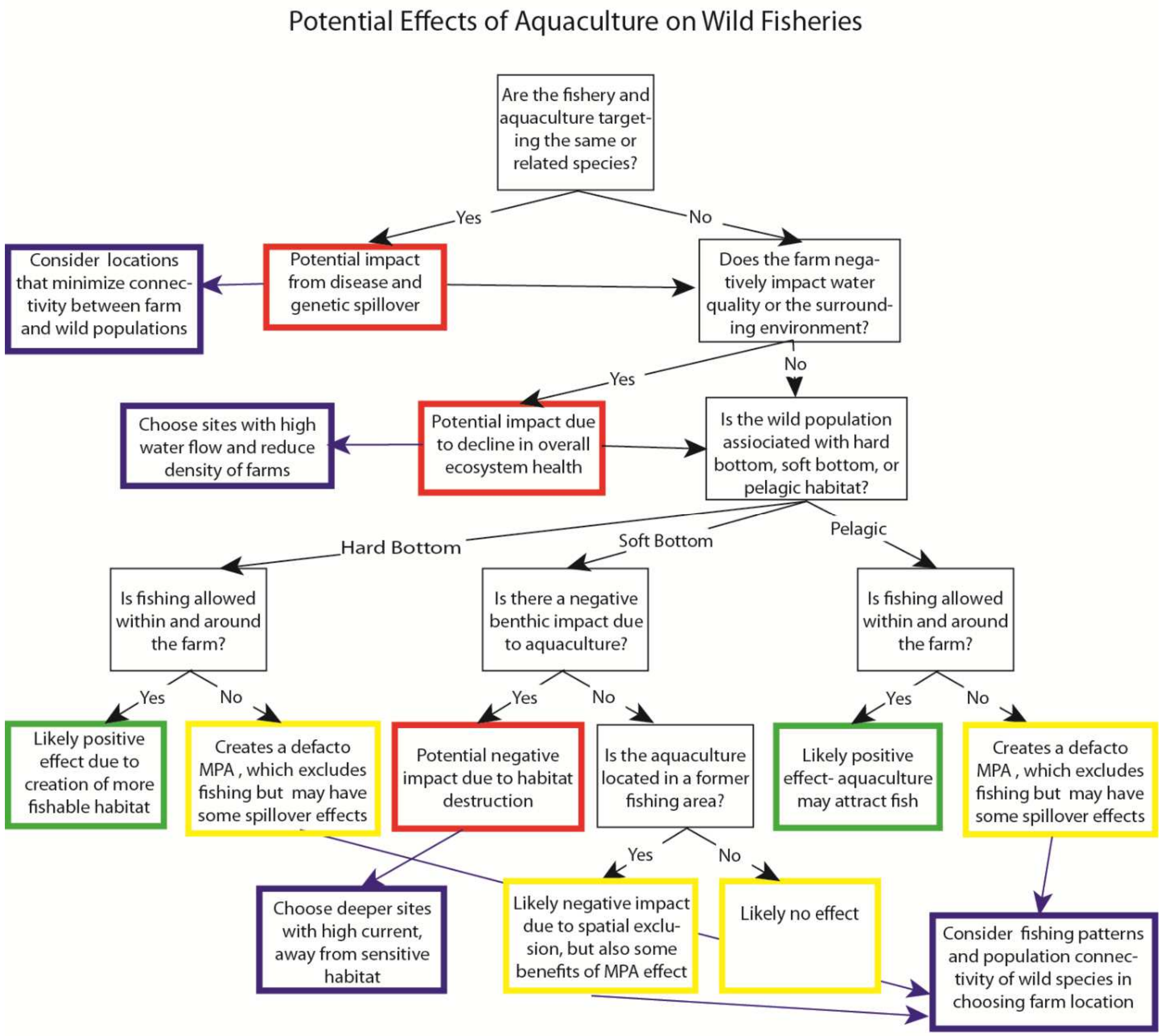

Figure 2. A flow chart for assessing the potential risks of an open ocean fish farm on wild fisheries, assuming best practice on-farm management and siting of the farm over soft bottom habitat. Black boxes represent questions about the attributes of the farm or environment that affect the outcomes; red, yellow, and green boxes represent potential (not mutually exclusive) effects on wild fisheries (indicating a risk of negative effects, neutral or mixed effects, and positive effects, respectively); and blue boxes represent potential spatial planning solutions to help mitigate risks. See text for supporting references.

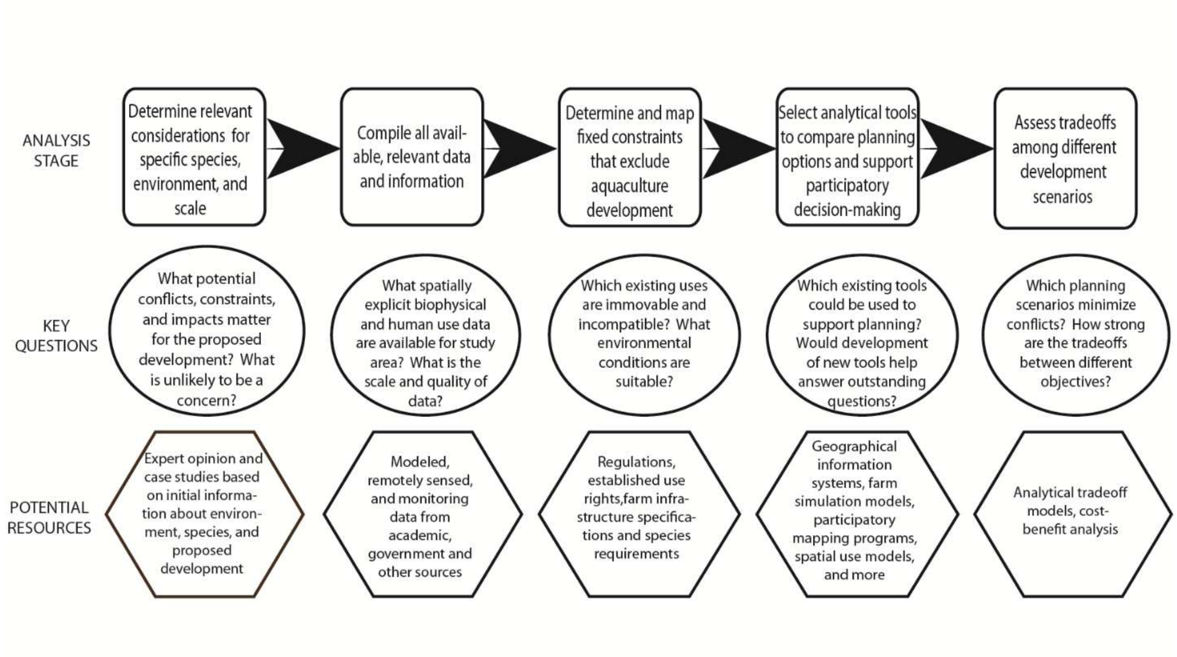

Figure3. Recommended approach to incorporating scientific analysis to support spatial planning for development of offshore aquaculture. The rectangles contain key analysis stages; the circles and hexagons include important questions and potential resources, respectively, to help guide each of these stages.

F. Tables

Table 1. Several key environmental risks for fed, unfed, and autotrophic aquaculture that can be mitigated by spatial planning, along with planning strategies that are likely to minimize risk, and examples of available analytical tools that can be used to evaluate these risks. We also qualitatively assess the overall risk of each environmental issue when aquaculture is well planned, i.e., assuming that the listed risk reduction strategies are incorporated into spatial planning processes and that farm operations are well-managed. See main text for supporting references.

Environmental risk	Aquaculture types affected	Risk reduced by:	Overall risk for well-planned offshore aquaculture	Available analytical tools
Benthic Impact	Fed, unfed	• Choosing sites with high current and/or deeper water • Avoiding sensitive benthic habitats	Low	Aquaculture modeling software, such as Depomod, AquaModel, and the FARM model

Disease Outbreak	All	• Reducing connectivity between farms growing similar species • Locating farms away from habitat of native populations • Reducing density of farms	Moderate	Oceanographic models, such as Regional Ocean Modeling Systems (ROMS); species distribution mapping
Water Column Pollution	Fed	• Locating farms in environments with high natural productivity and low levels of existing nutrient pollution • Using multi-trophic farming techniques • Reducing density of farms	Low	Aquaculture modeling software, such as Depomod and AquaModel
Marine Mammal Interactions	All	• Locating farms away from marine mammal haul outs, migration routes, and important foraging grounds	Low risk of entanglement; moderate risk of behavioral change	Spatial analysis of wildlife movement patterns
Food and Nutrient Depletion in the Water Column	Unfed and auto-trophic	• Locating farms in areas with high natural productivity • Reducing density of farms	Low	Ecopath modeling

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II. Mapping the Global Potential for Marine Aquaculture

This chapter is in review. Authorship on the manuscript is as follows: Rebecca R. Gentry, Halley E. Froehlich, Dietmar Grimm, Peter Kareiva, Michael Parke, Michael Rust, Steven D. Gaines, and Benjamin S. Halpern

A. Introduction

As the human population grows to 10 billion people by 2050(United Nations Department of Economic and Social Affairs 2015), our food systems will be under intense pressure to produce animal protein for an increasingly urban and middle-class population(Tilman and Clark 2014). Faced with plateauing wild fisheries catches and high impacts from land-based agriculture (Maxwell et al. 2016; Pelletier and Tyedmers 2010), momentum is building to look towards marine aquaculture to meet growing protein demand (Lovatelli, Aguilar-Manjarrez, and Soto 2013; Merino et al. 2012). The relative sustainability of marine aquaculture in comparison to land-based meat production (Hall et al. 2011) and the human health benefits of diets rich in fish (Tacon and Metian 2016) make it even more pressing that we consider aquaculture's potential. Oceans represent an immense opportunity for food production, yet the open ocean environment is largely un-tapped as a farming resource.

Despite the perception that marine aquaculture has high growth potential (Troell et al. 2014; Godfray et al. 2010), little is known about the extent, location, and productivity of potential growing areas across the globe. To rectify this shortfall, we drew on physiology and growth theory to quantify and map global potential for fish and bivalve aquaculture. These categories represent two major types of culture: fed aquaculture, where food is provided from an external source, and unfed aquaculture, where nutrition comes from the environment. We focus on quantifying a realistic biological baseline given the diversity of existing ocean uses, thus providing novel insight into potential global aquaculture production and the role it might play in addressing future food security. Ultimately, this baseline can be combined with economic and social constraints and drivers of aquaculture production to further refine realistic production potential in particular locations.

B. Methods

To characterize aquaculture's potential we used a three-step approach (see Appendices for detailed methods). First, we analysed the relative productivity for each 0.042 degree^2 patch of global oceans for both fish and bivalve aquaculture. To do this we constrained production potential for each of 180 aquaculture species (120 fish and 60 bivalves) to areas within their respective upper and lower thermal thresholds using 30 years of sea surface temperature data (Fig. A1). We then calculated the average (multi-species) growth potential index (GPI) for each patch for all suitable fish and bivalve species, resulting in a spatially explicit assessment of general growing potential (Fig. A2). GPI is derived from the von Bertalanffy Growth equation, and uses species-specific parameters (growth rate and maximum length (Froehlich, Gentry, and Halpern 2016)) to create a single metric to describe the growth potential of a species (Pauly and Munro 1984). GPI has been used frequently to assess growth suitability for culture, and is particularly useful for fed species or those not subject to food limitation (Pauly, Moreau, and Prein 1988; Mathews and Samuel 1990; Alvarez-Lajonchère and Ibarra-Castro 2012). Locations with high GPI are expected to have better growth conditions for a spectrum of aquaculture species and, thus, are well suited to development. Using a multi-species average of GPI to assess growth potential provides a more general growth suitability metric than is possible when making detailed assessments for a single species. Moreover, this approach provides a conservative assessment, since we are considering an average rather than maximum growth potential.

Second, once production potential was determined, we removed unsuitable areas with environmental or human-use constraints. We excluded areas with unsuitable growing conditions due to low dissolved oxygen (fish only) and low phytoplanktonic food availability (bivalves only). We also eliminated areas >200m depth because they are generally too deep to anchor farms and areas already allocated to other uses, including marine protected areas, oil rigs, and high-density shipping areas (Fig. A5; Table 1). For the third step, we estimated idealized potential production per unit area by converting average (multi-species) GPI into biomass production, assuming a low density farm design.

A. Results and Discussion

Overall, we found that over 11,400,000 km^2 are potentially suitable for fish and over 1,500,000 km^2 could be developed for bivalves. Both fish and bivalve aquaculture showed remarkable potential across the globe, including both tropical and temperate countries (Figs. 1&2; Table 3). However, as would be predicted by metabolic theory (Brown et al. 2004), many of the areas with the highest GPI were located in warm, tropical regions. Total potential production is considerable: if all areas designated as suitable in this analysis were developed, we estimate that approximately 15 billion metric tons of finfish could be grown every year – over 100 times current global seafood consumption.

Although this analysis clearly shows vast aquaculture potential, there are important additional environmental, economic and social factors that would rule out seemingly suitable space. For example, a more refined assessment may exclude environmentally sensitive or high biodiversity areas such as coral reefs. Other areas might be ruled out by economic considerations such as distance to ports, access to markets, shore-side infrastructure, and intellectual or business capital. Understanding the social interactions with wild fisheries, jobs, prices, and cultural heritage should also be taken into consideration. Actual zones for aquaculture development will certainly be much smaller than the identified suitable areas. However, the scale of potential space suggests enormous flexibility in siting farms within the context of more nuanced constraints.

Nearly every coastal country has high marine aquaculture potential and could comfortably meet its own domestic seafood demand, typically using only a minute fraction of its ocean territory (Fig. 3). While the global potential is vast, certain countries show particular promise. Indonesia, for example, has among the highest potential annual production for both fish and bivalves. Developing only 1% of Indonesia's suitable ocean area could produce >24 million MT of fish per year or >3.9×10^{11} individual 4 cm bivalves. If consumed entirely within Indonesia, this amount of additional fish production would increase per capita seafood consumption by six times.

The large production potential per unit area for marine aquaculture enables the possibility of producing significant amounts of seafood using limited space. For example, we calculate that, if the most productive areas of the ocean are developed for fish aquaculture, the amount of seafood that is currently captured by all wild fisheries(FAO 2016) could be grown using less than 0.015% of the ocean's surface area, comparable to less than the area of Lake Michigan. Notably, many countries with the highest potential are not currently producing large quantities of marine aquaculture (FAO 2015) (Fig. 4). This vast untapped aquaculture potential suggests that other factors, such as social, economic, or regulatory constraints are limiting aquaculture development far more than biological constraints or conflicting uses.

Given the breadth of locations that are potentially suitable for marine aquaculture, there is ample opportunity for well-managed aquaculture expansion to increase resiliency to future environmental, social and economic shocks. Notably, some of the countries with highest aquaculture growth potential are predicted to experience large population increases, such as India and Kenya (United Nations Department of Economic and Social Affairs 2015) (Fig. 1; Table 3). In addition, four of ten countries with the highest average GPI for finfish aquaculture are Pacific island nations, a region with both high per capita fish consumption and looming food security concerns (Bell et al. 2013; Cheung et al. 2010). It may be worthwhile for these high potential high need countries to consider economic development opportunities by pursuing policies to enable marine aquaculture development. However, the effects of aquaculture development on local food security can vary considerably(Golden et al. 2016; Belton, Bush, and Little 2016; Béné et al. 2016), and continued research on the interactions between aquaculture policy and socially sustainable development is needed(Krause et al. 2015).

While our aquaculture suitability assessments are based on current ocean conditions, the environment is changing at an unprecedented rate (IPCC 2014). Future efforts to assess how climate risks will modify this potential will improve long-term predictions of aquaculture potential. Nonetheless, given the relatively small amount of space needed for aquaculture to meet global and national seafood demands, the breadth of physiological tolerances found across cultured species (Froehlich, Gentry, and Halpern 2016), and the ability of selective breeding to adapt organisms to future agroecosystems, the over-arching conclusions of this paper are likely robust. Indeed, marine aquaculture could be used to mitigate some aspects of climate change(National Oceanic and Atmospheric Administration 2016).

Given the huge potential for marine aquaculture, why is development of farms still rare? Restrictive regulatory regimes, high costs, economic uncertainty, lack of investment capital, competition, and limitations on knowledge transfer into new regions are often cited as impediments to aquaculture development (Fairbanks 2016; Knapp and Rubino 2016). In addition, concerns surrounding feed sustainability, ocean health, and impacts on wild fisheries have created some resistance to marine aquaculture development (Naylor et al. 2009; J. Ramos et al. 2015; Holmer 2010) and merit ongoing investigation to ensure good practices. These cultural and economic dimensions of development, along with the regulatory systems that will help guide sustainable growth, are critically important to understanding and shaping realistic growth trajectories. Our results provide a foundation to help guide this rapidly growing food production sector towards enhancing the well-being of people while maintaining and perhaps enhancing robust ocean ecosystems.

D. Appendices

1. Methodological approach and overview

To determine the relative productivity potential of ocean areas for marine aquaculture, we used an approach that considers the temperature tolerance of aquaculture species to estimate location-specific growth potential. We then used growth rate and allometric principles to estimate potential annual production per unit area for both fish and bivalve aquaculture.

Finally, we constrain suitable extent for fish and bivalve aquaculture to areas of allowable depth, environmental conditions, and use restrictions. Globally, such constraints provide an initial, simplified framework for considering marine aquaculture development and represent only some of the key constraints that would be required for a more detailed regional analysis. In some cases these constraints will be conservative (e.g., some existing uses could be moved to allow aquaculture to expand) and in other cases too liberal (e.g., other factors such as ecological hotspots, current speed or prime fishing zones will likely further limit ideal aquaculture locations).

All analyses and visualizations were performed in R *v*3.3.2(R Core Team 2016); the following packages were used in this analysis: raster, rgdal, RasterVis, maps, dplyr, tidyr, ggplot2, RColorBrewer, ncdf4.

2. Calculating Growth Performance Index

Species Data and mapping

A total of 180 consumable marine aquaculture associated species were included in the analysis (120 fish and 60 bivalves). Information was collected on each species' temperature tolerance range (maximum and minimum temperature) and von Bertalanffy growth function (VBGF) parameters (K and Linf). All methods used for species selection are described in detail in Froehlich *et a*l.(Froehlich, Gentry, and Halpern 2016); see Table 4 for a full list of included species and attributes.

Global sea surface temperature (SST; °C) values were used to map each species to the locations where they could potentially be grown, given their respective thermal limits. In order to compare the range of temperatures in the marine environment to species' temperature tolerance ranges, we extracted annual maximum and minimum SST over a 30-year period (1982-2011). All SST data were provided by the NOAA World Ocean Atlas (Locarnini et al. 2010)at a resolution of 0.042 degrees For each year and for each given unit area in the ocean, we determined which aquaculture species could tolerate the thermal environmental ranges in each location; all of the years were averaged to determine the mean number of fish and bivalve species that can be grown in each location (Fig. A1). In general, temperate locations show the highest numbers of potentially suitable species.

Growth Performance Index Calculation

The two VBGF parameters (K and Linf) were then used to calculate the Growth Performance Index (GPI) for each species. GPI is a single, unitless metric derived from the VBGF, which can be used to describe and compare the growth potential of species and is most accurate when food is not constrained (Pauly and Munro 1984). GPI values typically range between 0 to 5, with most aquaculture fish species exhibiting values above 2 (Mathews and Samuel 1990; Alvarez-Lajonchère and Ibarra-Castro 2012). GPI (ϕ') is described as follows:

$$\phi' = log_{10}K + 2log_{10}L_{\infty} \qquad \text{(Eq. 1)}$$

For each unit area and each year, we calculated the average GPI across all species that were mapped to each given location. We then averaged all years together to get the mean GPI calculation for each unit area (Fig. A2). The standard deviation of GPI (Fig. A3) gives an indication of the variability of GPI for each location over time. In subsequent analysis, we cut out areas for fish aquaculture that had an average GPI value below two and for bivalves below an average GPI of one, as not having consistently warm enough water for commercial aquaculture development.

Sensitivity of GPI

To determine the sensitivity of our global average GPI metric to species selection, we re-created global average GPI maps with a reduced number of species. Specifically, instead of using all fish and bivalve species (the complete model), we took a bootstrap-like approach and created 10 alternative scenarios where we randomly selected (without replacement) half of the species, and ran the same process of assigning species to locations based on temperature tolerance range. We calculated average GPI for each location in the same method as described above. This allowed us to evaluate how species selection affected overall patterns of growth potential.

In order to understand how the highest production growing regions compared across these alternative models, we assessed whether specific locations that have the highest productivity (top 10%) in our complete model are also high productivity (top 20%) in our alternative models. A high percentage would indicate that the locations of high production areas are consistent across the complete and alternative models. For fish, we found high consistency between the complete model and the alternative model runs; across all alternative models, 90% of the highest productivity locations from the complete model were in the top 20% of productivity areas in the alternative models (Table 2). The bivalve model was not quite as robust to species selection, which is not surprising given the smaller sample size. On average, 60% of the highest productivity bivalve areas from the complete model were captured in the top 20% of growing areas in the alternative models, but there was considerable variation between the different alternative scenarios, with many runs showing high consistency with the complete model, and a few being extremely different.

We also compared the difference between GPI in the complete model to each alternative model for every given location. We took the average of the differences from all the iterations to determine which locations are the most sensitive to species selection. The variation was fairly uniform for the fish model, but areas around Korea and the Middle East showed some increased variability, indicating a greater sensitivity of GPI to species selection. For the bivalve model, high latitude areas, the Gulf of California, the Gulf of Mexico, and parts of the tropical Indo-Pacific showed elevated sensitivity to species selection (Fig. A4). The already limited number of species that can occur in these thermal envelopes is likely contributing to these results.

3. Constraint Mapping

For each constraint, we set a threshold beyond which we would exclude aquaculture development. In general, we chose conservative thresholds for each of these variables, which resulted in the elimination of some areas that may be suitable for marine aquaculture. Each constraint layer, its source, resolution, and threshold for aquaculture development are listed in Table 1. The areas found unsuitable for aquaculture for each constraint are shown in Fig. A5. All layers were converted to geographical latitude/longitude coordinates. Our final map showing potential productivity areas includes all regions with a minimum phi-prime score that were not eliminated due to any of the constraints. The original resolution of each constraint layer is noted in Table 1; the final resolution of the potential production map is 0.0083 degrees, which is equivalent to the layer with the finest resolution (depth). Each constraint layer is described in more detail below:

Depth

Most aquaculture operations are anchored to the seafloor, which becomes increasingly expensive as depth increases(Rubino 2008). We chose a maximum depth of 200 meters, which we suggest reflects the outer bound of current industry practice. While aquaculture can take place in deeper water, and can even be free-floating without any anchoring, we introduced this constraint to provide some economic realism to the analysis.

Dissolved Oxygen:

Low dissolved oxygen (DO) can be a significant problem for aquaculture operations, causing reductions in fitness and ultimately death if oxygen concentrations are reduced to lethal levels (Harris et al. 1999). Low dissolved oxygen is a naturally occurring condition in some environments, but can be exacerbated by anthropogenic nutrient producing activities, such as high-density fed aquaculture, terrestrial-based nutrient pollution, and climate change(Diaz, 2001). While it is possible to increase the DO in culture area through use of aerators, it is generally preferable to avoid locations that commonly experience chronic low DO conditions. Alternatively, nutrient removing aquaculture such as algae and filter feeders could be used to improve oxygen levels in some cases. Conversely, areas that are nutrient poor may benefit from the nutrients released from fed aquaculture.

We used DO data from the National Centers for Environmental Information, measured at 30 meters depth (since most aquaculture is grown below the surface), and averaged across all available decades (1921-2008); data are too sparse to assess inter-annual variability. We assumed that chronic low DO would not be an issue in ocean areas with less than 30 meters depth due to current and/or wind action. All areas that had an annual average below the sub-lethal limit for fish (4.41 mg/L) (Vaquer-Sunyer and Duarte 2008) were excluded as potential aquaculture locations. This constraint led to a total of 1,041,975 km^2 (3.9% of total area after constraining to 200m depth regions) being removed from potential aquaculture areas (Table 1). For bivalve aquaculture, we set the lethal limit at an annual average less than 1.99 mg/L (Vaquer-Sunyer and Duarte 2008), which is the sub-lethal limit for molluscs. No areas fell below this threshold, so DO was not a constraining factor for bivalves.

Chlorophyll-a Concentration

Bivalve culture requires adequate natural food supply for growth. Ideal growing environments have both a high and steady source of food to allow for continuous growth. While filter-feeding bivalves can get nutrition from a variety of sources, including detritus, chlorophyll-a concentration has been found to be a good proxy for food availability (Blanchette, Helmuth, and Gaines 2007; Page and Hubbard 1987), and is the most robust available measurement at a global scale.

We used monthly average global chlorophyll a data from MODIS satellites. Data from 2003 to 2014 was averaged to produce both a monthly and annual average concentration for each unit area. When no data were available for any given month (which occurred in high altitude areas over winter), those months were excluded from the annual mean calculation.

The GPI metric is most accurate when food availability is not constrained, therefore we limited bivalve growing regions to areas that have both high and consistent food availability. As a result, bivalve aquaculture areas were limited to regions that had annual chlorophyll-a concentrations with an annual mean above 2 mg/m^3 and had at least 10 months with a chlorophyll-a concentration greater than 1 mg/m^3. This constraint led to an additional total of 23,932,076 km^2 (89.5% of total area after constraining to 200m depth regions) being excluded from potential aquaculture area.

These chlorophyll-a requirements were drawn from existing publications and reports (Saxby 2002; Inglis, Hayden, and Ross 2000; Langan 2008). The satellite data often had missing data for high latitude locations during winter months due to darkness and cloud cover; therefore, we allowed up two months that do not to meet the 1 mg/m^3 threshold (i.e., only requiring at least 10 months with chlorophyll-a values). This allows some high latitude areas to be included as suitable bivalve growing regions in our analysis regions without sacrificing the need for consistent food availability. Since our chlorophyll-a requirements are quite conservative, we have excluded some areas that are successful existing bivalve growing regions. The success of bivalve farming outside of our suitable areas may be attributable to growers that are able to create a profitable enterprise with relatively lower food availability (e.g., semi-intensive culture) or because food sources, such as detritus, that were not captured by our data are relatively more important in certain regions.

Shipping traffic

Marine aquaculture operations are not compatible with heavy shipping traffic, and planning processes generally eliminate shipping lanes as potential locations for aquaculture (Rubino 2008; Puniwai et al. 2014). We used data on global shipping intensity from Halpern *et al* 2015 (Halpern et al. 2015) to exclude ocean area with the highest shipping traffic. To do this, we divided the entire ocean area into 20 quantiles based on shipping intensity within each unit area; we then excluded aquaculture from the top 5% of highest intensity shipping areas. While 5% is only a small fraction of the total ocean area, it is disproportionately concentrated in the coastal areas (see Fig. A5), and therefore has a significant effect on the total area available to aquaculture development. This constraint led to an additional total of

6,755,497 Km^2 (25.3% of total area after constraining to 200m depth regions) being excluded from potential aquaculture area.

Oil rigs

Oil rigs are used as an example of other ocean development that in general excludes aquaculture. There have been some suggestions that aquaculture development could utilize inactive oil platforms, but developing aquaculture on an active oil platform remains unlikely (M. J. Kaiser, Snyder, and Yu 2011). Therefore, for this analysis we excluded all active oil rigs as locations for potential aquaculture development. Oil rig presence/absence data are from Halpern et al (2015) (Halpern et al. 2015). This constraint led to an additional total of 680,126 km^2 (2.5% of total area after constraining to 200m depth regions) being excluded from potential aquaculture area.

Marine protected areas

Marine protected areas (MPAs) vary substantially in their purpose and restrictions. For this analysis, we used data from the World Protected Areas database (IUCN and UNEP 2009), which categorizes protected areas into seven different categories (Ia, Ib, II, III, IV, V, VI), which capture the primary stated management objectives of a marine protected area (Day et al. 2012). Categories V and VI are protected areas whose objectives explicitly acknowledge human interactions and resource use, so these areas were not excluded for marine aquaculture. However, evaluation of whether aquaculture would be consistent with the objectives of these MPAs would need to be done at a local planning scale. The other five MPA categories focus primarily on conservation, so aquaculture was deemed to be an incompatible activity and was excluded for our analysis. This constraint led to an additional total of 30,980 km^2 (0.1% of total area after constraining to 200m depth regions) being excluded from potential aquaculture area. It is important to note that current levels of marine protection are well below conservation targets and not representative spatially across the globe(Wood et al. 2008). Therefore, actual area that should be set aside for protection is likely larger than we apply in this analysis.

After all of these constraints were applied, the total area within continental shelf regions (depth <200m) was reduced from 26,748,980 km^2 to 11,402,629km^2 for fish and 1,501,709km^2 for bivalves.

4. Biomass Calculations

In order to understand what GPI means in terms of potential aquaculture biomass production, we used the VBGF and species specific growth parameters to assess the amount of time it would take each aquaculture species used in our analysis to grow to a generic harvestable size. For fish we estimated that average marketable size is approximately 35 cm ("plate size"), and for bivalves we estimated that a marketable product would be approximately 4 cm long. Including all species that reached our harvestable size, we used least squares regression to estimate how GPI relates to time to harvest (Fig. A6). To determine the most accurate functional form, we used hold out sampling to remove 10% of the observations then calculated the mean square error for linear, polynomial, and exponential models. The chosen model had the lowest mean square error when comparing the actual to the estimated values. The resulting equations are as follows:

$$\text{Log}(T_F) = 7.68 - 5.82 * \log(\phi') \qquad \text{(Eq. 2)}$$

$$\text{Log}(T_B) = 2.99 - 1.66 * \phi' \qquad \text{(Eq. 3)}$$

where T_F is the time for a fish to reach 35 cm and T_B is the time for a bivalve to reach 4 cm. The resulting R^2 values for these models are 0.90 and 0.88 for fish and bivalves, respectively.

For fish we used principles of allometry to convert from length to weight (Keys 1928):

$$W=aL^b \quad \text{(Eq. 4)}$$

where W is Weight, L is length, and a and b are species specific parameters. We used median values for a and b based on Froese (Rainer Froese 2006), so that a=3.025 and b=0.01184. Using this equation, we determined that our generic 35 cm fish would weigh approximately 548 grams at harvest.

The relationship between length and weight is quite variable across bivalve species(Gaspar, Santos, and Vasconcelos 2001), so we did not convert the potential production approximations to tonnage. Rather, we report potential production as the number of 4cm individual bivalves.

To understand how the time to harvest estimation related to harvest per unit area, we assumed a consistent farm design for both fish and bivalve harvest. For fish, we assumed that each km^2 would contain twenty four 9,000 m^3 cages, each stocked with 20 juveniles per meter cubed. This low stocking density would result at a density at harvest below the European organic standard maximum of 15 kg/m^3 for most marine finfish(European Union 2009) and results in conservative production per unit area estimates. For reference, farming densities for some marine fish can be up to or beyond 30kg/m^3 at harvest(Sim-Smith and Forsythe 2013). If a stocking density in this range was used, production per unit area estimates in this paper would approximately triple.

For bivalves, we based our design on offshore longline growing for mussels, and assumed 100 long lines placed in each km^2 of growing area; each long line would have 13,000 feet of fuzzy rope, and that each foot of fuzzy rope would be seeded with 100 bivalves. The space required for anchoring would vary with depth and design, and was therefore not included in this analysis. We acknowledge that farm design varies significantly, and could be adjusted to meet local conditions; however, a uniform design allows us to most clearly differentiate between areas at a global scale.

The production per unit area per year was calculated by dividing the total farm output by the number of years between stocking and harvest. This is based on the assumption that re-stocking would happen immediately post-harvest.

In order to calculate overall production estimations, all potential aquaculture cells were rank-ordered by their average GPI value. The production for each cell and the total area of all cells were calculated as a running sum, thereby allowing for the assumption that the most productive locations would be developed first. Since our production maps are based on a latitude/longitude coordinate system, the resolution of each cell is equivalent in degrees latitude and longitude, but not in area. The variation in cell area was taken into consideration throughout the analysis, and all calculations of area and potential production accounted for the variability of cell size.

5. Country-level estimates and comparisons

Each unit area was assigned to a country, based on the country and territory specifications used in Halpern *et al*. (Halpern et al. 2012). Average weighted GPI (the value for each cell was weighted by its area) and total developable area for each country and territory are listed in Table 3. Consistent with the global production estimations, country production estimations also assumed sequential development of locations from the highest to lowest GPI.

Current aquaculture production and seafood consumption data comes from Food and Agricultural Association (FAO) and was extracted using the FishStatJ software (FAO 2014).

E. Acknowledgements

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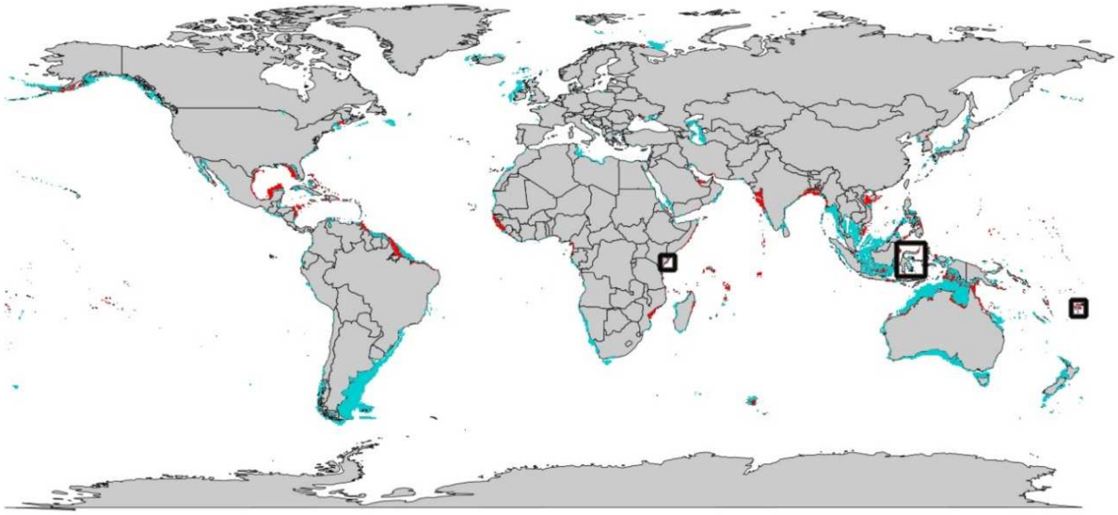
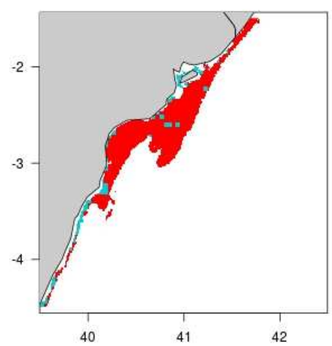
F. Figures

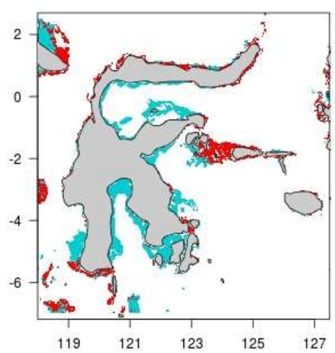
a.



b.



c.



d.

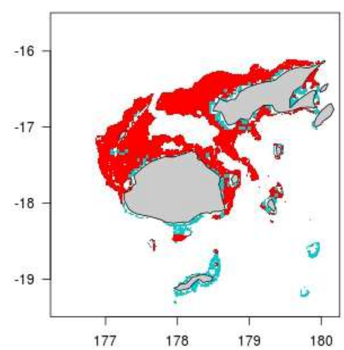
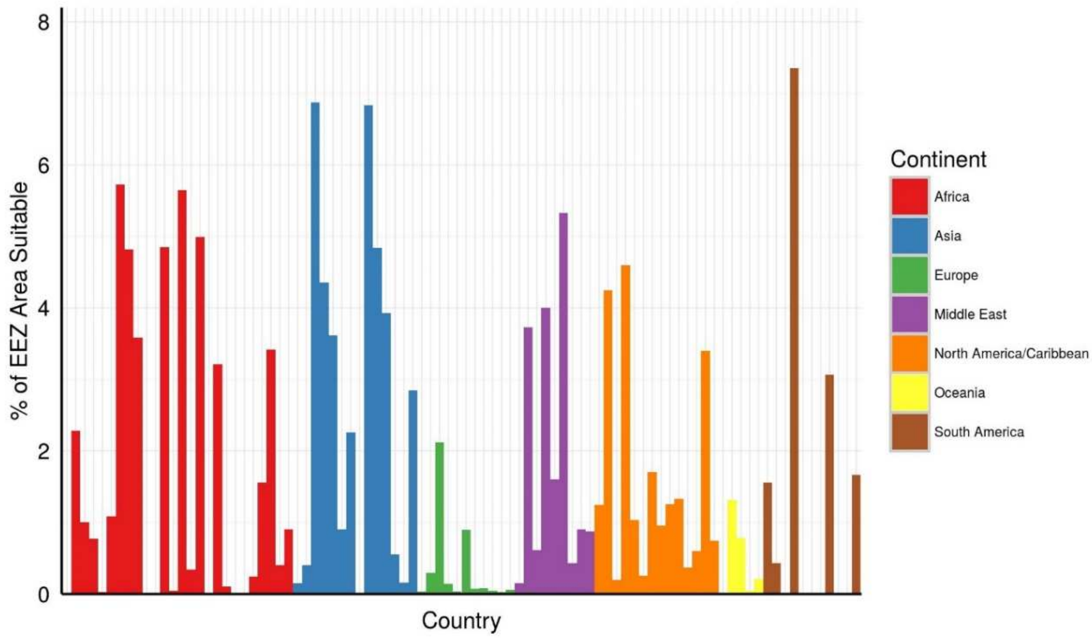


Figure. 1. Global hotspots for finfish aquaculture (panel a). Blue and red areas depict locations that have potentially suitable growing conditions for marine aquaculture and no known conflicting uses. Red coloration signifies areas with the highest (top 20%) potential productivity. Panels **b**, **c**, and **d** show zoomed in areas from the southern coast of Kenya, central Indonesia, and Fiji, respectively (locations of detail areas indicated with black rectangles in panel **a**.

a.



b. **c.** **d.**

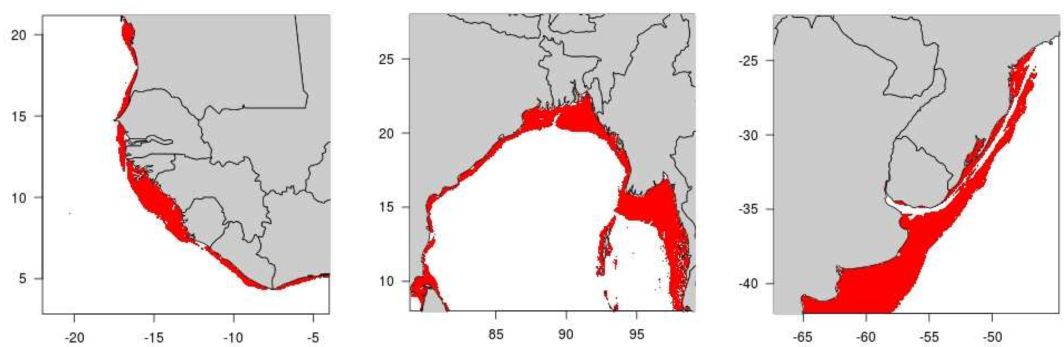


Figure 2. Potential growing area for bivalves by country. Panel **a** shows the percentage of each country's Exclusive Economic Zone (EEZ) that has potentially suitable growing conditions for bivalves and no known conflicting uses. Each bar represents a single country, grouped by continent. Panels **b**, **c**, and **d** show potential bivalve growing areas (in red) centred on Guinea, Bangladesh, and Uruguay. These are the countries with the highest percentage suitable area for bivalves in Africa, Asia, and South America respectively. Refer to Fig. A7 for expanded figure detail.

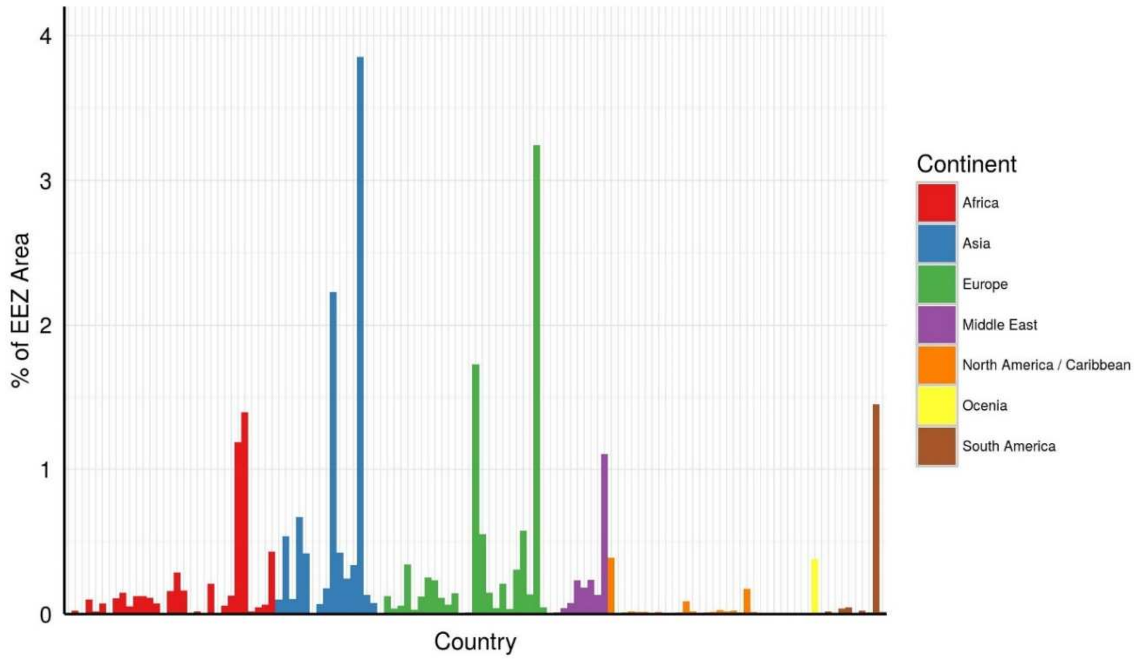
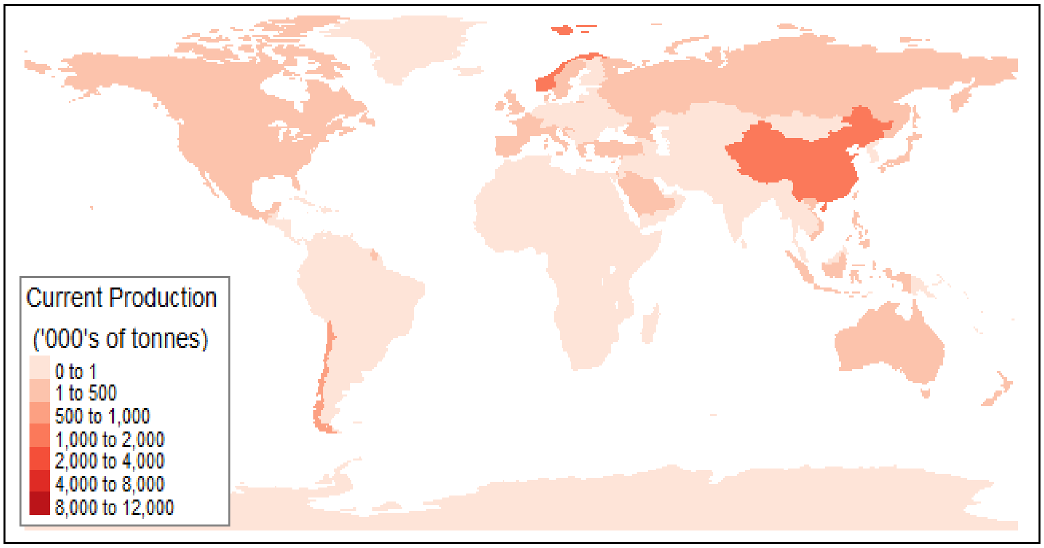


Figure 3. Percent of each country's EEZ required for finfish aquaculture to supply its current seafood consumption. Each bar represents a single country, grouped by continent. The vast majority of countries would need to farm much less than 1% of their EEZ to produce all of the seafood they are currently consuming. Refer to Fig.A8 for expanded figure detail.

a.



b.

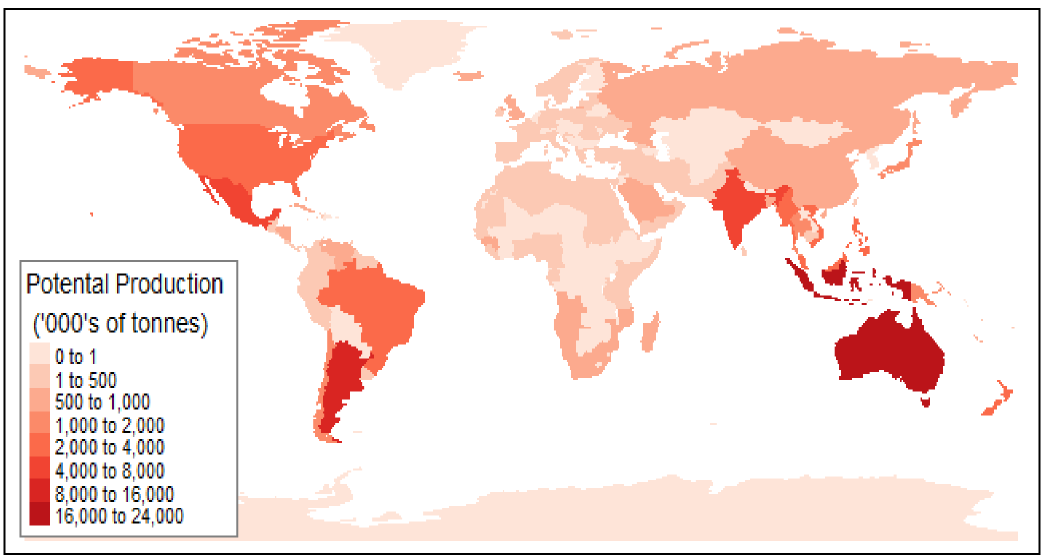
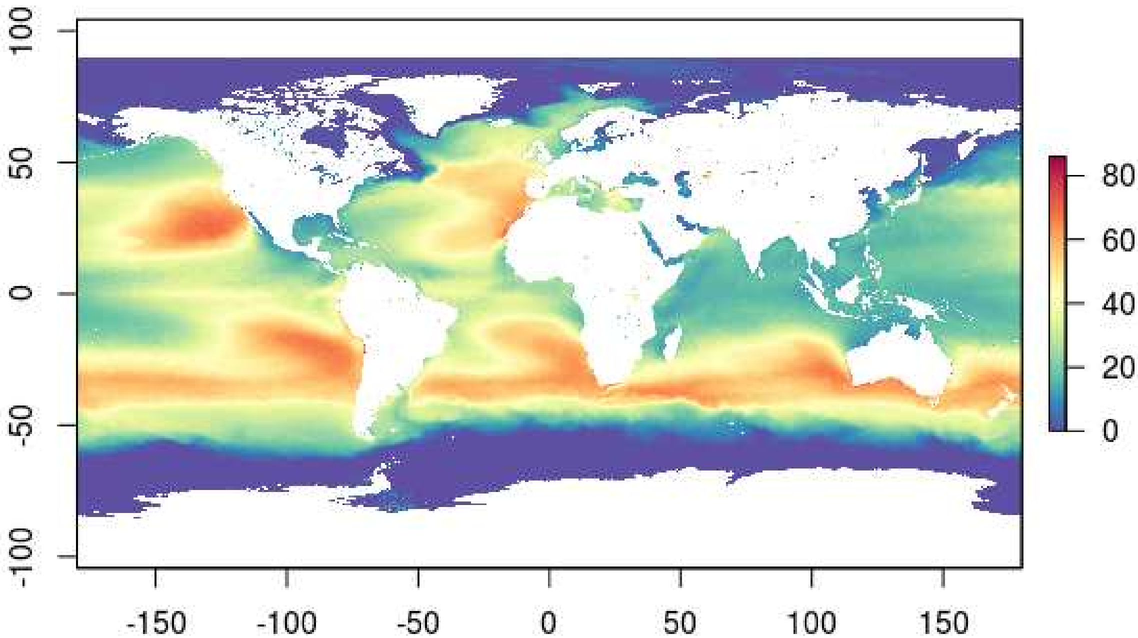


Figure 4. Marine aquaculture production and potential. Current marine aquaculture fish production (**a**), and potential production if 1% of suitable area in each country were to be developed for low density marine finfish aquaculture (**b**). Note that certain countries, such as China and Norway, already produce more marine finfish than the projected potential, which could reflect more intensive production or a larger fraction of marine area already developed for aquaculture.

a.



b.

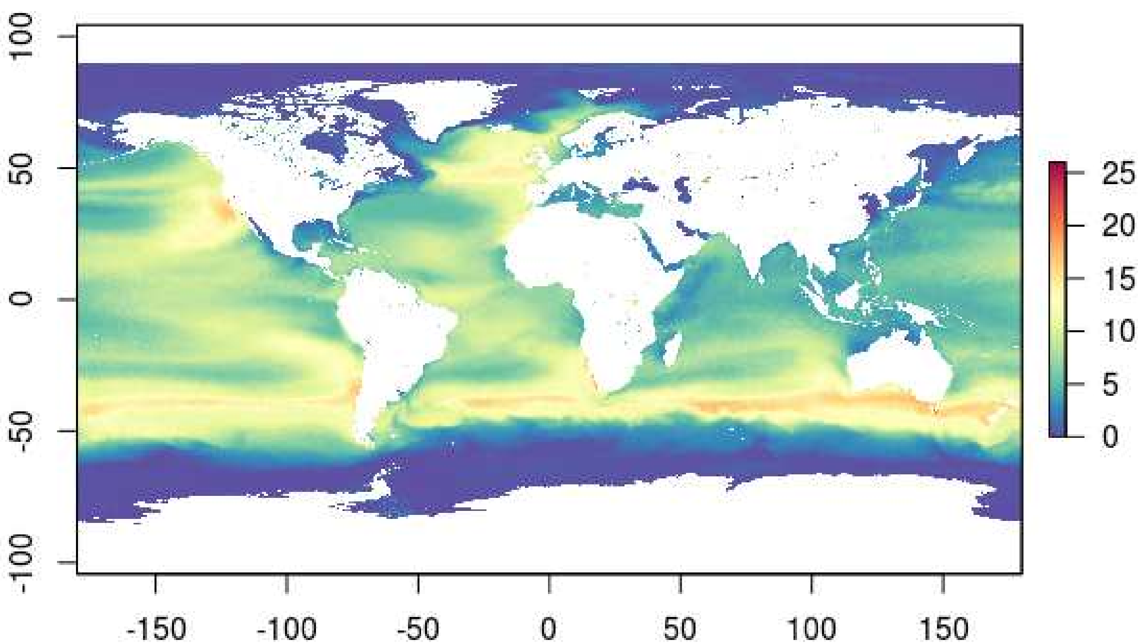
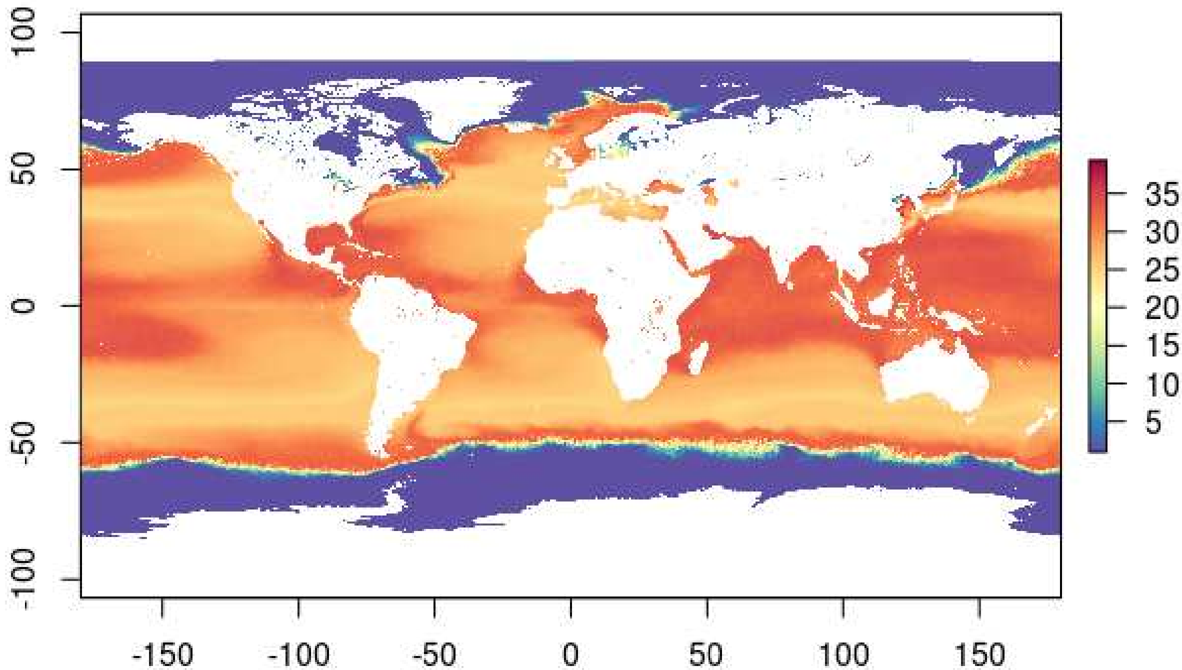


Figure A1. The mean number of species that can be grown (due to temperature tolerance) across all aquatic environments. Panel **a** shows the results for fish and **b** for bivalves

a.



b.

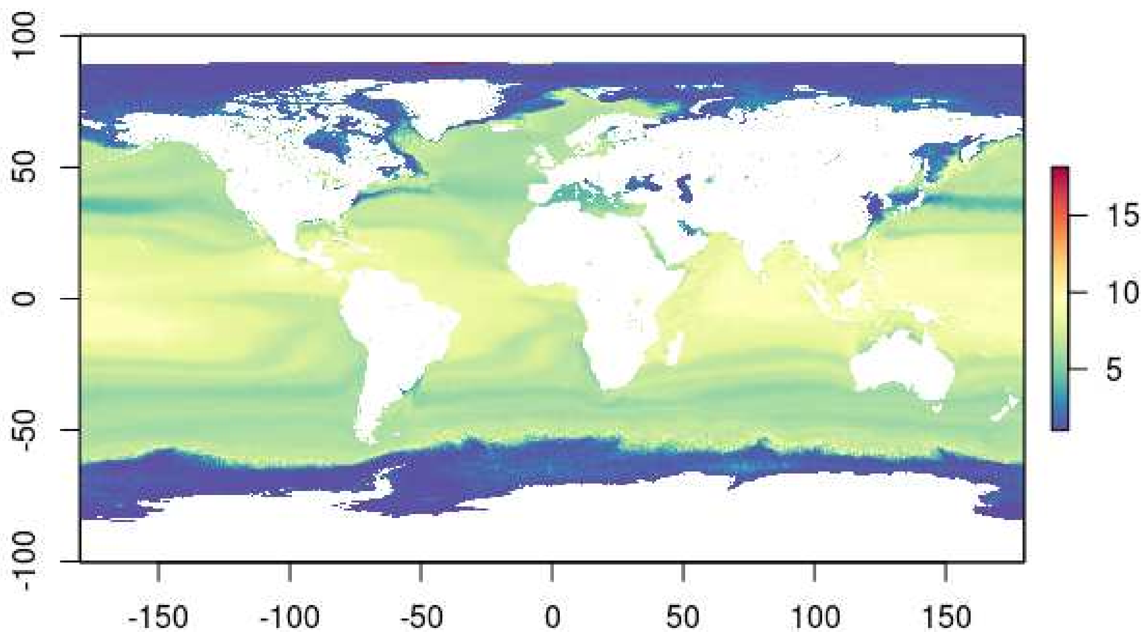
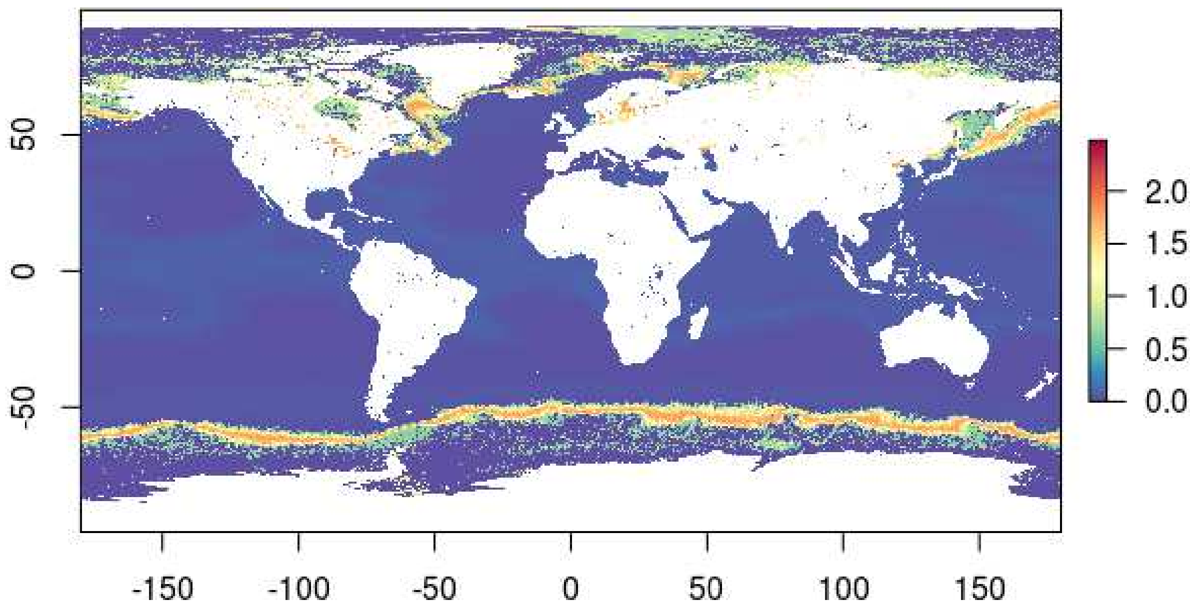


Figure A2. Mean Growth Performance Index across all aquatic environments. Panel **a** shows the results for fish and **b** for bivalves. The Growth Performance Index values have been exponentially transformed in order to more clearly show the variation in values near the top end of the scale.

a.



b.

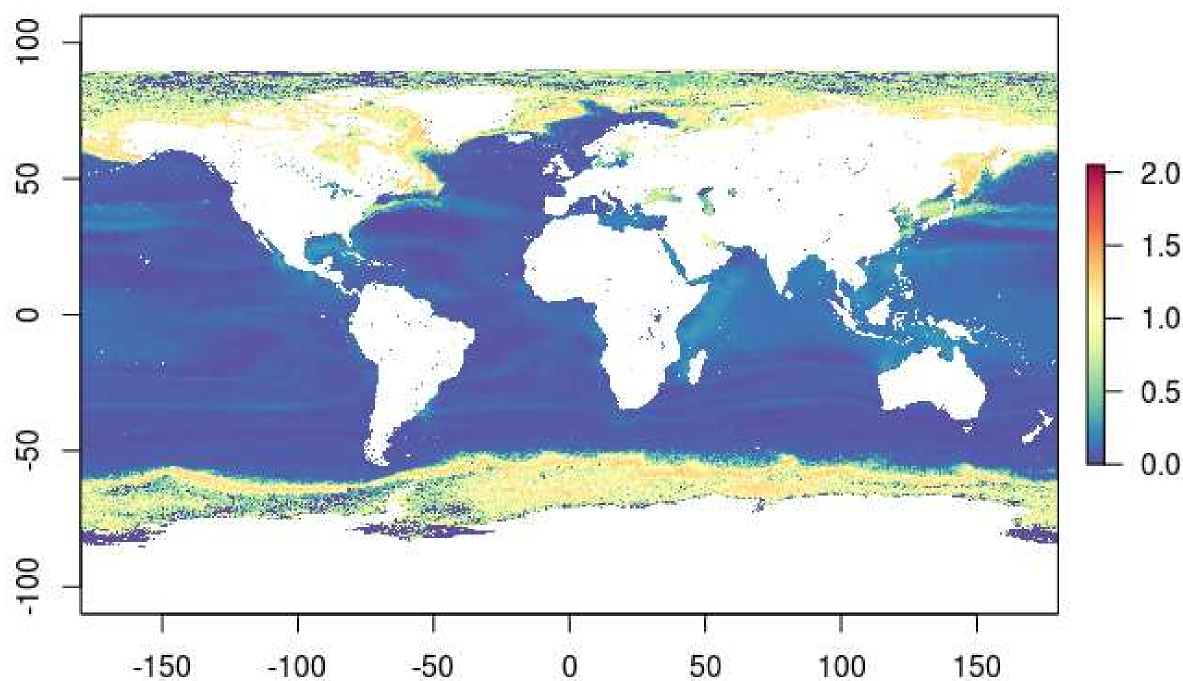
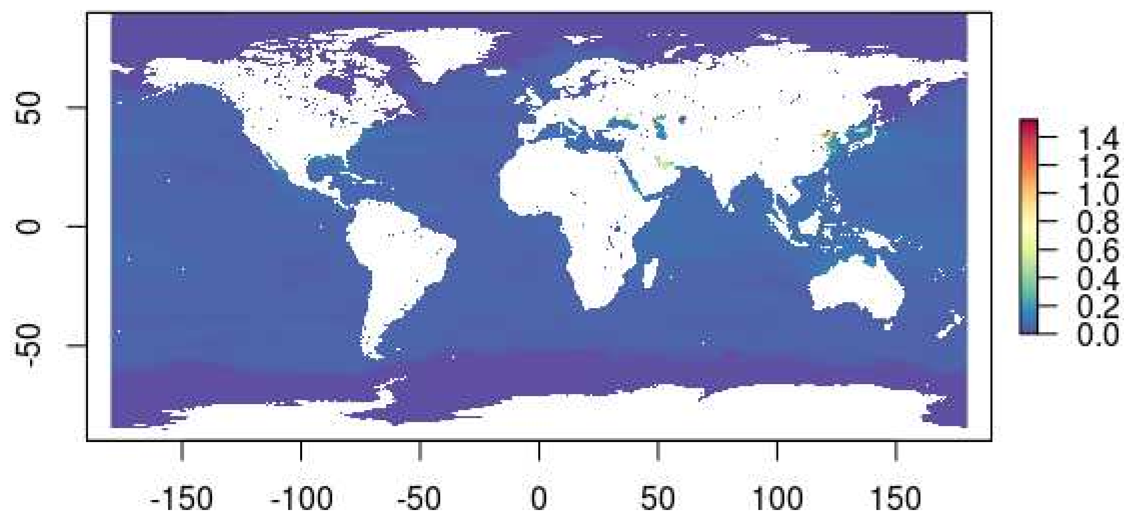


Figure A3. **Standard Deviation of Growth Performance over the period from 1982-2011.** Panel **a** shows the results for fish and **b** for bivalves.

a.



b.

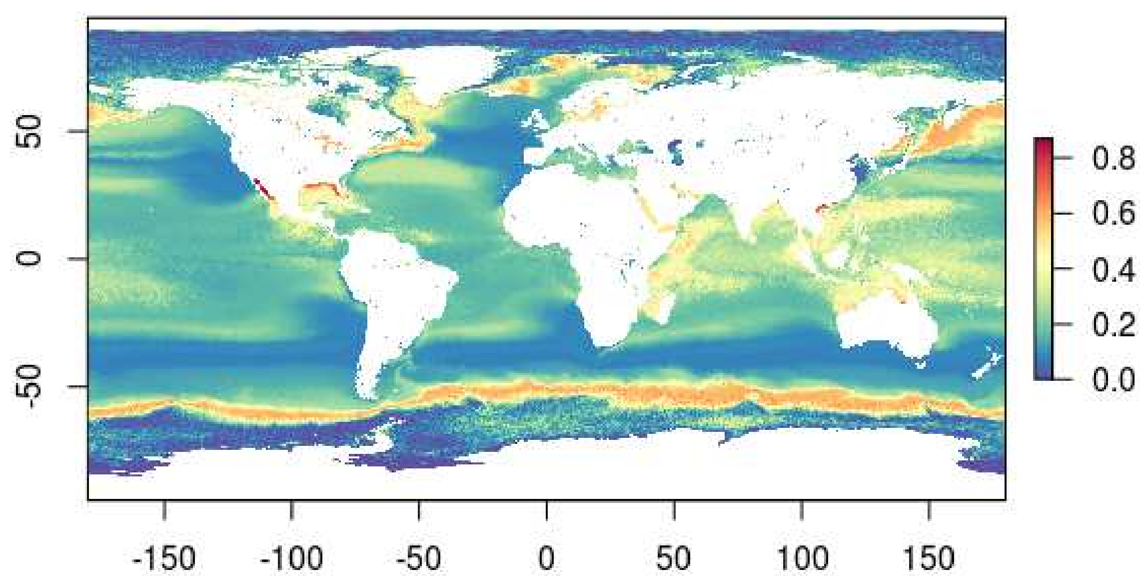


Figure A4. The average difference of GPI between the complete model and the 10 alternative reduced species scenarios. Panel **a** shows the results for fish and **b** for bivalves. Warmer color areas indicate regions where our phi prime measurements are likely to be most sensitive to the species chosen in the analysis.

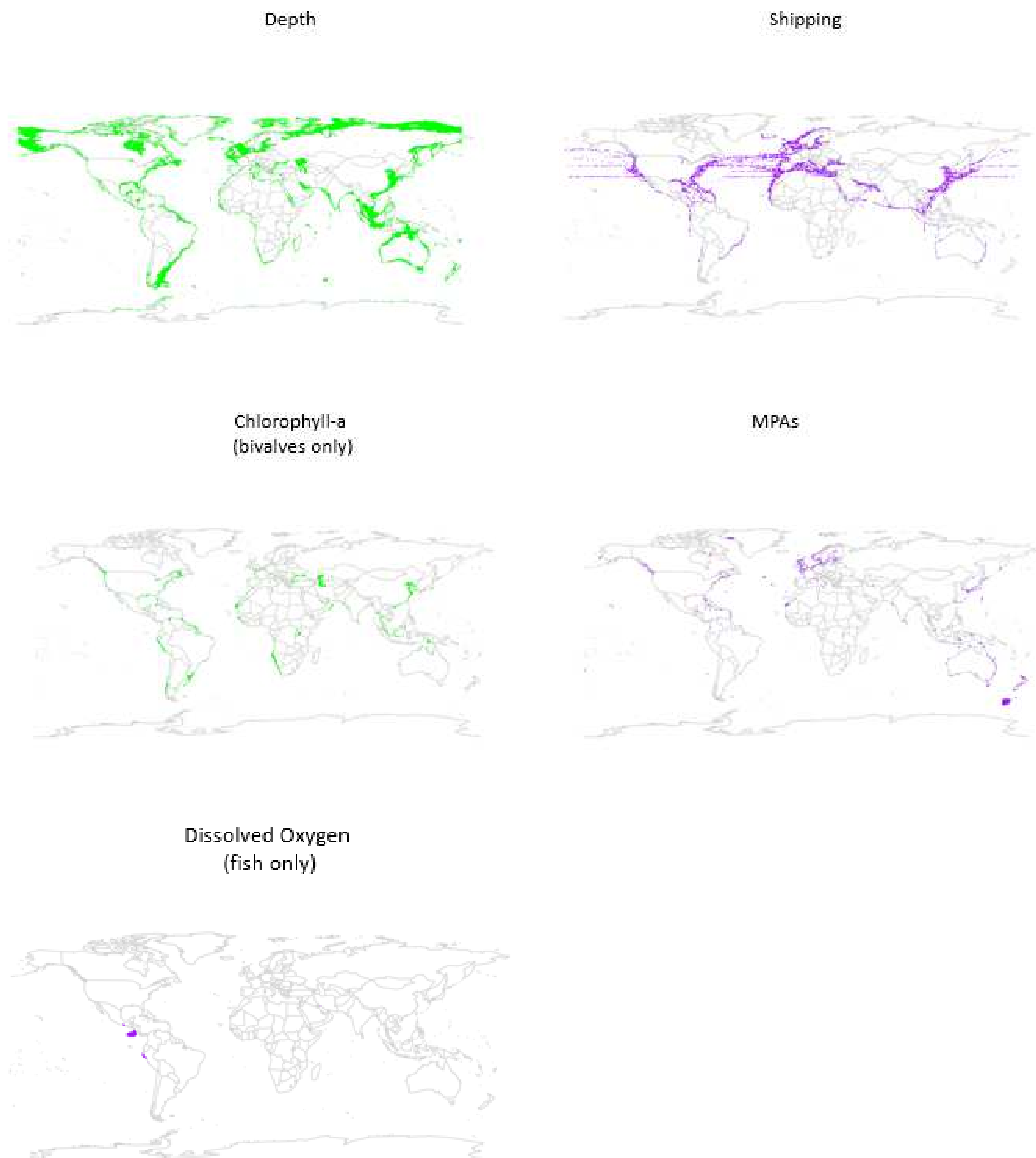
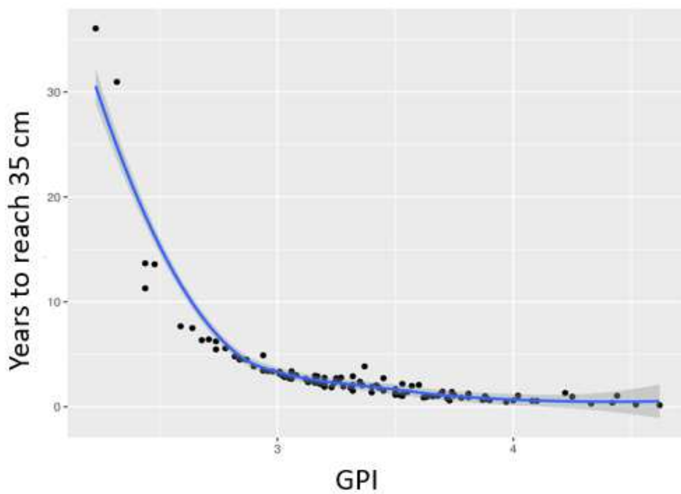


Figure A5. Excluded areas for each constraint listed in Table 1 (except for oil rigs, for which excluded areas were not easily visible on the global map). For depth and Chlorophyll-a concentration, the suitable areas are shown in green. For the other constraints, the excluded areas are shown in purple. Unless specified, each constraint map applies to both finfish and bivalve aquaculture.

a.



b.

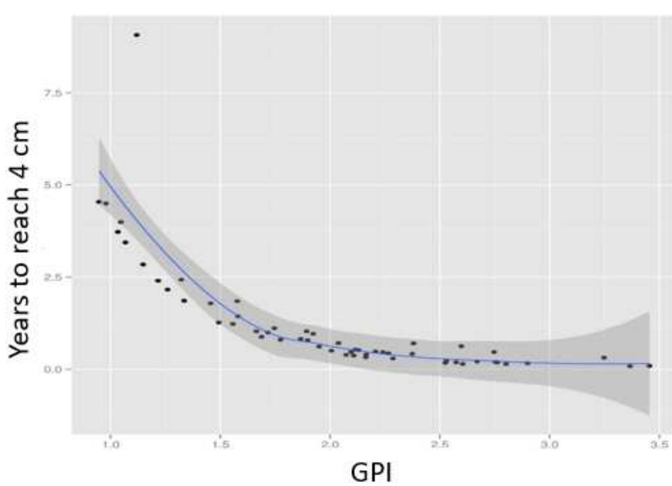


Figure A6. The estimated amount of time to reach harvestable size as a function of GPI. Panel **a** shows the relationship for fish and **b** for bivalve species used in this analysis.

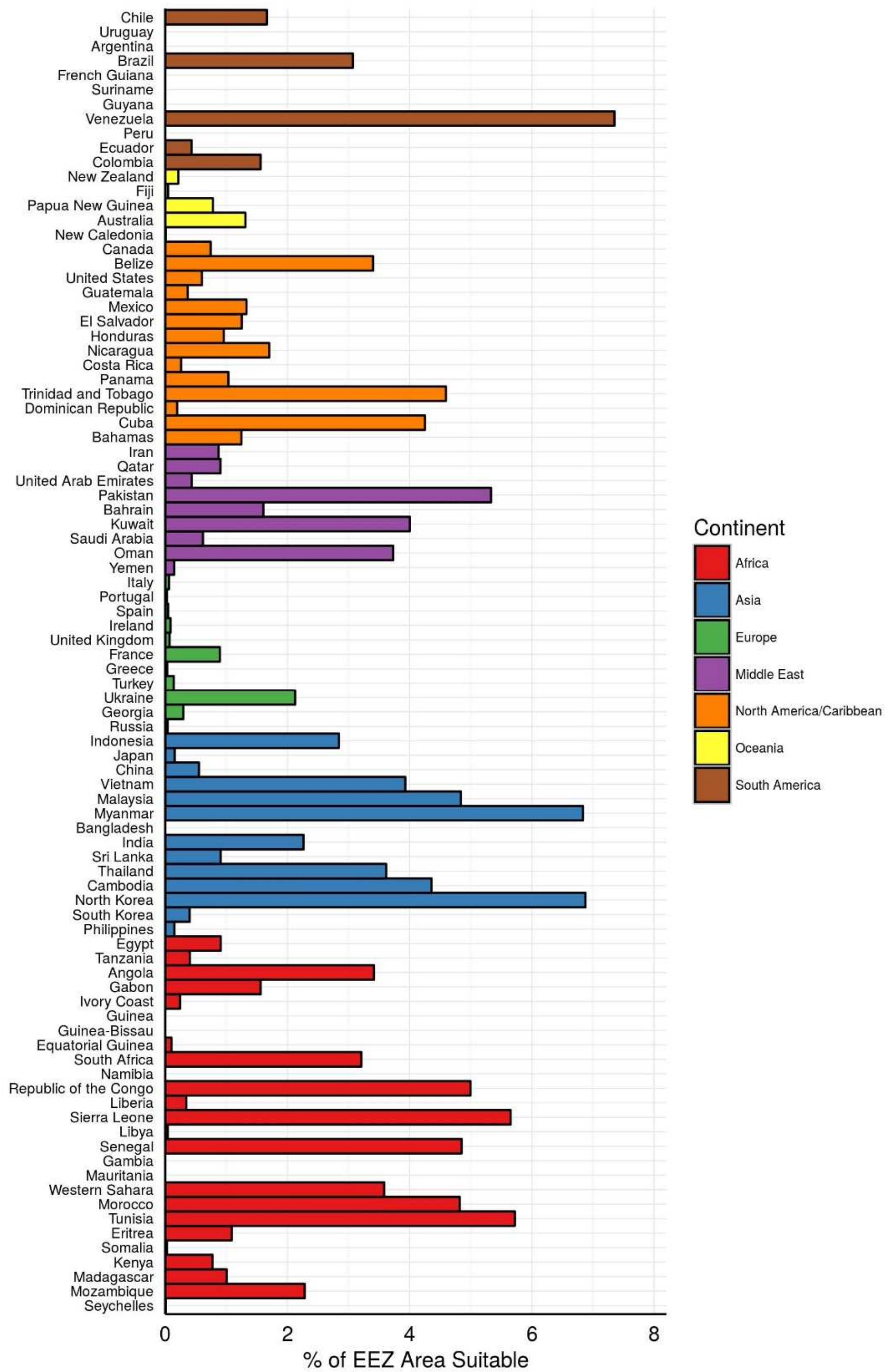


Figure A7. Potential growing area for bivalves by country. The percentage of each country's Exclusive Economic Zone (EEZ) that has potentially suitable growing conditions for bivalves and no known conflicting uses. Each bar represents a single country, grouped by continent. This figure is an expanded version of Fig. 2.

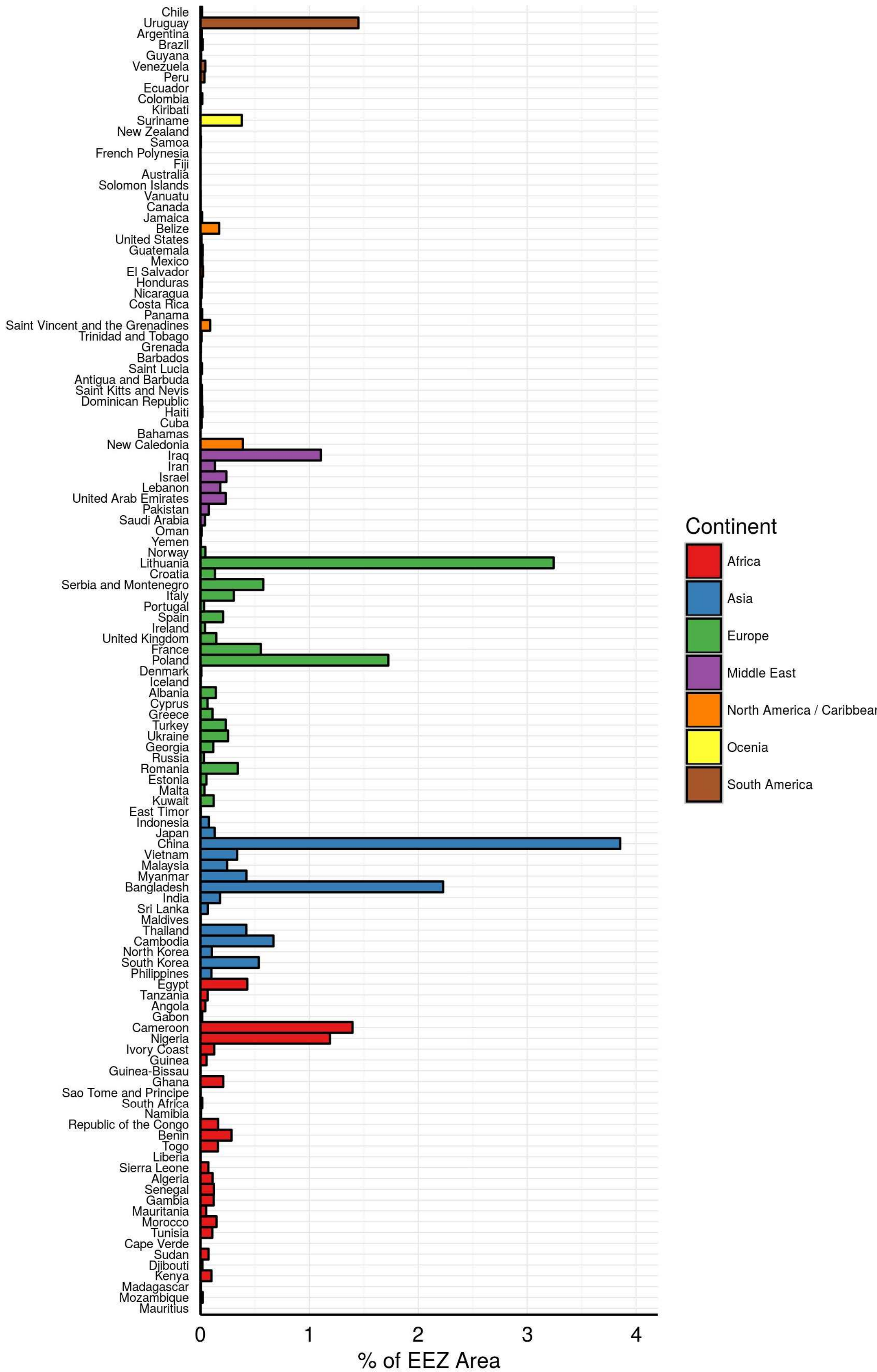

Chile
Uruguay
Argentina
Brazil
Guyana
Venezuela
Peru
Ecuador
Colombia
Kiribati
Suriname
New Zealand
Samoa
French Polynesia
Fiji
Australia
Solomon Islands
Vanuatu
Canada
Jamaica
Belize
United States
Guatemala
Mexico
El Salvador
Honduras
Nicaragua
Costa Rica
Panama
Saint Vincent and the Grenadines
Trinidad and Tobago
Grenada
Barbados
Saint Lucia
Antigua and Barbuda
Saint Kitts and Nevis
Dominican Republic
Haiti
Cuba
Bahamas
New Caledonia
Iraq
Iran
Israel
Lebanon
United Arab Emirates
Pakistan
Saudi Arabia
Oman
Yemen
Norway
Lithuania
Croatia
Serbia and Montenegro
Italy
Portugal
Spain
Ireland
United Kingdom
France
Poland
Denmark
Iceland
Albania
Cyprus
Greece
Turkey
Ukraine
Georgia
Russia
Romania
Estonia
Malta
Kuwait
East Timor
Indonesia
Japan
China
Vietnam
Malaysia
Myanmar
Bangladesh
India
Sri Lanka
Maldives
Thailand
Cambodia
North Korea
South Korea
Philippines
Egypt
Tanzania
Angola
Gabon
Cameroon
Nigeria
Ivory Coast
Guinea
Guinea-Bissau
Ghana
Sao Tome and Principe
South Africa
Namibia
Republic of the Congo
Benin
Togo
Liberia
Sierra Leone
Algeria
Senegal
Gambia
Mauritania
Morocco
Tunisia
Cape Verde
Sudan
Djibouti
Kenya
Madagascar
Mozambique
Mauritius
0
1
2
3
4
% of EEZ Area
Continent
Africa
Asia
Europe
Middle East
North America / Caribbean
Ocenia
South America

Figure A8. Percent of each country's EEZ required for finfish aquaculture to supply its current seafood consumption. Each bar represents a single country, grouped by continent. This figure is an expanded version of Fig. 3.

G. Tables

Table 1. Environmental and conflict constraints that excluded aquaculture development.

Constraint Layer	Source	Resolution of input data	Area exclusion threshold for fish aquaculture	Area exclusion threshold for bivalve aquaculture	Additional area within 200m depth area excluded
Depth	Satellite geodesy data (Sandwell et al. 2014)	.0083 degrees (30 arc seconds)	>200 meters depth	> 200 meters depth	N/A
Dissolved Oxygen	World Ocean Atlas (H. E. Garcia et al. 2010)	1 degree	<4.41 mg/L	N/A	1,041,975 km^2
Chlorophyll-A Concentration	Vertically generalized production model (VGPM) chlorophyll-based primary production estimate(NASA Goddard Space Flight Center 2014)	0.083 degree	N/A	Chlorophyll – required an annual average equal to 2 mg/m^3 and no more than 2 months below 1 mg/m^3	23,932,076 km^2
Shipping traffic	Halpern *et al.* (Halpern et al. 2015)	934.5 m	The top 5% of ocean area with the highest shipping density was excluded	The top 5% of ocean area with the highest shipping density was excluded	6,755,497 km^2
Oil rigs	Halpern *et al.* (Halpern et al. 2015)	934.5 m	Excluded if oil rig present	Excluded if oil rig present	680,126 km^2
Marine protected areas	2010 World Database of protected Areas (UNEP-WCMC IUCN and 2010)	Originally as a shapefile	excluded in categories Ia, Ib, II, III, and IV	excluded in categories Ia, Ib, II, III, and IV	30,980 km^2

Table 2. Results from robustness testing. This analysis showed that locations with the highest production potential are relatively robust to species selection for fish, but that species selection has more impact on the locations of highest productivity for bivalves.

	Percent of 10% highest production cells from complete model that are also in the top 20% most productive cells in the alternative models	
Alternative Scenario	FISH	BIVALVES
1	98.9	98.4
2	80.8	57.4
3	91.5	1.4
4	98.8	10.7
5	91.0	96.5
6	92.4	71.8
7	75.8	6.7
8	83.3	74.8
9	91.8	84.2
10	99.9	98.6
Mean	90.4	60.0

Table 3. Phi prime values and potential productive area for each country / territory included in the analysis

Country/ Territory	Total Area for Fish (km2)	Total Area for Bivalves(km2)	Fish GPI Average	Bivalve GPI Average
Albania	2013	0	3.24	NA
Algeria	2358	0	3.22	NA
Angola	40271	17245	3.41	1.88
Antarctica	68	0	2.71	NA
Antigua and Barbuda	2288	0	3.45	NA
Argentina	779603	107769	3.33	1.79
Australia	1891412	90867	3.39	1.83
Australian Southern Ocean Territories	4674	0	2.99	NA
Australian Tropical Territories	4102	0	3.30	NA
Bahamas	77441	7434	3.49	1.94
Bahrain	1595	135	3.50	1.31
Bangladesh	60980	15548	3.49	1.99
Belize	9641	1364	3.46	2.04
Benin	1942	0	3.47	NA
Brazil	517115	111718	3.41	2.02
British Caribbean Territories	8141	0	3.48	NA
British Indian Ocean Territory	21243	0	3.50	NA
British Pacific Territories (Pitcairn)	92	0	3.32	NA
British Southern Ocean Territories	171621	0	3.43	NA
Cambodia	34968	2109	3.46	2.14
Cameroon	8625	0	3.49	NA
Canada	136533	42706	3.12	1.67
Cape Verde	4180	0	3.31	NA
Chile	161312	59747	3.32	1.83
China	71442	4864	3.48	1.90

Colombia	35742	12459	3.46	2.16
Comoros	1123	0	3.49	NA
Costa Rica	10194	1490	3.49	2.21
Croatia	1781	0	3.25	NA
Cuba	50476	15602	3.45	1.85
Cyprus	728	0	3.36	NA
Democratic Republic of the Congo	128	0	3.48	NA
Denmark	24618	0	3.16	NA
Disputed	68755	3707	3.45	1.77
Djibouti	1641	0	3.43	NA
Dominica	335	0	3.45	NA
Dominican Republic	7237	527	3.49	2.14
East Timor	1972	0	3.44	NA
Ecuador	26716	4620	3.35	2.01
Egypt	14476	2424	3.39	1.89
El Salvador	13252	1203	3.43	2.06
Equatorial Guinea	9361	315	3.49	2.12
Eritrea	41002	879	3.48	1.66
Estonia	810	0	2.47	NA
Fiji	40055	591	3.49	2.15
Finland	170	0	2.18	NA
France	7560	3005	3.27	1.87
French Caribbean Territories	2074	0	3.46	NA
French Guiana	43197	23168	3.48	2.14
French Indian Ocean Territories	4747	0	3.49	NA
French Polynesia	26061	0	3.47	NA
French Southern Ocean Territories	67085	0	3.43	NA
Gabon	31617	3047	3.46	2.00
Gambia	3237	2259	3.47	1.96
Georgia	1636	74	3.37	1.48
Germany	934	0	3.21	NA

Ghana	7928	0	3.44	NA
Greece	5231	163	3.24	1.78
Grenada	971	0	3.48	NA
Guatemala	10696	442	3.42	1.93
Guinea	42376	18494	3.50	2.11
Guinea-Bissau	21143	17608	3.50	2.05
Guyana	49658	19640	3.49	2.16
Haiti	3566	0	3.48	NA
Honduras	47133	2104	3.50	2.12
Iceland	48863	0	3.19	NA
India	316124	51791	3.48	2.06
Indian	487	0	2.63	NA
Indian	42031	0	3.51	NA
Indonesia	1601956	169103	3.46	2.11
Iran	11127	1466	3.43	1.46
Iraq	153	0	3.33	NA
Ireland	55432	353	3.27	1.83
Israel	780	0	3.40	NA
Italy	7297	329	3.24	1.26
Ivory Coast	10728	428	3.44	2.06
Jamaica	10532	0	3.50	NA
Japan	111186	6209	3.34	1.80
Kenya	7752	873	3.50	2.14
Kiribati	5771	0	3.48	NA
Kuwait	3440	515	3.32	1.12
Latvia	277	0	2.60	NA
Lebanon	309	0	3.37	NA
Liberia	17125	852	3.47	2.12
Libya	56319	145	3.29	1.58
Lithuania	789	0	2.74	NA
Madagascar	114940	12034	3.44	1.99
Malaysia	267886	22987	3.43	2.08
Maldives	27133	0	3.50	NA
Malta	416	0	3.29	NA
Marshall Islands	19279	0	3.51	NA
Mauritania	19248	14566	3.31	1.92
Mauritius	39094	0	3.47	NA
Mexico	343827	43421	3.45	1.93
Micronesia	22926	0	3.51	NA
Morocco	32006	13163	3.24	1.88
Mozambique	82357	13091	3.48	2.03

Myanmar	212762	35551	3.45	2.11
Namibia	91055	79330	3.24	1.78
New Caledonia	49912	157	3.37	2.04
New Zealand	251162	14251	3.25	1.82
Nicaragua	62497	2579	3.49	2.11
Nigeria	18644	0	3.48	NA
North Korea	17840	8017	3.31	1.63
Norway	14844	0	3.08	NA
Oman	33865	20004	3.38	1.96
Pakistan	16182	11838	3.45	1.95
Palau	2963	0	3.50	NA
Panama	29974	3442	3.48	2.13
Papua New Guinea	163089	18678	3.47	2.02
Peru	45494	69431	3.24	1.84
Philippines	213333	2733	3.47	2.13
Poland	970	0	3.04	NA
Portugal	2599	464	3.24	1.78
Qatar	3553	317	3.52	1.64
Republic of the Congo	4448	2083	3.47	1.89
Romania	602	0	3.45	NA
Russia	80467	2969	2.86	1.58
Saint Lucia	341	0	3.46	NA
Saint Vincent and the Grenadines	1705	0	3.47	NA
Samoa	1759	0	3.51	NA
Sao Tome and Principe	1661	0	3.45	NA
Saudi Arabia	57084	1366	3.45	1.32
Senegal	14266	7627	3.44	1.96
Serbia and Montenegro	2260	0	3.23	NA
Seychelles	50222	146	3.49	2.12
Sierra Leone	22802	9094	3.49	2.12
Solomon Islands	26625	0	3.48	NA
Somalia	45922	236	3.48	1.98
South Africa	90053	49231	3.24	1.81
South Korea	8798	1297	3.38	1.46
Spain	2333	468	3.24	1.59

Sri Lanka	23621	4818	3.45	2.05
Sudan	10967	0	3.44	NA
Suriname	53973	17159	3.46	2.12
Sweden	422	0	2.77	NA
Syria	291	0	3.38	NA
Taiwan	595	0	3.50	NA
Tanzania	17407	988	3.49	2.07
Thailand	157310	11056	3.44	2.05
Togo	970	0	3.45	NA
Tonga	7915	0	3.39	NA
Trinidad and Tobago	9634	3658	3.49	2.16
Tunisia	31665	5809	3.24	1.32
Turkey	5314	359	3.35	1.42
Tuvalu	4161	0	3.50	NA
Ukraine	32211	2864	3.16	1.24
United Arab Emirates	14272	236	3.54	1.27
United Kingdom	56028	560	3.31	1.89
United States	643610	51933	3.36	1.69
Uruguay	48377	34784	3.25	1.62
USA Caribbean Territories	1443	0	3.50	NA
USA Pacific Inhabited Territories	1345	0	3.51	NA
USA Pacific Uninhabited Territories	449	0	3.43	NA
Vanuatu	5401	0	3.47	NA
Venezuela	72232	34644	3.46	2.12
Vietnam	251378	25429	3.48	2.05
Western Sahara	12333	10763	3.23	1.88
Yemen	35000	803	3.48	1.83

Table 4. All species included in the analysis, along with key attribute information. Attribute information were initially extracted from the FishBase (R. Froese and Pauly 2016)SeaLifeBase (Palomares and Pauly 2016), and/or Encyclopedia of Life (EOL) ("Encyclopedia of Life" 2007)online databases; additional references used to check initial values and fill in missing information are noted.

Scientific Name	Common Name	Minimum Temperature	Maximum Temperature	L_∞	K	Additional References
FISH						
Acanthopagrus berda	Goldsilk seabream	14.6	25.7	56	0.29	
Acanthopagrus latus	Yellowfin seabream	4.9	38.2	35.2	0.17	
Acanthopagrus schlegeli schlegelii	Blackhead seabream	10.4	26.3	50	0.22	
Acipenser gueldenstaedtii	Danube (diamond) sturgeon	10	20	236	0.04	www.orchardfisheries.co.uk/
Acipenser nudiventris	Fringebarbel sturgeon	10	20	200	0.07	
Acipenser stellatus	Starry sturgeon	10	20	218.7	0.08	www.sturgeon-web.co.uk/
Acipenser transmontanus	White sturgeon	10	23.3	610	0.04	(Crocker and Chech 1997; Conte et al. 1988),
Anarhichas lupus	Atlantic wolffish	0	13	152	0.09	(O'Dea and Haedrich 2003)
Anarhichas minor	Spotted wolffish	4	12	190	0.1	(Imsland et al. 2006; Foss et al. 2004)
Anguilla anguilla	European eel	4	33	152.8	0.24	(Sadler 1979)
Anguilla rostrata	American eel	4	25	120	0.33	
Anoplopoma fimbria	Sablefish	1.8	14.6	120	0.25	
Argyrosomus japonicus	Japanese meagre	12	28	200	0.14	
Argyrosomus regius	Meagre	11.9	23	185.5	0.14	
Atherina boyeri	Big-scale sand smelt	6	25	10.9	0.62	

Bolbometopon muricatum	Green humphead parrotfish	26.3	29	125	0.12	
Carangoides malabaricus	Malabar trevally	19.9	28.4	37.3	0.82	
Caranx hippos	Crevalle jack	9.6	27.8	80	0.65	
Caranx sexfasciatus	Bigeye trevally	21	30	74.1	0.24	(Gilbey 2011)
Centropomus undecimalis	Common snook	25	31	140	0.4	
Chaetodipterus faber	Atlantic spadefish	2.5	28	50.4	0.34	
Chanos chanos	Milkfish	15	42.5	180	1.03	https://www.spc.int/aquaculture/ ; http://www.fao.org/fishery/culturedspecies/search
Chelon macrolepis	Largescale mullet	20	28.9	23	0.1	http://www.fao.org/fishery/culturedspecies/search
Coregonus lavaretus	European whitefish	4	29.8	59.7	0.38	(Vielma, Koskela, and Ruohonen 2002)
Coryphaena hippurus	Common dolphinfish	21	30	157.9	1.67	
Cromileptes altivelis	Humpback grouper	26.5	29	65.4	0.35	
Dentex dentex	Common dentex	9.7	17.6	100	0.09	
Dentex tumifrons	Yellowback seabream	10.4	26.3	35	0.25	
Dicentrarchus labrax	European seabass	8	24	77	0.2	
Dicentrarchus punctatus	Spotted seabass	10.5	23.5	70	0.11	
Diplodus puntazzo	Sharpsnout seabream	24.3	24.3	60	0.47	(B. G. Garcia et al. 2011)
Diplodus sargus sargus	White seabream	14.7	18	42.3	0.16	
Diplodus vulgaris	Common two-banded seabream	14.7	19.7	40.8	0.26	

Dormitator latifrons	Pacific fat sleeper	24.6	33	41	0.57	
Eleutheronema tetradactylum	Fourfinger threadfin	27.6	27.7	128.7	0.37	
Epinephelus akaara	Hong Kong (redspotted) grouper	19	30.2	54.5	0.36	
Epinephelus areolatus	Areolate grouper	18.5	28.6	40.6	0.31	http://library.enaca.org/Grouper/Research/Breeding/2000/0803.htm
Epinephelus coioides	Orange-spotted grouper	17	35	108	0.15	(Lin et al. 2008)
Epinephelus fuscoguttatus	Brown-marbled grouper	10	36.5	113.3	0.18	(Cheng, Chen, and Chen 2013)
Epinephelus lanceolatus	Giant grouper	26.3	26.3	270	0.36	Hseu *et al.*(Hseu et al. 2007)
Epinephelus malabaricus	Malabar grouper	19	30.2	163.6	0.8	
Epinephelus tauvina	Greasy grouper	17	29.2	115.4	0.13	http://library.enaca.org/Grouper/Research/Breeding/2000/0803.htm
Evynnis japonica	Crimson seabream	10.4	26.3		0.22	
Gadus morhua	Atlantic cod	0	15	115	0.19	(Schurmann and Steffensen 1992);
Gnathanodon speciosus	Golden trevally	23	29.3	108.2	0.39	saltwater.aqua-fish.net/?gold-trevally
Hippoglossus hippoglossus	Atlantic halibut	0.9	18	470	0.08	(Stuart, Keller, and Drawbridge 2010)
Huso huso	Beluga	10	20	800	0.04	
Konosirus punctatus	Dotted gizzard shad	8.5	27.2	19.7	0.27	
Larimichthys crocea	Large yellow croaker	9	30	80	0.32	

Lateolabrax japonicus	Japanese seabass	13	23	25	0.18	
Lates calcarifer	Barramundi	15	38	176	0.39	
Lethrinus miniatus	Trumpet emperor	21	29.3	80	0.3	
Liza aurata	Golden grey mullet	10.8	18.8	56	0.25	
Liza ramada	Thinlip grey mullet	8	24	62.5	0.26	
Liza saliens	Leaping mullet	9	32	30.5	0.25	(Katselis, Koutsikopoulos, and Kaspiris 2002)
Lutjanus argentimaculatus	Mangrove red snapper	16	30	119.5	0.19	
Lutjanus goldiei	Papuan black snapper	18.3	27.2	100	0.28	
Lutjanus johnii	John's snapper	20.8	26.8	70	0.21	
Lutjanus russelli	Russell's snapper	23.3	26.4	45	0.56	
Megalops atlanticus	Tarpon	4.3	27.5	189.5	0.09	
Melanogrammus aeglefinus	Haddock	2	15.5	74.5	0.27	
Miichthys miiuy	Mi-iuy (brown) croaker	6	25	70	0.32	
Morone saxatilis	Striped bass	6.4	25	200	0.19	(Breitburg et al. 2003)
Mugil cephalus	Flathead grey mullet	8	24	71.2	0.29	
Mugil curema	White mullet	10	29.3	28	0.57	txstate.fishesoftexas.org/
Muraenesox cinereus	Daggertooth pike conger	10	27.9	111.2	0.37	(Golani and Ben-Tuvia 1982)
Mycteroperca bonaci	Black grouper	16	28	133.3	0.15	www.sms.si.edu/irlspec/Mycter_bonaci.htm
Oncorhynchus gorbuscha	Pink salmon	0.3	21	76	0.54	(Robert F. Raleigh and Nelson 1985)
Oncorhynchus keta	Chum salmon	0	23.7	95	0.35	

Oncorhynchus kisutch	Coho salmon	0	24.8	98	0.98	(Carter 2005)
Oncorhynchus mykiss	Rainbow trout	0	29	89.5	0.54	(Molony 2001; Elliott 1982)
Oncorhynchus nerka	Sockeye salmon	0	24.9	84	0.48	
Oncorhynchus tshawytscha	Chinook salmon	0	24.9	120.8	0.54	
Pagellus bogaraveo	Blackspot seabream	9.8	19.7	35.3	0.14	
Pagellus erythrinus	Common pandora	7.1	20.2	37.6	0.2	
Pagrus auratus	Silver seabream	9.2	29.3	130	0.13	
Pagrus major	Red (Japanese) seabream	7.7	22	100	0.15	(Foscarini 1988; Ishibashi et al. 2005; Woo and Fung 1980)
Pagrus pagrus	Red porgy	8.3	25.4	62.9	0.18	
Paralichthys olivaceus	Bastard halibut	14	23	103	0.15	
Platax orbicularis	Orbicular batfish	22	28	53.3	0.56	
Platichthys flesus	European flounder	5	25	43.3	0.37	
Plectropomus maculatus	Spotted coralgrouper	22	28.9	100.3	0.21	
Pleurogrammus azonus	Okhotsk atka mackerel	10	29	50	0.35	
Pleuronectes platessa	European plaice	2	25	100	0.15	(Freitas et al. 2010)
Pollachius pollachius	Pollack	6.5	12.3	130	0.19	
Polydactylus sexfilis	Sixfinger threadfin (moi)	25.3	40	60.7	0.56	(Halwart and Gupta 2004)
Pomatomus saltatrix	Bluefish	6.1	27.4	103	0.17	
Psetta maxima	Turbot	8	20	60.3	0.29	(Imsland et al. 1996; Burel et al. 1996);
Pseudocaranx dentex	White trevally	13.3	26.3	89.3	0.22	
Pseudopleuronectes americanus	Winter flounder	0.8	23.9	39.7	0.38	

Rachycentron canadum	Cobia	26	32	152.8	0.33	(J. B. Kaiser and Holt 2005)
Rhabdosargus sarba	Goldlined seabream	21.1	26.9	63.1	1.36	
Salmo salar	Atlantic salmon	2	28	128.6	0.37	(Elliott and Elliott 2010) ; http://www.fao.org/fishery/culturedspecies/search
Salmo trutta	Sea (brown) trout	0	24	69.2	0.29	(Elliott 1976; Elliott 1982; Elliott and Elliott 2010)
Salvelinus alpinus alpinus	Arctic char	4	22	92.5	0.04	(Elliott and Elliott 2010)
Salvelinus fontinalis	Brook trout	0	25	67.5	0.32	(R.F. Raleigh 1982; Elliott 1982)
Sciaenops ocellatus	Red drum	9.6	26	104.5	0.4	
Sebastes schlegelii	Korean (Schlegel's) rockfish	15	24	65	0.27	
Seriola dumerili	Greater amberjack	3.2	26.8	144	0.23	
Seriola quinqueradiata	Japanese amberjack	18	29	150	0.44	
Seriola rivoliana	Longfin yellowtail (Almaco jack)	18	26.9	114.7	0.56	
Siganus canaliculatus	White-spotted spinefoot	21	34	27.7	1.87	(Grandcourt et al. 2007)
Siganus guttatus	Goldlined spinefoot	24	28	39	1.66	
Siganus javus	Streaked spinefoot	25	28	44.6	0.56	
Siganus rivulatus	Marbled spinefoot	15	28.7	40	0.46	(Galil 2006)
Solea senegalensis	Senegalese sole	15	21	60	0.18	(Campos et al. 2014)
Solea solea	Common sole	5.7	27	50.3	0.35	(Pörtner and Peck 2010)

Sparidentex hasta	Sobaity seabream	17.8	26.3	66.5	0.35	
Sparus aurata	Gilthead seabream	11.5	22.7	70	0.3	
Takifugu rubripes	Tiger pufferfish	10	29	80	0.52	
Thunnus albacares	Yellowfin tuna	15	31	180.6	0.38	(NOAA Fisheries 1999)
Thunnus maccoyii	Southern bluefin tuna	5	30	212.7	0.14	(Patterson et al. 2008); http://www.fao.org/fishery/topic/16082/en
Thunnus orientalis	Pacific bluefin tuna	13.6	29	50	0.16	
Thunnus thynnus	Atlantic bluefin tuna	2.8	31	298	0.12	www.newworldencyclopedia.org/entry/Bluefin_tuna
Tilapia guineensis	Guinean tilapia	14	33	30	2.13	http://www.fao.org/fishery/culturedspecies/search
Trachinotus blochii	Snubnose (silver) pompano	20	31	96.7	0.56	(Kalidas et al. 2012; Wen, Ku, and Wang 2013)
Trachinotus carolinus	Florida pompano	13.2	25.9	64	0.27	
Trachinotus goodei	Great pompano	12	34	150	0.29	(Jory, Iversen, and Lewis 1985)
Trachurus japonicus	Japanese jack mackerel	10	29	31.7	0.35	
Umbrina cirrosa	Shi drum	9.6	26	73	0.63	
BIVALVES						
Aequipecten opercularis	Queen scallop	4.9	19.2	11	0.74	
Anadara grandis (tuberculosa)	Grand ark	26	37.5	63.2	0.14	(Broom 1985; Stern-Pirlot and Wolff 2006)
Anadara granosa	Blood cockle	25	32.8	9	1.8	(Yurimoto et al. 2014; Broom 1985)

Anadara tuberculosa	Black ark	22	31	63.2	0.71	(Nieves-Soto et al. 2013; Stern-Pirlot and Wolff 2006);
Argopecten purpuratus	Peruvian calico scallop	16	20	12	2.32	(Navarro et al. 2000)
Argopecten ventricosus	Pacific calico scallop	20	29	17.5	0.6	(Maeda-martinez et al. 1997)
Aulacomya ater	Cholga mussel	0	25.6	6.3	0.35	(Urban 1994)
Cerastoderma edule	Common edible cockle	6.8	12	5.6	0.58	
Chamelea gallina	Striped venus	6.5	13.1	5	0.43	
Chlamys varia	Variegated scallop	3.5	19.2	9	0.57	
Choromytilus chorus	Choro mussel	20	26.3	5	0.35	(Urban 1994)
Crassostrea gasar	Gasar cupped oyster	18	26	15.4	1.58	(C. D. O. Ramos et al. 2014)
Crassostrea gigas	Pacific cupped oyster	15	30	45	1.15	
Crassostrea iredalei	Slipper cupped oyster	14	34	9	1.58	
Crassostrea madrasensis	Indian backwater oyster	30	45	11.6	1.44	(Rajagopal et al. 2003; Alam and Das 1999)
Crassostrea rhizophorae	Mangrove cupped oyster	24.8	24.8	12	2.79	
Crassostrea virginica	American cupped oyster	-1.6	24.3	30	0.88	
Cyclina sinensis	Oriental cyclina	20	35	5	0.87	(Ying-Jie et al. 2006)
Hippopus hippopus	Bear paw clam	24.7	29.2	40	0.15	
Lyropecten subnodosus	Pacific lion's paw	15.5	25.1	17.8	0.55	(Arellano-Martínez et al. 2011)
Mactra glabrata	Smooth mactra	10	30	27.6	0.02	

Mactra veneriformis	Globose clam	10	30	27.6	0.02	(Yu et al. 2009; Nakano et al. 2012)
Mercenaria mercenaria	Northern quahog (Hard clam)	9.2	24.4	13	0.33	
Meretrix lusoria	Japanese hard clam	5.5	15.9	5	0.47	
Mya arenaria	Sand gaper	4.7	23.6	10	0.29	
Mytilus chilensis	Chilean mussel	12	16	10.2	0.5	(Duarte et al. 2014; Gray, Seed, and Richardson 1997);
Mytilus coruscus	Korean mussel	2.9	20	10	0.21	(Wang et al. 2015)
Mytilus edulis	Blue mussel	-1.4	23.4	11	0.31	
Mytilus galloprovincia lis	Mediterranea n mussel	7.6	9	15	0.58	
Mytilus planulatus	Australian mussel	12.3	21.3	6	0.46	(Allen 1955)
Mytilus platensis	River Plata mussel	13.7	20.9	9	0.73	
Ostrea chilensis	Chilean flat oyster	14	14	10	1.01	
Ostrea conchaphila	Olympia oyster	6	20	12.5	0.47	
Ostrea edulis	European flat oyster	8.4	11.9	12	1.01	
Panopea generosa (abrupta)	Pacific geoduck	8.5	10.2	12.5	0.47	(Hidalgo-De-La-Toba et al. 2015)
Paphia gallus	Rooster venus	21.8	28.3	7.5	0.87	
Patinopecten yessoensis	Yesso scallop	5	23	25	0.93	(Gosling 2003)
Pecten fumatus	Southern Australia scallop	12	21	8.6	1.6	(Heasman, O'Connor, and Frazer 1996; Gwyther and Mcshane 1988)
Pecten maximus	Great Atlantic scallop	7.9	15.9	17	0.56	

Perna canaliculus	New Zealand mussel	18.2	18.2	15	0.6	
Perna perna	South American rock mussel	10	30	17	0.38	http://www.biosecurity.govt.nz/pests/perna-perna
Perna viridis	Green mussel	23.6	23.6	16.5	1.24	
Protothaca staminea	Pacific littleneck clam	9.2	10.2	7.5	0.17	
Ruditapes decussatus	Grooved carpet shell	11.8	11.8	6	0.87	
Ruditapes philippinarum	Japanese carpet shell	10.2	24.7	8	0.56	
Saccostrea commercialis	Sydney cupped oyster	10.8	19.7	22.4	0.93	http://www.fao.org/fishery/culturedspecies/search
Saccostrea cuccullata	Hooded oyster	18.7	25.6	20	1.58	
Saxidomus giganteus	Butter clam	9	11.8	13	0.47	
Scapharca broughtonii	Inflated ark	22	25	17.8	0.26	
Scrobicularia plana	Peppery furrow	9.6	12.3	17.8	0.55	
Sinonovacula constricta	Constricted tagelus	15	20	25.6	0.87	http://www.fao.org/fishery/culturedspecies/search
Soletellina diphos	Diphos sanguin	21.8	28.3	12	0.87	
Tresus nuttallii	Pacific horse clam	2	20	22.5	0.47	(Lauzier et al. 1998)
Tridacna crocea	Crocus giant clam	26.8	28.4	15	0.17	
Tridacna derasa	Smooth giant clam	28.5	28.5	60	0.11	
Tridacna squamosa	Fluted giant clam	24.5	28.9	45	0.22	
Venerupis aurea	Golden carpet shell	7.2	10	4.5	0.55	
Venerupis pullastra	Pullet carpet shell	10.3	12.3	5	0.47	

Venerupis rhomboides	Banded carpet shell	7.2	10	4.5	0.55	
Venus verrucosa	Warty venus	9.6	15.9	17.8	0.25	

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III. Farming Endangered Species:

Looking beyond Rhinos, Tigers, and Bears

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A. Introduction

Iconic species such as the elephant, rhinoceros, and tiger face threats of extinction from continued poaching driven by illicit international trade. Despite significant conservation effort and investment in anti-poaching measures, poaching pressure on high demand species is continuing (Challender and MacMillan 2014). One of the major drivers is the lure of lucrative profits on the black market; prices can be very high for rare species that are highly coveted in international trade (Hall, Milner-Gulland, and Courchamp 2008). For example, a single high quality totoaba, a critically endangered fish whose swim bladder is in high demand in the Asian medical trade, can fetch over $10,000 USD on the black market (Environmental Investigation Agency 2016). The global illegal trade in wildlife products is massive and widespread, with a total estimated annual value of $15-20 billion USD (UNEP 2016).

In the face of these conservation crises, one potential solution has been proposed repeatedly in both the scientific literature and popular press – reduce prices by farming endangered species (e.g. Bulte & Damania 2005; Damania & Bulte 2007; Latimer 2015; Tensen 2016). Recently, proposals to open up legal trade for rhinoceros horns and elephant ivory have renewed debate about the interactions between legal markets, illegal markets, and conservation of hunted species (Lusseau and Lee 2016; Collins, Fraser, and Snowball 2015). The concept is that a legal market (supplied by farming, ranching, or legal stores of a product such as ivory) will increase supply and lower prices, which should decrease poaching incentives. Although this idea is appealing, the majority of theoretical work and case studies have come to the conclusion that farming is unlikely to help the endangered species, and in some cases may even contribute to its decline (Crookes and Blignaut 2015; Kirkpatrick and Emerton 2010; Livingstone and Shepherd 2016; Damania and Bulte 2007; Gratwicke et al. 2008; Brooks, Roberton, and Bell 2010; Tensen 2016). A growing legal market can make the problem worse by increasing competition between suppliers, decreasing the stigma associated with the wildlife product, or providing opportunities for laundering poached products through legal trade channels.

The limited conservation value from farming endangered species, however, has been concluded primarily through studies examining very slow growing, low fecundity species, such as rhinoceroses and tigers. In these cases, farming is very expensive – typically far more expensive than poaching. As a result, there is no potential to greatly reduce prices in the market without large subsidies, which likely limits any potential conservation benefits from legal markets. Stepping back and looking beyond these high-profile endangered species, there are many examples of endangered species where farming could produce animal products at far more competitive prices. This raises the question of whether the potential benefits of wildlife farming as a conservation tool are underappreciated because we have not pursued the most promising species targets. Here, we critically examine the conservation implications of the relative costs of hunting and farming threatened species, focusing specifically on how hunting and farming costs can be used to predict the potential upside of conservation-motivated farming. Finally, we examine which biological characteristics of endangered species may indicate a high potential for conservation farming, and the role of ongoing poaching enforcement in the success of this strategy.

B. Theory- The Importance of Costs

To explore the circumstances when legal farming of a threatened species could be a market solution for species conservation, we develop a series of simple conceptual models for hunting and farming a threatened species. Initially, we assume that hunting and farming can produce products that are substitutable in the market and share a common downward sloping demand curve. We begin with a bioeconomic model for hunting drawn from theory for an unregulated, open access fishery (Clark 2010). Hunting a threatened species is (usually) illegal and therefore takes place outside of any formal management structure, making an open-access fishery an appropriate starting model framework.

We assume a population (of size x) reaches a pre-farming bioeconomic equilibrium (x_{BE1}) at the point where x equals the ratio of cost per unit effort *(c)* to price per individual animal (p) multiplied by catchability (as measured by the catchability coefficient, q, which describes the efficiency of capture for the wild population per unit effort):

$$x_{BE1} = \frac{c}{pq} \qquad \text{(eq.1)}$$

The cost of hunting (c) a protected species represents the sum of the fixed operating costs per unit effort plus the product of the fines or other punishment for poaching and the probability per unit effort of being caught. Therefore both the severity of punishment and the effectiveness of enforcement drive up the cost of hunting.

For this simple model, we assume that poachers (and farmers) are price takers, and that hunting will take place as long as it is profitable on average. At equilibrium the price of hunting stabilizes where profit approaches zero, and the price that can be obtained for the product equals the cost of producing it. Therefore, we can also think of p as the cost of hunting the marginal animal at equilibrium.

As with hunting, farming of the threatened species will occur so long as it is profitable—i.e., when the marginal price per animal produced is greater than the cost of farming that animal. We assume that costs per unit of production are fixed as production increases (i.e. a horizontal supply curve). See appendix 1 for discussion of the implications for a supply curve of farmed product where cost per unit changes with quantity produced. Using these models, we can now examine how the initial relative costs of farming and hunting an endangered species can help predict when farming could promote species' recoveries.

While much of the literature is focused on animals that can be hunted more cheaply than they can be farmed, when farming can produce a product below the cost of hunting there is a much greater potential for farming to relieve hunting pressure (Bulte and Damania 2005; Tensen 2016). With a horizontal supply curve, we assume that the production of the farmed product will expand until it is no longer profitable, at which point the quantity supplied equals the quantity demanded at the cost of farming production per unit. The cost of farming production thus becomes the market price, assuming that the farmed and wild products are perfect substitutes and share the same market price—see appendix 2 for a more detailed discussion of this assumption. Since hunting is more costly than farming, hunting will no longer be profitable at the margin and will cease. This will allow the population of the exploited species to recover.

As the wild population increases, the cost of hunting could decline; for example, less effort may be needed to hunt or the penalties associated with illegal activity could decline if fines are lowered or enforcement becomes less effective during the rebound. If the cost declines enough so that hunting is cheaper per unit than farming, hunting will start again and displace farming. As hunting depletes the wild population, the cost of hunting is likely to increase; for example hunting effort or penalties increase. Eventually we will reach a new post-farming bioeconomic equilibrium (x_{BE2}), where the cost of farming the animal (π) now substitutes for the pre-farming market price:

$$x_{BE2} = \frac{c*(1-r)}{\pi q} \qquad \text{(eq. 2)}$$

The addition of *r* represents the discount to the cost per unit of hunting that may occur between the two equilibriums (e.g. a value of $r = 0$ represents that there has been no change in cost per unit effort and a value of $r = 0.4$ represents a reduction in cost per unit effort of 40%). From this equation, we can see that the lower the costs of farming (π) and the higher the cost per unit effort of hunting (c), the higher the potential population recovery post farming. In addition, species that are less efficient to hunt (as measured by q) have more recovery potential. However, if the per unit cost of hunting declines, the predicted recovery would be reduced.

To forecast the expected population recovery from farming we define the percentage population increase (x_{inc}) between the period before farming was introduced and the period post farming:

$$x_{inc} = \left(\frac{x_{BE2} - x_{BE1}}{x_{BE1}}\right) * 100 \qquad \text{(eq. 3)}$$

Substitution provides a convenient expression of population increase as a function of p, π, and r expressed as a percentage:

$$x_{inc} = \left(\frac{p(1-r)}{\pi} - 1\right) * 100 \qquad \text{(eq.4)}$$

The key value in Eq. 6 lies in the replacement of several variables that can be difficult to measure (specifically *q)* with a ratio that is easier to communicate and measure. The ratio between costs can then be used to estimate the upside benefit of establishing conservation farming or can help elucidate the cost differential between farmed and wild production that would be necessary to achieve a conservation target. For example, given a goal to triple the population of a given species where the current cost of poaching an animal is $100, farming could be a tractable solution for achieving this goal if an animal could be farmed for $33 or less (assuming there is no reduction in the per unit cost of hunting).

In this simple model, the costs of hunting vs farming a species demonstrates the potential upside for conservation success through farming of threatened species. While the real world offers significant complexities beyond the scope of this model, if farming can be done cheaply enough and scaled quickly, some of the key concerns about the efficacy of wildlife farming diminish. Specifically, one concern with wildlife farming is that the introduction of a legal farmed product could reduce the stigma associated with an animal product, resulting in an increase of demand (e.g. Livingstone 2016). However, as long as farming can expand to meet this demand without the farming costs rising above the costs of hunting, then an increase in demand should not have a negative effect on the success of farming as a conservation tool. Another oft-cited concern, that farming can have a negative effect on the wild population, such as through capture of adults or juveniles to replenish or diversify the farming stock (e.g. Haito 2007) also does not necessarily doom conservation-motivated farming as a solution. If farming effects the wild population, but the population growth rate is still positive, then the equilibrium post-farming population should still be reached, it would just take longer. However, any impact on the wild population may make the species more vulnerable to other stressors (such as climate change, habitat destruction, etc.), and therefore may not be acceptable.

C. Application and Discussion

1. Farming Costs: Time Is Money

For many endangered species, especially those for which farming has never been attempted, we do not have a clear indication of the potential costs of farming the animal. However, we can consider which species might be suitable for farming by looking at the types of species characteristics that have the strongest influence on farming costs. One important issue is the time in captivity before harvest. As the time in captivity increases, so do the costs invested in the animal (due to feed, space, labor, etc) and the costs associated with depreciation of money invested in the animal (Harris & Newman 1994). In nature, species have an enormous range of growth strategies. However, if we look at the small subset of wild species that have historically been commercially farmed, they are overwhelmingly species that grow to a commercially valuable size relatively quickly. This is a key constraint on profitability. Fast maturation is often associated with high growth rates and fecundity, all characteristics that would make a species suitable for cost-effective farming. Indeed, looking across the most commonly farmed and traded land species we found that these animals are harvested from within a few weeks to a few years of birth; typically under a year (Salmon 1979; Knízetová et al. 1994; Dalle Zotte & Ouhayoun 1998; Dhanda et al. 2003; Baéza et al. 2012; FAO). Time to harvest for aquatic species is slightly more variable, however considering only the post-nursery grow out phase, the most commonly farmed aquatic animals are usually harvested in less than two years, and often in less than one year (FAO 2017). The relatively fast growth and maturation of many commercially farmed animals contrasts with the life history of many threatened species for which farming has been suggested (Fig 1). One of the notable examples of successful wildlife farming, the short-tailed chinchilla, has a time to harvest of approximately nine months (Bieniek et al. 2011). This is in line with other commercially farmed species, making it unsurprising that the chinchilla could be a successful farming candidate.

While much of the conservation farming literature has focused on land animals, only a handful of land animals are farmed at a large scale, highlighting the challenge of finding species that are suitable for farming (Diamond 2002). In contrast, over 500 aquatic species are already farmed, and there is wide diversity in the types of species that are raised profitably by aquatic farming (i.e. aquaculture) (FAO 2016). In addition, aquatic species, on average, have a faster rate of domestication and higher success rate than land animals (Duarte, Marba, and Holmer 2007), making the case that conservation farming should more closely consider the potential of aquatic species.

Intensely exploited aquatic species such as the totoaba and seahorse have already been successfully bred in captivity and are being produced at a small scale. The fast growth rate of the totoaba (Román Rodríguez and Hammann 1997) and relatively rapid maturation of seahorses (FAO 2017) signal that they may be able to be produced at a large scale and at competitive price, though more in-depth analysis of their farming potential (particularly in terms of the time needed to produce a high quality totoaba bladder) would be necessary. Aquaculture potential is also high for a variety of threatened marine species that have been under capture pressure due to their high value in the aquarium trade (Tlusty 2002). The Banggai cardinalfish is a notable example of a species that is endangered primarily due to the aquarium trade and has growth and reproductive characteristics that make it suitable for culture. Until recently, some cardinalfish were bred in captivity, but not at a price or scale that was competitive with wild capture. However, recent development of large-scale aquaculture for the Banggai cardinalfish in Thailand shows potential for producing farmed fish at competitive prices (Conant 2015). This example demonstrates an important opportunity for conservation intervention: providing assistance to scale-up farming and making production more efficient may provide the jumpstart that is needed for farming to achieve low enough costs that it can have meaningful conservation benefits.

2. Hunting Costs: Enforcement Matters

Returning to our base model, the overall cost of hunting an animal depends on the ease of capture, the costs per unit effort of hunting, and the population size. Animals that are difficult to find, are highly dispersed from one another, or are far away from human settlements are likely to be more difficult to catch. In addition, those that require specialized equipment or significant manpower to hunt, will also have higher hunting costs. Similarly in the oceans, those species that require more labor or fuel intensive fishing methods due to depth, distance from shore, or behavior are generally more expensive to fish (Lam et al. 2011). Species characteristics such as aggregation behavior, habitat, animal size and behaviour would all influence the cost of hunting.

Beyond these biological characteristics of the hunted species, one of the major costs associated with illegal hunting – the risks associated with breaking the law – depends mostly on management effectiveness. Better enforcement and higher penalties can drive up harvest costs greatly to increase the conservation benefits of farming. However, enforcement comes at a cost to the enforcers, which may be hard to sustain, especially if the species is recovering. In addition, the introduction of farming may also reduce the risk costs of hunting if enforcement effectiveness declines when illegal product evades detection in legal trading channels (Fischer 2004). If the hunting costs per unit effort decline while a species is recovering, the species will have less total recovery than would be predicted from the initial costs of hunting and farming.

3. Will Farming Work for Conservation?

Farming species to promote conservation is not a panacea, but we can predict that success is most likely when farming is much cheaper than hunting (e.g. Tensen 2016). Identifying species than lend themselves to farming is an important first step, and would help conservationists re-focus this strategy in a direction that is more likely to be successful. Many of the same characteristics that make a species expensive to farm (such as slow growth rates, low fecundity) also make it more vulnerable to a given level of human impacts, which makes the pool of potential candidates seem constrained. Nonetheless, by looking towards aquatic environments we have shown that there are species that are both threatened by human exploitation and have the characteristics that would make farming a potentially promising conservation solution.

For species that do not currently have a low enough ratio of farming to hunting costs to achieve conservation benefits from farming, increasing the consequences of breaking the law can make farming a more tractable solution. For some species, such as the rhino, the cost related to hunting would have to be extremely high, which could only be achieved through greatly increasing fines and enforcement. For example to achieve a doubling of the population, the current cost of hunting a kilogram of rhino horn would have to be more than

$120,000[1]. In contrast, we suggest that the current cost of hunting an adult (100kg) totoaba would need to be about $600 to see a population doubling due to farming[2] . While increasing the cost of hunting to the point that hunting is more expensive than farming may be unrealistic for the rhino, coupling increased enforcement with a captive breeding program could be far more realistic for a species like the totoaba.

As demonstrated in the preceding example, if we can estimate just the farming or hunting costs for any threatened species, we can use the equations presented in this paper to estimate the cost levels that would be needed to make conservation farming a tractable strategy. While investment in anti-poaching efforts could drive up the costs of hunting, these investments would need to be ongoing to offer long-term protection. As an alternative, investing in farming, either in short term research and development, or longer term to subsidize the costs of farming could provide similar conservation improvements (by driving down the relative costs of farming to hunting) and be more cost effective in the long term. In certain cases, initial farming costs may be artificially high due to the extra steps needed to certify the farming of an endangered species so that it can be legally traded(CITES 2010). Conservation efforts to establish and certify wildlife farms for international trade may make wildlife farming more feasible.

Further focus on the relative costs of farming different types of animals can help direct conservation farming efforts on the species that show the most promise from a cost

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[1] Based on the cost of rhino farming (approximately $31,000 kg^{-1}) as reported in Crookes and Blingnaut (Crookes and Blignaut 2015), and that a single hunted rhino wold produce 2 kgs of horn. Assuming no change in per unit effort cost of hunting.

[2] Based on a cost of 3 Euros/kg^{-1} for farming red drum (which is a fish in the same family as totoaba) in semi-industrial farm in Reunion (Mariojouls et al. 2008). Assuming no change in per unit effort cost of hunting.

standpoint. Before conservation farming should be established for any species, in depth analysis of species and market specific conditions would need to be carefully considered. However, none of these issues are likely to matter if farming cannot be done profitably. So far, much of the literature on farming endangered species has focused on slow growing, low fecundity animals for which this approach was unlikely to bring much conservation success. Going forward we need to look beyond these large land mammals to identify species where farming has far greater conservation potential.

D. Appendices

1. Average and marginal costs of farming

In figure A1(a) we can see how the average costs of farming (blue lines) and hunting (red line) can be used to estimate whether farming or hunting can be produced for lower cost at any given level of production in the long term. As is standard, the long term supply curve for hunting is backward bending because beyond the maximum sustainable yield, it will cost more to yield less product as the population diminishes (Copes 1970). Initially, we have assumed that the marginal costs of farming are constant, and do not change with the quantity produced.

If the marginal cost of farming is always less than the cost of hunting (line 3), then farming will fill all production and hunting will never take place. The opposite is true when hunting is always cheaper than farming (line 1): farming would almost never make sense from a market perspective unless the species was on the brink of extinction. However when farming is less expensive than hunting only when the population is reduced to some point (line 2), then eventually an equilibrium will exist where the two marginal cost lines meet:

hunting will take place when it is less expensive (when the population is large); beyond this point farming will meet the rest of the demand.

In Panel B we have introduced line 4, which assumes an upward sloping marginal cost curve for farming. As long as the marginal cost curve of farming increases more slowly than the marginal cost curve of hunting, slightly upward sloping marginal costs of farming will not make a difference to the conclusions. However in line 4, the marginal cost of farming is increasing more steeply than the marginal cost of hunting at low production levels, which causes the marginal cost curves to cross twice. In this example, a small amount of farming will take place even at low levels of output, but production will not become large until after the marginal cost lines have crossed a second time. At high levels of production, all additional output will come from farming.

2. Imperfect Substitutes

In order for farming to have a market-based effect on the price for an endangered species product, there needs to be some effect from the availability of a farmed product on the demand for the wild product. In cases where the farmed product does not act as a substitute for the wild product (e.g. Drury 2009) conservation motivated farming would not be a good strategy (Tensen 2016). In the base model, we assumed that the two products are perfect substitutes and are indistinguishable in the market. However, in some cases these two products may have separate demand curves, but the supply of one effects the demand of the other.

In the simplest example, the two products may have parallel demand curves and the supply of one can fully fulfil the demand of the other at a constant rate of substitution. In this case they are still substitutes, but they command different prices in the market. For example, if consumers would be indifferent to pay p for the wild product or $f*p$, where f is a constant between 0 and 1, for a farmed product then the post farming population equilibrium could be described as:

$$x_{BE2} = f * \frac{c}{\pi q} \qquad \text{(eq.5)}$$

Therefore, it is clear that the closer f is to 1, the higher the post-farming equilibrium population that would be expected from introducing farming. As long as f is not small enough to cause x_{BE2} to fall below x_{BE1}, we can expect that there will be a conservation benefit from farming. However the cost difference between the farmed and wild product will need to be larger in order to see an equivalent population increase.

In some cases the substitutability between the two products is more complex in that the supply of one product effects the demand of the other, but does so in a variable way along the supply curve, in which case the two products are referred to as imperfect substitutes. In this case f in equation S1 above would refer to a function relating the supply and price of the two products. The form of this relationship can vary, but in general the same principal as the fractional substitutes remains: the closer the farmed product is to the wild, the more our model will hold true.

E. Figures

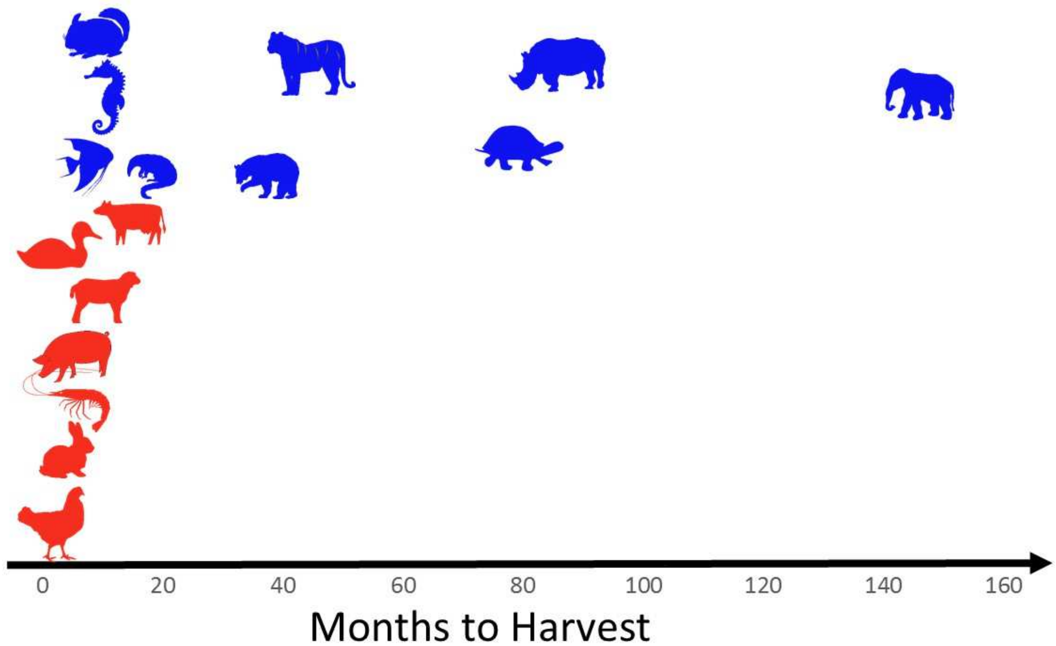

Figure 1. Typical time to harvest for commonly farmed non-threatened land animals (red) and for species for which conservation farming has been suggested or attempted (blue). When the typical time to harvest is not known for a species, time to maturity was used as a proxy.

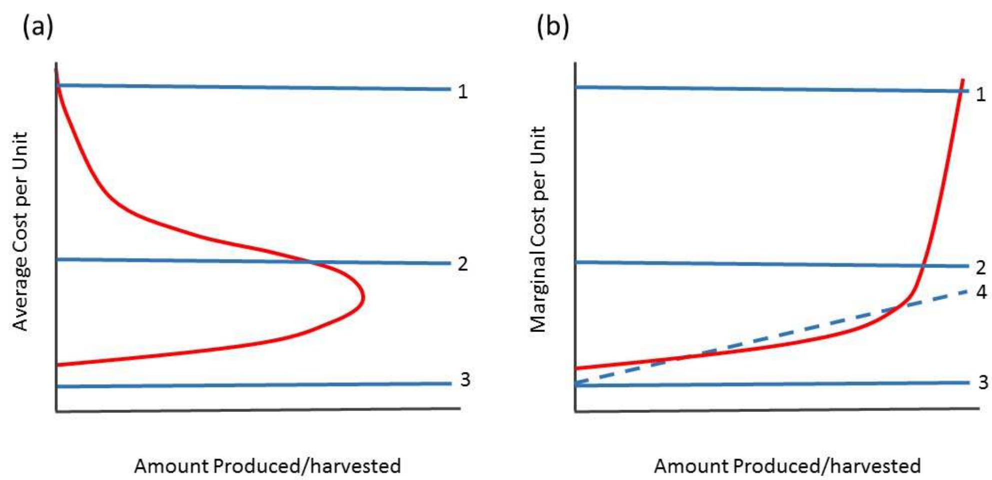

Figure A1. The long term average cost (panel a) and marginal cost (panel b) per unit of production for farmed (blue line) and hunted (red line) species. Lines 1,2,3, assume a constant marginal cost of farming. Line 4 assumes an increasing marginal cost of farming.

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