

Diversity and Resilience of Sea Gardens Across the Pacific Ocean

**by
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Abstract

In a time of rapid global environmental change, it is important to identify the practices that promote resilient social-ecological systems. Indigenous systems of stewardship offer insight into social-ecological resilience given that they reflect long-term use and adaptation over periods of environmental change. To gain insight onto what practices can support resilient food systems, we analyzed twenty-one Indigenous mariculture innovations from around the Pacific Ocean. We examined the extent to which latitudinal patterns in species diversity influence the diversity of species harvested within these systems. We also assessed the diversity of life history traits, trophic groups, modes of reproduction, migration strategies, and population growth strategies that exist among the species cultured within these innovations and the diversity of management strategies used to maintain them. Lastly, we compared these social-ecological attributes of mariculture diversity to contemporary commercial aquaculture practices. We found that globally, Indigenous mariculture systems cultivate a diversity of species with a range of ecological and life history traits, unlike contemporary commercial industrial mariculture systems which rely on fewer species and are thus less biologically diverse. We also found that the diversity of species cultivated across the Pacific Ocean was not driven by a latitudinal gradient in species diversity suggesting that these biodiverse food systems are not incidental, but rather are the result of intentional stewardship rooted in a diversity of management practices informed by observations and experimentation and honed over many generations. Our research demonstrates the importance of biodiversity in resilient social-ecological systems, and that building resilient and biodiverse coastal food systems must include the lived knowledge and leadership of Indigenous People.

Keywords: Social-ecological resilience; Indigenous stewardship; Marine food systems; Marine ecology; Mariculture; Aquaculture

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Statement of Positionality and Identity

I am a non-Indigenous person with mixed European ancestry, and a settler. I grew up in what is called the United States, on land stolen from Indigenous Peoples. I was educated in Western, capitalist, and colonial paradigms under patriarchy and white supremacy. White supremacy explicitly and implicitly grants privilege and power to Whiteness while discriminating against and devaluing the knowledge of non-Western cultures. This has biased my beliefs, understanding and assumptions about the world, and I still have a great deal of unlearning to do.

As a non-Indigenous person conducting research about Indigenous systems of management, I am lucky and privileged to be part of this conversation. I hope that my research advances agendas of decolonization and revitalization by pointing to the lived knowledge, experiences, and authority of the Indigenous stewards of these places.

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Introduction

In a time of accelerating loss of ocean biodiversity and global environmental change, there is a need to identify the practices and strategies that promote biodiverse and resilient social-ecological systems (Folke et al., 2021; Hughes et al., 2013). It is well-established that diversity is a key characteristic of social-ecological resilience because it facilitates greater adaptive capacity under changing conditions (Biggs et al., 2012; Kotschy et al., 2015; Nyström et al., 2019). For example, in marine systems, diverse fisheries portfolios allow harvesters to adapt to ecological and social disturbances, and more biologically diverse ecosystems allow for a more stable delivery of ecosystem functions (Cline et al., 2017; Isbell et al., 2015). Studying diversity within resilient social-ecological systems can help identify what practices are more likely to sustain productivity when a system is confronted with change (Lepofsky & Salomon, In Press).

Resilience refers to the ability of a system to recover from unexpected change and to maintain its functioning and identity by adapting to a disturbance (Biggs et al., 2012; Liggs et al., 2015). Specifically, a resilient social-ecological system adapts to disturbance and reorganizes to retain vital ecosystem functions that support human well-being (Biggs et al., 2015; Chapin et al., 2010; Folke et al., 2016; Poe et al., 2016; Walker & Salt, 2012). Social-ecological resilience emphasizes the embedded and linked human-nature system.

Social-ecological systems are considered self-organizing and complex adaptive systems that exhibit non-linear behavior and emergent properties between components (Biggs et al., 2012; Levin, 1998). Interactions between the components of complex adaptive systems can feed back and influence subsequent interactions, adding uncertainty and non-linearity to the system (Levin, 1998; Mahon et al., 2008). Diversity confers social-ecological resiliency because it provides heterogeneity, and thus more pathways to adapt and recover from unexpected perturbations within a complex system (Kotschy et al., 2015).

A hallmark of Indigenous stewardship of food systems is diversity, which encompasses species diversity as well as a variety of management strategies along a continuum of habitats (Armstrong et al., 2021; Hoffman et al., 2021; Marshall et al., 2018; Schuster et al., 2019). For example, on the Oregon coast, fishing weirs were

operated year-round and targeted both resident and migratory species in estuaries, rather than solely relying on salmon for food (Byram, 2002; Tveskov & Erlandson, 2003). In Hawaii, Indigenous Hawaiians employed complex food intensification strategies across a variety of habitats in terrestrial and aquatic environments (Winter et al., 2020). Fish were cultivated along a salinity gradient; from inland freshwater ponds (loko i'a kalo) within taro fields to help reduce pests and promote soil enrichment for taro, all the way to large seawater ponds (loko kuapa) along the coast (Costa-Pierce, 1987). This diversification of species and cultivation techniques across different habitats promotes resiliency by providing the ability to adapt during unexpected environmental changes (Berkes, 2007). Understanding how humans have secured food production while encouraging environmental feedbacks that promote productivity is important in the context of global food security. Studying systems that are diverse and socially-ecologically resilient can provide insight and innovation to promote resiliency in other regions.

Western conservation science typically considers human-altered environments a recent and destructive phenomenon on an otherwise pristine and unaltered planet (Bliege-Bird & Nimmo, 2018; Williams et al., 2020). This perspective ignores the stewardship of landscapes by many Indigenous Peoples, who have long been selectively transforming and enriching local biodiversity and ecosystems in complex and enduring ways (Armstrong et al., 2021; Hoffman et al., 2021; Jackley et al., 2016a; Marshall et al., 2018). Multiple lines of evidence demonstrate that Indigenous Peoples all over the world have been stewards and engineers of ecosystems for millennia, and have engaged in management to increase the productivity of the local environment (Armstrong et al., 2022; Balée et al., 2023; Jackley et al., 2016a; Lepofsky et al., 2021; Palace et al., 2017). These management actions are part of larger goals and objectives, and can be understood as a spectrum of human influence, with a gradient of intensity and influence on the environment (Lertzman, 2009). In these management systems, people were not passive recipients of the environment but are active engineers of ecosystem processes and drivers of local diversity (Boivin et al., 2016). For example, in Australia, Indigenous fire stewardship creates greater landscape diversity and heterogeneity, leading to greater abundance of a keystone lizard species despite high harvest pressure (Bird et al., 2013). On the Atlantic coast of North America, pre-contact shell middens elevated soil nutrients and increased local plant species richness (Cook-

Patton et al., 2014). Along the Pacific coast of North America, clam gardens double the productivity and abundance of edible clam species by expanding and enriching ideal intertidal clam habitat (Groesbeck et al., 2014). In these contexts, humans have been in relationship with their local environment for millennia, altering and managing it to increase productivity and produce a stable food supply despite environmental and social change.

Indigenous systems of stewardship offer insight into social-ecological resilience given that they are built on generations of accumulated knowledge and wisdom and have persisted through times of environmental change (Berkes et al., 2000; Turner & Reid, 2022). Along the Pacific coast, Indigenous Peoples have maintained intricate relationships and management practices with local intertidal environments for millennia, and these practices have helped enable a predictable and long-term food supply (Gauvreau et al., 2017; Jackley et al., 2016; Kobluk et al., 2021; Reeder-Myers et al., 2022). Some of these strategies include mariculture innovations: coastal technologies such as tidal fish traps, fish weirs or sea gardens which are embedded within a suite of cultural, spiritual and governance practices (Lepofsky & Caldwell, 2013a; Mathews & Turner, 2017). Archaeological evidence has shown that these innovations lasted through changes in sea level, changes in temperature, and other environmental variability (Holmes et al., 2022; Toniello et al., 2019).

Global patterns of species richness and biodiversity are the result of ecological, evolutionary, and climatic processes over hundreds of thousands of years. Notable biogeographical patterns like the latitudinal diversity gradient describe the striking increase in species richness for all taxa from the Earth's poles to the equator (Hillebrand, 2004). Additional studies have shown that in marine environments, warmer sea surface temperatures are associated with higher biodiversity (Gagné et al., 2020; Tittensor et al., 2010). Studying the patterns between global biodiversity and the environmental mechanisms that drive it can provide perspective for conservation and management, especially in the face of global climate change.

Understanding how humans have secured and managed marine resources in the past is important in building resilient food systems during environmental change. To lend insight into what makes for resilient resource management systems, we analyzed twenty-one Indigenous mariculture innovations from around the Pacific Ocean (Figure 1)

(*Sea Gardens Across the Pacific*, 2022). We investigated how global patterns in the natural environment might influence biodiversity within these mariculture innovations. We assessed the diversity of life history and ecological traits amongst the species cultivated, as well as the diversity of management strategies within these management systems. Finally, we assessed the species richness of these innovations compared to the species richness in commercial industrial mariculture. We asked the following questions: 1) Does the diversity of species cultivated within Indigenous mariculture innovations follow global patterns of marine biodiversity driven by latitude and sea surface temperature? 2) What is the diversity of trophic levels, reproductive guilds, migratory strategies, population doubling time, thermal ranges, and management strategies amongst the species cultivated? And 3) How does the species diversity within Indigenous mariculture systems compare to that of commercial industrial mariculture today? We predicted that there would be weak evidence for an effect of latitude and sea surface temperature on the diversity of species cultivated. For question two, among ancestral mariculture innovations, we also expected relatively more low trophic level species with less complex reproductive needs, non-migratory species, and/or species with lower population doubling times. Alternatively, given that these systems are part of a linked social-ecological system, we also predicted there maybe evidence for a broad range of species cultivated from each of these categories. Finally, due to the values of longevity of harvest and sustainability within many Indigenous management systems, we predicted that there would be a higher number of species cultivated in Indigenous mariculture systems compared to commercial industrial mariculture (Atlas et al., 2021b). This synthesis of resilient management systems, which span thousands of years and thousands of kilometers of coastline, shed light onto what practices can support resilient food systems into the future.

Methods

Study Area

The mariculture innovations examined in this study represent a Pacific-wide compilation of mariculture technologies. They encompass innovations located from 58N (Intertidal Fish Traps of Southeast Alaska) to 55S (Corrales de Pesca of the Chiloé archipelago in Patagonia) (*Sea Gardens Across the Pacific*, 2022). The locations of unique innovation sites span the breadth of temperate, subtropical, and tropical climates, and currently experience average sea surface temperatures ranging from 10°C-29°C. The source collection by no means represents all mariculture innovations across the Pacific. However, they collectively reflect a diversity of technologies across many marine environments.

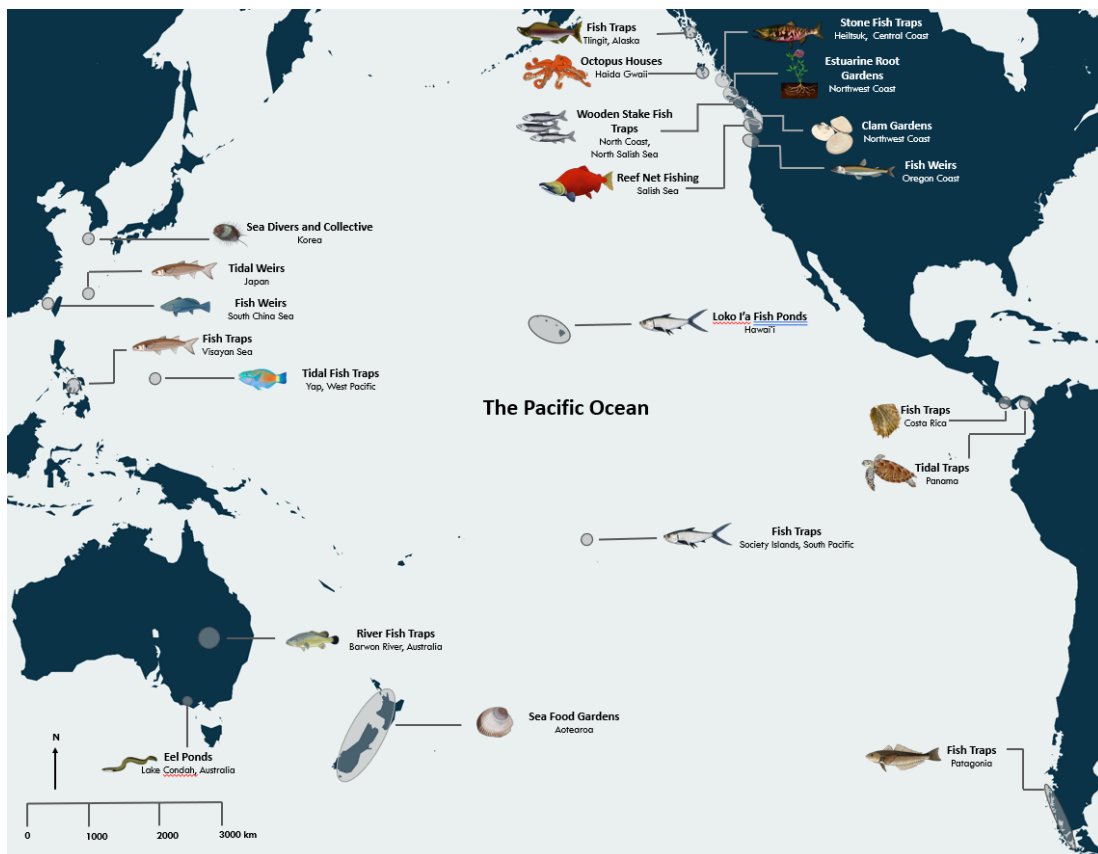


Figure 1 Locations of the 21 Indigenous mariculture innovations across the Pacific Ocean from which this analysis was based.

Data Collection

Species Richness

To classify the species harvested in each mariculture technology, we conducted a systematic review of published papers, books, and government reports (n = 282) gathered by experts from the Pacific Sea Garden Collective (2022). These included natural and social science researchers and practitioners, both Indigenous and non-Indigenous. We made one record for each species, family, or class explicitly stated as being currently or previously stewarded using the innovation technology. In areas where there is a limited published ethnographic record or remaining knowledge holders (e.g., Costa Rica, Panama), we included species that were observed within the mariculture innovations by researchers today and present in the nearby (<50km) archaeological record. We recognize, however, that faunal remains represented in the archaeological record will likely encompass marine species not influenced by the Indigenous mariculture innovation studied. We calculated gamma species richness per innovation by summing the number of species found to be associated with each unique innovation.

Species Traits and Spatial Data

For each species documented, we gathered species-specific ecological and biological information using global fish database FishBase (Froese and Pauly, 2023) and global invertebrate database SeaLifeBase (Palomares and Pauly, 2022). Specifically, we gathered data on each species' trophic level, migratory strategies, population doubling time, reproductive guild, preferred thermal ranges (Table A1).

Spatial Data

For each unique mariculture innovation, we calculated a latitudinal midpoint and sea surface temperature. The latitudinal midpoint was calculated from spatial polygons, which encompassed the range within which each unique innovation exists. These ranges come from published maps from the same body of literature as the species dataset, and we prioritized Indigenous territory maps over those of colonial government systems. Latitudinal midpoints (N-S/2) were calculated from these spatial polygons.

We acquired sea surface temperature data from the European Space Agency to calculate the average monthly mean sea surface temperature from 1990-2010 (Merchant et al., 2019). We used the same spatial polygons as the species richness dataset.

Industrial Mariculture

We retrieved industrial mariculture data from 1980-2009 using the Sea Around Us database (Pauly, Zeller, Palomares, 2020). Industrial mariculture data is defined as “production that is commodity-driven and export-based”, with a minimum 1 tonne per year of total wet weight (Pauly, Zeller, and Palomares, 2020; Campbell & Pauly, 2013). This database excludes artisanal and subsistence mariculture, freshwater aquaculture, and kelp production. We used similar spatial parameters as the Indigenous mariculture data. Since the industrial mariculture data on the Sea Around Us database is by region, province, or state whereas our dataset is by Indigenous territory, there are a total of $n = 14$ sites for industrial mariculture compared to $n = 21$ for Indigenous mariculture.

We chose to compare Indigenous and industrial mariculture owing to their similarities in technologies and methods; these similarities among mariculture approaches were better pairings than industrial fishing and Indigenous mariculture, for example.

Management Practices Within Mariculture Systems

To assess the diversity of management practices within the Indigenous mariculture innovations, we pooled management categories using Indigenous marine resource management literature from the Northwest Coast of North America (Lepofsky et al., 2017; Lepofsky & Caldwell, 2013b; Mathews & Turner, 2017). We chose this body of literature because these systems have been extensively studied and include multiple lines of evidence (ethnographic, archaeological, and paleo-ecological). We created a table of management strategies and asked experts from the Pacific Sea Garden Collective to fill in “yes”, “no”, or “no information” regarding the strategies used in each mariculture technology (Table B1).

To explore the types of innovations within our dataset, we further classified each innovation as “pond”, “garden”, or “fish traps/weirs”. A pond refers to the construction of pools and channels to breed and grow different species for later harvest (Costa-Pierce, 1987). We defined fish traps or weirs as structures built into rivers or intertidal environments to block, direct, catch, or strand fish (Moss, 2012). Gardens are intertidal areas constructed or altered to extend and enhance available habitat, often with joined tending and cultivation practices (Deur et al., 2015).

Publication Bias

Publication bias refers to research in the published literature not representing the population of completed studies. Some mariculture innovations are more thoroughly documented in published literature than others. To ensure that our study did not measure higher species richness in mariculture innovations with published literature, we quantified the relative amount of research effort for each mariculture innovation using the number of papers published for each unique innovation. We included “number of published papers” as a covariate in our model determining the relative effect of latitude and sea surface temperature on species richness.

Biases, Assumptions, and Limitations

Data Sources

Additional bias in our data sources exists. We used available published literature written in English, often by western ethnographers, which may exclude the lived knowledge of current and past stewards. For transparency we recorded the types of data sources we drew upon and acknowledge that our data provide a snapshot of and likely an underestimation of the species harvested and of the techniques used in mariculture innovations.

Management Systems

We acknowledge that the classification of mariculture innovations as “gardens”, “ponds”, or “weirs”, or by different management strategies is a heuristic device created by non-Indigenous researchers. Innovations placed in one category could also be placed

in another category, and these classifications may not encompass the full suite of their role in a broader management system. For example, holding ponds might also be built into fish traps to extend harvest periods (White, 2011). A distinguishing characteristic of Indigenous mariculture innovations is that they are part of an embedded system. Separating out these mariculture technologies risks overgeneralizing or overlooking their broader contexts and roles within an integrated social, cultural, spiritual, and government system.

Species Naming

Western scientific (Linnean) nomenclature is used here as one avenue to explore ecological diversity, and we acknowledge that that these innovations are places of biocultural diversity. There are many ways that taxonomy is reflected in Indigenous languages and practices. An Indigenous name for an animal, plant, or alga, might refer to a group of species in Linnean classification, or to a single life history stage (Gillman & Wright, 2020). In our case, we chose to use Western science nomenclature because it allowed us consistency in comparing species use across cultural contexts.

Statistical Analysis

To determine the relative effect of latitude, sea surface temperature and number of papers published on the number of species associated with Indigenous mariculture innovations, we fit generalized linear models with a negative binomial likelihood and log link function. We selected this likelihood distribution because it best described the discrete nature of our response variable and ensured that model residuals met assumptions of linearity, homoscedasticity, normality, and independence. Given that latitude co-varied with sea surface temperature, and some innovations did not have known sea surface temperature data, we chose latitude as a covariate in this model over sea surface temperature.

Using a model selection approach, we compared all candidate models including a null model using ΔAIC_c values and weights (Burnham, 2015; Burnham & Anderson, 2002). Models were built in R using the MASS package and model comparison was conducted in the MuMin package in R (Bartoń, 2022; Ripley et al., 2023).

Results

Drivers of Species Richness

We found no evidence for an effect of latitude, sea surface temperature, or number of papers published on species richness across the mariculture innovations (Figure 2, Table 1). Model averaging results revealed relative variable of importance for latitude to be less than 0.4 (sum of Akaike weights = 0.28) (Burnham, 2015).

Analyses using sea surface temperature yielded similar results. Sea surface temperature was second to the null model, with ΔAIC_c of 2.04 (Figure C3, Table C3). Model averaging revealed relative variable of importance for SST to be less than 0.4 (sum of Akaike weights = 0.25) (Burnham, 2015).

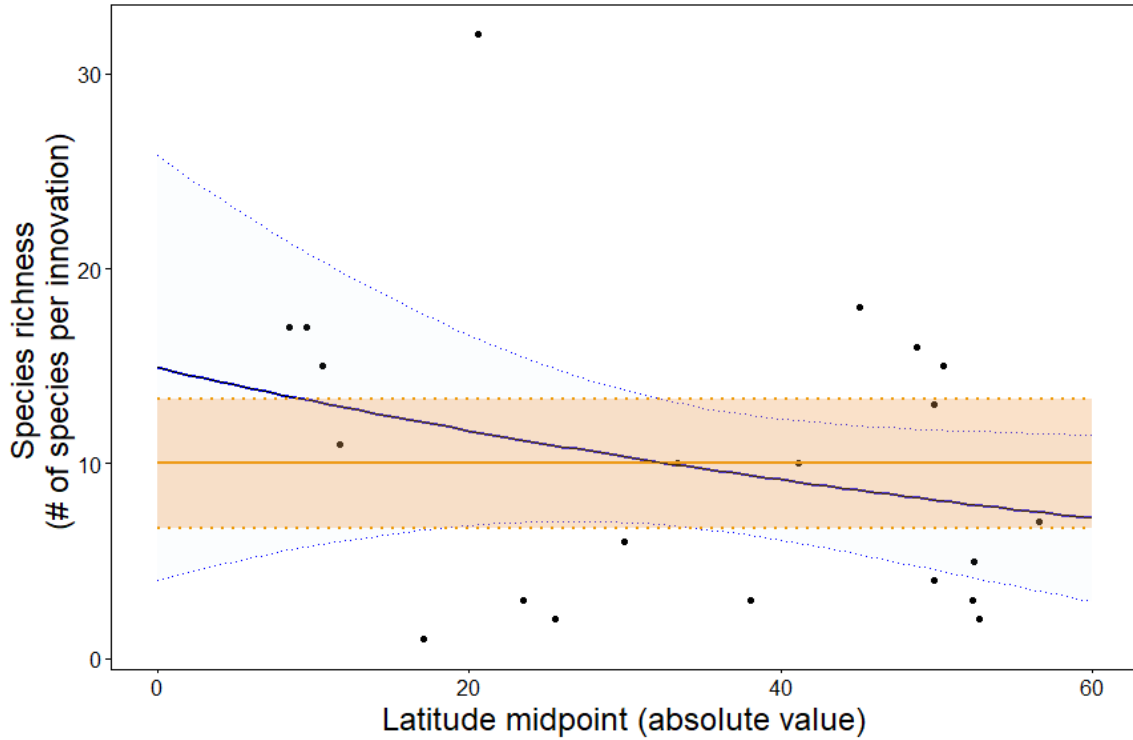


Figure 2 Diversity of species associated with Indigenous mariculture innovations. Null model (orange line) vs latitude model (blue line) with 95% confidence intervals (shaded areas). Black dots represent raw data points. The predictor line for latitude is almost fully within the confidence intervals of the null model.

Table 1 Strength of evidence for alternative models predicting the effect of latitude and number of papers published on species richness.

Model	N	LL	AIC _c	Δ AIC _c	R ² adj	Weight
Response variable - Distribution						
Species Richness – Negative Binomial						
Null	21	-68.5	141.8	0.0	0.000	.52
Latitude Midpoint	21	-67.8	143.0	1.20	0.071	.28
Number of Papers Published	21	-68.5	144.4	2.67	0.004	.14
Number of Papers Published + Latitude Midpoint	21	-67.8	146.0	4.26	0.073	.06

Species Life History and Ecological Traits

Trophic Groups

We found that 44% of the species associated with Indigenous mariculture innovations across the Pacific were secondary consumers (n = 92, Figure 3A). Examples include sockeye salmon (*Onchorhynchus nerka*), Pacific herring (*Clupea pallasii*) and many species of Jack or Trevally (papi'o, amaka and ulua) from the Carangidae family. Primary consumers made up the next largest trophic group (n = 61, 29%) and include bivalve species like toheroa clams (*Paphies ventricosa*), butter clams (*Saxidomus gigantea*) and rabbitfish (garmiy, daruy, limreq, biywod) from the Siganidae family. Tertiary consumers like coho salmon (*Oncorhynchus kisutch*) make up the third largest group (n = 40, 19%). Very few species were primary producers (n = 17, 8%) (N=210 species). Examples of primary producers include feather boa kelp (*Egregia menziesii*) or springbank clover (*Trifolium wormskioldii*).

Migratory Strategies

We found that non-migratory species were the primary group of species used in these mariculture innovations (n = 138, 69%, Figure 3B). This number includes sedentary invertebrates such as butter clams (*Saxidomus gigantea*), and kelp species. We observed that the total number of migratory species is still relatively high (n = 61, 31%), and that there are diverse migratory strategies including species that are: anadromous (n = 24), oceanodromous (n = 18), amphidromous (n = 8), catadromous (n = 6), and potadromous (n = 5) (N = 199). Examples of anadromous species include pink salmon (*Oncorhynchus gorbuscha*) or green sturgeon (*Acipenser medirostris*). Oceanodromous species include honu (sea turtles, Hawaiian).

Population Doubling Time

Most species in these mariculture innovations have an average population doubling time of 1.4-4.4 years (n = 67, 64%, Figure 3C), such as róbalo (*Eleginops maclovinus*), and eulachon (*Thaleichthys pacificus*). Species like black rockfish (*Sebastes melanops*) with 4.5-14 years' doubling time were relatively less common (n = 21, 20%). Very few species with a population doubling time of less than 15 months were

represented (n = 17, 16%) (N = 105) (Figure 3C). Examples include nehu (anchovy, *Encrasicholina purpurea*) or parrotfish (taroeq, choy or marib, *Chlorurus spilurus*). (N= 105 species).

Reproductive Guild

Most species used in these mariculture innovations belong to the non-guarder reproductive guild (n = 161, 81%), followed by bearers (n = 25, 12%) and guarders (n = 14, 7%) (N = 200) (Figure 3D). In the non-guarder guild, most species are broadcast spawners (87%), such as venus clams (*Venus antiqua*) or California sea cucumbers (*Apostichopus californicus*). Within the guarder guild, 67% of species are nest spawners such as green sea turtles (*Chelonia mydas agassizi*), and 33% are substratum choosers. In the bearers' guild, most species are external bearers (80%) such as sea catfishes (Ariidae) followed by internal live bearers (20%) like sharks (Carcharhinidae, 17%). Out of N = 210 species, there were 10 species whose main reproductive guild (guarder, non-guarder, or bearer) were unknown or not applicable (pollinators).

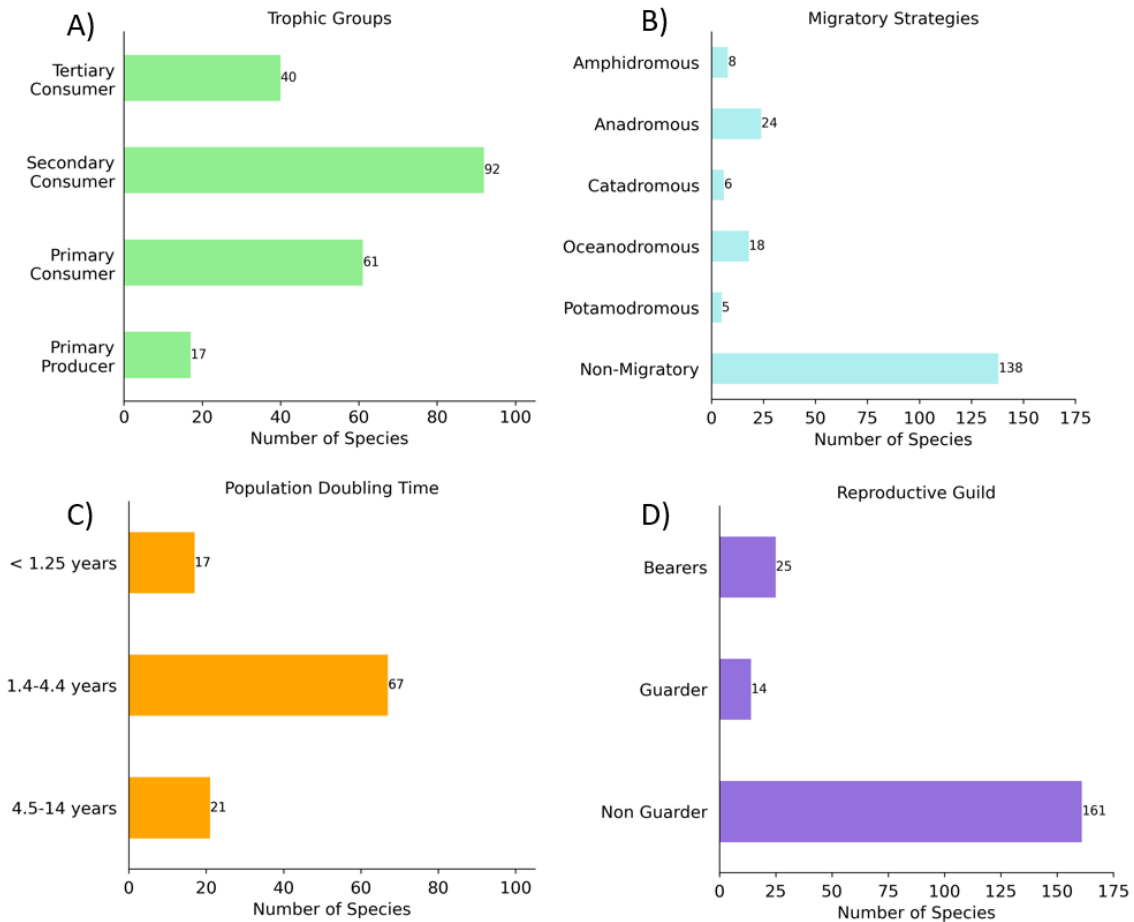


Figure 3 The diversity of traits for species in Indigenous mariculture innovations, shown by different trophic groups (A), unique migratory strategies (B), variety of population doubling times (C), and reproductive guilds (D). Harvesting species from a variety of ecological niches means stewardship of many environments, which might be one way that diversity contributes to social-ecological resilience.

Thermal Preferences

The preferred thermal range for fish species within the mariculture innovations varied from 0°C - 35°C (N = 123) (Figure 4). While latitude and sea surface temperature did not explain species richness (Figure 2), we did see that species with a diversity of temperature ranges were cultivated within these innovations.

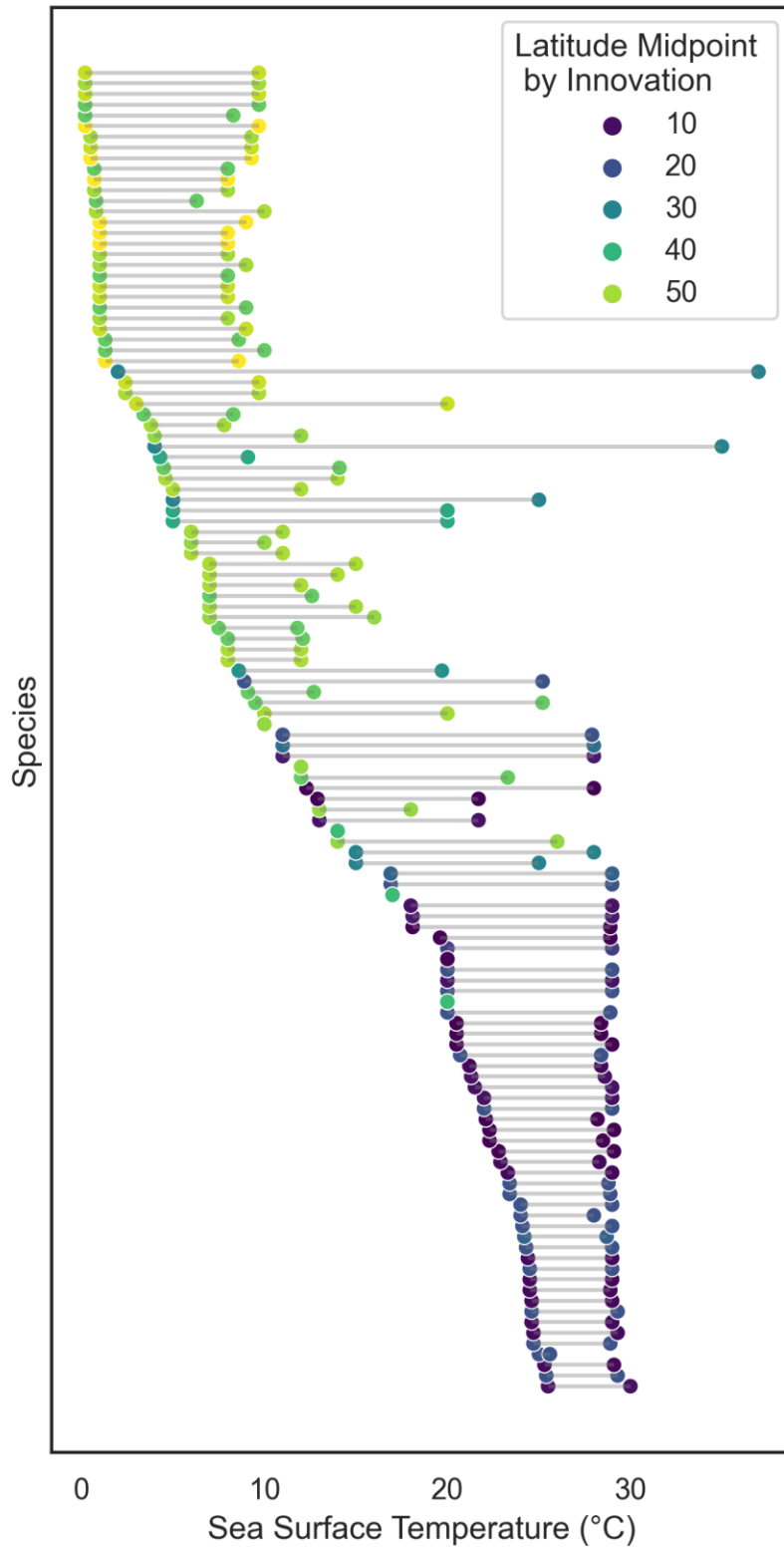


Figure 4 Thermal ranges for species within mariculture innovations. Each connected line is the temperature range for a species. N = 123

Management Systems

While there is a range in the number of management strategies employed in the mariculture innovations, the majority have at least 3 unique management strategies (mean = 4.0, +/- 3.0) (Figure 5C). Most of these innovations were classified as fish traps or weirs (13), followed by gardens (5) and ponds (3) (Figure 3A). We found that most of our data sources came from both ethnographic and archaeological data (18), and relatively fewer innovations were informed by archaeological data (2) or ethnographic data (1) (Figure 5B, Table D1).

We found that there was a variety of management strategies used in these innovations (Figure 3D). The top two categories were tenure systems and selective harvest (16). Documented evidence of tenure systems existed for 16 of the 21 mariculture innovations, and there was a lack of evidence for the remaining 6. The next most used practices in these innovations were clearing or cleaning of habitat (13) and terracing or ditching (13).

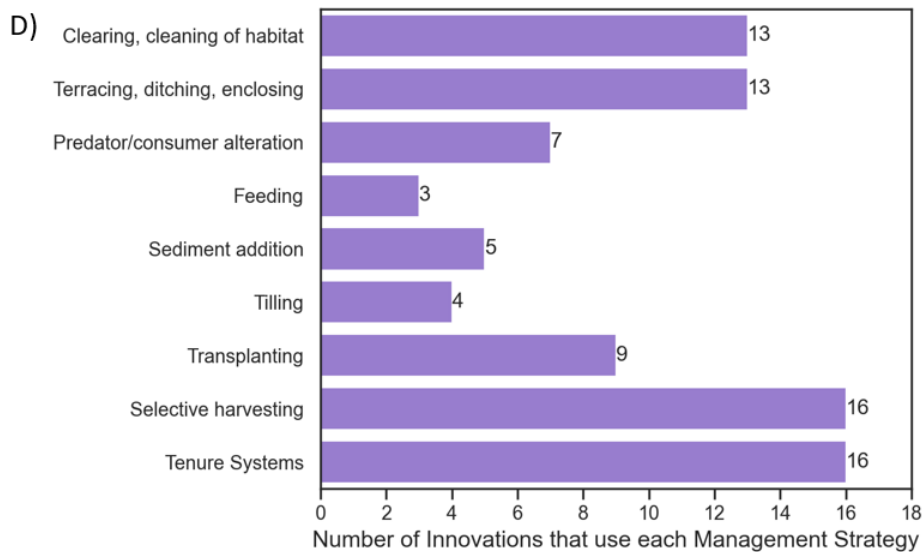
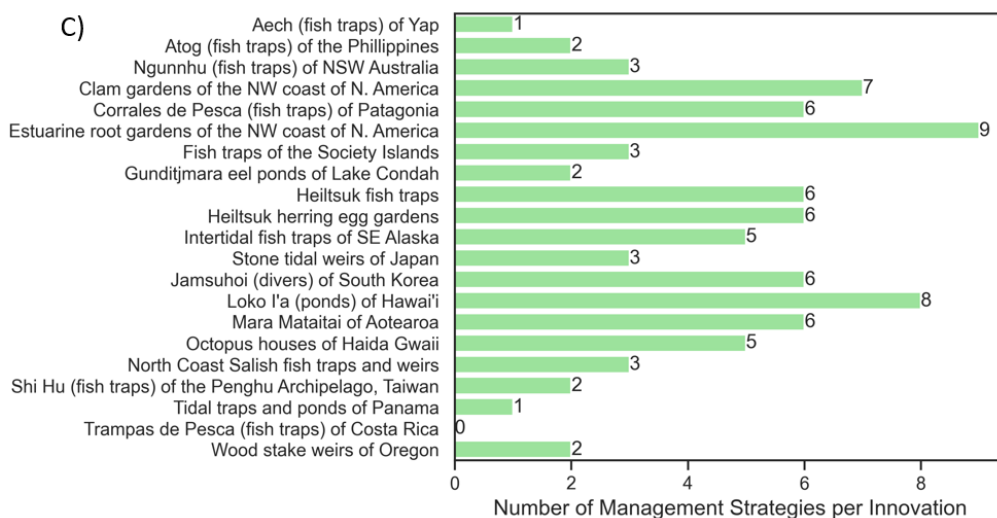
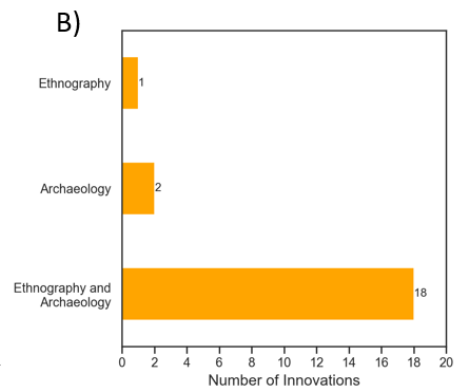
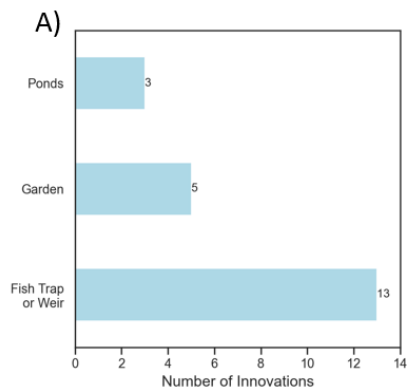


Figure 5 Management practices of Indigenous mariculture technologies. (A) Number of different types of innovations in this study, (B) Types of data used to collect management data, (C) Number of management strategies by innovation (mean = 4.0, standard deviation +/- 3.0) and (D), Number of innovations that employ each management strategy, as sourced from experts in the Pacific Sea Garden Collective.

Industrial Mariculture

Total Species Richness

From 1990- 2009, across the Pacific Ocean, the total species richness number for industrial mariculture was 113, compared to 210 for Indigenous mariculture (Figure 6A). This is 46% more total species richness for mariculture innovations compared to industrial mariculture.

Trophic Groups

Most species from industrial mariculture since 1980 are primary consumers (n = 50, 45%, Figure 6B), such as the Pacific cupped oyster (*Crassostrea gigas*) or White leg shrimp (*Litopenaeus vannamei*). Next are secondary consumers (n = 41, 37%), such as White spotted grouper (*Epinephelus coeruleopunctatus*) followed by tertiary consumers (n = 21, 19%) like Atlantic salmon (*Salmo salar*) (N = 113 species). This is a different order than the trophic groups used in Indigenous mariculture, which were: secondary consumers (44%), followed by primary consumers (29%), tertiary consumers (19%), and primary producers (8%).

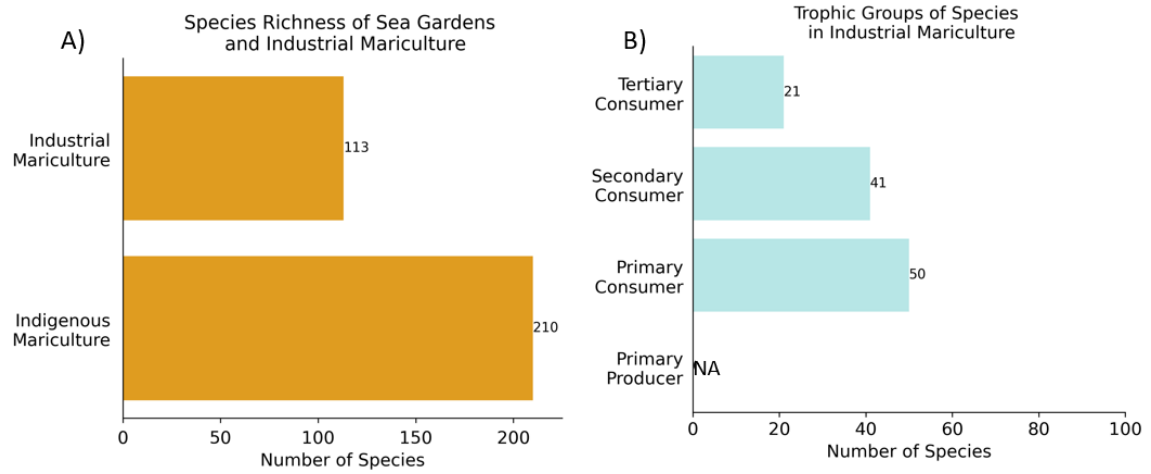


Figure 6 A) Species richness for mariculture innovations and industrial mariculture, and B) the trophic groups of species within industrial mariculture. Industrial mariculture data does not include primary producers like kelp or seaweed. Data retrieved from the Sea Around Us from 1980-2009.

Discussion

Our research provides additional evidence of the importance of biodiversity in promoting resilient social-ecological systems and the importance of recognizing diverse cultural practices influencing these systems. Globally, Indigenous mariculture systems support a diversity of species with a range of life history and reproductive traits (Figure 3), while commercial industrial mariculture systems rely on fewer species and are thus less biologically diverse (Figure 6). We found that latitude does not drive the diversity of species stewarded via Indigenous mariculture, suggesting that a biodiverse food system is not incidental, but is the result of intentional and transformative stewardship (Figure 2). This stewardship is rooted in a diversity of management practices informed by environmental observations and experimentation and honed over many generations (Figure 5) and during changes in environmental conditions. Indigenous mariculture systems are embedded in dynamic place-based societies and intertwined with diverse spiritual, cultural, and government systems and many practices that drive their resilience and persistence. A compelling attribute of these social-ecological systems is their relationship to a diversity of species.

Diversity as an Attribute of Indigenous Mariculture

Globally, Indigenous management systems support biodiversity (Brondízio et al., 2021; Fa et al., 2020). Across terrestrial landscapes, Indigenous-led management helps to protect biodiversity and key ecosystem functions (Estrada et al., 2022; Fa et al., 2020; Garnett et al., 2018; Schuster et al., 2019). Our results lend support for this in coastal environments, as we found that across the Pacific Ocean, using mariculture systems, Indigenous Peoples cultivate species with a diversity of trophic levels, reproductive guilds, migratory strategies, population doubling times, and temperature ranges.

At first glance, our findings about the diversity of trophic levels stewarded within these innovations might seem surprising, as they contradict our original hypothesis. We predicted that there would be a preference towards species that require less energy to maintain, such as those in lower trophic levels. Instead, we found that secondary consumers made up a relatively higher amount of the species stewarded, and that the percentages for primary, secondary, and tertiary consumers (44%, 29%, and 19%,

respectively) were not radically uneven. This evenness across trophic groups suggests niche redundancy, which allows adaptation under change and a continuity of species-specific ecosystem functions. Cultivating a diversity of species in similar trophic levels may increase the stability of the food web, as stability is highest in systems with multiple species harvested in each trophic level (Gross et al., 2009). In contrast, large levels of harvest at a single trophic level can have reverberating consequences through the food web (Smith et al., 2011). Furthermore, cultivating a diversity of species in similar trophic niches might also allow the substitution when environmental or social disturbances might reduce the availability of one of these species. It was not surprising to see that relatively more of the species cultivated in these mariculture innovations are secondary consumers, as there are many instances of Indigenous People selectively altering the local trophic environment to enhance the productivity of certain species (Table B2). For example, in the northeast Pacific Ocean, sea otter populations were held below carrying capacity for millennia, in order to increase the availability and size of California mussels for human consumption (Slade et al., 2022). Building sustainability and resilience in marine food systems means increasing adaptive capacity, through diverse harvest portfolios with multiple species in each trophic group.

We found that 31% of the species stewarded in these Indigenous mariculture systems were migratory, and 69% of the species were non-migratory. This seems like a relatively high proportion of migratory species, which require complex management, as they use multiple habitats and require specific environmental conditions at each life history stage. However, Indigenous stewardship is rooted in values of reciprocity, respect, and fundamental sustainability practices, and many Indigenous fisheries have continually harvested migratory species without the overharvest and population collapses often seen in industrial fishing (Atlas et al., 2021). Indigenous fisheries have been able to harvest migratory species at high intensities, such as salmon (Turner & Mackie, 2006). The harvest of species with both migratory and non-migratory strategies might confer more resiliency to the system than the harvest of either alone. For example, migratory species spend their growth period in environments external to the nearshore system where these innovations are located. Their return to their natal environment results in an allochthonous transport of biomass and a provision of nutrients and biomass to the nearshore food system, without as much direct ecological competition for resources with local species. Additionally, because migratory and non-migratory species

occupy different habitats for much of their lives, they are exposed to different disturbances and experience population fluctuations at a different cadence. These differences in exposure to different disturbances, as well as in the timing of migration patterns relative to local species' growth and reproduction patterns allows for year-round access to food. Our research suggests that promoting redundancy and diversity through the cultivation of both migratory and non-migratory species confers diversity and resiliency to local food systems.

Furthermore, we found that multiple species were harvested across the life history categories in this study. We chose to examine migratory strategies, reproductive guilds, trophic levels, and population parameters because each of these categories represents a diversity of niches from different ecological perspectives. The presence of multiple species in each of these categories within Indigenous mariculture demonstrates functional redundancy. Across ecosystems, functional redundancy allows a mechanism for adaptation and can confer community stability during disturbance, allowing for the continued provision of key ecosystem functions (Biggs et al., 2020; van der Plas, 2019). Several mariculture innovations in this study managed or altered ecosystem functions. For example, 5 out of 21 of the innovations added sediment, nutrients, or fertilizer to the system, and 7 out of 21 added species to provide predation or herbivory functions as needed (Figure 5D). In Hawaiian mariculture systems, some species were cultivated in the Loko i'a (ponds) to enhance ecosystem functions for other species: such as intentional addition of species that filter water, reduce algal growth, or add fertilizer, like honu (sea turtles) (Keala et al., 2007). A diversity of niches, functional groups, and ecological groupings confers social-ecological resiliency in mariculture systems.

People Enhanced and Maintained Diversity

We did not see evidence for an effect of latitude on the diversity of species in Indigenous mariculture systems, and the results follow our hypothesis. Our null result suggests that in these systems, the natural environment alone is not the driver of the species that are being cultivated in these mariculture innovations. A diverse food system is not incidental, and the stewards of these systems were and are active contributors and co-participants in the environmental system, enacting intensification techniques to enhance biodiversity and productivity. This perspective re-affirms the deep reciprocal relationship with and stewardship of place that is present in Indigenous stewardship.

Management Systems

As expected, we see that Indigenous mariculture systems employ a diverse range of practices that contribute to a resilient food system. We found that most mariculture innovations are associated with at least 3 management strategies, with selective harvest being the most common. Selective harvest refers to only taking a portion of a plant, some individuals from a population, or allowing individuals at a specific size or life history stage to return to spawn (Lepofsky et al., 2017; Lepofsky & Caldwell, 2013b; Mathews & Turner, 2017). Many Indigenous stewardship practices embody principles of reciprocity, respect, and conservation, so it was not unexpected to find that selective harvest was a common practice (Lyver et al., 2017; Oliveira, 2014; White (Xanius), 2006). Only 16 of the 21 innovations had documented evidence for tenure systems, however, it is likely that all these systems were associated with some form of tenure, for which evidence has yet to be found.

Most of our data sources came from both ethnography and archaeology, while fewer innovations were informed solely by archaeological data or ethnographic data. Source diversity in studying these systems is important, as data sources shape what can be inferred about management and can contribute a diversity of evidence about people's connection with and enhancement of the local ecosystem. Source diversity does not compensate for researcher biases, but joining multiple lines of evidence together can create a more complete picture of how landscapes were managed to enhance diversity, and help to reinvigorate past examples of resilient management practices (Armstrong & Veteto, 2015; Lepofsky et al., 2017).

Industrial and Indigenous Mariculture

We found 46% more species diversity in Indigenous mariculture systems compared to that of industrial mariculture, indicating that Indigenous mariculture builds social-ecological resilience in part by cultivating a diversity of species. Literature in industrial aquaculture supports our result, and higher species diversity can be associated with higher rates of production and resilience (Dumont et al., 2020; Metian et al., 2020; Oboh, 2022; Thomas et al., 2021). A reliance on a diversity of local species reduces the ecosystem consequences from the introduction of non-native species, but there are other well-documented negative ecological outcomes from industrial

mariculture (De Silva et al., 2009; Herbeck et al., 2013; Quiñones et al., 2019). Over the last 50 years, industrial mariculture has dramatically increased in production, but is trending towards less species diversity, in addition to a variety of harmful ecological outcomes (Campbell & Pauly, 2013; Troell et al., 2014). In contrast, Indigenous systems have harvested over several thousand years without the extraordinary environmental consequences often seen in industrial mariculture (Atlas et al., 2021a; Reeder-Myers et al., 2022). Promoting social-ecological resilience in mariculture means fostering biodiversity and redundancy, as well as centering the knowledge and wisdom of Indigenous People.

Future Management and Revitalization

The deep time scale and broad spatial dimensions of our data demonstrate that Indigenous systems were managed to include a wide variety of diverse species with redundant ecological roles. We see evidence for diverse harvest portfolios, and species with complex and spatially broad ecosystem niches. Indigenous management systems are embedded within social, cultural, and spiritual frameworks that drive the social-ecological resilience of these systems. Globally, the revitalization of Indigenous management confers social-ecological resilience (Brondízio et al., 2021; Reyes-García et al., 2019). For example, across multiple continents, land managed by Indigenous communities has higher rates of vertebrate biodiversity compared to conventional protected areas (Schuster et al., 2019). Indigenous Peoples have broad tenure across ecologically valuable land, and Indigenous knowledge systems hold critical pieces to preserving global biodiversity. (Garnett et al., 2018; O'Bryan et al., 2021). Building resilient and biodiverse social-ecological systems must promote the revitalization of Indigenous systems of management and center the perspective and leadership of Indigenous stewards.

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Appendix A – Life History Trait Definitions

Table A.1. Definitions for life history traits from FishBase (Froese and Pauly, 2023).

Category	Definition	Subcategory	Definitions of Subcategory
Migratory Type	Relocation to from one body of water to another, usually for reproductive purposes. Generally cyclical and predictable in nature.	Oceanodromous	Migration between feeding and spawning areas within ocean. Cyclical, predictable, covers >100km
		Anadromous	Organism that ascends rivers to spawn
		Catadromous	Migration down from freshwater to sea to spawn. Cyclical, predictable, covers >100km
		Amphidromous	Migrating to and from freshwater/sea at some life stage but not for breeding
		Potamodromous	Migratory in freshwater. Cyclical, predictable, covers > 100km
		Non-migratory	No migratory behavior for spawning
Reproductive Guild	Organisms within each guild display similar reproductive strategies, like parental care, nest building, or spawning/egg dispersal adaptations.	Non-guarder	No parental care provided for eggs after spawning.
		Guarder	Some parental care provided for eggs after spawning.
		Bearer	Fertilized eggs retained in/on body for part or all of the developmental period

Trophic Group	The position an organism occupies in a food web, based on the food it consumes.	Primary Producer	Consumes primary producers and detritus.
		Primary Consumer	Consumers of primary producers and detritus. (herbivore/detritivore).
		Secondary Consumer	Consumers of herbivores (carnivore)
		Tertiary Consumer	Consumers of primary or secondary consumers (carnivore).
Population Doubling Time	How long it takes a population to double in size, based on model estimations.	< 1.25 years	Less than 15 months.
		1.4 - 4.4 years	Between 1.4 and 4.4 years.
		4.5 - 14 years	Between 4.5 and 14 years.

Appendix B – Management Strategies

Table B.2 Management strategies and descriptions (Lepofsky et al., 2017; Lepofsky & Caldwell, 2013b; Mathews & Turner, 2017).

Management Strategy	Description
Clearing or cleaning of habitat	Manual removal of large rocks, driftwood, seaweed, debris, etc. from estuaries, fish ponds, clam beaches, spawning areas, to enhance productivity.
Terracing, ditching, enclosing	Creating new habitats through rock and log terracing, ditching, etc., to extend available habitat, or to create holding ponds for later harvest.
Predator/consumer removal or addition	Applying knowledge of predation and consumer interactions to enhance productivity of the desired species. E.g, removing predators who compete with or consume the target species, introducing herbivores to control algal growth
Feeding	Providing food for growing fish; or putting fishguts, bones, and dead salmon back into the river to nourish young fish, crabs, etc.
Sediment addition	Adding nutrients or moisture retaining materials to soil, or nutrients to water, or other materials E.g, adding shell hash to clam gardens.)
Tilling	Aerating soil or substrate to enhance moisture penetration, recycle nutrients, etc.
Transplanting	Moving young fish, larvae, root fragments, etc. from one location to another, including transplanting salmon eggs, spawning herring, shellfish spat, or rhizomes
Selective harvesting	Includes selective, partial, rotational, or nondamaging harvesting: Taking only a portion of a plant, or only some individuals from a population, allowing individuals to return to spawn, selectively harvesting males or females, or other selection practices to maintain and promote population growth.
Tenure systems	Laying of plot boundaries or establishing borders and site-specific ownership and management. E.g, in estuarine root gardens, crabapple trees, edible red laver seaweed picking areas, clam gardens.

Appendix C – Model with Sea Surface Temperature and Species Richness

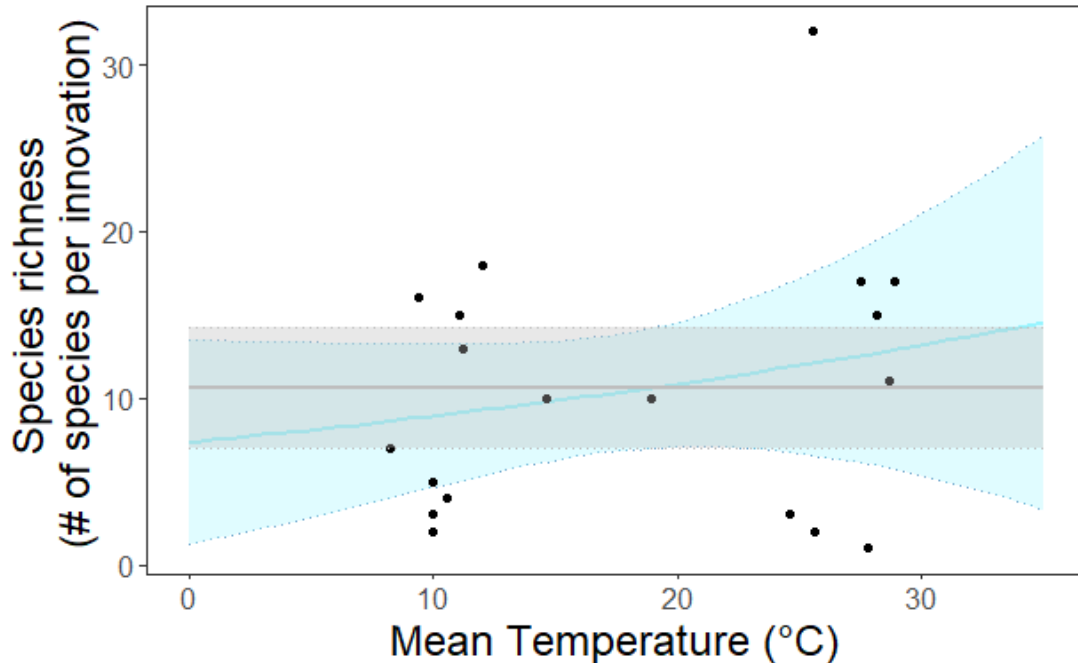


Figure C1 Diversity of species associated with Indigenous mariculture innovations vs mean sea surface temperature. Null model (grey line) vs temperature model (blue line) with 95% confidence intervals (shaded areas). The predictor line for sea surface temperature is almost fully within the confidence intervals of the null model.

Table C1 Strength of evidence for alternative models predicting the effect of SST and number of papers published on species richness

Model	N	LL	AIC _c	Δ AIC _c	R ² adj	Weight
Response variable - Distribution						
Species Richness – Negative Binomial						
Null	19	-63.0	130.8	00.0	0.000	0.58
Sea Surface Temp	19	-62.6	132.8	2.04	0.042	0.21
Number of Papers Published	19	-62.8	133.3	2.51	0.017	0.17
Number of Papers Published + Sea Surface Temp	19	-62.6	136.0	5.22	0.046	0.04

Appendix D – Management Strategy Responses

Table D1 Expert responses to about which management strategies are used within each mariculture innovation.

Innovation Name	Clearing, cleaning of habitat	Terracing, ditching, enclosing	Predator or consumer alteration	Feeding	Sediment addition	Tilling	Transplanting	Selective harvesting	Tenure Systems
Aech (fish traps) of Yap	No information	No information	No information	No information	No information	No information	No information	Yes	No information
Atog (fish traps) of the Philippines	Yes	No	No information	No information	No	No information	No information	No information	Yes
Ngunnhu (fish traps) of NSW Australia	No information	Yes	No information	No information	No information	No information	No information	Yes	Yes
Clam gardens of the NW coast of N. America	Yes	Yes	Yes	No information	Yes	Yes	No information	Yes	Yes
Corrales de Pesca (fish traps) of Patagonia	Yes	Yes	No	No	No	Yes	Yes	Yes	Yes
Estuarine Root Gardens of the NW coast of N. America	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Fish traps of the Society Islands	Yes	Yes	No information	No information	No information	No information	No information	No information	Yes
Gunditjmara eel ponds of Lake Condah	No information	Yes	No information	No information	No information	No information	No information	Yes	No information
Heiltsuk fish traps	Yes	Yes	No	No	Yes	No	Yes	Yes	Yes
Heiltsuk herring egg gardens	Yes	Yes	Yes	No information	NA	NA	Yes	Yes	Yes
Intertidal fish traps of SE Alaska	No	Yes	No	No	Yes	No	Yes	Yes	Yes
Stone tidal weirs of Japan	Yes	Yes	No	No information	No information	No	No	Yes	No information
Jamsuhoi (divers) of South Korea	Yes	No information	Yes	Yes	No information	No information	Yes	Yes	Yes

Loko l'a (ponds) of Hawai'i	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes
Mara Mataitai of Aotearoa	Yes	No information	Yes	No information	Yes	No information	Yes	Yes	Yes
Octopus houses of Haida Gwaii	No information	Yes	Yes	No information	No information	No information	Yes	Yes	Yes
North Coast Salish fish traps and weirs	Yes	No	No information	No information	No information	No information	No information	Yes	Yes
Shi Hu (fish traps) of the Penghu Archipelago, Taiwan	No information	Yes	No information	No information	No information	No information	No information	No information	Yes
Tidal traps and ponds of Panama	Yes	No information	No information	No information	No information	No information	No information	No information	No information
Trampas de Pesca (fish traps) of Costa Rica	No	No	No	No	No	No	No	No	No
Wood stake weirs of Oregon	No information	No information	No	No information	No information	No information	No	Yes	Yes