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Ecology and the science of small-scale fisheries: A synthetic review of research effort for the Anthropocene

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ABSTRACT

Human-driven changes to aquatic environments threaten small-scale fisheries (SSFs). Ensuring a livable future for SSFs in the Anthropocene requires incorporating ecological knowledge of these diverse multi-species systems beyond the long-standing reliance on populations, a management paradigm adopted from industrial fisheries. Assessing the state of ecological knowledge on SSFs is timely as we enter the United Nations Decade of Ocean Science and Sustainable Development and with the upcoming International Year of Artisanal Fisheries and Aquaculture. Synthesizing research effort can help identify existing knowledge gaps and relatively well-researched ‘bright spots’ that can inform strategies to achieve global sustainability commitments. Yet trends in ecological research of SSFs are not well understood compared to better-studied industrial fisheries. To address this void, we conducted a synthetic review of SSF publications in ecology journals ($n = 302$), synthesizing trends in research subjects and methodologies over time. Wide geographic and habitat disparities in the coverage of publications are identified, with marine fisheries in Latin American receiving the greatest coverage while inland and Asian fisheries are understudied relative to the global distribution of SSFs. Bony fish and invertebrates received substantial coverage compared to endangered cartilaginous fishes. Studies have increasingly focused on human dimensions and ecosystem ecology compared to earlier emphasis on population ecology. Methodologically, studies rarely incorporate experiments despite their efficacy in testing interventions. To achieve a ‘wider view’ of fisheries that is reflective of the needs of SSFs in the Anthropocene, future ecological studies should expand their geographic, taxonomic, and methodological breadth to better assess understudied SSF interactions.

1. Introduction

More than 20 years ago fisheries science was described as a field “at a turning point”, in need of a dramatic cognitive shift and viable alternatives to conventional management practices (Pitcher et al., 1998, p. xxiv). The collapse of iconic fisheries like Atlantic cod cast doubt upon the efficacy of scientific fisheries management at the turn of the century, as these methods resulted in the “destruction of the very object it was designed to protect” (Bavington, 2010, p. 509). This diagnosis remains relevant and is even more pertinent in light of the Anthropocene, the present geological epoch defined by the nature, scale, and magnitude of human influence on earth systems processes (Crutzen, 2002). Novel challenges and uncertainties are characteristic of the Anthropocene,

where the dynamics of intertwined drivers, complex systems, and emergent phenomena occurring across scales are transforming our environments (Bai et al., 2016). Warnings that we face a “critical and narrowing window of opportunity” (Palsson et al., 2013) to act and alter our present course underscores the urgency of identifying alternatives to environmental management-as-usual: the centralized, command-and-control strategies applied in conventional ‘managerial approaches’ to natural resources (Bavington, 2002). In fisheries, conventional management has focused on stock-assessments of just a few commercially important fish populations (Bavington, 2002; Smith and Link, 2005). This dominant management paradigm assumes that biological outcomes can be regulated at the population level and will result in broader ecosystem sustainability (Wilson, 2006). Yet, this population-centric

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approach is ill-suited to dealing with the cumulative effects of the Anthropocene, where human-driven climate change, habitat loss, pollution, and resource degradation are dramatically altering marine and freshwater ecosystems and the livelihoods of human communities who depend on them (Poe and Levin, 2017; He and Silliman, 2019). Arguably, the human communities most affected by these interacting forces are small-scale, non-industrial fisheries (SSFs), which typically rely on multi-species catch in near-shore ecosystems to sustain their livelihoods and food security. Compared to industrial fisheries, SSFs lack the technology and capital required to easily adapt to the negative effects of human-driven alterations in aquatic ecosystems, for example by fishing further offshore and poleward following species range shifts (Dubik et al., 2019; Rogers et al., 2019). While scientists have been tracking and modelling the impacts of climate change on fisheries, SSFs risk being overlooked in such assessments given the uneven history of fisheries science which was not conceived for multi-species SSFs. The application of conventional fisheries management techniques to SSFs has repeatedly failed across both social and environmental dimensions (Pitcher et al., 1998; Charles, 2001; Berkes, 2003).

The social and environmental stakes surrounding the future of SSF management are high. The small-scale sector plays a vital role in fish supply chains, landing nearly half the world's seafood and the vast majority of inland catch (World Bank, 2012; Welcomme et al., 2010). Primarily destined for direct human consumption, fish landed by the SSF sector provides protein and micronutrients critical to human health and nutrition and is particularly important for the food security of coastal communities in less developed countries (Béné et al., 2015; Golden et al., 2016). As the world needs to feed an estimated 9 billion people by 2050, fish will continue to play an important role as food (Béné et al., 2015; Koehn et al., 2017). Balancing the needs for food security and equitable access to fish with the negative effects of overfishing, which can alter the structure and function of aquatic ecosystems, is a critical social and ecological challenge for the Anthropocene. Given that, on a global scale SSF are generally considered to be more ecologically sustainable than industrial fisheries, employing by some estimates 25 times the number of people while only using a quarter of the fuel to land the same amount of catch for human consumption (Chuenpagdee et al., 2006), SSF will continue to play an important role in realizing sustainable food systems (Levkoe et al., 2017). Ensuring that SSFs are sustainably managed requires expanding the present scientific fisheries management paradigm to encompass a "wider view of fisheries" that includes multi-species interactions among harvested populations and their ecologically relevant environment (Smith and Link, 2005).

We argue that the novel challenges of the Anthropocene also present an opportunity to rethink scientific fisheries management to be more inclusive and responsive to the characteristics of SSFs, where notions of system dynamics and sustainability are reflective of the social-ecological complexity and interdependency of aquatic commons. This process would benefit from incorporating broader ecological knowledge, correcting the earlier overemphasis on isolated fish populations and stock assessment methods, which are dominant in fisheries science but are incompatible with SSF management needs and realities (Mahon, 1997).

1.1. Fisheries science: past and present

From the mid-20th century onwards, fishing pressure has generally increased, in line with the 'great acceleration' observed in many human activities around 1950, now proposed as the start of the Anthropocene epoch by global change scientists (Steffen et al., 2015). Aided by new technologies in abundance post-WWII, fishing boats were able to locate and capture fish deeper and further offshore, expanding their range and accuracy in targeting fish (Cushing and Cushing, 1988). The western institution of scientific fisheries management also rapidly changed at this time, away from qualitative description and observation and towards statistical means of identifying fish populations (Bavington, 2002; Smith, 1994). As industrial fisheries rapidly expanded alongside

growing awareness of the risks of potential over-exploitation, statistical methods were popularized to calculate the dynamics of commercially exploited stocks in the Global North (Ricker, 1954; Beverton and Holt, 1957). Bioeconomic models became the norm, assuming that fish populations were self-regulating systems which tended towards equilibrium (Mahon et al., 2008; Wilson, 2006). However, there is mounting empirical evidence for an alternative model of aquatic environments as complex biophysical systems, where fish population adapt to temporally and spatially complex environments at finer scales, often in non-linear ways (Wilson, 2006). The social dimensions of fisheries are also distorted by this bioeconomic lens, with fishers aggregated into a single variable, with unidirectional effects on the environment (i.e., removal of fish). Such models assume that all fishers behave as economically rational, self-interested actors (St. Martin, 2005). While the stock-recruitment heuristic simplifies the calculation of fisheries management and has reigned for decades, there is a growing consensus that both the underlying logic of this model and the applied results are deficient, serving to "disguise the complexity of the ocean in a way that is adaptively dysfunctional" (Wilson, 2006).

The assumption of equilibrium in scientific fisheries management appears particularly inaccurate in the face of climate change, where alterations in water temperature, circulation, and productivity are predicted to dramatically alter global catch (Brander, 2007; Cheung et al., 2010), driving local extinctions and species range shifts that will create novel species assemblages (Cheung et al., 2009; Pinsky et al., 2013). The environmental requirements and restricted mobility of freshwater and sessile organisms will constrain many species ability to adapt through migration (Woodward et al., 2010; Muir et al., 2015). Ocean acidification further negatively affects many invertebrates, particularly calcifiers (Kurihara, 2008), a sensitivity which is enhanced when coupled with temperature changes (Kroeker et al., 2013). Changes in temperature, salinity, streamflow, and surface water availability threaten inland fisheries (Paukert et al., 2017), which, in extreme cases, can lead to the complete disappearance of lakes and waterways (Coe and Foley, 2001). Climate driven alterations of marine systems are now evident at the very base of marine food webs, with global shifts in phytoplankton community structure affecting upper trophic levels as evidenced by a drop in the availability of vital fatty acids in predatory fish (Lorrain et al., 2020). Such shifts are predicted to negatively impact the health of more vulnerable human populations reliant on fish catch for critical micronutrients (Golden et al., 2016; Colombo et al., 2019). These interacting forces raise new questions about ecological function and what adaptable and sustainable fisheries management should look like (Pinsky and Selden, 2017). Considering the escalation of numerous pressures in the Anthropocene, rethinking the relationship between the social and ecological elements of wider aquatic systems and the dynamics of fisheries reflected in models is warranted.

1.2. Looking forward: science and policy commitments to future SSF sustainability

Scientific communities are being called upon to respond to the complex environmental challenges and novel information needs of the Anthropocene by "casting their analytic nets wider" (Arbo et al., 2018). The Anthropocene concept can serve as a bridge between disciplinary silos, encouraging new collaborations and hybrid perspectives (Bron-dizio et al., 2016). Diverse social science and humanities perspectives on the environment are needed to address global change in general (Palsson et al., 2013), and marine conservation in particular (Arbo et al., 2018). Radical changes in the science and management of coral reefs are being called for if they are to survive and remain functional in the Anthropocene (Hughes et al., 2017). Here, we argue that broader ecological knowledge beyond 'population thinking' is critical for a forward-looking fisheries science that can address the interdependence of ecosystems and human wellbeing for a livable Anthropocene (Poe and Levin, 2017). A recent high level convening on fisheries sustainability at the FAO

underscored the imperative of managing systems for variability rather than stability (FAO, 2019), a paradigm shift which will require a better understanding of how fishing pressures combined with large-scale biophysical, climatological, and anthropogenic drivers are affecting fish populations across all levels of biological organization in inland and marine fisheries (Rijnsdorp et al., 2009; Barange et al., 2014). Moving beyond the blinders of a few commercially important target stocks (which are skewed towards industrial fisheries) will require greater knowledge of the ecology of overlooked species, interactions, and processes that sustain functioning ecosystems (Gelcich et al., 2010; Rijnsdorp et al., 2009; Barange et al., 2014). Reconsidering how human dimensions in fisheries are categorized and depicted in models also matters for sustainability goals and the targets and policies created to achieve them. The causes and consequences of the Anthropocene are not equal, and SSF communities will be disproportionately affected by environmental change. Instead of depicting fishers as a unidirectional force upon natural systems (Sayre, 2012)—drivers of degradation in the Anthropocene (Steneck and Pauly, 2019)—differences in power, responsibility, and history should also be taken into consideration in the broader dialogue on sustainability and within efforts at climate change adaptation.

As we enter the United Nations (UN) Decade of Ocean Science for Sustainable Development (2021–2030) and the upcoming International Year of Artisanal Fisheries and Aquaculture (IYAFA) in 2022, it is timely to assess the state of ecological knowledge regarding SSFs as these high-level commitments lay the groundwork for innovation and concrete policy actions. Accordingly, to elucidate the present distribution of research effort and identify knowledge gaps for future research, we reviewed the geographic and thematic areas of SSFs that ecologists have studied, and the methods employed. Conducting such an assessment aligns with the mandate of SDG 14 (conserving and sustainably using the oceans and aquatic resources), which outlines the need for increased scientific knowledge and research capacity for sustainability (indicator 14a). The importance of better understanding ecological processes in the context of SSFs is further highlighted by the FAO Voluntary Guidelines for Securing Sustainable Small-Scale Fisheries (SSF Guidelines), in their call for increased policy action to address the accelerating impacts of climate change on SSFs. Together, recent international meetings, commitments, and instruments reflect an emerging global consensus that SSFs are important social-ecological systems facing complex and evolving management challenges. Realizing global sustainability commitments will require greater ecological knowledge and better models of fisheries systems to disentangle impacts, predict changes, and mitigate threats to SSFs and enable their ongoing adaptation in the Anthropocene.

1.3. Current intersections between ecology and SSFs

Across many dimensions, “small” is a misnomer in SSFs. Diverse gear types, fishing methods, modes of organizing labor, and ecological knowledge are employed by SSFs as fishers pursue multiple fish species, often adapting their targets on both short time scales (e.g. daily) and in accordance with seasonal and annual changes (Wilson, 2006). In contrast to industrial fisheries, SSFs are found in nearly every aquatic environment on earth and make up 90% of fishers worldwide (World Bank, 2012) and are the ocean’s largest employer (OECD, 2016). Given their outsized role in aquatic economies and food security, SSFs demand specialized attention. The popularity of the social-ecological systems (SES) approach and ecosystem-based management demonstrate that scientists recognize the need to integrate a wider set of ecological and social interactions into fisheries analysis, especially in the context of small-scale systems (Leslie and McLeod, 2007; Ostrom, 2009; Basurto et al., 2013). Ecologists are well positioned to inform a fuller understanding of SSFs as part of interconnected ecological communities, rather than as isolated fish stocks, helping to unpack the complex dynamics between aquatic communities, fishers behavior, and abiotic

physical factors—all of which are impacted by unprecedented rates of change affecting SSF human and non-human communities. A more comprehensive and dynamic view of the ecology of SSF systems would help inform a ‘wider view of fisheries’ and meet global calls for greater research effort to inform the design of innovative, adaptive, evidence-based management. As a first step towards strengthening the interface between ecological knowledge and innovative SSF management, we conducted a systematic, vote-count review of ecological research across the diverse geographies, habitats and taxa SSF depend on to illustrate the current distribution and focus of SSF research published in ecology journals.

Existing vote-count synthesis reviews have offered useful insights for the fields of ecology (Neff and Corley, 2009), conservation biology (Lawler et al., 2006), restoration ecology (Zhang et al., 2018), and tropical marine science (Partelow et al., 2018). Several studies have synthesized patterns in fisheries research effort through bibliometric methods (Jarić et al., 2012; Johnson et al., 2013; Aksnes and Browman, 2015; Oliveira Júnior et al., 2016; Syed et al., 2018). Except for an analysis of co-authoring networks and author origins for artisanal fisheries research (Oliveira Júnior et al., 2016), these reviews cast a broad scope towards ‘fisheries’ or ‘fisheries science’ in general, not distinguishing between industrial fisheries and SSFs. Such reviews do not capture SSF-specific values and impacts which are eclipsed in broader fisheries reviews, overshadowed by industrial fisheries (Basurto et al., 2017; Smith and Basurto, 2019). Recent syntheses of SSF studies generally demonstrate that researchers have studied SSFs for decades, with output and disciplinary breadth expanding since the early to mid-2000s (Oliveira Júnior et al., 2016; Smith and Basurto, 2019; Purcell and Pomeroy, 2015). As the field has grown, thematic syntheses have contributed to our understanding of social dimensions of SSFs and their management (Gutierrez et al., 2011), the effects of protected areas on fisheries (Gill et al., 2017), and the overlooked connections between fishing environments and gender (Kleiber et al., 2015), among others.

Given the growing and diversifying body of research on SSFs and the unprecedented management challenges the Anthropocene poses, an overview of the trends in the geographical and topical focus of existing ecological research on SSFs is timely and merited. To begin to respond to this need, this study addresses the following questions: What aspects of SSFs have ecologists studied and how? What are key areas where ecologists can contribute to a more holistic understanding of SSFs that is relevant for management in the Anthropocene? By addressing these questions, our study highlights well-studied thematic and geographic areas or ‘bright spots’ ready to be leveraged by policy-makers to meet management challenges and global sustainability commitments, as well as under-studied areas where more basic ecological research is needed.

2. Materials and methods

We conducted a systematic search in Web of Science (WOS) and ProQuest’s Earth, Atmospheric, and Aquatic Science Collection for relevant literature using the search terms “small-scale fisher*” OR “artisanal fisher*” OR “inland fisher*” OR “subsistence fisher*” within the subject category “ecology.” Subject categories offer the most systematic search protocol reducing researcher bias and have been successfully implemented in other reviews of fisheries science (Aksnes and Browman, 2015) and ecology (Neff and Corley, 2009). WOS subject categories contain core subject-area journals and are not exclusive, meaning journals can be indexed to more than one category. Despite the advantages of using subject areas as a search strategy, articles published on the ecology of SSFs in journals that are categorized differently (e.g., as “biology” or “fisheries” but not “ecology”) are not included in this study. As other authors using a similar approach note, this is an inherent limitation of journal-based field delimitations applied in bibliometric analyses (Aksnes and Browman, 2015). While multiple search databases were used, this study likely underestimates publications on the ecology of SSFs, particularly given that our study was limited to peer-reviewed

publications in English.

After screening all publications returned by our search protocol to remove false positives (i.e. publications about industrial fisheries, aquaculture, or other topics without parallel inclusion of small-scale fisheries), the remaining 302 articles retrieved by WOS and ProQuest were each coded by two readers for attributes of the study geography, methods employed, the sub-field of ecology, and the habitat(s) and taxa studied (see supplementary materials). Article-level bibliometric information (e.g., year published, journal) and coding results were analyzed using a vote-count approach, providing an overview of the state and development of published literature on SSF in ecology journals over time (hereafter referred to as “SSF ecology publications” or “SSF ecological literature”).

3. Results

3.1. Late emergence but rising interest in the ecology of SSFs

The SSF ecological literature is young and relatively sparse with research output increasing over time. While peer-reviewed studies of SSFs started being published in the early 1960s, SSF publications in ecology journals only appeared in 1991 (Fig. 1). Both bodies of scholarship (e.g., all SSF publications and those in ecology journals) have risen in the last decade, but SSF ecological research is not increasing as rapidly as research output from the wider field of SSF studies. Regarding publication outlets, SSF ecological research is published in a variety of self-identified ecology journals, including interdisciplinary conservation, marine science, and social science journals (Table 1). The top ten ecology journals publishing the most SSF research included two of the top ranked ecology journals (*Conservation Biology* and *Ecological Applications*, based on SCImago 2016 rankings), indicating that SSF ecology research is often directed to a broader interdisciplinary audience (such as the readership of *Ecology & Society*, the most common outlet) rather than specific ecology fields and their top ranked journals.

3.2. Mismatch between research effort and the global distribution of SSFs

Far more papers are published on the ecology of marine SSFs compared to inland SSFs (76% versus 24%). However, the relative distribution of marine and inland research does not reflect the actual percentage of SSFs by landings nor employment: inland SSFs account for nearly one-third of total annual catch and over half of all fishers (Fig. 2). Among studies of marine SSFs, the Atlantic (40%) and Pacific (40%) oceans received the most research coverage, followed by the Indian

ocean (11%) and Arctic (2%). The most studied inland systems were the Amazon river (11%), Tonlé Sap (7%), and the Ganges-Brahmaputra-Meghna River Basin (4%), with remaining research effort spread thinly across different inland systems with three or fewer publications. The geographic spread of studies also did not align with the global distribution of SSFs. Latin America was the region with the most studies (48%) whereas Asia is the region with the most small-scale fishers (World Bank, 2012; Fig. 3b). The three countries with the most SSF ecological studies published were Brazil, Chile, and Mexico (Fig. 3a).

3.3. Methods employed and ecological level of analysis studied

Methods used to study SSF ecology are primarily observations and models, whereas experiments are neither widely used nor markedly increasing (Fig. 4). Across the entire study period, 75% of studies used observations, 50% used models and only 8% used experiments without much variation in the relative proportion over time. The focal level of ecological analysis of SSF studies has changed over time, with population and community ecology dominating in earlier decades giving way to a more recent rise in human dimensions and ecosystem ecology from the early 2000s to 2016 (Fig. 5). The rise in publications focused on human dimensions (e.g., governance systems, traditional ecological knowledge, community perceptions of environmental change, fishers' attitudes towards management, gear and fishing technologies) largely accounts for the recent upturn in SSF publications in ecology journals, comprising 58% of studies in the dataset.

3.4. Taxa and habitats studied

Bony fish and invertebrates were the most studied taxonomic groups (45% and 29% of studies respectively) compared to others that are targeted or directly interact with SSFs (Fig. 6a). Marine mammals, cartilaginous fish, and turtles are understudied relative to their threatened status and importance to SSF as target species and as taxa subject to unintended interactions with fisheries (e.g., bycatch, depredation, competition, gear entanglement, boat strikes). Most studies focused on benthic systems (47%) compared to pelagic (23%). Coral reefs (16%) and rivers (15%) were the most studied habitats. All other habitat types including lakes (8%), lagoons (7%), rocky reefs (6%), estuaries (5%) were less commonly studied (Fig. 6b). Other vital habitats including wetlands, mangroves, seagrass beds, and inter and sub-tidal systems were not well studied despite direct and indirect importance to SSFs as fishing grounds and nurseries for juveniles. One quarter (25%) of studies did not provide sufficient description to classify habitat type, which hinders aggregating ecological knowledge on diverse SSFs and their

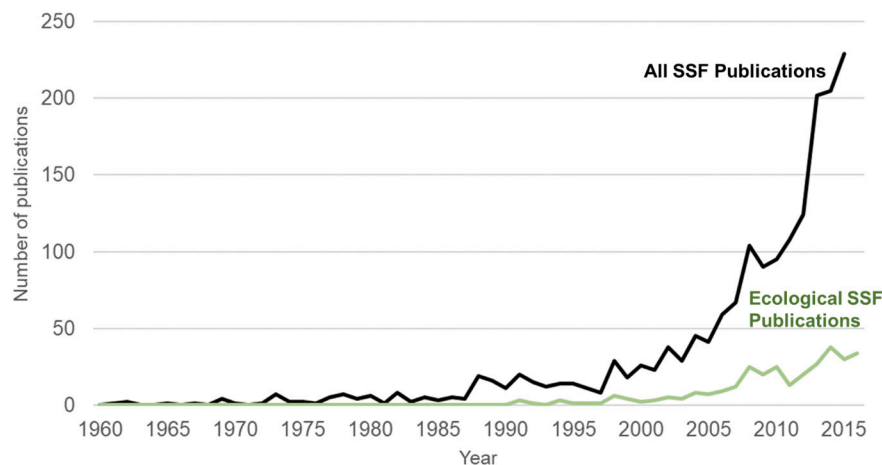


Fig. 1. Comparison of all SSF publications (Smith and Basurto, 2019) and ecological SSF publications over time. Ecological publications on SSF emerged relatively recently and have not expanded as rapidly as the wider field of SSF studies has in the last decade.

Table 1
Top 10 ecology journals publishing SSF research.

Top 10 journals ranked by number of SSF publications		
Journal	Number of publications	2016 Impact factor
Ecology and society	37	2.84
Marine ecology progress series	28	2.29
Biological conservation	23	4.02
Conservation biology	19	4.84
Ecological modelling	19	2.36
Ecological economics	16	2.97
Aquatic ecosystem health & management	14	0.88
Environmental biology of fishes	12	1.26
Ecological applications	9	4.31
Journal of experimental marine biology and ecology	7	1.94

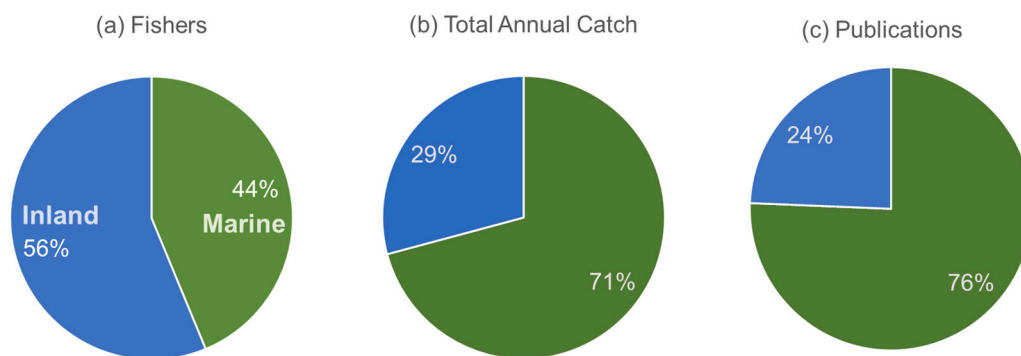


Fig. 2. Global comparison of the proportion of inland and marine SSFs across three dimensions, (a) number of fishers, (b) total annual catch, and (c) publications in this study, demonstrating that research efforts is skewed towards marine SSF and inland SSF are understudied particularly in comparison to their contribution to employment. Catch (b) is based on estimated total annual landings for marine SSF (34 million tons) and inland SSF (14 million tons) and the number of fishers employed (a) in marine SSF (14 million) and inland SSF (18 million) (World Bank, 2012).

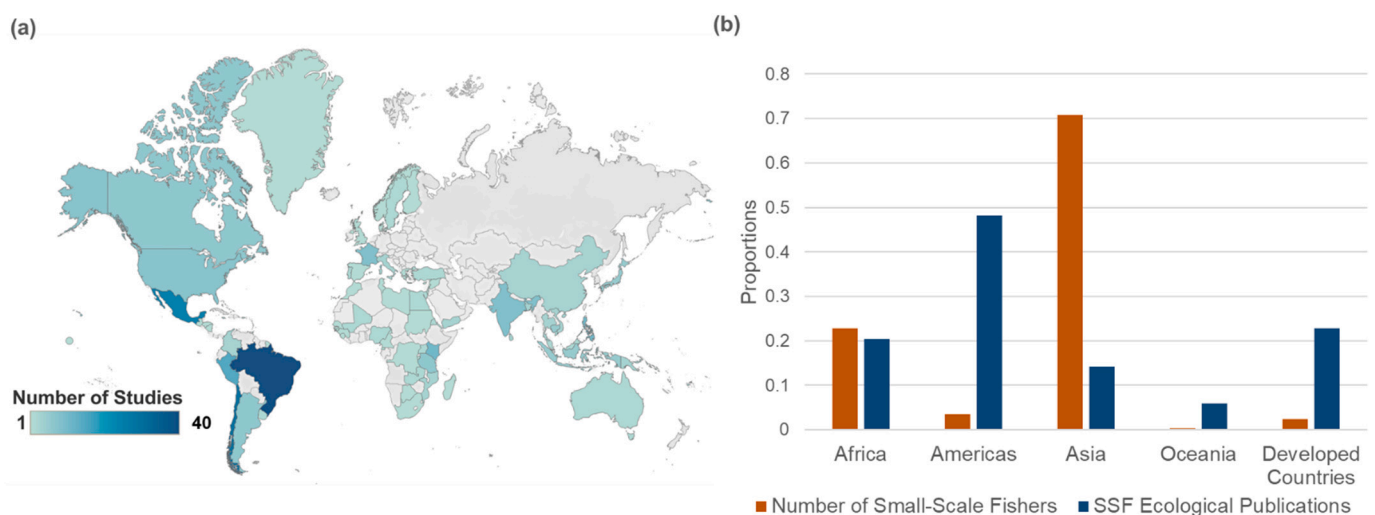


Fig. 3. Geographic comparison of the (a) number of SSF ecological studies mapped by country and (b) studies grouped by regions in contrast to the distribution of the number of small-scale fishers by regions (proportions). Most SSF ecological research is in Latin America and the Caribbean (“Americas” in 2b) whereas the most small-scale fishers are in Asia. Numbers underlying the proportions of small-scale fishers come from the Hidden Harvest study as well as regional classifications for developing and developed countries (Table 3.4; World Bank, 2012).

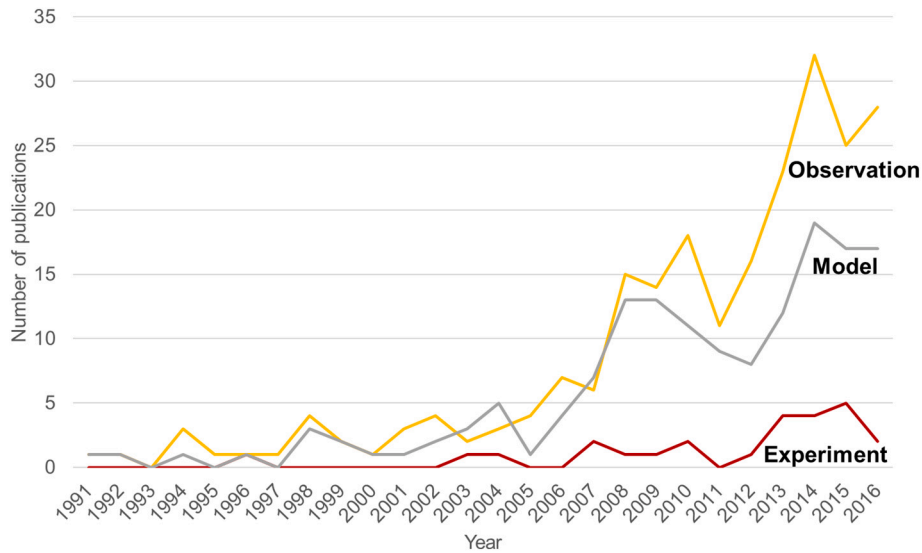


Fig. 4. Methods used in SSF ecology publications over time. Observational studies and modelling have tracked together and increased over time along with the overall rise in publications, while experiments have not been widely used.

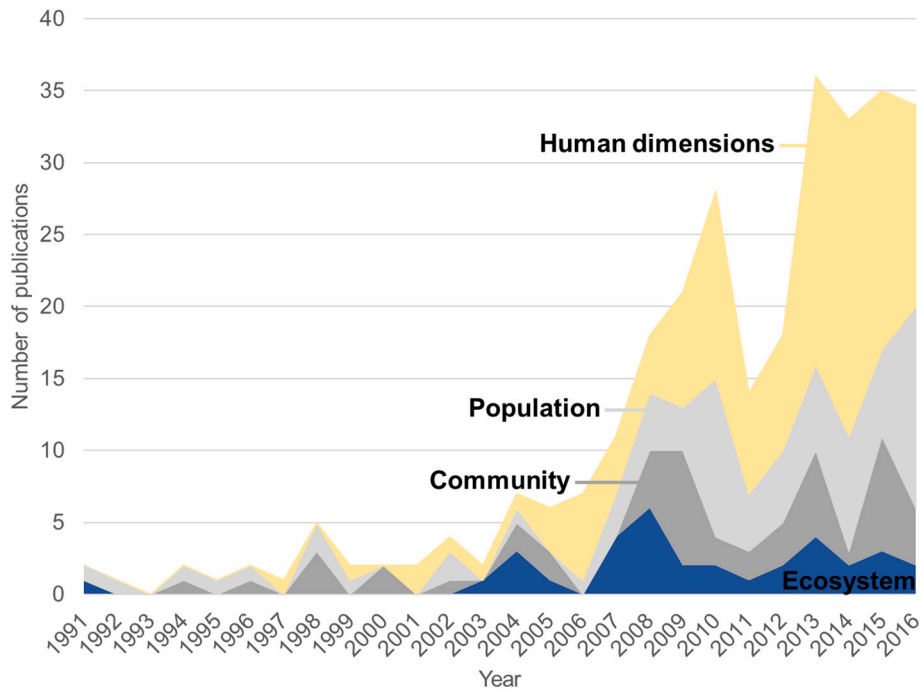


Fig. 5. Level of ecological analysis studied over time. The rise in human dimensions studies largely accounts for the upturn in SSF ecological publications in the past 15 years, whereas community and ecosystem ecology are not widely studied.

underlying habitats.

4. Discussion

4.1. Current trends reveal bright spots, gaps, and opportunities in ecological research of SSFs

After decades of neglect relative to research on industrial fisheries, SSF research has rapidly grown and diversified in the last decade (Smith and Basurto, 2019). Ecological perspectives and methods could help illuminate relationships critical to understanding and sustaining these multi-species SESs. Our analysis of SSF research in ecology journals demonstrates that this is a young and growing body of scholarship,

nearly two thirds of which has been published since 2010 (62%). The expanding body of SSF research published in ecology journals reveals bright spots and knowledge gaps: (i) marine SSFs and SSFs in Latin America are relatively well-studied, yet there is an overall mismatch between the global distribution of SSFs and ecological research; (ii) bony fish and invertebrates inhabiting coral reefs and rivers are relatively well-studied, but threatened taxa and habitats which are critical to SSFs are not presently well-studied by comparison; and (iii) there is rising interest in the human dimensions of SSFs and research output in interdisciplinary journals, but studies seldom incorporate ecological data or experimental methods. Below we outline the implications of these trends for our present understanding of SSFs and highlight areas where more targeted research could enhance the comprehensiveness of our

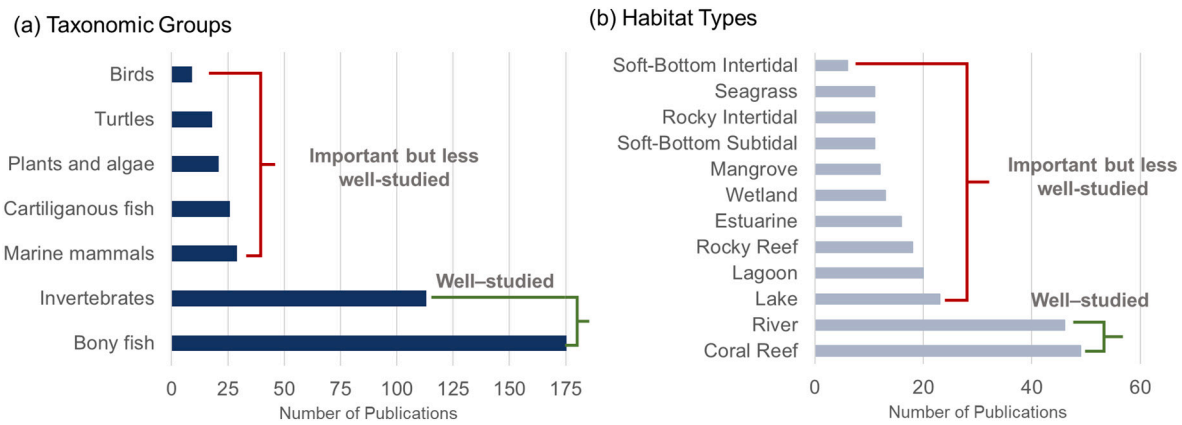


Fig. 6. Counts of SSF studies by different (a) taxonomic groups and (b) habitat types. The panels show a similar pattern with two dominant types emerging as relatively well-studied and a range of important but relatively less well-studied groups and habitat types that SSF directly and indirectly depend on and interact with.

knowledge and effective management strategies in the Anthropocene.

4.2. Global mismatch between research output and distribution of SSFs

4.2.1. Inland fisheries understudied relative to global distribution of SSFs

Currently, 76% of SSF research in ecology journals focuses on marine systems, which does not reflect the global balance of inland versus marine SSFs for overall catch and employment. Inland fisheries are overwhelmingly small-scale and play an outsized role in household food security and employment (Paukert et al., 2017; Lynch et al., 2016a; Bennett et al., 2018) but have historically been marginalized in fisheries policy, overshadowed by higher profile interest in marine fisheries. Our study shows that this pattern is replicated in ecological SSF research, leaving freshwater ecosystems that underpin inland fisheries understudied. Inland fisheries are plagued by issues of unreported catch, inconsistent national statistical monitoring systems, and issues of data disaggregation, yielding data deficiencies which contribute to misperceptions about their global scale and magnitude. However, most ecological SSF research in our dataset was not reliant on fisheries-dependent data, thus a lack of reliable inland fisheries data should not necessarily impede ecological research on the dynamics of freshwater fisheries systems. Therefore, while the pattern of imbalance in research attention between marine and inland fisheries in our study conforms with wider trends in fisheries science and policy, data deficiency is not likely the limiting factor, instead this is likely due to the fact that research on freshwater systems often emphasize non-fisheries uses of these systems (Funge-Smith and Bennett, 2019). Further, the general lowly status of inland fisheries in the sphere of capture fisheries may also contribute to this trend, where present knowledge gaps perpetuate the sector's lack of recognition and a dearth of resources assigned to inland fisheries by national and international institutions (Welcomme et al., 2010; Funge-Smith and Bennett, 2019). For example, the Sustainable Development Goals (SDGs) highlight the importance of marine fisheries (e.g., SDG14b), without a corollary recognition of the role of inland SSFs (Funge-Smith and Bennett, 2019; Lynch et al., 2017).

However, threats to freshwater ecosystems and the simultaneous importance of inland fisheries to food security are increasingly recognized, where a better understanding of these systems dynamics is needed to achieve sustainability in the Anthropocene. In 2015, inland fisheries experts at the FAO made high-level, global recommendations for inland fisheries including the need to recognize and account for their ecological diversity in assessment processes. Additionally, experts recommended basing inland fisheries management on scientific evidence and within their broader ecosystem and sociopolitical contexts (Cooke et al., 2016). Thus improved ecological characterization of inland SSFs, informed by policy needs, is vital to sustaining what are already among the most altered ecosystems in the world (Vörösmarty et al., 2010), inhabited by

some of the most threatened vertebrates on the planet (Sala et al., 2000). Currently, our understanding of how climate change will affect inland fisheries has lagged assessments of marine systems, leaving critical research gaps on the tolerance of freshwater fisheries to changes in temperatures, stream flows and volume, and salinity. Ecological knowledge on the dynamics of fish populations beyond changes in species phenologies and distributions are needed, including possible changes in population dynamics, assemblages, and interspecific interactions (Lynch et al., 2016b). Current assessments of freshwater fishes' response to climate change have been species-specific (e.g., Kovach et al., 2016) and concentrated on developed country contexts (e.g., Whitney et al., 2016; Lynch et al., 2016b). More comprehensive ecological knowledge of inland fisheries impacts and responses to climate change could enhance decision-support tools, identifying opportunities to aid the adaptive capacity of these systems to respond to climate change (Paukert et al., 2017; Lynch et al., 2016b), which is particularly important in developing countries where these systems are critical to food security.

4.2.2. Latin America and the Caribbean is the best studied region, Asian SSFs are understudied

Currently, the Latin American and Caribbean region has the greatest number of SSF ecology publications; a pattern which diverges from the geographic distribution of SSFs. Based on the best global estimates, five out of six of the countries with the greatest number of marine SSFs are in Asia (World Bank, 2012) and Asia accounts for 67% of inland production (FAO FishstatJ, 2019). The under-representation of research in Asia may be linked to our study's focus on English language journals. Nonetheless, assessing the ecological dynamics and sustainability of SSFs in Asia is important to ensure that research effort aligns with environmental impact and the importance of fish for food security. Future efforts to synthesize ecological knowledge of SSFs in Asia would be beneficial for painting a more complete picture. Geographic bias in the study of ecological systems is common (e.g. Lawler et al., 2006; Zhang et al., 2018), where scientists tend to return to their same study sites, building labs and research networks with a strong geographic focus, some of which reflect historical colonial relationships or Diaspora Knowledge Networks (DKNs) (Meyer and Wattiaux, 2006; Oliveira Júnior et al., 2016). The disproportionate coverage of Latin American SSFs is likely explained by the presence of several productive fisheries ecologists from the region (Oliveira Júnior et al., 2016), the prevalence of English within Latin American research institutions, and the region's accessibility to researchers in the United States and Canada. Further, our observation that developed nation's fisheries are better studied is notable and concerning as the "the research needs associated with tropical artisanal fisheries are immense and are predominantly located in developing countries of the Global South" (Oliveira Júnior et al., 2016). Oliveira

Júnior et al.'s review of artisanal fisheries research found that developed countries dominated co-authoring networks (in terms of author origins), our study adds to their conclusions about the global mismatch between research needs and capacity, demonstrating that this gap is mirrored in the geographic foci of research effort. The geographic bias we identify in ecological research on SSFs presents opportunities to leverage existing knowledge on better-researched areas such as Latin America and developed nations into regional overviews, while under-researched areas in the Global South will require greater attention to meet the objectives of sustainable fisheries set by the UN.

4.3. Threatened taxa and understudied habitats

Species of bony fish and invertebrates are the best studied in current ecological research of SSFs and make up most of the global catch (FAO, 2018). Yet gaps exist in our understanding of the impacts of SSFs on vulnerable species, including both target species and non-target species interactions with fisheries and fish assemblages. Sharks and rays are common in multispecies catches characteristic of SSFs, but landings often go unregulated and unreported, making global estimates difficult (Dulvy et al., 2014). Though sharks and rays play critical functional roles as predators in both oceanic and freshwater ecosystems, their life history traits make them particularly sensitive to overfishing (Cortés, 2000). Over half of shark and ray species are estimated to be threatened or near threatened, with coastal sharks and rays at a greater risk due to combined threats of fishing pressure and habitat degradation (Dulvy et al., 2014). While the consequences of shark fishing have received attention in recent years (Stevens et al., 2000; Clarke et al., 2007), estimates do not typically distinguish between the impacts of small-scale and industrial fisheries, where the latter often include sharks and rays as bycatch. Targeted studies of the ecology of freshwater, estuarine and marine sharks and rays' interactions with SSFs are needed to disentangle the drivers of declining populations (e.g., coastal degradation versus direct fishing pressure and the differences between industrial fisheries and SSFs). Given that shark and ray species have one of the highest data deficiency ratings of any taxonomic group (Hoffmann et al., 2010), fisheries-independent ecological assessments are particularly important to understand the relationship between SSFs and these vulnerable species.

Coral reefs were the most studied habitat type. Given the importance of coral reefs as foundation species and fishing grounds, sustained research effort is important. Particularly in light of climate change impacts on coral reefs (Hughes et al., 2003; Hoegh-Guldberg et al., 2007) predictive ecological models are necessary (Yates et al., 2018), especially if models can help with data-deficiency in many fisheries (Basurto et al., 2017). However, as the principles of landscape ecology and ecosystem-based management are increasingly applied to fisheries, a better understanding of interactions across habitat types is important for holistic 'seascape' management (Pittman and Brown, 2011; Weeks, 2017), such as the role of mangroves and seagrass beds for juvenile fish and other landscape-scale interactions across habitats (e.g., coral reefs and mangroves; Mumby et al., 2004). Habitats are connected through the dispersal of larvae and post-settlement migration of commercially and ecologically important fish species (Weeks, 2017). Given that SSFs are typically multispecies, with fishers themselves utilizing multiple habitats, more research on the social-ecological dynamics of connectivity across habitats in SSF would be a valuable contribution by ecologists.

4.4. Rise of interdisciplinarity and human dimensions

Research on the human dimensions of SSFs is on the rise in ecology journals. Many of these studies draw on social-ecological systems (SES) literature to represent SSFs as coupled human and natural systems. The increase in studies of human dimensions may reflect a shift in funding priorities and towards SES-themed research (Kittinger et al., 2013).

Balanced research that addresses human and ecological dimensions of these systems and their interactions is essential to a more holistic scientific understanding of SSFs. However, many SES studies coded as 'human dimensions' in our data set lacked basic ecological data. Our observation supports the critique by Epstein et al. (2013), that SES research often better elucidates human dimensions with limited incorporation of ecological principles, methods, or data. This imbalance in treatment of the "social" and "ecological" may result partly from the cost and difficulty of measuring ecological variables and a lack of expertise among SES researchers (Basurto, 2008). While the desire to understand linkages between the human and ecological dimensions of SSFs is apparent, the ecological gap (i.e., in expertise and substantive ecological data) in current SES research is an area where ecologists could contribute. Research would benefit from enhancing SES studies through the wider incorporation of core ecological theories and methods in study design, particularly experiments. While experimental manipulations are powerful approaches to test for causal linkages in science and have long been employed in non-human ecological studies (Connell, 1961; Paine and Gould, 1977), our review found their use in studying SSFs was uncommon. SSFs are relatively small and manipulable systems, and thus more amenable than large scale fisheries to experimental studies. Experiments could help resolve problems stemming from confusion between correlation and causation, testing possible variables to isolate drivers behind observed SSF dynamics and evaluating insights drawn from observations and modelling.

5. Conclusions and future directions

The Anthropocene provides a powerful bridging concept cross-cutting social and natural science disciplines (Sullivan et al., 2017). The term's rise has brought reexamination of long-standing dualisms that shape how scientists and policymakers think about, model, and manage global change (Brondizio et al., 2016). In the context of fisheries, responding to the unprecedented planetary changes that mark this era requires thinking outside the confines of traditional fisheries science metrics (Barreto et al., 2020), shifting attention to social and ecological connectivity and variability, with greater attention to the specific dynamics of SSFs. Global bodies such as the UN have committed to ensuring the future viability and sustainability of SSFs, and called for scientists from diverse disciplinary perspectives to work with policymakers, managers, fishers, aid organizations, and civil society to collaboratively respond to emergent sustainability challenges. Social scientists have answered this call, translating different theories of human behavior and methods to the study of environmental systems and SSFs. Ecological knowledge is needed to understand how resource degradation, climate change, and worsening natural disasters are affecting population dynamics, species ranges and assemblages, species interactions, habitat connectivity, and ecosystem stability. Ecologists can therefore help inform evidence based SSF policymaking to meet global commitments to support SSF sustainability, such as those outlined by the SDGs and the FAO. But general calls for "more research" must be guided by an understanding of what the field has already undertaken.

Our review demonstrates that research on SSFs published in ecology journals is growing, with the greatest research effort thus far focused on marine fisheries in Latin American and the Caribbean, on bony fish and invertebrates, and on coral reef and riverine habitats. Studies have primarily utilized observations and models in their methods, historically focusing on population ecology and more recently, on human dimensions. Knowledge of these relatively well-researched areas (e.g., taxa, habitats, and geographies) on the ecology of SSFs should be leveraged by policymakers, managers, fishers, and the public to help meet UN goals of managing SSFs sustainably. Yet at present, effective synthesis and communication of existing research may be lacking. In addition to these 'bright spots', our review found relatively understudied areas, which we suggest are key directions for future research: inland fisheries, SSFs in Asia, SSF interactions with threatened species

such as cartilaginous fishes, and habitat connectivity across ‘seascapes’. Understanding the effects of and preparing SSFs to respond to widespread environmental changes requires greater use of experimental methods and more extensive study of community and ecosystem ecology in these systems. In this pursuit, experimental methods could be used to simulate changing conditions under different climate change scenarios, the results of which could help test the efficacy of possible management interventions and inform strategies to support the resilience of SSFs.

Our synthesis represents an initial effort to illustrate what aspects of SSFs ecologists have studied and encourage greater engagement by ecologists with SSFs and interdisciplinary collaborations with other natural and social scientists already studying them. Given the rising concerns about the societal impacts of climate change upon SSFs (Barange et al., 2014; Golden et al., 2016; Blasiak et al., 2017), career opportunities likely await ecologists able to fill knowledge gaps, assess the impacts of possible interventions, and clearly communicate recommendations for managers. By working directly with policymakers, managers, and fishing communities, future ecological research can be best aligned with the evolving informational needs and sustainability challenges all fisheries, large and small, face in the Anthropocene.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary materials: methods, coding protocol, and data

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