Fish Flow: following fisheries from spawning to supper

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Novel methodologies now make it possible to track the complete geographical movements of seafood species from reproduction to human consumption. Doing so will better inform consumers and assist resource managers in matching fisheries and conservation policies with natural borders and pathways, including stock boundaries, networks of marine protected areas, and fisheries management areas. Such mapping necessitates an unprecedented synthesis of natural and social sciences, including knowledge of adult fish population abundance and movements, egg output, larval dispersal, and recruitment to juvenile and adult habitats, as well as fisheries stock assessment, capture, and distribution through human social networks. The challenge is to fully integrate oceanography, population genetics, ecology, and social sciences with fisheries biology to reveal the patterns and mechanisms of "Fish Flow" from spawning to supper. As practitioners representing all five of these disciplines, we believe that Fish Flow analyses will promote sustainable fisheries management and marine conservation efforts, and may foster public knowledge, wise seafood choices, and appreciation of social–ecological interconnections involving fisheries.

"Managing fisheries is hard: it's like managing a forest, in which the trees are invisible and keep moving around" – John Shepherd *(unpublished lecture at Princeton University, 1978)*

I ncreasing demand for seafood puts escalating pressure on marine resources, incentivizing overfishing and harmful fishing practices that damage marine ecosystems. Over

In a nutshell:

- Most exploited ocean species live in "stocks" or "marine metapopulations" (groups of isolated local populations connected by dispersal of larvae), which have proven difficult to delineate and study
- Recent methodological breakthroughs now allow mapping of fisheries stocks from spawning to human consumption, yet doing so will require unprecedented integration of oceanography, population genetics, ecology, fisheries biology, and social sciences
- Partial examples are now available for this developing synthesis, which will eventually culminate in web-based, interactive "Fish Flow" maps depicting the many connections and interdependencies between marine ecosystems and human communities
- Development of Fish Flow maps will inform sustainable fisheries and marine conservation efforts in unprecedented detail

one-third of global fish stocks are currently exploited unsustainably (FAO 2020), and this will likely only worsen as human populations continue to grow. At the same time, the healthiest fish stocks globally are those subject to modern fishery management (Hilborn *et al*. 2020). Beyond conventional management and more recent ecosystem-based approaches (Francis *et al*. 2007), marine conservation efforts in developed nations often focus on consumer choice to curtail industrial overfishing (Oken *et al*. 2012). Various means of educating seafood consumers include online monitoring of fishing vessels (eg Global Fishing Watch), blockchain technology to securely trace seafood supply chains (eg Two Hands), informational cards and smartphone apps (eg Seafood Watch), and seafood sustainability certifications (eg Marine Stewardship Council). The flow of seafood from fisheries to human consumption can be quite complicated, as illustrated by recent mapping efforts at local (Glazier *et al*. 2013), regional (Fuller *et al*. 2017), and global (Ramesh *et al*. 2019) scales; this complexity can hinder effective management and conservation, and impede informed consumer choice regarding seafood sources.

To address this gap, an interdisciplinary "Fish Flow" analysis would allow consumers, fishing communities, conservationists, marine resource managers, and policy makers to resolve the origin, status, and fate of seafood stocks, as well as appreciate the many connections and interdependencies among widely separated marine ecosystems and human communities. Although there have long been calls for multidisciplinary approaches to fisheries, to the best of our knowledge none have focused on spatially explicit mapping of the flow of fish from their origins at spawning to the dinner table. Here, we first briefly review the ecological and social context of Fish Flow, define it explicitly, and list how such analyses will benefit fisheries management and conservation. We then summarize

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recent breakthroughs in the component disciplines, including examples of studies that have partially integrated these components, and explore why a comprehensive Fish Flow analysis has yet to be accomplished. We conclude with our vision of future web-based, interactive Fish Flow maps that inform the public, policy makers, and managers in unprecedented detail, which may also foster wise stewardship based on tangible knowledge of social–ecological interconnections.

■ Marine metapopulations and the pathways of marine fisheries

Most marine invertebrates and fishes have larval and adult forms so distinct that at times in the past they were formally described as different species. Adults of most of these species do not move around very much, being either sessile or roaming a localized home range associated with the seafloor. The exceptions are open-ocean (pelagic) species that can migrate over vast ranges. Regardless of adult movements, spawners produce miniscule larvae that are capable of riding ocean currents and can settle either close to the spawning site or be dispersed great distances. This larval dispersal process connects groups of locally open populations into a relatively closed "marine metapopulation", known as a "stock" in fisheries (Kritzer and Sale 2004). Larval dispersal was long one of the great unknowns of marine science, yet recent breakthroughs now both predict and track patterns from spawning to "settlement", the transition from larval to juvenile life for seafloor-associated species (Cowen and Sponaugle 2009). Juveniles eventually undergo "recruitment" to the local population, and if captured as juveniles or adults, to the fishery (Caley *et al.* 1996). The combination of these biological cycles with fishery "stock assessments" (analyses of demographic data determining changes in stock size in

response to fishing), as well as patterns and pathways of catch, distribution, and consumption by humans, comprises the complete social–ecological system of a marine fishery.

■ What is Fish Flow and what are its benefits?

The Fish Flow concept was originally used by social scientists to describe the post-catch distribution of seafood through social networks on land (Severance *et al.* 2013), and has been assessed empirically on shore for some coastal fisheries (eg Glazier *et al.* 2013; Kittinger *et al.* 2015). Here, we incorporate marine natural sciences and expand the concept to be a fully integrated analysis that tracks the movement of seafood from spawning through larval dispersal, then juvenile and adult survival and growth, to capture, distribution, and consumption (Figure 1).

By revealing the details and mechanisms underlying marine metapopulation and fisheries dynamics holistically, a complete Fish Flow analysis will provide a variety of benefits to both management and conservation. Here, we provide just a few examples. Fish Flow will (1) elucidate the geographical boundaries of stocks in unprecedented detail, which is important because mismatches between natural fish population boundaries in the sea and often-arbitrarily delineated management areas can cause major errors in fishery policies (Berger *et al.* 2020); (2) enable biologically realistic design of community-based fisheries management areas, identifying the extent to which adjacent communities are linked both by movement of fisheries species at sea and by catch distribution on shore (Krueck *et al.* 2019); (3) facilitate the design of networks of marine protected areas by helping to pinpoint sites that seed other locations with particularly high numbers of larvae (Pelc *et al.* 2010); (4) identify explicit sources of seafood for consumers, enabling informed decisions regarding environmentally conscious diet choice (Richter and Klöckner 2017); and (5) illustrate the many interconnections between humans and marine ecosystems, which we hope will foster a conservation ethic based on the appreciation that all things are connected (Muir 1911).

Although the scientific benefits of Fish Flow are straightforward, it may be less clear that these analyses are also critical for influencing people's behavior regarding seafood choice. Conservation psychologists report that such behavioral change involves "background knowledge" like that provided by Fish Flow, which increases the willingness of consumers to make environmentally friendly choices (Almeida *et al.* 2015; Richter and Klöckner 2017). In general, knowledge that enhances a sense of connection with nature and appreciation of ecological interconnections (eg a Fish Flow map) tends to foster sustainable behaviors (Nisbet *et al.* 2009).

Figure 1. Conceptual diagram of the Fish Flow interdisciplinary approach for tracking fish from spawning to supper. The four colored blocks show the conventional domains of different disciplines: blue (oceanography and population genetics), green (ecology), yellow (fisheries biology), and pink (social sciences). Cumulatively, these blocks and the overlap between adjacent blocks cover the complete life cycle and fisheries of typical seafood species (cod [*Gadus* sp] illustrated). The arrow from *stock dynamics* to *spawning* indicates that the adult population is the source of reproduction.

■ Fish Flow will integrate breakthroughs in five disciplines

A complete Fish Flow analysis will require an interdisciplinary synthesis of five fields of research. It is important to
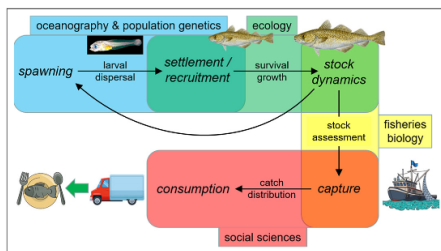
note that on its own, each discipline can reveal only a por-
tion of the overall system (Figure 1). As practitioners of all
five essential disciplines, we believe that fully integrated Fish
Flow analyses will be forthcoming soon because of recent
methodological breakthroughs, as well as the fact that partial
(mostly pairwise) syntheses of the constituent fields are already
occurring. Recent advances in each of the five constituent
disciplines are discussed in the sections below.

Oceanography

Tracking dispersal of diminutive larvae over vast areas of the
world's oceans has until recently been virtually impossible.
Coupled physical-biological oceanographic models of ever-
higher resolution can now simulate larvae as passive and/or
active particles, tracking virtual larvae from spawning to set-
tlement, thereby providing estimates of larval dispersal pathways
and population connectivity (Swearer et al. 2019). The physical
component of these models calculates water movement and
physical structure within a defined ocean area, while the bio-
logical components attempt to emulate biotic processes during
the larval lifespan. Life-history characteristics such as pelagic
larval duration, as well as behaviors like depth selection, are
critical to the accuracy of these coupled models (Metaxas and
Saunders 2009). Although small larvae are typically incapable
of swimming against horizontal currents, many can swim
vertically (Mileikovsky 1973). A species that can orient itself
relative to various physical features can vastly alter its hori-
zontal transport distance (Woodson and McManus 2007).

Population genetics

Genetic techniques are now essential tools for characterizing
connectivity in the ocean, revealing patterns of larval dis-
persal (Weersing and Toonen 2009). Population genetic
methods historically used one or a few genomic regions
(loci) to describe larval dispersal as gene flow over hundreds
to thousands of kilometers. However, these methods are
ineffective at identifying patterns of gene flow at smaller
spatial scales relevant to ecology and fisheries. Using tiny
tissue samples, advances in genomic techniques now allow
parentage studies that use hundreds or thousands of loci
to track individual larvae from spawning to settlement
(D'Aloia et al. 2015). Parentage analyses, akin to the DNA
fingerprinting used in forensic science, can link the location
where the parent spawned to the location of the offspring,
thereby resolving patterns of connectivity as well as self-
recruitment back to the same local population (Abesamis
et al. 2017). Fortunately, the costs of genetic analyses are
declining rapidly, allowing the large sample sizes required
to detect parent-offspring pairs in the sea.

Ecology

Detailed demographic studies of juvenile and adult fish and
invertebrates now provide information on the rates of set-
tlement/recruitment, growth, survival, and movements that

drive and regulate local population dynamics (Hixon et al.
2012). Varying in time and space, these demographic rates
ultimately form the foundation of fisheries production.
Measures of input to local populations are provided by
counts of new settlers (by divers) or of young-of-the-year
recruits (by surface-based sampling gear). Demographic tools
include mark–recapture studies (Pine et al. 2003) and anal-
yses of rings in fish otoliths (calcium carbonate structures
in the inner ear of fish that aid in orientation and hearing)
(Campana 2005), both of which provide data on growth,
survival, and movements. Tracing juvenile and adult move-
ments has benefited from advances in miniature telemetry
tags, along with subcutaneous microtags and markings that
enable rapid individual identification (Pine et al. 2003).
Otolith analyses include detection of the duration of the
larval dispersal period and microchemical signatures locked
in growth rings, which provide information about habitats
used during different stages of fish development (Campana
2005). Measurements of egg production and spawning output
provide estimates of larval production for the next gener-
ation. The rate at which larvae are produced is an essential
parameter for calculating the volume of larval dispersal
contributing to Fish Flow (Johnson et al. 2018). Mapping
of spawning locations also reveals the time and place of
gamete release that feed into larval dispersal models (Ciannelli
et al. 2015).

Fisheries biology

Fisheries biology documents interactions among fish pop-
ulations, the environment, and fishing communities to man-
age seafood resources. Traditionally, fishery-dependent data
provided time series of effort and catch that informed the
stock status of exploited species (Hilborn and Walters 1992).
More recently, fishery vessel tracking systems collect high-
resolution spatial and temporal patterns of effort and catch
that support geographic analyses (Gerritsen and Lordan
2011). These systems provide information for examining
fishery interactions with target stocks and their habitats,
assessing fishing behavior and vessel interactions, and eval-
uating fishing activity relative to area closures. In addition,
fishery-independent surveys provide unbiased data on
metapopulation-scale abundance or biomass indices and life-
history information for target species (Hilborn and Walters
1992). Of the five disciplines involved in Fish Flow, fisheries
biology is the most integrative, with many fisheries scientists
now making use of oceanographic models, population genet-
ics, ecology, and social sciences (Essington et al. 2017).

Social sciences

Social sciences are as diverse as natural sciences, yet are amal-
gamated here with respect to how fishery catch connects to
the dinner table (Figure 1). Marine social sciences can help
illuminate social, economic, and cultural values, drivers, and
factors associated with seafood capture, distribution, and

consumption. Research on human dimensions of seafood catch distribution has grown in complexity, sophistication, and overall breadth, and is now viewed as critical for informing sustainability dialogues in policy and governance (Bennett 2019). As a prelude to more holistic Fish Flow analyses described here, recent studies have mapped the distribution of seafood among communities on shore, helping elucidate the structure of social networks relating to a fishery, as well as the food and livelihood security function of artisanal fisheries (Glazier *et al.* 2013; Severance *et al.* 2013; Kittinger *et al.* 2015). Related research has focused on the cultural dimensions of fishing activities and the role of social drivers, along with traditional and cultural practices, in determining catch distribution patterns and their value to communities. Social sciences have also focused on characterizing complex value chains for fisheries, examining the extent to which catch is channeled through commercial markets, as well as subsistence use and barter (Grafeld *et al.* 2017). Examples of now-common methodologies that social scientists use to assess Fish Flow include ethnographic and interview-based research, participatory mapping, and social network analysis.

■ Ongoing interdisciplinary syntheses move toward Fish Flow

In addition to the development of new tools reviewed above, partial (mostly pairwise) syntheses of the constituent Fish Flow fields are already occurring, albeit not yet with the goal of mapping overall movement from spawning to supper. The most extensive integration to date has occurred between marine ecology and fisheries biology. Indeed, "fisheries ecology" is now a recognized subdiscipline that includes tracking fish stocks from spawning to capture (Hidalgo *et al.* 2017). Social sciences, especially socioeconomics, have also long been an essential component of fisheries management, but only recently in the context of mapping catch distribution on land (Figure 2; Kittinger *et al.* 2015).

Pairwise integration of natural-science disciplines is also evident in the non-fisheries components of Fish Flow, though again, not yet in the context of holistic mapping. Oceanographic models are often now integrated with regional ecological studies. For example, Lipcius *et al.* (2001) found that the effectiveness of marine reserve sites for Caribbean spiny lobster (*Panulirus argus*) in the Bahamas, measured empirically within sites, was a function of connectivity among sites estimated from a larval dispersal model. Studying multiple fishery species, Treml *et al.* (2015) integrated a range of demographic parameters that affect reproductive output into a larval dispersal model for Port Phillip Bay, Australia, and concluded that the primary factors determining recruitment success across species were larval mortality, duration of the pelagic larval stage, and the period over which larvae are competent to settle.

Integration of oceanographic models (predicting larval dispersal pathways) and genetic kinship analyses (documenting actual larval dispersal start and end points) is developing rapidly and at increasing resolution (Cowen and Sponaugle 2009). Examples include studies of reef fishes and invertebrates in Hawaii (eg Christie *et al.* 2010), California (eg White *et al.* 2010), the Red Sea (eg Raitsos *et al.* 2017), and the Great Barrier Reef (eg Bode *et al.* 2019). Genetic studies of larval dispersal have also been integrated with ecological studies of the reproductive output of local populations, providing estimates of the actual volume of larval flow from one location to another (Figure 3; Johnson *et al.* 2018). Such analyses have socioeconomic ramifications. Almany *et al.* (2013), for instance, used genetic kinship analyses to show that larval dispersal from a spawning aggregation of squaretail coral grouper (*Plectropomus areolatus*) located in one community tenure area in Papua New Guinea seeded both that area and adjacent tenure areas. These communities embraced their new knowledge of their ecological interdependence by subsequently establishing a "resource development network" of managed and protected areas to ensure sustainability of their collective fishery resources (Almany *et al.* 2015).
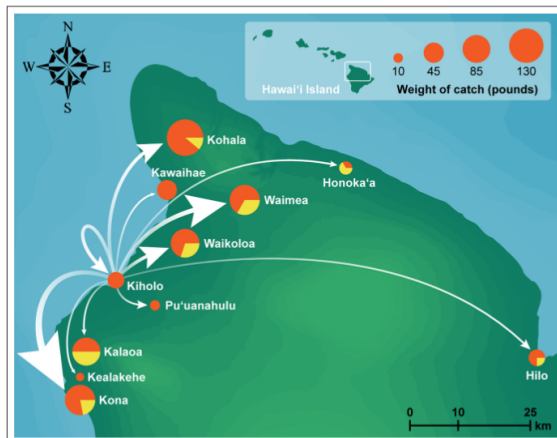

Figure 2. Spatial patterns of reef-fish catch distribution among local communities from landings at Kīholo Bay, Hawaii. The thickness of each arrow represents the number of distribution events studied, and the size of the pie chart indicates the weight of the catch. Within each community's pie chart, orange slices are Kīholo-landed fish that were kept for home consumption, and yellow slices are Kīholo-landed fish that were given away (not sold) for home consumption. Redrawn from Kittinger *et al.* (2015).
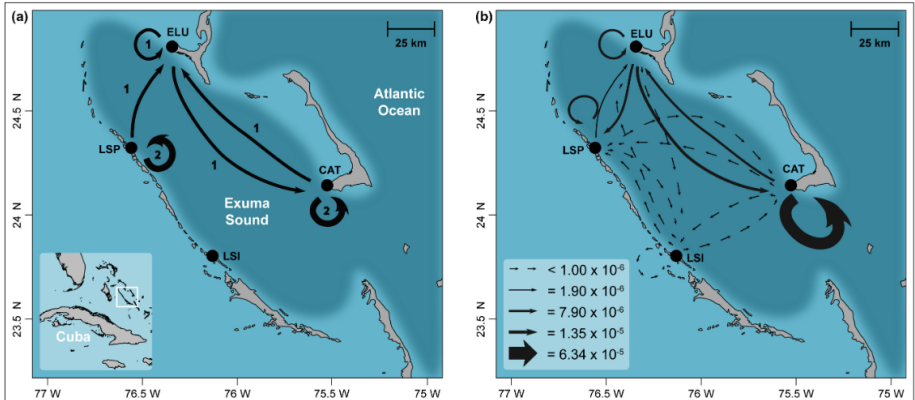
Figure 3. Integration of population genetics with population ecology elucidates larval dispersal of the coral-reef fish *Stegastes partitus* (bicolor damselfish) in Exuma Sound, Bahamas. (a) Number of genetically detected parent–offspring pairs, showing connectivity between sample populations (arrows connecting sites) as well as self-recruitment (circular arrows). (b) Integrating genetic patterns with larval production at each population, "demographic connectivity" is the estimated proportion (illustrated by relative arrow thickness) of eggs produced by each population that survived and dispersed as larvae to other populations (arrows connecting sites) or returned to their natal populations (circular arrows). Eleuthera (ELU), the Exuma Cays Land and Sea Park (LSP), Cat Island (CAT), and Lee Stocking Island (LSI). Redrawn from Johnson *et al.* (2018).

Integration of at least three of the five disciplines required for a full Fish Flow analysis has thus far been relatively rare. A combined suite of oceanographic, ecological, and fisheries models employed 39 years of data to evaluate spatial trends, physical-biological interactions, and biological reference points for Alaskan fisheries in the eastern Bering Sea (Ortiz *et al.* 2016). These models elucidated a cross-shelf gradient of higher variability in physical and biological patterns inshore versus offshore, a latitudinal gradient in the timing of ecological processes, and an effect of temperature on recruitment and recommended fishery yield. In the Philippines, Abesamis *et al.* (2017) compared genetic studies of larval dispersal of the coral-reef fish *Chaetodon vagabundus* (vagabond butterflyfish) with the geographic distribution of community-based marine protected areas for fisheries production. The social-science conclusion was that spatial patterns of larval connectivity demonstrated the importance of instituting cooperative fishery management among local communities within the region.

■ **Challenges to implementing Fish Flow**

Why has there not yet been a complete Fish Flow analysis from spawning to supper? Despite recent methodological breakthroughs in the constituent disciplines, as well as partial syntheses (summarized above), there remain several challenges to achieving full implementation. The most general issues plague all large-scale, interdisciplinary projects: silos and funding. Scientific silos – the reluctance to collaborate outside one's discipline – is a social/psychological issue that is fortunately waning as it becomes increasingly clear that solutions to major environmental issues require interdisciplinary collaboration (Cochrane 2017). The fact that limited funding is a perennial issue for interdisciplinary science is common knowledge. There are also some limits to which each of the five constituent disciplines can presently contribute to Fish Flow analyses effectively, constraints that hinder but do not actually preclude Fish Flow analyses and which we believe will soon be overcome. These are discussed in the following sections.

Oceanography

One crucial component that is often excluded from coupled biological-physical oceanographic models – usually due to a lack of relevant information – is larval behavior (Leis 2021). As mentioned above, although small larvae are typically incapable of swimming against horizontal currents, many can swim vertically, and more recent models are exploring ways to successfully integrate this larval behavior (Swearer *et al.* 2019).

Population genetics

Because of larval dispersal, identifying parents and offspring in the sea requires large sample sizes, which can impose daunting logistical constraints. Moreover, although the cost of genetic analyses to identify parent-offspring pairs is declining rapidly, further development of analytical approaches is still needed (Christie *et al.* 2017).

Ecology

Gathering the demographic data required for Fish Flow analyses is labor intensive, and ideally requires study species and systems where individual survival, growth, movement, and reproductive output can be measured directly. Although there are promising new approaches for securing such data from otoliths and other indirect methods, detailed demographic analyses are presently constrained to shallow marine systems, such as temperate rocky reefs and tropical coral reefs (eg Hixon *et al.* 2012; Johnson *et al.* 2018). Fortunately, these systems include major fisheries, especially in developing nations.

Fisheries biology

Collection of fisheries data required for detailed stock assessments – effort, catch, stock abundance, and life-history characteristics – is expensive, and will continue to be for the foreseeable future. Spatial stock assessments can reduce bias in estimates caused by spatial population structure, yet substantial data inputs are required (Punt 2019). We

Figure 4. Larval dispersal patterns of a species of surgeonfish among studied coral reefs (dark blue arrows connecting black circles; data from Christie *et al.* [2010]) compared with reef-fish catch distribution patterns among local communities (white arrows connecting white circles) from landings at Kīholo Bay, Hawaii (white star; data from Kittinger *et al.* [2015]). Although the two studies were not integrated originally and did not involve the same species, together they suggest that people on the north side of the Island of Hawaii may depend on fish spawned off the southern end of the island, far from where the fish were captured and landed. If substantiated, such knowledge would inform fisheries management regarding stock boundaries and catch distribution, and may increase public appreciation of and engagement with their connections to island-wide fisheries management and conservation.

encourage developed nations to continue to share their scientific expertise and fisheries biology resources with developing countries.

Social sciences

Analysis of the social dynamics that affect both fishing effort and post-catch distribution of seafood can require considerable investment in survey efforts. Intensive creel surveys are necessary to monitor and track effort and catch at a meaningful geographic scale (eg Delaney *et al.* 2017), and survey efforts for post-catch use also require extensive planning for successful execution. In addition, designing the scale of social surveys to match the biological scales of pre-catch population dynamics can require substantial investment and planning.

Further considerations

Beyond implementation challenges, non-expert public perception of the relevance of Fish Flow analyses will likely vary with geographical scale. At the scale of islands and isolated archipelagos, such information will be extremely important in fostering a sense of socio–ecological interdependence, as is evident in Papua New Guinea (Almany *et al.* 2013, 2015) and the Philippines (Abesamis *et al.* 2017). At broader scales of continental coastlines, Fish Flow will likely be of interest to people directly or indirectly affected by and concerned about regional fisheries. At global scales, we imagine that those with preexisting environmental perspectives will embrace Fish Flow maps as evidence of planetary interconnectedness, and use this information to support international marine conservation and sustainability efforts.

■ Future vision of Fish Flow for social–ecological sustainability and resilience

Given recent methodological breakthroughs and successful partial syntheses of oceanographic modeling, population genetics, ecology, fisheries biology, and social sciences summarized here, we believe that the time has arrived for the implementation of full Fish Flow analyses. The timing could not be more critical as the oceans rapidly change in ways that are clearly affecting patterns of connectivity in the sea, causing shifts in the distribution, function, and productivity of marine metapopulations (Gerber *et al.* 2014). The clear challenge will be to implement adaptive management based on changes in these parameters documented by Fish Flow analyses.

We envision that there will be web-based, dynamic, interactive Fish Flow maps depicting the movement of fish from where they were spawned to settlement/recruitment locations to adult population ranges to sites of capture by fisheries and finally to shore-based distribution and consumption. A precursor to such maps can be constructed by combining two recent, albeit unrelated, studies on the Island of Hawaii (Figure 4).
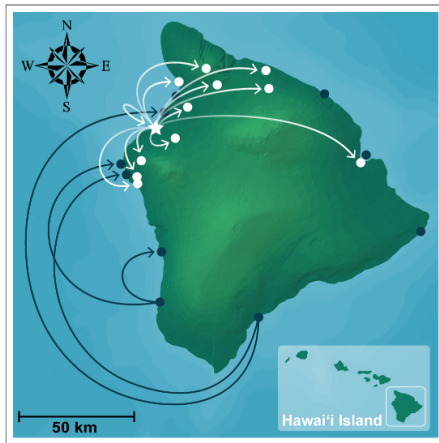
Christie *et al.* (2010) mapped patterns of larval dispersal of the coral-reef fish *Zebrasoma flavescens* (yellow tang), documenting that the western half of the island is seeded by fish populations at the southern end. Kittinger *et al.* (2015) mapped patterns of catch distribution of a variety of other reef-fishery species from a northwestern bay on the island, showing that seafood landed there was distributed across the entire northern region. Taken at face value and assuming these patterns are representative of local fishery species in general, combining these two studies into a single map may convince people living on the northern half of the island that they are connected to and should be concerned about the management and conservation of coral reefs in the southern region. From a fisheries management perspective, this particular synthesis suggests that stock boundaries encompass the entire western shore of the island, delineating the realistic domain of community-based management and networks of marine protected areas. Clearly, the studied fishery landings site is also important to human communities across the northern region of the island. A true Fish Flow map would focus on particular species or groups of species over ecologically and socially relevant scales of space and time, with dynamic arrows whose thicknesses would be proportional to the level of flow of fish both at sea (Figure 3b; eg Johnson *et al.* 2018) and on land (Figure 2; eg Kittinger *et al.* 2015).

Over a century ago, naturalist John Muir warned that, "when we try to pick out anything by itself, we find it hitched to everything else in the universe" (Muir 1911). Visually explicit Fish Flow maps will help to ensure that everyone – from interested non-specialists to high-level policy makers – understand and appreciate how clearly connected and dependent humans are on seafood produced in various, and sometimes very distant, regions of the ocean. In addition to informing fisheries management, such knowledge will help to foster an effective marine conservation ethic, enabling future generations to reap sustainable benefits from resilient ocean ecosystems.

◼ Acknowledgements

◼ References

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