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Editor's Choice

Characterizing fisheries connectivity in marine social–ecological systems

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Marine social–ecological systems are constantly changing, and fishers who make a living from working the seas are continually adapting in response to different sources of variability. One main way in which fishers can adapt to ecosystem change is to change the fisheries they participate in. This acts to *connect fisheries*, creating interlinked networks of alternative sources of income for fishers. Here, we synthesize fisheries data and construct fisheries connectivity networks for all major ports in the US California Current Large Marine Ecosystem. Fisheries connectivity networks are comprised of nodes, which are fisheries, connected by edges, whose weights are proportional to the number of participating vessels. Fisheries connectivity networks identify central fisheries in the US California Current Large Marine Ecosystem, specifically Dungeness crab and Spiny Lobster, and systematic topological differences, e.g. in network resilience and modularity. These network metrics directly relate to the social vulnerability of coastal fishing communities, especially their sensitivity and capacity to adapt to perturbation. Ultimately, improving knowledge of fisheries connectivity is vital if policy makers are to create governance institutions that allow fishermen to adapt to environmental, technological and management change while at the same time enhancing the social and economic value of fisheries. In doing so, new policies that account for fisheries connectivity, will lead to improved sustainable fisheries management, and enhanced socioeconomic resilience of coastal communities.

Keywords: climate change, complexity, cross-scale, fisheries management, food-web, harvest portfolio, livelihoods, resilience, social–ecological systems, vulnerability.

Introduction

Marine social–ecological systems are constantly changing over a range of spatial and temporal scales (Stommel, 1963), and fishers who make a living from working the seas are continually adapting in response to different sources of variability (Holland and Kasperski, 2016; Cline *et al.*, 2017). Fishers can adapt to ecosystem and management change in three main ways. First, they can change their spatial distribution of effort, tracking shifting species distributions as they move with the climate for example (Perry *et al.*, 2005). Second, they can find alternative sources of income and even stop fishing altogether (Cinner *et al.*, 2009). Third and last, they can change how they distribute their effort among the fisheries in which they participate. Indeed, it is well-known that fishers diversify when possible and work in multiple fisheries to minimize income risk. For example, harvest portfolio diversification significantly reduces exposure to inter-annual variability in revenue for US West Coast and Alaskan fishers (Kasperski and Holland, 2013; Cline *et al.*, 2017). An important consequence of fishers diversifying their harvest portfolios is that this connects fisheries, even when ecological links between the harvested species are absent.

Fisheries connectivity creates networks of alternative sources of income, which are critical to the ability of fishing communities to adapt to oceanographic, ecological, technological, and management change (Cinner and Bodin, 2010; Kasperski and Holland, 2013). For instance, in the US California Current Large Marine Ecosystem (CCLME), fishermen participate in multiple fisheries, moving between them throughout and between years, adapting their participation in response to changes in relative profitability, species spatial distributions, and regulations (Holland and Kasperski, 2016). Indeed, a combination of natural, regulatory, spatial and technological factors will make participation in certain fisheries highly complementary, while participation in other combinations will be incompatible. Consequently, a direct shock to one fishery, such as a climate-driven drop in recruitment; or a decrease in price; or a change in management, can impact a set of fisheries at once, solely as a result of shifts in fishing effort. For example, depressed returns of California Central Valley fall Chinook salmon in 2007 led to a nearly complete closure of West Coast salmon troll fisheries in 2008 and 2009 (Upton, 2011). Many fishermen left fishing completely while others shifted effort into the Albacore tuna, Dungeness crab and groundfish fisheries. Such responses in fisheries participation are likely to vary significantly between fishers, and as a function of numerous factors including their home port, vessel type, and size, and importantly their portfolio of fishing permits.

Key questions surrounding fisheries connectivity remain unanswered. Most importantly, fisheries connectivity has yet to be systematically characterized for any marine social–ecological system. As a consequence, while fishers, policy makers, and scientists acknowledge that diversification of fisheries participation, and hence fisheries connectivity, is important (Kasperski and Holland, 2013; Cline *et al.*, 2017), there remains no consistent method for quantifying it. Furthermore, its structure and topology remain largely unknown, and management policies are not designed to account for it. Indeed, Ecosystem-Based Fisheries Management (EBFM; Pikitch *et al.*, 2004) has focused predominantly on dealing with food-web complexity in fisheries (Smith *et al.*, 2007), marginalizing the equally complex social–ecological networks resulting from how fishers participate and shift effort among fisheries (Holland and Kasperski, 2016). Without knowledge of fisheries connectivity, EBFM will find it difficult to predict fishers' adaptive responses to even relatively simple management actions—much less complex, environmentally-driven perturbations to a range of interconnected target species. Understanding these responses is critical to predicting the direct implications of these changes for the sustained well-being of fishers and fishing communities. This is all the more important when one considers that fishers' behaviour may feed-back to substantially influence the very biological variation that initially influenced fishing behaviour, potentially amplifying or dampening it as a result (Essington *et al.*, 2015; Fryxell *et al.*, 2010). Fisheries connectivity is thus an essential social component of EBFM. Improving knowledge of fisher behaviour, in general (Fulton *et al.*, 2011; Lubchenco *et al.*, 2016) and in terms of fisheries participation, is vital if policy makers are to create institutions that allow fishermen to adapt to environmental change while at the same time enhancing the social and economic value of fisheries and creating resilience in both ecosystems and livelihoods (Levin and Lubchenco, 2008; Kasperski and Holland, 2013).

In this article, we have examined the spatial variability in fisheries connectivity among ports in the CCLME. Fisheries connectivity networks are defined by nodes, which are fisheries, connected by edges, whose weights are proportional to the number of participating vessels. The CCLME is an ideal case-study for examining differences in fisheries connectivity networks, because of its large spatial extent and its food-web and fisheries diversity (Field *et al.*, 2006). This allowed us to assess the influence of individual fisheries within fisheries connectivity networks, calculated at a range of spatial scales, from the scale of ports to that of the whole Large Marine Ecosystem. Further, we quantified properties of fisheries connectivity networks relating to their potential resilience to perturbation (Carpenter *et al.*, 2012), and their relevance for the social vulnerability of coastal human communities, in terms of their sensitivity and adaptive capacity (Adger, 2006). This analysis represents a comprehensive and quantitative analysis of the social–component of marine social–ecological systems, and underscores the fundamental importance of social dynamics for successful fisheries stewardship.

Methods

In order to quantify and explore fisheries connectivity in the US CCLME, we first synthesized fisheries landings ticket data for the entire region, from which we defined fisheries and subsequently fisheries connectivity. We analysed fisheries connectivity using network theoretic metrics applied at the port-group level (i.e. clusters of geographically proximate ports), and relating them to the social vulnerability framework (Adger, 2006), with a focus on sensitivity to change and adaptive capacity. The port-group spatial scale was chosen so as to best represent fisheries connectivity in terms of coastal fishing communities. However, we also calculated fisheries connectivity at larger spatial scales, specifically at the scale of the whole CCLME. All our calculations were performed for a short period (2009–2010; 2 years without El Nino or La Nina conditions, and without major management changes) and in the discussion, we mention the importance of collecting longer time-series data, from which changes in fisheries connectivity could be observed

Data synthesis and analysis

Vessel landings tickets for all commercial landings on the US West Coast between 2009 and 2010 were collected from the Pacific Fisheries Information Network database (PacFIN: http://pacfin.psmfc.org/). These commercial landings account for $\sim$1.25 million metric tons of 197 species, resulting in approximately half a billion dollars in revenue (adjusted to 2009 levels) by a total of 3121 vessels. To examine patterns of fisheries participation and construct fisheries connectivity networks, we grouped landings into distinct fisheries. Fisheries are defined as harvest assemblages caught with a specific gear (Deporte *et al.*, 2012). The Pacific Fisheries Management Council has developed a set of sector-based definitions similar to this approach for the federally managed groundfish landings (www.pcouncil.org), but no equivalent currently exists for non-groundfish fisheries. Therefore, in order to treat the landings dataset uniformly and build an objective set of fishery definitions, we applied our own fisheries (otherwise known as "métier") analysis to the entire landing dataset (Deporte *et al.*, 2012). At its heart, a fisheries analysis identifies clusters of trips based on the gear used, and the revenue and species composition of landings (Smith *et al.*, 2011; van Putten *et al.*, 2012; Boonstra and Hentati-Sundberg, 2016). This methodology requires choices in the way similarity among trips are measured, a clustering algorithm for grouping similar trips together, and scalability so that it can be applied to the 197 472 trips we had data for.

For every pair of trips, landings similarity was measured using the Hellinger distance (Legendre and Legendre, 2012) D. This distance metric has the benefit that it is asymmetric, where the presence of a species in both trips is considered more informative than the absence of a species. The Hellinger distance is calculated from the species composition of two fishing trips A and B as follows:

$$D_{AB} = \sqrt{\sum\nolimits_{i=1}^{S} (a_i - b_i)^2}, \tag{1}$$

where a_i is the fraction of revenue derived from species i on trip A, b_i is the fraction of revenue derived from species i on trip B, and S is the total number of species collected in both trips. With this metric, trips A and B become increasingly similar (and the Hellinger distance declines) as the difference in the proportion of revenue attributable to each of the S species diminishes. Once calculated for all pairs of trips (stored as a distance matrix), we identified fisheries as groups of trips with similar target assemblages using the infoMap community detection algorithm (Rosvall and Bergstrom, 2008). This algorithm examines networks for subgraphs more interconnected to one another than the whole network in which they are embedded. It requires a similarity matrix as an input, hence we transformed the distance matrix by subtracting the maximum value of D from each pairwise value D_{AB}. The result is a weighted and undirected network, where trips are nodes and edges are trip similarities. However, because our dataset contained 340 466 unique trips, we were not able to implement the infoMap algorithm using a single matrix containing all pairwise similarities. To overcome this computational challenge, and obtain manageable matrix sizes, we first performed the fisheries analysis on 1 year's worth of landings data, specifically 2010. Then, for each trip in 2009 we identified which 2010 trip was "nearest" to it, in terms of species composition, by means of a k-nearest neighbours algorithm. Each trip in 2009 then inherited the fisheries of its nearest 2010 trip. In this way, we managed to assign all trips from the whole dataset to specific fisheries.

Constructing participation networks

Fisheries are linked by vessel participation. If a vessel k fishes in two fisheries i and j in year t, they are linked by vessel k in that year. Over all vessels, the edge-weight between two fisheries is determined by the total number of vessels that participate in fishery i and j, for any given year. These calculations can be made at a range of spatial scales, from the whole US west coast, to the port-level. We focused on fisheries connectivity at the port-group level to address its differences across fishing/coastal communities. Ports were grouped based upon geographic proximity, capturing the range of ports that any given fisher regularly visits over the course of a year. Port-groups were defined as: **NPS** (Bellingham Bay, Port Townsend, Port Angeles, Anacortes, Sequim, La Conner, Neah Bay, Friday Harbor, Blaine, other north Puget Sound ports); **SPS** (Seattle, Olympia, Everett, Shelton, Tacoma); **CWA** (Westport, La Push, Willapa Bay, Grays Harbor, other Washington coastal ports); **CLW** (Ilwaco/Chinook, other Columbia River ports); **CLO** (Astoria, Cannon Beach, Seaside-Gearhart); **TLA** (Tillamook/Garibaldi, Pacific City, Netarts Bay, Nehalem Bay); **NPA** (Newport, Depoe Bay, Waldport, Siletz Bay); **CBA** (Winchester Bay, Charleston (Coos Bay), Bandon, Florence); **BRA** (Brookings, Port Orford, Gold Beach, Crescent City, other Del Norte county ports); **ERA** (Trinidad, Eureka, Fields Landing, other Humboldt county ports); **BGA** (Fort Bragg, Albion, Point Arena, other Mendocino county ports); **BDA** (Bodga Bay, Bolinas, Point Reyes, Tomales Bay, other Sonoma and Marin county ports); **SFA** Princeton/Half Moon Bay, San Francisco, Berkley, Richmond, Oakland, Sausalito, Alameda, other SF Bay and San Mateo county ports); **MNA** (Santa Cruz, Moss Landing, Moneterey, other Santa Crus and Monterey county ports); **MRA** (Morro Bay, Avila, other San Luis Obispo county ports); **SBA** Santa Barbara, Port Hueneme, Oxnard, Ventura, other Santa Barbara Ventura county ports); **LAA** (Long Beach, San Pedro, Dana Point, Terminal Island, Newport Beach, Wilmington, other LA and Orange county ports); **SDA** (Oceanside, San Diego, other San Diego county ports). For these port-groups, fisheries connectivity is calculated as:

$$A_{i,j,t} = \sum\nolimits_{k}^{m} \frac{R_{i,k,t} R_{j,k,t}}{R_{k,t}} (R_{i,k,t} + R_{j,k,t}), \tag{2}$$

where k is the vessel index from 1 to m (the total number of vessels), is the revenue made by vessel k from fishing in fishery i in year t, and similarly is the revenue made by vessel k from fishing in fishery j in year t. is the total revenue made by vessel k in year t. This measure of fisheries connectivity is proportional to the evenness with which vessel k participates in fisheries i and j. That is, if vessel k makes lots of money in one fishery, and not a lot from another, then these fisheries are less strongly connected by this vessel than if participation was divided equally. Fisheries connectivity is also proportional to the total revenue made by vessel k from working in both fisheries (i.e.). Last, fisheries connectivity is inversely proportional to the total revenue made by vessel k, for example a vessel may make all its money from fisheries i and j, but if that total is small, relative to other vessels, this should have a relatively small contribution to the overall calculation of fishery connectivity, which integrates over all vessels (i.e. the summation over m vessels), and hence is a measure of the fishing community. We focused on the largest fisheries in each port group, and for confidentiality reasons, we included only those that had >3 participating vessels, and that were responsible for >25% of those vessel's revenue. Once fisheries connectivity networks were calculated for each year of the data, we averaged edge weights across years.

Node-level analysis: identifying important fisheries

To measure the importance of individual fisheries in fisheries connectivity networks, we calculated node strength, betweenness and fragmentation centrality. Node strength is a generalization of node-degree for binary networks, which is simply the number of connections to a given node. For weighted edges, node strength s_i is the summation over edges: $S_i = \sum_j A_{ij}$. Because fisheries connectivity networks varied by orders of magnitude in the total number of vessels moving among fisheries, we normalized this value by the sum of all edge weights in a network, thus providing a measure ranging between 0 and 1 where 1 indicates that all connections in the network were to fishery i, and 0 means that no connections involved fishery i. In other words, for a given fisheries connectivity network, fisheries with node strength close to one are those that were consistently connected to the majority of other fisheries in the network and/or were involved in the strongest connections present.

This measure of node strength, while intuitive, only takes into account the local structure around each node. To incorporate both node strength and the position of fisheries in a given fisheries connectivity network, we calculated betweenness centrality (Barthelemy, 2004). This metric is calculated as the number of shortest paths which travel through a given fishery. Because betweenness scales with network size, and because fisheries connectivity networks vary in size, we normalized this value by the number of pairs of nodes (N−1)(N−2)/2, so that the betweenness score is in the interval [0,1] for all networks. In networks that measure the flow of quantities, for example information, money or electricity; betweenness centrality identifies nodes that play an important role in moderating or controlling flow. Our fisheries connectivity networks do not measure flow explicitly, as they are based on trip similarities (see Equation 2). However, fisheries *participation* can be thought of as being able to "flow" across a given fisheries connectivity network, and further it is proportional to *trip similarity*. As a consequence, betweenness centrality can be used to identify nodes, from the fisheries connectivity networks, that are important to the overall ability of fishers, in a given port-group, to redistribute their effort.

In contrast to betweenness, fragmentation centrality identifies nodes that are important to a given network's ability to withstand directed perturbations (Borgatti, 2006). For example, if nodes are removed preferentially based upon fragmentation centrality, a network will rapidly break apart, relative to if nodes are removed at random. Hence, in the context of fisheries connectivity, fisheries with high fragmentation centrality are those that hold the whole network together, and connect different sets of fishing strategies (groups of connected fisheries that make up a given fishers' harvest portfolio). Fragmentation centrality is calculated from network geodistances, which are used to compute the level of fragmentation after a given node is removed (Borgatti, 2006).

Network-level analysis: sensitivity and adaptive capacity

Node strength, betweenness and fragmentation centrality are node-level metrics, and are related to the concept of social vulnerability (Adger, 2006). Social vulnerability is comprised of three parts: exposure and sensitivity to perturbation, and the capacity to adapt and maintain welfare in the face of the perturbation. The node-level metrics above relate to sensitivity and adaptive capacity because the more dependent a port (group) is on a particular fishery, indicated by the presence of a highly central fishery for example, the less able fishers are to shift effort to other fisheries (Steneck *et al.*, 2011) and the more sensitive they are to disturbances directed to the important fishery. However, the nature of the perturbation is key. For instance, networks with highly central nodes can better withstand perturbations affecting all nodes uniformly (Watson *et al.*, 2011). Furthermore, vulnerability in this context is a community-level concept, and as a consequence, in order to better summarize the sensitivity and adaptive capacity of fishing communities in the CCLME, we also calculated a number of network-level metrics.

First, edge density was calculated to summarize the overall connectivity of the fisheries networks. Edge (or link) density *LD* is the number of edges divided by nodes in a given network, and it scales both with network size and interconnectedness. Since the fisheries connectivity networks are undirected, this value can be interpreted as the average number of fisheries to which any given fishery is connected, at a given port for example. In the context of vulnerability, edge density can be considered inversely related to sensitivity because being connected to multiple fisheries indicates that fishers have income flexibility, being able to shift between fisheries when one suffers a perturbation such as a closure (Kasperski and Holland, 2013).

We also calculated the universal resilience function (Gao *et al.*, 2016), which is designed to measure the general ability for a complex system (with an underlying network topology) to withstand perturbation, e.g. the removal of a node, or a uniform decrease in edge weights. The universal resilience function is calculated as, where *s* is the average edge weight in a given network, and *S* is the edge symmetry (here, because the fisheries connectivity networks are undirected, symmetry is equal to one) and *H* is the edge heterogeneity measured as the variance in edge weights divided by *s*. In terms of vulnerability, this resilience metric is directly related to the sensitivity of human communities to perturbation.

Last, network modularity *Q* measures whether a given network contains distinct modules (groups of relatively well connected nodes) or not (Pons and Latapy, 2006). It is calculated as the average difference in the summation of edge weights within a given module, minus the summation of edge weights from nodes in the module to those nodes outside the module, over all modules. In our context, it measures to what extent a given fisheries connectivity network is comprised of clusters of highly connected fisheries. This relates to the concept of fishing strategies (Boonstra and Hentati-Sundberg, 2016), which is described in more detail in the discussion. Modular networks have low sensitivity to perturbation because a disaster in one network module will be largely contained (Levin and Lubchenco, 2008). However, such modularity in fisheries is thought to simultaneously reduce adaptive capacity by constraining participation of fishers to certain fishing strategies (Stoll *et al.*, 2016).

Results

Fisheries connectivity varies greatly across port groups in the CCLME, reflecting differences port size, and in the spatial distribution of harvested species over this large spatial scale. For example, in Figure 1 we show the fisheries connectivity networks for port-groups at Newport, Oregon; Santa Barbara and San Diego, California. These port-groups span the latitudinal range of the CCLME, and differences in which fisheries are present in part reflect differences in the marine ecology that these port-groups are adjacent to. For example, in Newport, which is the northernmost port-group of the three, the Dungeness crab fishery dominates the fishery connectivity network. However, for Santa Barbara it is the squid fishery; and in San Diego in the south, it is the Spiny Lobster fishery. These three example fisheries connectivity networks also vary in their overall connectance, in terms of the total number of fisheries and how well connected the networks are. Of the three, Santa Barbara has the most nodes, and is the most connected, suggesting that this fishing community is the most diversified and hence potentially better able to withstand shocks (i.e. relatively low sensitivity). Further, within any of these fisheries connectivity networks, the importance of each fishery, in terms of total revenue generated, varies greatly (Figure 1, relative size of nodes within a given network; node size should not be compared between networks). For example, in Santa Barbara, the squid fishery is the largest, while there are numerous smaller fisheries, including the lobster, crab, and urchin fisheries.

The differences in the overall topology of these example fisheries connectivity networks is reflected in differences seen between networks for all port-groups in the CCLME (see Figure 2; small inset networks on right, and our Supplementary Material, where we show in detail the fisheries connectivity networks for each port-group in the CCLME; in these networks node colours represent broad gear groups, yellow = hook and line, green = troll, brown = trawl, pink = shrimp trawl, teal = nets, purple = miscellaneous, and orange = pots). In addition, an important characteristic of fisheries connectivity is its cross-scale nature. For example, it can be calculated at a range of spatial scales, from port-group to county to state to whole LME scales. The port-group scale reflects the scale at which fishing communities exist. However, for certain applications, such as relating to federally managed fisheries, calculating connectivity at a larger scale may provide different and more useful information. For example, we show the whole CCLME fisheries connectivity network (calculated using all the vessel-landings data) in Figure 2 (large network on left). Similarly to many of the port-level networks, this large-scale network identifies the Dungeness crab pot fishery as most important (in terms of revenue generated). However, the number of nodes and density of edges are much greater than the port-level networks.

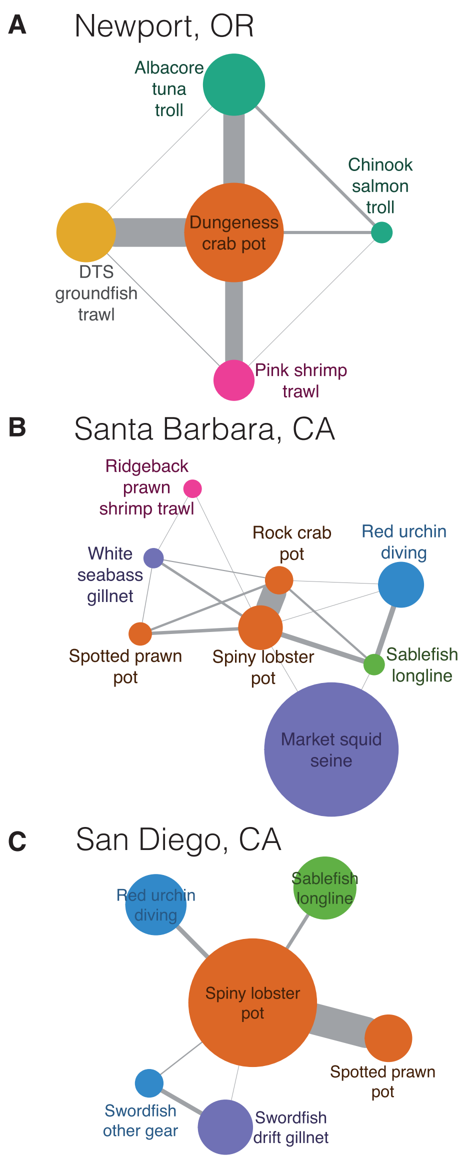

Figure 1. Differences in fisheries connectivity networks for (a) Newport, Oregon; (b) Santa Barbara, California; and (c) San Diego, California. Edge width is proportional to fisheries connectivity and all fisheries (nodes) are sized in proportion to their total revenue generated. Node colours represent broad gear groups, yellow = hook and line, green = troll, brown = trawl, pink = shrimp trawl, teal = nets, purple = miscellaneous, and orange = pots. Node/fisheries are positioned to maximize visual clarity. In general, the fisheries connectivity networks varies greatly along the US west coast in terms of network topology, and the identity of present fisheries.

In general, virtually all fisheries were connected to at least one other fishery by vessel participation. This highlights that vessels in the CCLME are predominantly generalists, operating in multiple fisheries over the course of a year. Fisheries connections varied from port to port (e.g. Figure 1), but some clear patterns emerged. In particular, across all networks either the Dungeness crab pot or Spiny lobster pot fisheries were important, in terms of both node strength, betweenness and fragmentation centrality (Figure 3a–c, respectively). Large node strength identifies that these two fisheries are much more connected than the other fisheries in any given network. This also reveals that many different types of fishers will operate in one of these two fisheries, gaining some (large) fraction of their income. In addition, the high betweenness centrality of the crab and lobster fisheries identifies that those fishers/vessels that participate in these fisheries (that being most of them) have heterogeneous harvest portfolios, and operate in numerous other fisheries. The relatively high fragmentation centrality of Spiny lobster and Dungeness crab identifies that if these fisheries were to experience some sort of perturbation, this would also then impact the overall topology of the fisheries connectivity networks in which they are embedded. In general, these node-level results identify that the economic welfare of fishing communities in the CCLME will be sensitive to shocks directed to the crab and lobster fisheries.

At the network level, we found systematic differences in topological characteristics (Figure 4). Port-group participation networks had between 3 and 13 fisheries (nodes) and between 0 and 49 edges with a median of 7 and 14, respectively. Fisheries in these networks were connected to anywhere between 0 and 12 other fisheries. Edge density, the average number of connections to a given fishery, for these networks varied between 0.91 and 3.77 (Figure 4a). We found that the modularity (Q) of these networks varied between −0.33 and 0.305 (Figure 4b). In particular, a change in sign of network modularity was observed. This identifies extremely contrasting networks: those with negative modularity Q have uniformly connected fisheries, whereas those with $Q > 0$ are modular in structure, with groups comprised of highly connected subsets of fisheries, but with weak connections between these groups. This directly relates to the sensitivity and adaptive capacity of CCLME fishing communities: those communities that work in highly modular fisheries participation networks will have low sensitivity to directed perturbations, which will be contained to a given module; simultaneously, these communities will have low adaptive capacity, as modular boundaries describe limits on the ability of fishers to redistribute their effort. These

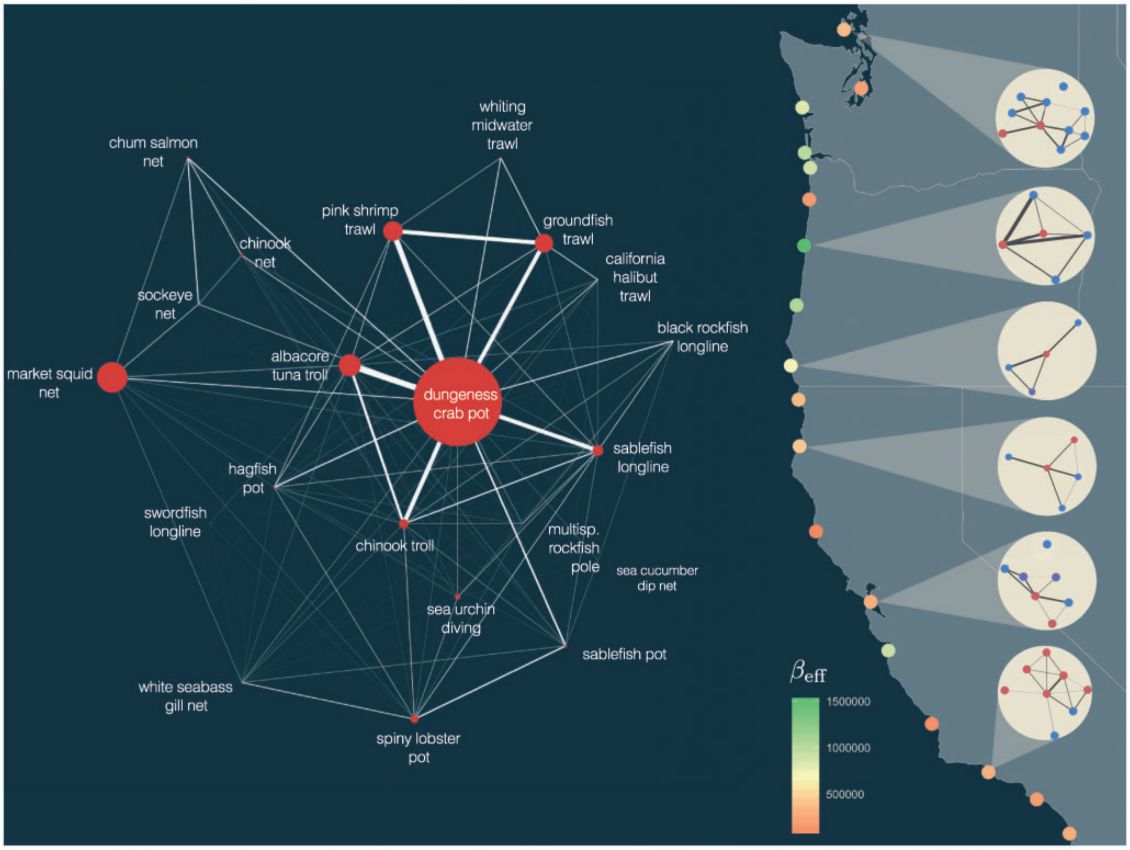

Figure 2. Summary of fisheries connectivity on the US west coast. The large network on the left is the fisheries connectivity network for the whole US CCLME. In scaling down, fisheries connectivity networks can be derived for each port or port-group (smaller networks on the right). These port-level networks vary in properties such as network resilience (colour of port-location dots: red is lower resilience, green is greater resilience), and they are also comprised of both state and federally managed fisheries (small networks on right: red and blue nodes, respectively).

consequences for vulnerability are reversed for networks with low modularity.

Estimates of the universal measure of network resilience also varied across port-groups, with the highest value many orders of magnitude greater than the lowest value (Figure 4c). This suggests that ports will vary greatly in their sensitivity and capacity to adapt to perturbation, for example the removal of a fishery or a general decrease in participation across a given network, created from either an environmental or management change. Further, the geographic distribution of network resilience, across port-group fisheries connectivity networks highlights an interesting latitudinal gradient (Figure 2: colour of port-location markers). Specifically, the port-groups towards the north of the CCLME (mainly in Oregon and Washington) are more resilient than those in the south (i.e. in California). This is somewhat counter to the comparison of connectance between Newport and Santa Barbara (Figure 1), but because the resilience metric is calculated from the mean edge weights of a graph, and those edge weights scale both with the absolute number of vessels and revenue, port-groups with relatively more vessels and revenue are more resilient. This is why Newport, for example is more resilient than Santa Barbara, even though the latter has more (connected) nodes.

In comparison to the port-group values, the fisheries connectivity network for the whole US CCLME had resilience $=$ 5 700 000, modularity $= 0.042$ and edge density $= 4.60$ (Figure 4; "CCLME" identifier). This highlights an important point about scale: both resilience and edge density for the CCLME network are far higher than those of the port-group level networks. This is because these quantities scale with network size. Hence, bigger networks (in terms of the number of nodes) naturally have larger values of resilience and edge density. In contrast, the modularity of the CCLME network is a middle ranked value (Figure 4b). This is a consequence of the CCLME network being comprised of the port-group level networks, and in essence "averaging" modularity at that lower level. In general, these differences in network metrics at the port-group and the CCLME scales highlight that the scale at which fisheries participation is assessed will determine measures of social vulnerability like sensitivity and adaptive capacity.

Discussion

In summary, contemporary fisheries connectivity networks for all port-groups in the US CCLME vary greatly in terms of the fisheries they are comprised of, in how these fisheries are connected by vessel participation, and their overall topology. These differences have strong implications for the vulnerability of fishing communities, in terms of their sensitivity and capacity to adapt to perturbation. Further, these results identify that US west coast fishing communities are comprised of highly generalist vessels, which participate in numerous fisheries over the course of any given

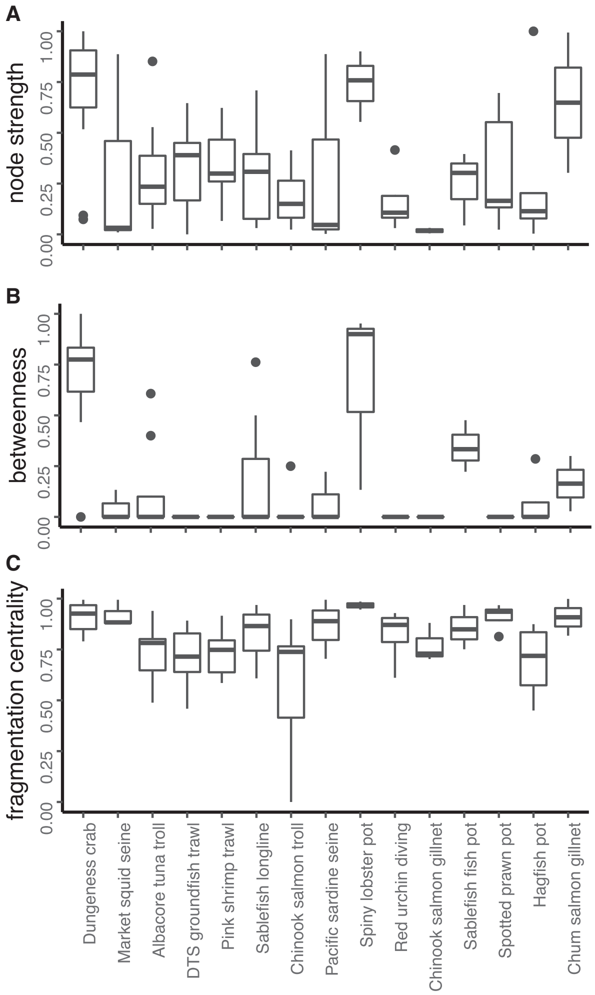

Figure 3. Distribution of (a) node-strength, (b) betweeness and (c) fragmentation centrality for major fisheries (ordered from left to right in terms of decreasing total revenue) in the CCLME, with between port-group variability captured by the width of the box and whiskers for each fishery. These distributions highlight the dominance of a few key fisheries. In particular, the Spiny Lobster and Dungeness Crab fisheries have the highest node strength, betweeness and fragmentation centrality. This reveals that almost all fishers on the US west coast will participate in and gain revenue from these fisheries at some point of the year.

year. This is important, because quantifying the topology of fisheries connectivity networks will improve our ability to anticipate the redistribution of fishing effort from one fishery to another, given a perturbation, whether due to a change in management, environmental conditions, or some other external shock.

The vulnerability framework is vital for connecting network theoretic metrics to concepts relevant to the economic prosperity of marine social–ecological systems. We have shown that metrics like edge density, resilience and modularity, calculated from fisheries participation networks, all provide information about the potential sensitivity and adaptive capacity of coastal communities. Node-level metrics like node strength and centrality also provide similar information. Importantly though, while the topology of a fisheries connectivity network holds vital information, far more powerful is to investigate how these networks change over time. We assessed the topology of fisheries connectivity networks for the years 2009 and 2010. This is a necessary first step, but in order to gain a better understanding of how fishing communities absorb and respond to perturbation, the next important step is to examine how these fisheries networks change over longer timescales (i.e. decades). For instance, if a particular port-level fisheries connectivity network exhibited a concentration of centrality over time, this would relate to the concept of the “gilded trap”, where fishers get locked into certain (perhaps highly profitable) fisheries (Steneck *et al*., 2011). This reduction in the portfolio of harvested species increases fisher’s sensitivity to perturbation, and potentially reduces their adaptive capacity. Many fisheries agencies already have the data required to create time-series of fisheries connectivity networks, and doing so will undoubtedly be fruitful future work, complementing other contemporary studies of vulnerability in fishing communities (Ekstrom *et al*., 2015).

In addition to the vulnerability framework, fisheries connectivity directly relates to livelihood diversification (Ellis, 1998; Cinner and Bodin, 2010). Work in this field has emphasized that there are always multiple reasons why livelihoods in a given community are diverse, from seasonality to risk aversion. Indeed, fishers are known to diversify their harvest portfolios as a means to manage income risk (Kasperski and Holland, 2013; Holland and Kasperski, 2016; Cline *et al*., 2017). This is important because policies that aim to minimize income risk could take advantage of information about fisheries connectivity, for example in reducing barriers to participation in key fisheries. These barriers will principally take the form of current governance institutions (e.g. licenses/permits), and a key challenge to designing policies that encourage fisheries connectivity to reduce income risk, is to do so without there being a concomitant increase in the risk of ecological problems driven by over-exploitation.

When designing management policies to take advantage of information about fisheries connectivity, it is vital to consider its cross-scale nature. Indeed, a main conclusion from this analysis is that the scale of governance institutions may or may not be synergistic with the topology of port-level fisheries participation networks. For instance, the emergence of the Large Marine Ecosystem concept was largely based on calls to better account for the ecology of marine systems by matching social and ecosystem scales. However, the observed heterogeneity in port-level fisheries participation may mean that governance strategies or policies undertaken with only the Large Marine Ecosystem level in mind will be ineffective or indeed have negative consequences for fishing communities. In contrast, management policies designed specifically to address the cross-scale nature of fisheries connectivity networks, for instance those designed using the principles of polycentricity (Ostrom, 2010), will be more uniformly effective across a given region.

This is easier said than done, for in any given marine social–ecological system, there will already be present various institutional constraints, operating at a range of scales. For example, presently there are numerous fisheries in the CCLME that are either state- or federally-controlled, and coastal communities will vary in which sets of rules and laws they must adhere to (see Figure 2, small networks on right). For example, on average “crab vessel” makes 70% of their revenue from crab, which was state-managed during the time-period of this analysis, and 30% of their annual revenue in non-crab fisheries, most of which are federally managed. Although governance institutions that acknowledge cross-scale and trans-boundary issues are not without precedent,

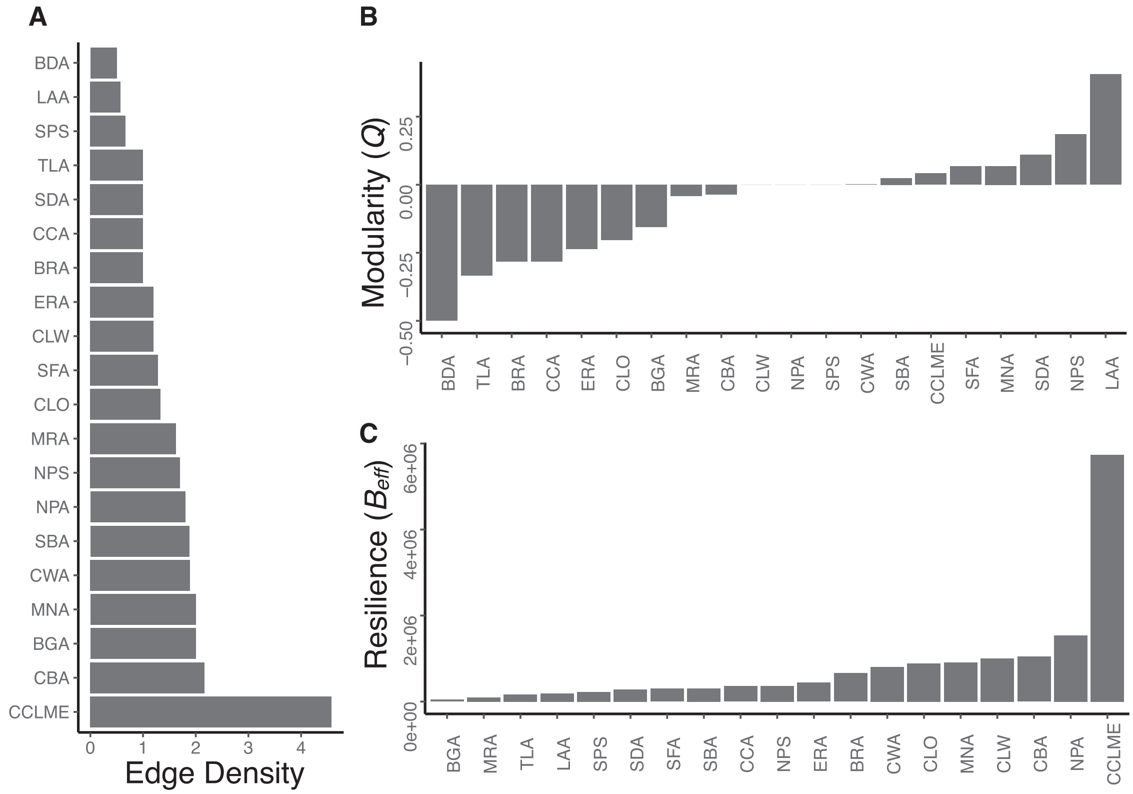

Figure 4. Distribution of (a) edge (or link) density (*LD*); (b) network modularity (*Q*) and C) network resilience (β_{eff}) across fisheries connectivity networks for CCLME port groups (group IDs are provided in the "Methods" section) including the region-wide CCLME network. These distributions reveal the wide ranging topologies observed across fisheries connectivity networks. In particular, a change in sign of network modularity is observed. This identifies extremely contrasting networks: those with negative modularity *Q* have uniformly connected fisheries, whereas those with positive *Q* are modular in structure, with groups comprised of highly connected fisheries, but with weak connections to other groups.

as on the US west coast where the Pacific hake fishery is jointly managed by the US and Canada, formal management structures that recognize the cross-scale nature of fisheries connectivity are the exception, not the rule. This variation from port-to-port in institutional constraints will play into the differing response of fishing communities to environmental and management shocks, in terms of adaptive fisheries participation.

One aspect of fisheries connectivity that directly informs management is the identity of "central" fisheries based upon vessel participation. This is in contrast to standard approaches to measuring importance, which mainly focus on the revenue generated by a fishery (Pauly *et al.*, 2003). For example, it is well known that the Dungeness crab fishery produces a large fraction of the revenue for CCLME fishers (in the north at least—see Figure 1a's relative size of nodes; Rasmuson, 2013). However, fisheries connectivity networks reveal that it is also centrally placed (also see Figure 2), meaning that in numerous fishing communities, it is not just "crab fishers" that depend on it as a major source of income. The Dungeness crab fishery is unique, in that it draws both large and small vessels (Botsford *et al.*, 1983; Rasmuson, 2013). This is important because it identifies that fishers with different "fishing strategies" all participate in the crab fishery. Fishing strategies describe the set of fisheries that fishers participate in over a given year, and they have been shown to be important to and systematically vary in other marine social–ecological systems (e.g. Aguilera *et al.*, 2015; Boonstra and Hentati-Sundberg, 2016). Fishing strategies can be identified from the fisheries connectivity networks using community detection algorithms (Pons and Latapy, 2006), similar to the calculation of network modularity performed here. We leave this for future work, but this again relates to the cross-scale nature of fisheries connectivity, and the scale at which management should be directed: should policies be designed for individual fisheries, fishing strategies, port-level fisheries connectivity networks, or at larger scales?

Fisheries connectivity networks also provide the means to evaluate the impact of new policies. For example, fisheries connectivity networks vary in both composition and topology, with the most complex networks having four times the connectivity of the simplest ones. As a consequence, we would expect a differing response from port to port, in the way fishers adapt to a management change, in terms of the fisheries they participate in. Similarly, one can pose fisheries connectivity in terms of how fishers' adapt to climate change (Perry *et al.*, 2005; Pinsky *et al.*, 2013; Kasperski and Holland, 2013). Whether management or environmental change, these perturbations will affect the topology of fisheries connectivity networks, and in general, these changes can be thought of happening in two ways. First, fishers can redistribute their effort over a given network. This type of change reflects "fast" behavioural decisions. In contrast, the second way connectivity changes is relatively "slow" and reflects fishers retooling and learning new skills which would allow them to operate in entirely new fisheries. This slow adaptation will result in new edges between fisheries, and subsequent changes in the overall topology of the fisheries connectivity networks. To quantify these changes requires estimating fisheries connectivity, at a chosen temporal (e.g. yearly) and spatial (e.g. port-group) scale, over a long period of time (e.g. decades).

Last, a key property of fisheries connectivity networks is that they can create connections between harvested species, even when there are no direct ecological links between them. For example, for many (northern) ports, the Albacore tuna and Dungeness crab fisheries are strongly connected by fisher participation. However, these species have no direct ecological link in the CCLME food-web, with one being pelagic in nature, and the other benthic. This means that taken as a whole, the social–ecological network of a fishing community is comprised of both interacting species (i.e. the food-web), vessels that extract species (i.e. harvest links), and importantly now—fisheries connectivity. Indeed, a vital next step will be to link quantitative descriptions of food-webs, for example using species/functional-group (e.g. Ruzicka *et al.*, 2012) or size-based (e.g. Watson *et al.*, 2015) depictions, to fisheries connectivity networks. These "end-to-end" constructs (Fulton, 2010) will be two-mode or bipartite networks, consisting of two types of nodes (species and fisheries) and two types of edges (species interactions and fisheries participation). Bipartite network analyses can then be employed to identify key social–ecological feedbacks. For instance, changes in social aspects such as management or technology, will potentially impact ecologically unconnected species due to fisheries connectivity. Identifying these multi-step links is critical for improving EBFM, which by and large has focused solely on incorporating knowledge of ecological links (i.e. food-web complexity) into fisheries policies (Fulton *et al.*, 2011). Ultimately, in doing so new policies that account for fisheries connectivity, will lead to improved sustainable fisheries management, and enhanced socioeconomic resilience of coastal communities (Levin and Lubchenco, 2008).

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

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