Chapter 18
Homogenization of Fish Assemblages Off the Coast of Florida

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Abstract Biological homogenization can alter the ecological function of systems as well as the economic value associated with those ecosystems through complex socio-ecological dynamics. The aim of this chapter is twofold: (1) to document evidence of biological homogenization across marine fish assemblages off the coast of Florida and (2) to discuss how social values may influence, and are influenced by, the biological homogenization of coastal fish assemblages. We measured biological homogenization by tracking taxonomic changes over a decade across 13 near-shore sites off the Atlantic coast of Florida. We created species-location matrices for each site, calculated recently and a decade prior, and quantitatively depicted assemblage similarity changes between sites using a hierarchical clustering algorithm. We found evidence of biological homogenization of some fish assemblages, but not all, and relatively little change in site species richness. Sites that were closer to populated coastlines, or have been subject to substantial disturbance events, are more likely to show homogenization. Protected reef sites show little evidence of homogenization. We postulate feedback mechanisms between societal values, diver practices, diver experience, and the severity of homogenization. We suggest that cultural values directly influence diver behavior, which in turn can affect assemblage homogenization. These socio-ecological feedbacks have received very little attention in the context of coastal fish conservation, but deserve attention given the perilous state of such ecosystems worldwide.

Keywords Ecotourism · Diving · Marine · Reefs · Fish · Homogenization · Florida · Caribbean

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18.1   Introduction

Marine fish assemblages have been substantially altered through the effects of over-fishing, habitat loss, and climate change (Levin et al. 2006; Airoldi et al. 2008; Nyitrai et al. 2012; Riegl et al. 2009). Such impacts have been measured almost exclusively in the context of loss of key species or fish biomass. Rarely has anyone measured these impacts through the lens of compositional change, which is a perspective that acknowledges that species losses and additions combine to increase or decrease spatial similarity in marine fish assemblages through time (Olden and Rooney 2006). The few studies that have adopted this perspective have highlighted the homogenizing influence of habitat simplification and phase shifts, especially among coral reefs (Thrush et al. 2006; Airoldi et al. 2008; Alvarez-Filip et al. 2015), or of heavy influxes of exotic species after the establishment of inter-ocean canals (Edelist et al. 2013). The data necessary to track longer-term changes in composition are hard to come by but especially so within marine ecosystems which are by default harder to track due to limited logistical access. Here we take advantage of a citizen science initiative to document near-shore fish assemblages to explore the extent to which we see homogenization within the Atlantic coastal waters of Florida, USA.

Florida has nearly 12,000 miles of coastline, which includes the string of small islands that lie at the southern extreme of the state called the Keys (Fig. 18.1). The near-shore marine waters of the Florida's Atlantic coast and Keys exhibit a diverse array of seabed types including significant expanses of coral and artificial reefs. These reefs, and other habitat types, are home to hundreds of fish species, some of which are important sources of commercial seafood or sold in the marine aquarium trade (Johns et al. 2014; Bruckner 2005). These fish assemblages also support a massive SCUBA and snorkel dive industry, which generates on average US$3 billion annually in the Keys alone (World Wildlife Fund Global, Accessed 12 June 2017). These reefs, and other near-shore marine habitats, thus represent significant sources of ecosystem services for the region (Lane et al. 2015).

Caribbean reefs, of which the Florida group are the northern-most members, have suffered several major disturbance events over the last decades including bleaching, the loss of top predators, and the emergence of diseases that have reduced reef structural complexity (Manzello et al. 2007; Green and Bruckner 2000). The fish that use these reefs have shown mixed responses to such changes, with some assemblages showing signs of recovery within a decade or less, with others showing strong lags whereby fish assemblages have yet to recover to their pre-disturbance composition and biomass (Alevizon and Porter 2015). There is recent evidence showing Caribbean-wide shifts in fish assemblages toward habitat generalists and away from specialists (Alvarez-Filip et al. 2015) and overall loss in fish abundance (Paddack et al. 2009). The reefs along the Florida Keys were included in these assessments; however, no one has explored whether the spatial similarity of these reefs has increased through time or if these reefs have become more similar to other non-reef habitats along Florida's Atlantic coast. We evaluate this possibility here, along with tracking how these reefs compare in their similarity to other near-shore habitats that are important for marine fishes.
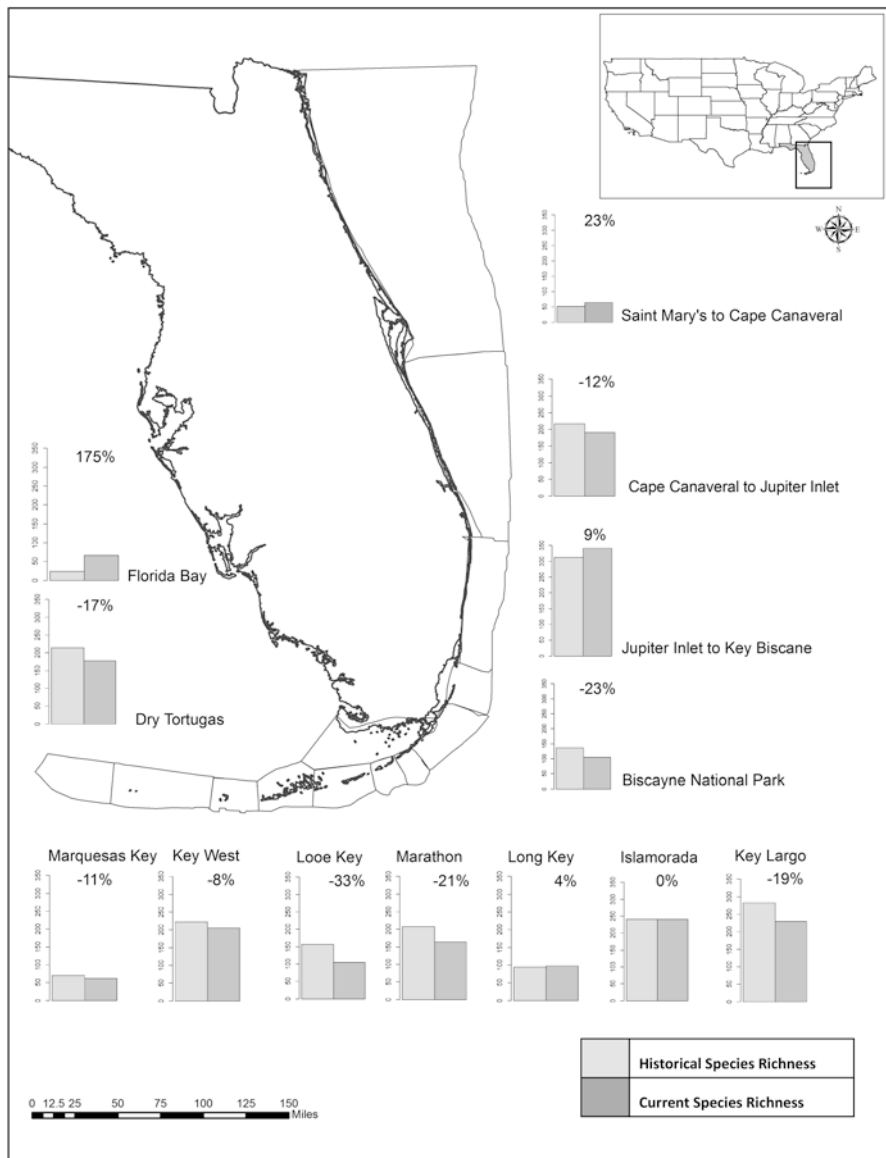
Fig. 18.1 Map of Florida showing the 13 REEF sites (sub-zones) considered in this study. Bar graphs correspond to site, with historical species richness in light gray and current species richness in dark gray. Overall changes in species richness from historical to current time frames are reported as percentages. Positive percentages indicate net gain in species richness per site, while negative percentages indicate net loss in species richness

18.2   Methods

18.2.1   Surveys

We queried the Reef Environmental Education Foundation (REEF) online database to obtain presence-absence data from across survey locations along the Atlantic coast of Florida (World Wide Web electronic publication; www.reef.org, date of download: 12 May 2017; Fig. 18.1). Our data comes from the REEF Florida East Coast and Keys (zone 3) of the tropical western Atlantic region. This zone covers survey locations from Saint Mary's River at the northern Atlantic coast boundary between Florida and Georgia, down to the Dry Tortugas, which is the western-most island group in the Keys (Fig. 18.1). Within this zone, there are 13 sub-zones within which surveys are conducted at various locations. Survey locations include natural coral reefs, artificial reefs, and other seafloor structures that attract relatively large numbers of marine fish (e.g., natural rubble, marine ridges).

In all REEF surveys, fish species presence is recorded by trained volunteer SCUBA divers using the Roving Diver Technique (RDT; Schmitt and Sullivan 1996, Hassell et al. 2013). Between 1994 and 2015, REEF volunteers conducted 37,695 RDT surveys at 1903 survey locations, summing to 34,305 dive hours with the average dive lasting 45 min. There are large differences in the total number of locations surveyed across sub-zones (from 14 to 502), with bigger sub-zones having more survey locations. The number of species detected is highly dependent on survey effort (in this case measured as dive time, and numbers of locations are surveyed); thus, we needed to standardize effort across the years within sub-zones to ensure relatively unbiased temporal assessments of compositional change. We chose years to include in our analyses so that they had dive times (effort) that were no more than 20% different in length. Based on this criterion, we selected 353 survey locations for inclusion in our analyses (20% of all sites surveyed). Initial surveys were conducted between the years of 1997 and 2004 and the later resampling surveys occurred from 2011 to 2017; thus, our data reflects on average a 20-year time span. We combined the species lists for each of these survey locations to create a scaled-up accounting of species composition across the 13 sub-zones, hereafter referred to as "sites" (Fig. 18.1). Note that there was necessarily a difference in the number of survey location information contained within each site, and thus our results cannot be fully corrected for differences in sampling intensity on species occupancy across sites.

18.2.2   Species Composition

We created two lists of species present for each of the 13 sites we analyzed. The first was composed only of species recorded as present in recent surveys ("current" time frame), and the second was only the species present in surveys at least 10 years prior ("historical" time frame). We used the cluster analysis R-package *hclust* to produce Bray-Curtis dissimilarity scores between all sites, calculated using only the

historical data and then again using the current data. We depicted similarity across all 13 sites within each time frame using a dendrogram where sites joined by short branches have very similar species composition, and longer branch lengths represent increasingly divergent species composition. Clusters of sites connected by short branch lengths are referred to as supergroups as these sites have very similar species composition to each other relative to other sites in the analysis. As a coarse measure of degree of homogenization, we calculated the overall branch lengths of each of these two dendrograms (historical and current). If sites have become more similar overall in species composition (homogenized), we expected to see that the current dendrogram has a lower summed branch length than the historical dendrogram; and we would take the opposite pattern (longer summed branch lengths) as evidence of differentiation. We can also more closely track how the cluster affiliation of each site may have changed between time frames by comparing the higher-order branching patterns between these two dendrograms. We would take as evidence of homogenization a shift toward branch nodes that indicated higher similarity (shift in branch location to the right between time frames). In contrast, substantive differentiation would be characterized by an increased dissimilarity score at higher-order branching nodes (shift in branch location to the left). This more detailed comparison of the two dendrograms allows us to pinpoint sites that are homogenizing, those that are not changing, and those that are differentiating.

There are several studies that suggest that species composition of a region can change substantially through time, while species richness remains largely unchanged (Dornelas et al. 2014). There is also a presumption within many discussions about biological homogenization that sites tend to become more similar in composition due mostly to the increasing presence of ubiquitous exotic species rather than the loss of endemic native species (Olden and Rooney 2006). To explore if these patterns were present in fish assemblages within Floridian coastal waters, we calculated historical and current species richness within each site. We calculated species richness as the simple sum of all species recorded as present within each site, repeating this calculation for each time frame. We also labeled each species as either native or exotic using USGS Nonindigenous Aquatic Species database (nas.er.usgs.gov).

Changes in richness within a site over time can occur in two ways. Species can either be absent from the historical list and present in the current or vice versa. The spatial pattern by which these temporal shifts in species presence occur dictates the extent to which compositional similarities are altered (Olden and Poff 2004; Olden and Rooney 2006). Thus, for example, across-site compositional similarity can increase (homogenize) through the addition of the same species across all sites across time frames; or similarity can increase when species found only in one or a few sites disappear between time frames. Differentiation can occur if formerly common species are lost in only a few scattered sites or if species enter the presence-absence record at only one or a few sites. In order to track such changes, we recorded the number of sites in which each of the 452 species was lost or gained between time frames. We then calculated the percentage change in site occupancy between time frames by dividing the change in number of sites by the number occupied in the historical time frame. We plotted all species according to their percentage change in site occupancy, as well as the number of sites they occupied in the histori-

cal time frame. This graphic allows one to visualize how individual species contribute to homogenization or differentiation patterns observed over time.

18.3   Results

Overall, sites along Florida's Atlantic coast and Keys experienced a 67% net gain in species richness, with Florida Bay experiencing the largest increase, over the 20-year time span of our data (Fig. 18.1). Most other sites experienced a slight loss in species richness or very little change through time (Fig. 18.1). Fifty-six species were observed within at least one site in the historical time frame, but were not observed in the current time frame. Over half (29) of these "disappearing" species were originally seen only within one site, suggesting that their loss from the current time species list is due to lack of detection and not true loss. However, 11 species were found within 3 or more sites in the historical time frame but not at any site in the current time frame, which is not as likely due to lack of detection. Seventy-two species were absent in the historical time frame but were recorded as present in the current period. Over two-thirds (55) of these "appearing" species were found only within one site in the current time frame, suggesting that they were rare in the historical period and not detected and are now experiencing local population increases. Nine species appear for the first time within three or more sites in the current time frame indicating rapid increases in local populations. Only two of these species are exotics: the Pacific lionfish (*Pterois volitans*) and brassy chub (*Kyphosus vaigiensis*). These exotic species account for the largest percentage increases in number of sites occupied within Fig. 18.2. The remaining seven species are considered native to the United States according to USGS. The reasons why these, and other increasingly observed species, are now found more commonly in the near-shore marine waters of Florida is not clear but may be due to either climate change or response of a narrow suite of local fish populations that are favored by the massive habitat alterations that took place prior to the time frame of our data (Alvarez-Filip et al. 2015; Lamy et al. 2016).

Of the 324 species that were present within at least 1 site across both time frames, 90 showed no change in the number of sites they occupied, with another 96 showing <20% shifts (positive or negative) (Fig. 18.2). Most of the 82 species that expanded the number of sites they occupied through time moved into only 1 more site, but 6 increased by 3 or more sites. No species that were originally found within four or more sites expanded to occupy other sites.

In terms of species composition, total branch length for the historical dendrogram was 4.3, whereas total length for the current dendrogram was 4.5, indicating slight overall differentiation in fish assemblage composition across sites through
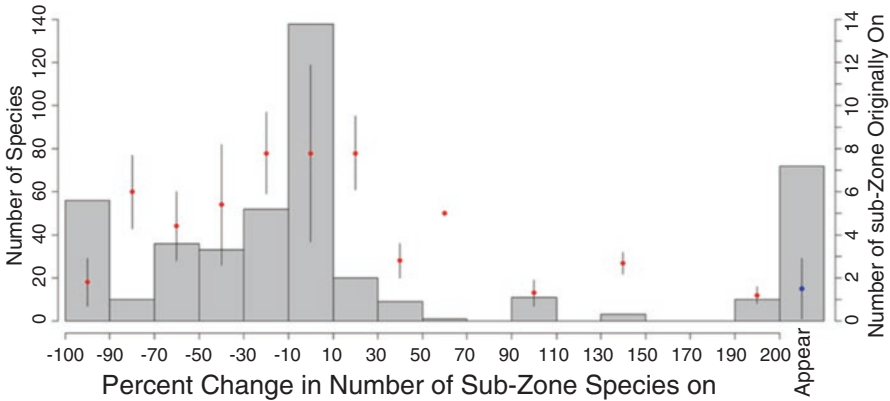
Fig. 18.2 Histogram showing the number of species that show a percentage change in number of sub-zones (sites) occupied between the historical and current time periods. Negative percentage change indicates species' range contraction, and positive change indicates species' range expansion. The y-axis indicates the number of species that fall within each percentage change bin. Also shown on the y-axis is the average number of sub-zones (sites) species within each percentile grouping occupied in the historical time period (red dots = average, bars = standard deviation). Many changes in percentage of sub-zones occupied are likely due to failure to detect species in surveys. However, large percentage decreases from species that occupied many sub-zones historically are likely true species declines, and large percentage gains from species that occupied few sub-zones historically likely represent true range expansions

time (Fig. 18.3). The Florida Bay site was consistently unique in fish assemblage composition as compared to all other sites no matter the time frame. The shift of the Saint Mary's Reef to Cape Canaveral site to become a member of the Looe Key, Biscayne National Park, Long Key, and Marquesas Key supergroup indicates that it currently has a species composition substantially more similar to the supergroup than it did historically. In contrast, the Jupiter Inlet to Key Biscayne site shifts from grouping with the other reef-dominated supergroup to becoming its own unique branch indicating that it has become much more distinct in species composition between time frames (Fig. 18.3). More subtle changes in compositional similarity occur within a supergroup consisting of the Marathon, Islamorada, Key West, Dry Tortugas, Key Largo, and Cape Canaveral to Jupiter Inlet sites (Fig. 18.3). Within this supergroup, there is a shift toward the sites becoming more similar to each other in their species composition across time frames, indicating homogenization (Fig. 18.3).
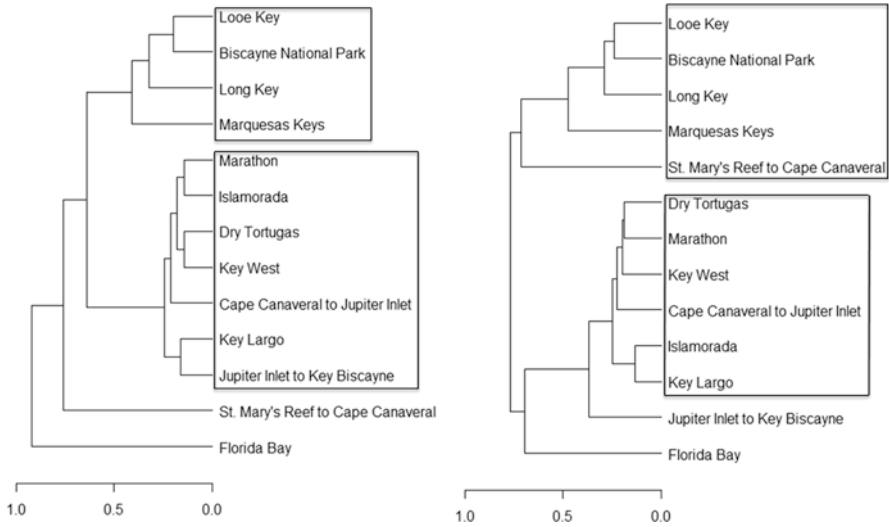
Fig. 18.3 Two dendrograms comparing fish assemblage similarity between reefs from historical (left) and current (right) time frames. Shorter branch lengths indicate higher degree of similarity, while longer branch lengths indicate lower degree of similarity, with similarity derived using Bray-Curtis scores (see main text)
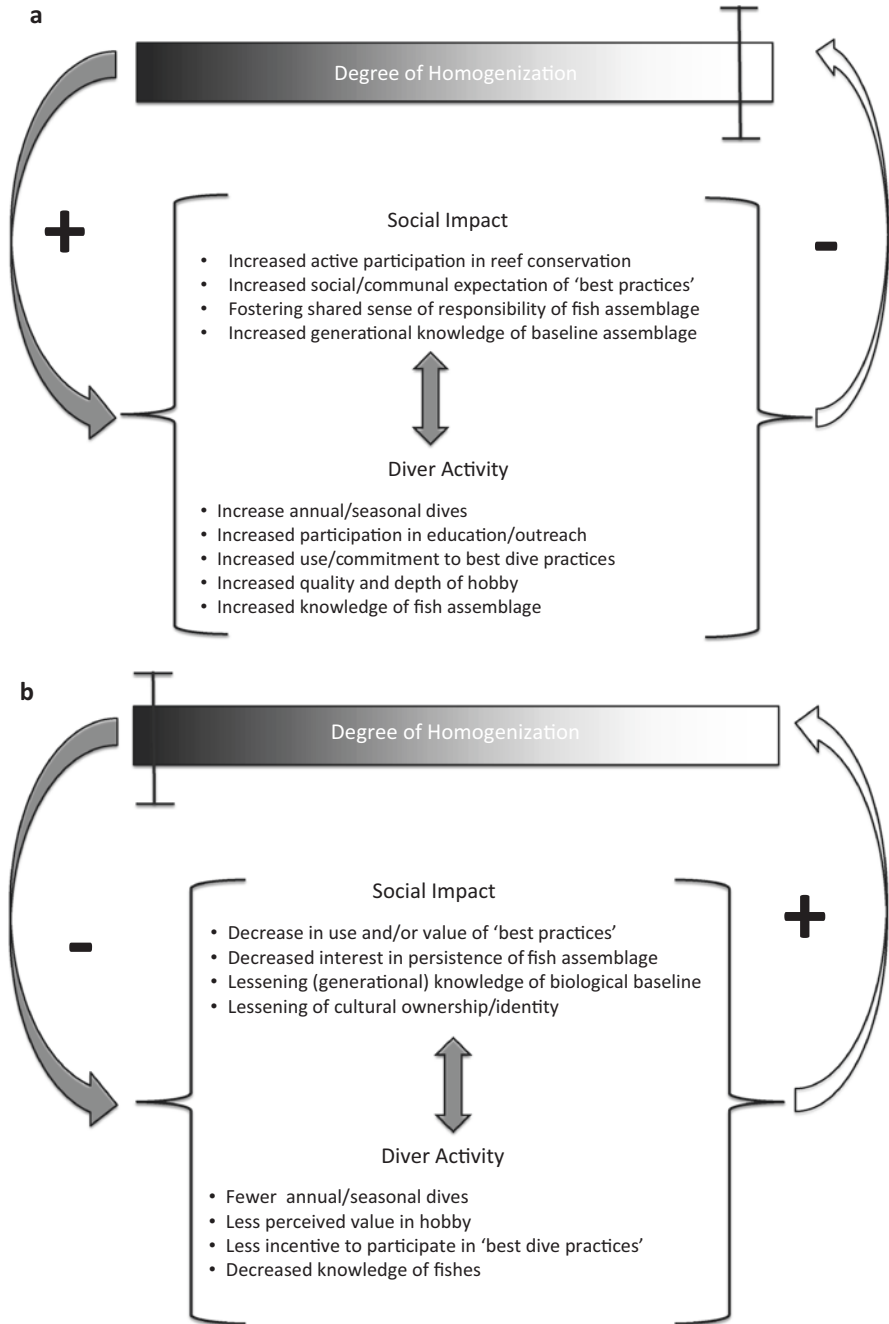
18.4 Discussion

We show that fish assemblages along the Atlantic coast of Florida and the Keys have shifted in their assemblage composition through time in a spatially complex manner but without experiencing large changes in species richness. Although there has been consistent focus on the loss of species and biomass within marine ecosystems, the possibility of changes in spatial diversity has largely gone unexplored (c.f., Alvarez-Filip et al. 2015; Edelist et al. 2013). We found that the Florida Atlantic coast fish assemblage is characterized by larger-scale differentiation; however, at a smaller scale, some regions have homogenized. In particular, the Jupiter Inlet to Key Biscayne site substantially differentiated from the others through time, while a supergroup of mostly coral-dominated sites homogenized. This pattern contrasts to what we observed among another supergroup of coral-dominated sites that experienced approximately similar changes in richness through time, but did not homogenize. These non-changing reef sites are some of the more geographically isolated of the set (e.g., Marquesas Key) or are under active protection as national marine sanctuaries or national parks (e.g., Looe Key and Biscayne National Park), which may explain their stasis in fish assemblage compositions over the time frame of our investigation.

The shifts in assemblage similarity we did observe are driven mostly by species losses and not by species colonization. Although some species are expanding into new sites, this spread seems to be smaller in spatial extent than the range contractions that many other species are undergoing. The two species that spread the most across time frames were exotic species; however, we recorded a very few exotic species in our dataset. Our results suggest the need to more closely examine the fish assemblages associated with the coral reefs around the Keys, Biscayne Bay, and scattered along the most southern Florida coastline. Narrowing the habitat focus of analysis, and thus also the suite of fish species considered, should increase clarity in regard to the role of changes in coral cover, predator diversity, and ocean temperatures that may be driving homogenization across habitats.

Finally, we posit that changes in fish assemblage spatial structure will influence the attractiveness of Florida marine habitats for dive tourism. One of the main motivations for diving any area is to experience the variety of fish species that use that site, with the more species variety, the better (Bhat 2003). Homogenization of fish assemblages across sites may provide a strong feedback into the dive tourism industry by reducing the attractiveness of Florida's diving locations. From a recreational diver's perspective, homogenization may lead one to conclude that once fish at one location have been seen, there is no reason to travel to other sites that have essentially the same diversity. However, this is only one factor in a complex matrix of factors that may go into a diver's decision to move from one site to another (Biggs et al. 2015). To our knowledge, the degree to which homogenization (or differentiation) influences the attractiveness of reefs and other habitats for dive tourism has not been explored. Therefore, we see our results as providing a starting point for this analysis by documenting the degree of homogenization realized among Florida's fish assemblages, in which parts of Florida contribute most to any observed homogenization and which species are "winning" or "losing."

We envision a feedback between fish assemblage composition and the cultural connections people maintain with these assemblages as a two-way interaction (Fig. 18.4a, b). Existing research links diver activity to their efforts to conserve the species and habitats they enjoy (Dearden et al. 2007; Arin and Kramer 2002), and this provides a framework for understanding when spatial compositional changes will elicit conservation actions from divers and when it will not. For example, novice divers may fail to recognize assemblage change since they are unfamiliar with how unique any given site was previously from all others in terms of fish assemblage. They thus likely will not experience an emotional response to experiencing a homogenized (or differentiated) fish assemblage and will not go on to engage in behaviors that lead to remediation of the site (Anderson and Loomis 2012). Such divers may also fail to recognize their own behaviors are contributing to fish assemblage change or species losses, and they may have low social inclination toward habitat conservation. These feedbacks for novice divers thus either fail to stem changes that lead to assemblage change or even encourage further change (Fig. 18.4a).

a

Degree of Homogenization

+

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Social Impact

- Increased active participation in reef conservation
- Increased social/communal expectation of 'best practices'
- Fostering shared sense of responsibility of fish assemblage
- Increased generational knowledge of baseline assemblage

Diver Activity

- Increase annual/seasonal dives
- Increased participation in education/outreach
- Increased use/commitment to best dive practices
- Increased quality and depth of hobby
- Increased knowledge of fish assemblage

b

Degree of Homogenization

‒

+

Social Impact

- Decrease in use and/or value of 'best practices'
- Decreased interest in persistence of fish assemblage
- Lessening (generational) knowledge of biological baseline
- Lessening of cultural ownership/identity

Diver Activity

- Fewer annual/seasonal dives
- Less perceived value in hobby
- Less incentive to participate in 'best dive practices'
- Decreased knowledge of fishes

Fig. 18.4 Conceptual diagrams illustrating the interplay of SCUBA and snorkel diver cultural and social behavior and its feedback with biological homogenization. We envision that divers' Fig. 18.4

Divers that regularly visit the same sites over many years have an expectation of what a healthy baseline fish assemblage looks like (Anderson and Loomis 2012). When that baseline begins to change, more experienced divers undergo an emotional response that may result in changes of their behavior (Fig. 18.4b). Those who rely on ecotourism are some of the most politically active demographics, which is reflected in the often mandatory requirement of state natural resource managing bodies to have individuals on the boards of these stakeholders (South Atlantic Fishery Management Council. Accessed 14 June, 2017). If conservation and natural resource managers aim to find compromises that satisfy both conservationists and stakeholders, we must to take into account the cultural and economic influences that are associated with natural systems. Future research on the cultural and social effects on biological homogenization should aim to gather information from individuals who engage with fish assemblages in both a casual and dedicated manner and connect their perceptions to what species they observe to their willingness to support conservation and management actions.

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Fig. 18.4 (continued) experience levels will play a strong role in how they respond to homogenization, depicted as a bar above the diagram with increases from right (light) to left (dark). Diver activity levels (experienced or novice) tend to engender particular behaviors relative to adherence to "best practices," interest in fish species ecology, knowledge of biological baselines, and claiming cultural identity in the fish themselves or dive site. Given this connection, we posit that experienced divers will respond with increased conservation vigilance when realizing that fish assemblages they frequently encounter are homogenizing. The increase in conservation action will then tend to decrease homogenization levels (panel A). In contrast, novice divers may not notice that assemblages have homogenized and thus will do nothing to prevent further homogenization or even act in ways that further increase homogenization (panel B)

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