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Shift in recreational fishing catches as a function of an extreme cold event

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Abstract. There is an increasing recognition that the influence of extreme climate events (ECE) can be more significant in structuring ecosystem dynamics than the gradual effects of climate change. Still, our understanding of the effects of climate extremes on ecosystem services such as marine fisheries lags behind those of effects of gradual change. The significance of ECEs depends on the severity of the disturbance event and the resilience of a fish community. South Florida experienced an extreme cold spell in 2010 that provided the opportunity to study recreational fisheries resilience to ECEs. Our main goal was to examine how recreational fishing catch structures responded to the cold spell, and illustrate any spatial-specific recovery trajectory dynamics after extreme ecological responses. To address this, we implemented multivariate and nonlinear statistics on fishing guide reports for 20 recreational species. A significant shift in the catch structure occurred after the event, suggesting a high sensitivity of fish populations and fisheries in the region to ECEs. All fishing regions considered were affected, but the trajectory of the response and recovery varied across study areas. While some fish species experienced an expected decline (due to mortality), other species manifested an increase in catch. Of the main seven species considered in nonlinear models, three experienced a decline (bonefish, snook, goliath grouper), two experienced an increase (red drum, gray snapper), and the two had various weak trends (tarpon, spotted seatrout). Three years after the event, the catch structure has not returned to the original state, indicating a possible state shift, whose stability needs to be determined in future tracking of affected populations. Future work should also address the extent to which harvest may interfere with resilience to ECEs. Our work highlights the need to account for rare environmental forcing induced by ECEs to ensure the ecological and economical sustainability of key services such as recreational fisheries.

Key words: cold spell; community composition; extreme climatic event; fishery resilience; recreational fisheries; Special Feature: Extreme Cold Spells.

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INTRODUCTION

Ecosystem dynamics are influenced by many local and regional processes including climate oscillations and episodic anomalies (Walther

et al. 2002, Hughes et al. 2005, Heenan et al. 2015). There is increasing recognition that extreme climate events (ECE; i.e., events that are rare, abrupt, and short in duration) can be more important in structuring ecosystem dynamics

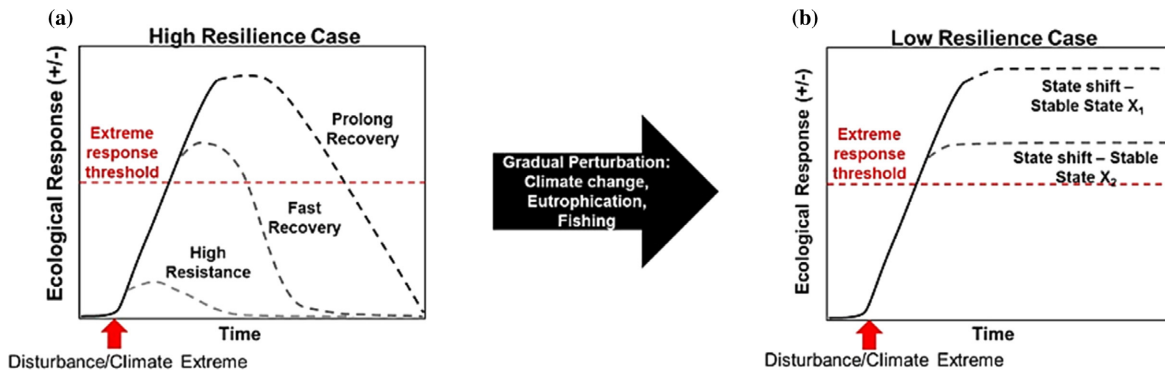


Fig. 1. Conceptual illustration of extreme responses, resilience, and recovery trajectories for an ECE. Shown are ecological responses in fish community with a low (a) and high (b) resilience, respectively. The trajectory of recovery after the ECE differs depending on the severity of the disturbance (red arrow) and resilience of the system. In (a), an ECE may not significantly push the fishery state across the extreme response threshold (high resistance), or may push the fishery state followed by a fast or prolong recovery. In contrast, when the resilience is eroded by other factors (b), an ECE has a higher likelihood of pushing the fishery to an alternative stable state (modified from Smith 2011).

than variation in average conditions (Smith 2011, Lynch et al. 2014). In particular, while the effects of more gradual changes in climatic conditions may be relatively unimportant at short time scales (e.g., months, years), the magnitude of the effect of ECEs can be disproportionate relative to their duration and frequency (Smith 2011). Thus, forecasted changes in the occurrence of ECEs should affect ecosystem structure and function, the productivity of resources, and the provisioning of socioeconomically valuable ecosystem services (Hughes et al. 2005, Jentsch et al. 2007, Brander 2010, Kreyling et al. 2011).

A disturbance event is considered an ECE if there is both a statistically rare climatic event and extreme ecological response (Smith 2011). Extreme responses cross critical thresholds where community structure and ecosystem function move outside their normal bounds (Jentsch et al. 2007, Smith 2011). This crossing of extreme response thresholds by an ecosystem (an extreme ecological response hereafter; red line in Fig. 1) may be induced by the reordering of dominant and/or functional species, widespread species loss, and/or invasion by novel species (Jentsch et al. 2007, Thibault and Brown 2008, Smith 2011). Post-ECEs, extreme responses may experience three different trajectories: a short recovery period, a prolonged period of recovery, or experience novel system trajectories characterized by state shifts (Fig. 1) (Kreyling et al. 2011, Möllmann and

Diekmann 2012). The likelihood of an ecosystem or community, and associated services, to recover, or switch to an alternative stable state depends on both the strength of the perturbation and the resilience of the system (Fig. 1a vs. 1b; Kreyling et al. 2011, Möllmann and Diekmann 2012). Communities that recover will return to the pre-disturbance state and experience only temporary effects on ecosystem and ecological services; however, if the ECEs lead to as state shifts, effects may be long lasting and hard to reverse, and may require drastic and costly management actions to mitigate the loss of services (Scheffer et al. 2001, Scheffer and Carpenter 2003, Suding et al. 2004).

Studies of the effects and recovery from ECEs on ecosystem services (i.e., the aspects of ecosystems that contribute actively or passively to human well-being; Fisher et al. 2009) are lacking. One important marine ecosystem services affected by ECEs is coastal fisheries (Brander 2010, Rocha et al. 2015), including recreational fisheries. Recreational fisheries are one of the most valuable ecosystem services (e.g., in terms of both provisional and economical values) provided by coastal ecosystems (Fedler 2009, Barbier et al. 2011, Post 2013). Recreational fisheries are characterized by a multispecies structure that encompasses various ecological and trophic attributes (Post et al. 2002, Post 2013). Thus, changes to community structure resulting from ECEs should directly affect the structure dynamics and

resilience of recreational fisheries (i.e., the ability of an exploited population to compensate for harvest and other environmental stressors; Post 2013). The resilience of recreational fisheries to ECE will depend on the diversity of the catch composition, the level of exploitation across species, and whether the traits of species within the catch are resistant or not to the abiotic or physiological stress caused by ECE (Planque et al. 2010, Britten et al. 2014). In this study, we explored the effect and resilience of the catch structure of a multispecies recreational fishery in response to an ECE. To our knowledge, few studies have tracked the response of fisheries to ECEs (but see Möllmann and Diekmann 2012).

In January 2010, South Florida experienced an extreme cold weather event that decreased air and sea surface temperatures to extreme lows for 10–14 d (Adams et al. 2012, Boucek and Rehage 2014). Associated with this ECE was mass mortality that affected a variety of species including important recreational fish species such as bonefish (*Albula vulpes*), common snook (*Centropomus undecimalis*), and Atlantic tarpon (*Megalops atlanticus*) (Fish and Wildlife Conservation Commission 2010, Rehage et al. 2010). Extreme cold events have led to fish kills in Florida approximately every 10 yr in the last 100 yr (Gilmore et al. 1977, Snelson and Bradley 1978, Boucek and Rehage 2014). However, this ECE was the most severe cold event over the last 85 yr (Boucek and Rehage 2014, Pirhalla et al. 2014).

For recreational fisheries, however, whether this disturbance event was in fact an ECE remains unresolved. Thus, the objective of this study was to assess the effect and resilience of recreational fisheries to a low-temperature ECE. Using a rich spatiotemporal creel survey data set from Everglades National Park (ENP, Florida, USA), we used a multivariate and nonlinear modeling approach to address the following research questions: (1) Did the 2010 cold spell result in a shift in the catch structure in Everglades recreational fisheries? (2) Did the nature of the shift vary across space? and (3) How did individual species contributed to shifts in the catch structure? Given previous documented effects on coastal species (Boucek and Rehage 2014), we expected to see a major impact on the recreational fishery. The catch data should reflect a shift from less to more cold-resistant species (i.e., tropical to temperate,

Boucek et al. this issue). Therefore, we hypothesized that the catch structure response to the cold spell reflected population dynamics of affected fishery species, by showing spatiotemporally dependent trajectories as a function of the biology of the fish (e.g., habitat requirements: marine vs. estuarine, physiology: temperate vs. tropical species, and life history traits: Allee effects, skip spawning) in combination with other habitat-specific disturbance regimes and stressors (e.g., water management and eutrophication).

MATERIALS AND METHODS

Site and data collection

Recreational fisheries data used in this study were collected throughout six areas in ENP (Fig. 2a). ENP, which includes Florida Bay and coastal mangrove estuaries, is an ideal model system for developing and testing approaches for assessing fisheries state shifts, long-term temporal trends, and the effects of climatic parameters. The Everglades is an iconic ecosystem of high socioecological value, subject to significant anthropogenic degradation, and presently the focus of the largest restoration effort ever attempted (Sklar et al. 2005). Recreational fisheries are economically vital to the region. One in five Florida anglers fishes the Everglades region, generating \$1.2 billion in economic activity (Fedler 2009).

We used fishery-dependent data obtained from professional guide logbooks. Professional guides are required to obtain an annual permit from ENP, and report their monthly catch and effort on a per trip basis via logbooks. Guides reported the area fished ($N = 6$ areas, Fig. 2a), number of fish kept and released per species, effort (number of anglers, hours fished), and species preference (Osborne et al. 2006). Further details on the methodology can be found in Tilmant et al. (1986) and Schmidt et al. (2002).

Only the top 20 species with the highest proportion of reports were considered in this study since they represented the majority of the catch (Appendix S1). These species encompass a diversity of geographical ranges (tropical, subtropical, and temperate), trophic levels, and life-history strategies. Over 25% of the time, anglers reported to catch these popular fish species: spotted seatrout (*Cynoscion ocellatus*), red drum

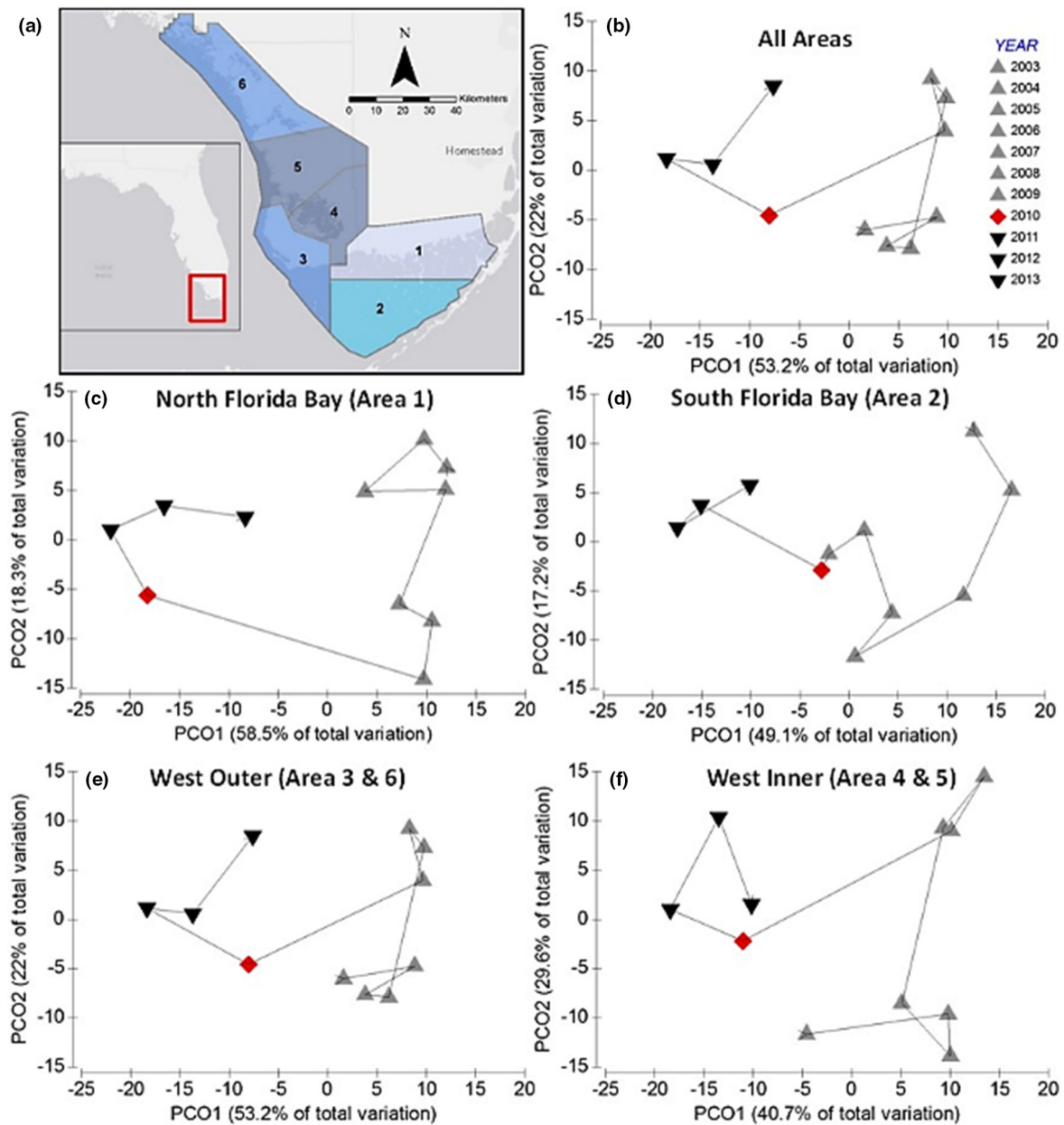


Fig. 2. (a) Map of the six fishing areas used in recreational catch reporting: 1: North Florida Bay, 2: South Florida Bay, 3: Cape Sable, 4: Whitewater, 5: Tarpon Bay/Shark River, 6: Ten thousand Islands. The degree of blue shading indicates how areas clustered spatially into four fishing regions with distinct catch structure (Appendix S1). PCO plots are shown for: (b) all regions combined, (c) North Florida Bay, (d) South Florida Bay, (e) West Outer, and (f) West Inner. Vector in PCOs illustrates the temporal trajectory of catch structure change (gray: before ECE, red: ECE, black: after ECE).

(*Sciaenops ocellatus*), common snook, and gray snapper (Osborne et al. 2006, Appendix S1). In addition, the professional guide fishery is largely directed at a few highly prized gamefish species

such as Atlantic tarpon and bonefish (Osborne et al. 2006, Fedler 2009). These species could be classified either as marine (gray snapper, bonefish, and tarpon) or estuarine (snook, spotted

seatrout, red drum) due to their varying habitat needs and physiological constraints. Also, these species have a temperate (red drum, spotted seatrout) or subtropical (snook, bonefish, tarpon, gray snapper) geographical range, which should influence their ability to cope with extreme low-temperature events (e.g., Boucek and Rehage 2014, Boucek et al. this issue). Thus, we expected to see a variation in species-level responses to the cold spell, which should cascade to major changes in catch structure.

Data processing

We used guide report data for 2003–2013, which included 7 years precold spell and 3 years postevent. Guides have reported their monthly catch and effort on a per trip basis since 1972; however, since the late 1990s the data set have been subject to sampling improvements (e.g., mandatory reporting after 1980, further stratification of the reported fishing areas after 1995), changes in fishing effort dynamics (e.g., GPS technological advances, economic incentives), and fishery management strategies (e.g., closure of commercial fishing in 1985, and changes in catch limits and fishery closures). Thus, the truncation of the data set from 2003 to 2013 was performed to control for major changes in catchability and data collection procedures, and isolate the disturbance event within a decadal period. This included a total of 15,341 guide reports. We combined the total catch reported (number caught + number released) and total hours fished by anglers to calculate catch per unit effort ($CPUE = (no. kept + no. release) / (no. hours fished \times no. anglers)$) for the 20 species with the highest reporting. We used monthly and yearly averaged CPUE in statistical analyses.

Statistical analyses

We performed separate univariate and multivariate analyses to address the three research questions. To examine if the catch structure varied across years and fishing areas, we used a two-way crossed permutational multivariate analysis of variance (PERMANOVA, type model III) with 1000 residual permutations under a reduced model. PERMANOVA allows the use of dissimilarity measures to test for significance of specific effects, similar to a multivariate analysis of variance (ANOVA), but uses a

permutation test that does not require the data to follow a particular distribution, and therefore is more robust than parametric alternatives (Anderson et al. 2008). We treated the spatial effect (fishing area), time effect (years), and the time by space interaction as fixed effects. To facilitate the interpretation of spatiotemporal patterns, a hierarchical clustering analysis was used to group the catch structure of the fishing areas into spatially distinct fishing regions (Appendix S1). Then, a series of principal coordinates analysis (PCOs) were used to illustrate the spatiotemporal patterns, and identify shifts or recovery signals in the catch structure in relationship to the cold spell (Question 1) and across regions identified in the hierarchical clustering analysis (Question 2). PCO is equivalent to principal component analyses (PCA), but with a higher flexibility of resemblance measures (Anderson and Willis 2003, Anderson 2008). PERMANOVA pairwise tests were used to more carefully examine patterns observed in the PCOs, and to determine how the catch structure varied over time (e.g., pre- vs. postevent years).

If significant spatiotemporal patterns in the catch structure were determined by the PERMANOVA and PCO, we used one-way similarity percentage (SIMPER) analysis to determine which fish species contributed most to the differences between the catch structure before and after the cold spell event (Question 3). Thus, this allowed us to determine the main fisheries that benefited (“winners”) or were negatively affected (“losers”) by the ECE.

We then used a series of generalized linear models (GAMs) to assess the nature of the CPUE response of the most abundant gamefish species and those driving variation between pre- and postevent years. This included bonefish, red drum, common snook, spotted seatrout, tarpon, gray snapper, and goliath grouper (*Epinephelus itajara*). A GAM is a semiparametric extension of a generalized linear model (GLM) that includes a linear predictor involving the sum of smooth functions of covariates (Guisan et al. 2002), and is a useful approach to identify ecological thresholds and break points (Samhuri et al. 2010). GAMs were used to determine whether any catch break-points in individual species CPUEs were due to the cold spell, and if recovery characteristics

were due to true nonlinear responses around the disturbance event (Question 3). For the GAMs, species CPUEs were log-transformed, and were fitted using a Gaussian distribution, or scaled T family distribution for heavy tailed data (family = scat in mgcv R package). To assess the general temporal patterns in CPUEs, GAMs were designed to have a smoother for year.month (i.e., time covariate) with all regions as random effects (e.g., one-way mixed GAM) (Zuur et al. 2009). Then, within each of the regions, the CPUE temporal trend of the main species was assessed with a year.month smoother as the main fixed effect.

All ordination procedures (PERMANOVA, PCO, SIMPER) were performed in PRIMER v6 with the add-on software PERMANOVA+ (Anderson et al. 2008). GAMs were done in R (R Core Development 2015) with the package “mgcv” (Wood 2006). Ordination multivariate procedures were based on Bray–Curtis dissimilarity matrix using the top 20 species’ CPUE standardized relative to the maximum catch reported for each species (Clarke and Gorley 2006).

RESULTS

Catch structure spatiotemporal response to the 2010 cold spell

We found evidence that the catch structure of recreational fisheries in the Everglades varied as a function of both space and time. The PERMANOVA indicated a significant interaction between year and fishing areas (Table 1). Spatially, the hierarchical clustering analysis showed that the catch clustered into four distinct groupings (or fishing regions hereafter): North Florida Bay (Area 1), South Florida Bay (Area 2), West Outer (Areas 3 and 6), and West

Table 1. Permutational multivariate analysis of variance (PERMANOVA; results degree of freedom, F and P values from Monte Carlo permutation test) testing for the spatiotemporal effects on the recreational catch structure.

Source	df	Pseudo F	P
Year	10	6.96	0.001
Area	5	50.01	0.001
Year × Area	50	1.47	0.001
Residual	198		

Inner (Areas 4 and 5) (Fig. 2a, Appendix S1). Temporally, the PCO showed a marked shift in catch structure as a result of the 2010 cold spell (Fig. 2b). Furthermore, when considering regions individually, this shift was consistently observed across all four regions (Fig. 2c–f).

However, we detected variation in how regions were affected by the 2010 cold spell over time, indicating possible lag times in the effects of the disturbance event or variation in recovery trajectories (Table 2). In North Florida Bay, catch structure in 2010 was significantly different from both the before and the after years, indicating the effect of the event and potential recovery from it, which was not evident in the other three regions (Fig. 2c, Table 2). In contrast, in these regions, the catch structure was similar between 2010 and the postevent years, suggesting a persistence of the effect from the cold snap and a lack of recovery over these postevent years (Fig. 2d–f, Table 2). The other notable finding among regions was that in South Florida Bay the catch structure varied only between the before and after years (Table 2), but 2010 was not distinct, suggesting perhaps a more gradual or delayed effect of the cold spell in the most marine of the regions (Fig. 2d).

Species contribution to the shifts in catch structure

Eight species contributed to over 60% of the catch structure dissimilarity between the pre- and postcold spell years, and these included bonefish, red drum, common snook, spotted seatrout, tarpon, goliath grouper, ladyfish, and gray snapper. The proportion of the contribution of each species to the dissimilarity depended on the fishing region (Table 3). For instance, spotted seatrout and red drum accounted for most of the separation pre- and postevent in Florida Bay, while red drum and tarpon drove the most separation in the outer and inner west region, respectively. The standardized CPUE for spotted seatrout and red drum (i.e., the species with the most temperate distributions out of the ones driving dissimilarity) had higher values after the cold spell event. In contrast, tropical gamefish species such as the common snook and goliath grouper had lower CPUE values after the disturbance event. These patterns of “winners” and “losers” species were evident and consistent in direction across fishing regions with one exception (Table 3). Gray snapper standardized CPUE both increased (in

Table 2. Permutational multivariate analysis of variance (PERMANOVA pairwise test, t and P values) showing differences in species catch structure between years classified as: before the ECE (Before), year of the ECE (ECE), and after the ECE (After).

Area	Test	t	P-value permutation
North Florida Bay	Before vs. ECE	2.86	P < 0.01
	Before vs. After	3.74	P < 0.01
	ECE vs. After	2.41	P < 0.01
South Florida Bay	Before vs. ECE	1.35	NS
	Before vs. After	2.94	P < 0.01
	ECE vs. After	1.32	NS
West Outer	Before vs. ECE	1.80	P < 0.05
	Before vs. After	3.17	P < 0.01
	ECE vs. After	1.56	NS
West Inner	Before vs. ECE	1.90	P < 0.05
	Before vs. After	2.83	P < 0.01
	ECE vs. After	1.31	NS

North Florida Bay) and decreased after the cold spell (in South Florida Bay). More localized fisheries such as bonefish and jack crevalle showed a decreased in CPUE after the 2010 cold spell only in certain regions (South Florida Bay and West Outer, respectively).

There was evidence of a change in CPUEs over 2003–2013 in most of the individual species

tested. The GAMs show that the direction, strength, and nature of the CPUE patterns in relation to the 2010 cold spell varied among species (Fig. 3), and among fishing regions (Fig. 4). The time (year.month) smoother was significant for five of the seven species ($P < 0.05$ in Figs. 3 and 4). Three species showed a decline over time (bonefish, common snook, and goliath grouper,

Table 3. SIMPER analysis results showing the species that contributed up to 60% to the dissimilarity of catch structure between the years before and after the ECE.

Area	Species	Before ECE	After ECE	Contribution(%)
North Florida Bay	Spotted seatrout	↓	↑	38.96
	Red drum	↓	↑	15.01
	Gray snapper	↓	↑	13.90
	Snook	↑	↓	8.28
South Florida Bay	Spotted seatrout	↓	↑	12.74
	Red drum	↓	↑	11.40
	Gray snapper	↑	↓	10.78
	Bonefish	↑	↓	8.67
	Ladyfish	↓	↑	6.65
	Goliath grouper	↑	↓	6.37
West Outer	Red drum	↓	↑	24.76
	Common snook	↑	↓	14.56
	Goliath grouper	↑	↓	10.27
	Crevalle jack	↑	↓	7.43
West Inner	Spotted seatrout	↓	↑	7.39
	Tarpon	↓	↑	17.25
	Goliath grouper	↑	↓	13.29
	Red drum	↓	↑	13.21
	Common snook	↑	↓	13.05
	Spotted seatrout	↓	↑	8.49

Note: The direction of the arrows (↑: higher averaged CPUE/max, ↓: lower averaged CPUE/max) illustrate how the CPUE of each species contributed to the dissimilarity relative to this group.

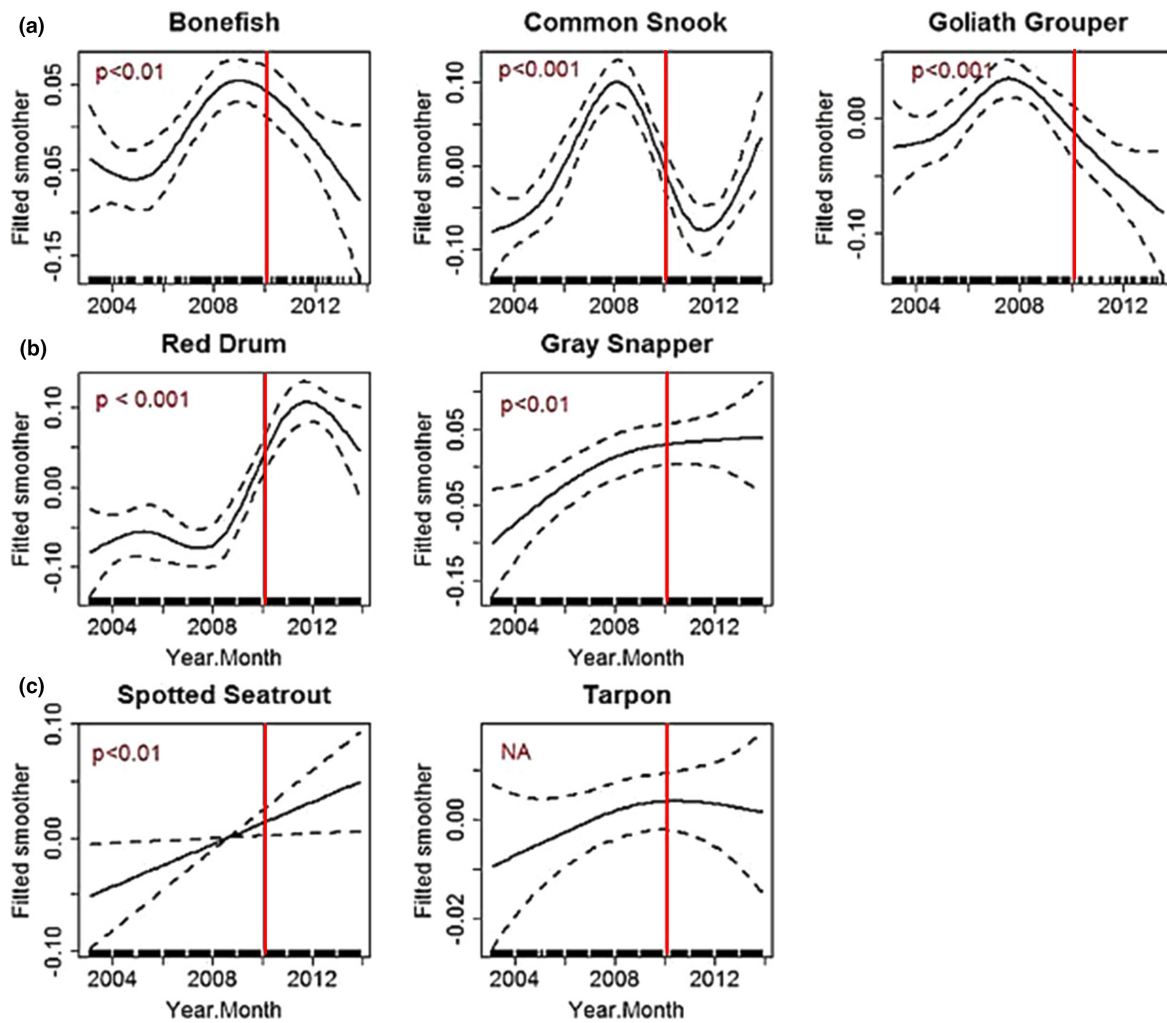


Fig. 3. Smoothed CPUE time series of species that experienced (a) declines (bonefish, goliath grouper, and common snook), (b) increases (red drum and gray snapper), and (c) weak temporal trends (spotted seatrout and tarpon) over 2003–2013. Trends are based on GAMS using fishing areas as a random effect. Solid line is the smoother, dotted lines are 95% point-wise confidence bands, and vertical line marks the ECE. P values are shown for each temporal trend.

Fig. 2a), two showed an increase (red drum and gray snapper, Fig. 4b), and two showed weak temporal trends (tarpon and spotted seatrout, Fig. 4c).

These species positive and negative temporal effects were variable across fishing regions, which we suspect relates to variation in distributions across space (i.e., species are affected where their catch was high) and not to differential spatial effects of the cold spell (Fig. 4). In North Florida Bay, a significant nonlinear response was observed for gray snapper (Fig. 4a). CPUE for

this species showed a positive linear trend preceding the cold spell, however, the trend slowed down postevent. A similar effect was seen for red drum in South Florida Bay, with a positive trend that preceded the cold spell but slowed down after the cold spell (Fig. 4b). In contrast, bonefish CPUE in South Bay peaked before the cold spell and declined after the ECE. In the West Outer region, red drum CPUE had an increasing CPUE immediately before and after the ECE, however, this pattern leveled off 2 years after the event (Fig. 4c). In contrast, both snook and goliath

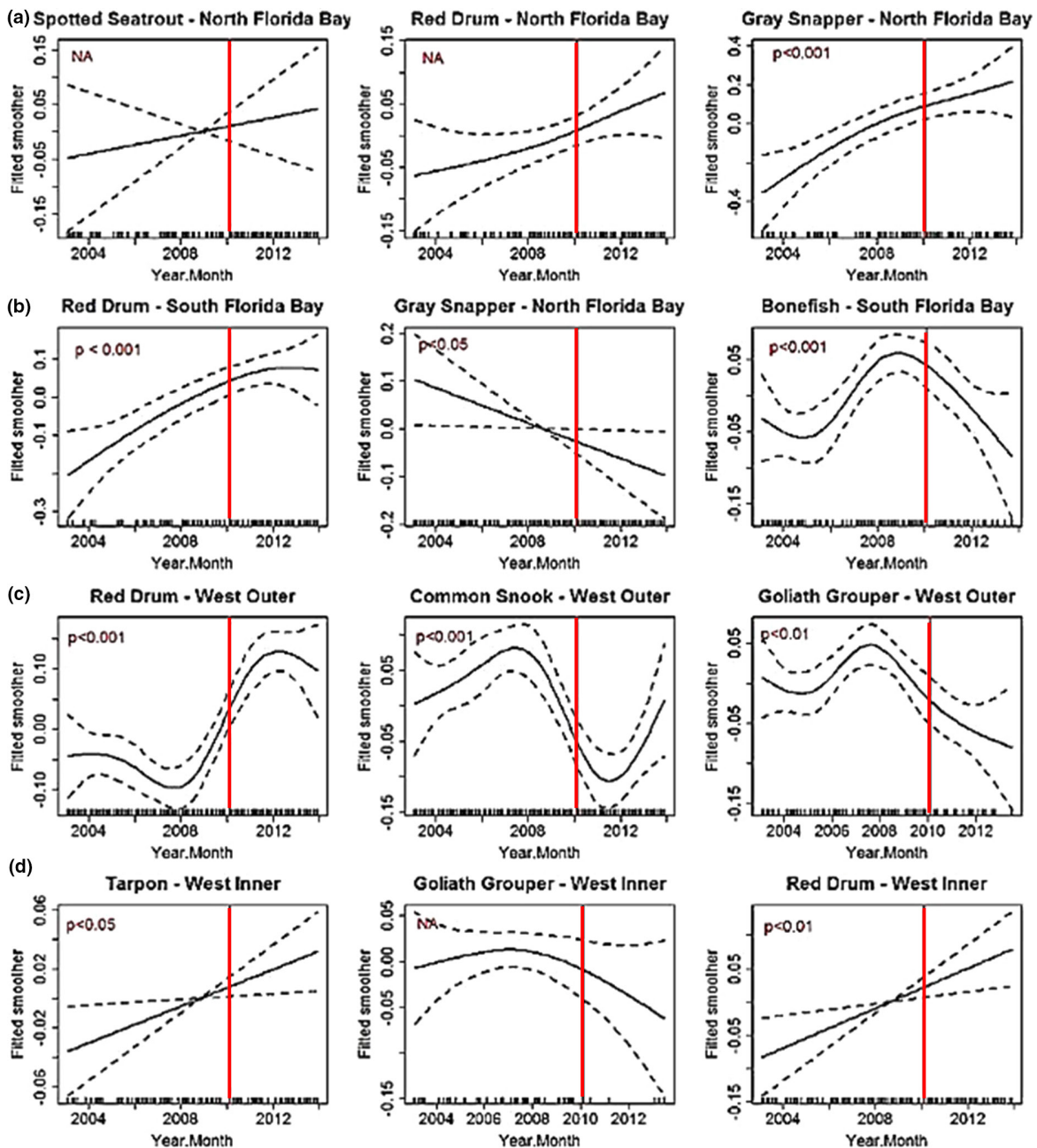


Fig. 4. Smoothed CPUE time series of the species that contribute the most to variation between pre and postevents years across the four fishing regions: (a) North Florida Bay, (b) South Florida Bay, (c) West Outer, and (d) West Inner. Species in each rows followed the same order as the SIMPER analysis in Table 3. Solid black line is the smoother, dotted lines are 95% point-wise confidence bands, and vertical line marks the ECE. P values are shown for each temporal trend.

grouper CPUE showed declining trends around the ECE in this region. Like bonefish, snook CPUE showed a peak preceding the ECE, but with the

highest rate of decline occurring concurrent with the cold spell. Finally, in West Inner Bay, the effects were weak and not significant (Fig. 4d).

DISCUSSION

Projected changes in the frequency and intensity of ECEs emphasize the importance of understanding how short time-scale events may influence the long-term dynamics of populations and the key ecosystem services that rely on them. Our main goal was to examine how Everglades recreational fisheries were affected by a severe cold spell, and track postevent recovery dynamics. Finding shows that the recreational catch structure suffered a major shift across all fishing regions as a result of the January 2010 extreme cold spell, highlighting the extreme response and vulnerability of recreational fish populations in this part of the world to low-temperature events. The shift resulted as a function of both a decline and an increase in the catch of top species. Subtropical species such as bonefish, goliath grouper, and snook suffered declines, while the catch of temperate species, like red drum and gray snapper, increased. In addition, 3 years after the event, recovery was not yet evident, except perhaps at one of the four fisheries regions examined.

The restructuring of the catch that we documented qualifies as an extreme response per Smith's (2011) definition, making the 2010 cold event a true ECE. One caveat, however, is the fact that we used a fishery-dependent data set, and thus were unable to completely discern changes in the catch structure that were due to "true" changes in fish abundance from changes in fishing effort alone. Fishing effort dynamics can disrupt how changes in CPUE track true changes in population size for a given fishery (Maunder and Punt 2004, Erisman et al. 2011, Post 2013). One common form of such disproportionality involves "hyperstability," in which CPUE remains stable while true abundance declines, leading to an overestimation of abundance and biomass (Erisman et al. 2011). Fishing effort may persist high even if fish abundance declines toward zero when there are substantial noncatch benefits of fishing (e.g., esthetics and leisure, travel cost, regulation enforcement; Post 2013). Furthermore, the interaction of fishing skills and spatially structured fishing may influence density-dependence effects in catchability. The catchability may change with fish abundance as

some anglers leave the fishery and other skilled anglers stay and allocate effort in different areas with distinct catchability among species/targeting tactics (Post 2013, Winker et al. 2013). Thus, shifts in catch structure, as those documented in our study may reflect changes in noncatch benefits, catchability, and/or effort dynamics, and not just changes in fish abundance. Nevertheless, fisheries-dependent data such as this study have been used successfully to assess how disturbance events influence ecological processes, community resilience dynamics, and regime shifts (Andersen et al. 2009, Möllmann and Diekmann 2012, Litzow et al. 2013, Britten et al. 2014).

In our study, several lines of evidence, however, support the notion that the documented changes in CPUE and catch structure are in fact reflective of changes in fish populations. First, we do know from previous fishery-independent studies that the cold spell caused significant fish mortality (Adams et al. 2012, Matich and Heithaus 2012, Boucek and Rehage 2014; P. Stevens et al., *unpublished manuscript*), which should have driven the observed CPUE declines in our study. For instance, Stevens et al. (*unpublished manuscript*) documented a 94% decline in common snook from fisheries-independent data in the West Inner zone of our study. Second, we did not document major shifts in fishing effort and angler behavior over time or space that could drive the changes in CPUE observed (Appendix S1:Fig. S3). Most importantly, we did not see major declines or increases in fishing effort across fishing zones that could drive CPUE up or down in significant way (Appendix S1). Similarly, aspects of angler behavior (species preference and harvest rate) remained largely constant despite the ECE. Angler preferences were spatially segregated before and after the cold event, and species harvest (the ratio of fish landed vs. released) remained constant in all regions over time, except the West Inner fishing region (Appendix S1:Fig. S3). In this region, harvest increased immediately post 2010. We hypothesize that this increase in harvest may relate to the closure of the snook fishery due to the cold event (mostly a catch and release fishery) and the increase in CPUE of species that are more harvestable (red drum and red snapper).

Fish community resilience and resistance should influence ECE outcomes. These outcomes may include periods of short or prolonged

recovery, or persistent state changes (Fig. 1; Smith 2011, Möllmann and Diekmann 2012). In this study, the lack of recovery 3 years after the event indicates a transitional catch structure state with some degree of persistence and a prolonged recovery. Spatially, we saw evidence of recovery at only one of four regions under study, which points to variation in local resilience (Dakos et al. 2015). Only North Florida Bay showed any indication of recovery, where the structure of the catch exhibited a directional trajectory toward the pre-event structure, and the event and post-event structures differed. In the rest of the fishing regions, the catch structure showed either a directional saltatory change (e.g., West Inner and West Outer) or a gradual change (e.g., South Florida Bay) with postevent trajectories exhibiting an overall tortuous pattern (i.e., lacking direction). Several studies have used the variation in recovery patterns (and the lack thereof) as indicator of low resilience, and potentially an early signal of a catastrophic shift (Van Nes and Scheffer 2007, Scheffer et al. 2012, Dakos et al. 2015). Other multispecies fishery studies have quantified changes in community size–structure, catch diversity, and biomass of functional groups to assess the stability of fished communities (Jensen et al. 2012, Fung et al. 2013). Community metrics like these ones could be combined with our approach (i.e., spatiotemporal catch structure dynamics) to integrate different functional components of marine communities (e.g., species interactions, prey–predator dynamics, catch variability, functional guilds, de- and compensation effects) that control both the resilience of ecosystems and associated fisheries.

One major question that remains unanswered at the end of this study is to what extent is the lack of recovery observed related to the harvest of these fisheries and to other unrelated stressors acting in this region? Previous work shows that variation in recovery patterns from disturbance is conditional on how the fishery resilience may be eroded by other environmental conditions (e.g., climatic oscillations) and anthropogenic stressors (e.g., eutrophication, salinity regimes, fishing pressure, and harvest) operating at varying spatiotemporal scales (Scheffer and Carpenter 2003, Möllmann and Diekmann 2012).

For example, the truncation of populations' size and age structure due to fishing increases

vulnerability to unfavorable environmental conditions by reducing the number of resistant age cohorts or those with a higher capacity to regenerate subsequent populations (Hsieh et al. 2006, Planque et al. 2010, Post 2013). In addition, age truncation can hinder the buffering capacity to stochastic environmental variation by fish species that use bet-hedging strategies (e.g., age-related differences in spawning location and time; Hidalgo et al. 2011). Hence, studies that incorporate varying combinations of climate disturbances and fishing levels are needed to disentangle and understand the intrinsic relationships between ECEs, fishing effects, and fish community resilience (ter Hofstede and Rijnsdorp 2011, Planque et al. 2010, Olds et al. 2014).

A longer time series will be needed to track recovery from the ECE, and determine whether the cold spell pushed the catch state to an alternative stable state, or if the catch structure is manifesting a prolonged recovery (i.e., Fig. 1a vs. 1b). In Florida, fisheries have recovered from previous cold spells, albeit not as severe (Gilmore et al. 1977, Bohnsack 1983). Elsewhere, previous studies have shown both prolonged recoveries and state shift in fish assemblages and fisheries catch structure in response to climate extremes and oscillatory patterns. For example, fisheries in the Eastern Scotian Shelf, the North and the Baltic Sea experienced a significant shift in structure due to a combination of overfishing and climate oscillations (Möllmann and Diekmann 2012). The dominant catch changed from a benthic to a forage fish species complex, but after sustained evidence of alternative stable states for 20 yr, signs of cod and benthic fish recovery pointed out to the reversibility of perturbed ecosystems. Other studies have shown that the resistance and recovery of coral and fish community assemblages after extreme events such as heat waves and coastal floods could be influenced by harvest control measures and improving the efficiency of marine protected areas (Olds et al. 2014, Williamson et al. 2014)..

As expected (Boucek et al. this issue) and evident in previous work (Boucek and Rehage 2014), the catch structure shifted as a result of the decline of subtropical species. The CPUE of species with a subtropical distribution and thus a limited cold tolerance declined, particularly common snook (e.g., 39° latitudinal limit; >15 °C

temperature lower limit; Shafland and Foote 1983) and goliath grouper (e.g., 36° latitudinal limit; >20 °C winter suitable habitat temperature for juveniles; Shideler et al. 2015). This decline likely resulted from a combination of severe lethal effects, resulting from hypothermal stress, as well as sublethal effects, such as reductions in reproductive fitness (e.g., spawning density-dependent mechanisms), which may be important contributing factors to the observed lack of recovery (Stenseth et al. 2002, Planque et al. 2010, Reuchlin-Hugenholtz et al. 2015). The lack of recovery 3 years after the event may have resulted from massive mortality of adults, and life history characteristics that contribute to slow population recovery for the affected species (e.g., long-lived fishes with slow growth, late maturation and low fecundity). For instance, bonefish and goliath grouper live between 20 and 35 yr, and would take 3 to 5 yr to reach a size where it would enter the fishery (Crabtree et al. 1997, Cass-Calay and Schmidt 2009). Snook juveniles suffered higher losses and adults manifested skip spawning following the cold spell. These effects influenced the size structure and population recovery which was estimated to take approximately 6 yr (Boucek and Rehage 2013). These life histories and changes in size structure can certainly increase the vulnerability of these species to disturbance events and associated stressors (Cass-Calay and Schmidt 2009, Adams et al. 2014, Shideler et al. 2015). In addition, temperature shock-related physiological stress can lead to behavioral impairments on foraging and movement capabilities (Donaldson et al. 2008, Szekeres et al. 2014), and cause translocation of available resources to the immune system and somatic growth with reproductive cost (Schreck et al. 2001, Planque et al. 2010) possibly contributing to the reduction in recruitment and lag responses. Throughout Florida, fisheries-independent data show that common snook suffered 80–90% population declines as a result of this event (Adams et al. 2012, Stevens et al. this issue) increasing the probability of density-dependent effects on the reproductive success of the species. Although bonefish, goliath grouper and common snook all showed preceding negative trends in CPUEs, the decline in catches observed between 2009 and 2010 were severe and larger in magnitude relative to these preceding trends.

One finding that was somewhat surprising was the increase in certain species (red drum, spotted seatrout, gray snapper) in the catch as a result of the ECE. Red drum and spotted seatrout are temperate marine species that experience variable winter conditions throughout their West Atlantic range (Anderson and Scharf 2014, Anweiler et al. 2014) and have lethal limits above the 6 °C minimum water temperature reported for this event (≤ 3 °C; Anderson and Scharf 2014, Anweiler et al. 2014). Surprisingly, gray snapper CPUE increased in certain fishing regions despite the fact this species is known to have a subtropical range. But, gray snapper display lower acute temperature tolerances (7–10 °C; Wuenschel et al. 2012), and are known to perform diel and ontogenic migrations from inshore/bay habitats to offshore reefs (Luo et al. 2009), where the cold spell effect was less severe (Lirman et al. 2011, Pirhalla et al. 2014). Possibly, red drum, spotted seatrout, and gray snapper populations may have benefited from a competition and/or predator release from negatively affected species (e.g., Gamble and Link 2012, Matich and Heithaus 2012). For example, the cold spell caused mass migration, high mortality, and age truncation of ENP bull shark juveniles (*Carcharhinus leucas*) (i.e., an apex predator in this system), which could have a net positive effect on mesoconsumers (Matich and Heithaus 2012). Else, these localized increases in CPUE may have been the outcome of shifts in fishing preferences and effort, a consequence of the low abundance and/or closed harvest for some highly valued fish species (e.g., 2-year closed harvest for snook harvest in Florida after the 2010 cold spell; Fish and Wildlife Conservation Commission 2010). Effort shift dynamics like this one have been reported as consequence of bag limits and other management strategies (Osborne et al. 2006, Post 2013).

In summary, by using a fishery-dependent data set, we demonstrated how a severe disturbance event resulted in persistent changes in the catch structure of a coastal recreational fishery as a result of both decreases and increases in the catch of target species. Recreational fisheries are economically important services to South Florida and other regions of the world, and their susceptibility to ECEs needs to be accounted for when considering their sustainability. The majority of stock assessment often rely on fishery-dependent or -independent indices of abundance that do

not take into consideration environmental conditions and low-frequency environmental forcing induced by ECEs (Brander 2010, King et al. 2015). Future work should aim to capture fish community and services responses to ECEs in areas with and without harvest (e.g., no take zones) to fully examine how exploitation (and other anthropogenic stressors) may affect fishery resilience to ECEs (Olds et al. 2014). A major challenge for sustaining the provisioning of valuable ecosystems services such as recreational fisheries in the future will be to increase our understanding of how and why fish communities and habitats may differ in their vulnerability and recovery to ECEs.

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