A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing

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Abstract. Overexploitation of predators has been linked to the collapse of a growing number of shallow-water marine ecosystems. However, salt-marsh ecosystems are often viewed and managed as systems controlled by physical processes, despite recent evidence for herbivore-driven die-off of marsh vegetation. Here we use field observations, experiments, and historical records at 14 sites to examine whether the recently reported die-off of northwestern Atlantic salt marshes is associated with the cascading effects of predator dynamics and intensive recreational fishing activity. We found that the localized depletion of top predators at sites accessible to recreational anglers has triggered the proliferation of herbivorous crabs, which in turn results in runaway consumption of marsh vegetation. This suggests that overfishing may be a general mechanism underlying the consumer-driven die-off of salt marshes spreading throughout the western Atlantic. Our findings support the emerging realization that consumers play a dominant role in regulating marine plant communities and can lead to ecosystem collapse when their impacts are amplified by human activities, including recreational fishing.

Key words: *Cape Cod, Massachusetts, USA; conservation; food web; human impacts; marine; overfishing; plant–herbivore interactions; recreational fishing;* Spartina alterniflora; *top-down control; top predator; trophic cascade.*

Introduction

The ecological collapse of marine ecosystems driven by human disturbances is one of the most critical environmental problems of our time (Jackson et al. 2001, Harvell et al. 2002, Hughes et al. 2003, Pandolfi et al. 2005, Lotze et al. 2006). Salt marshes are among the most valuable of marine ecosystems for their provision of food, fuel, filtration, and shoreline stabilization (Costanza et al. 1997, Millennium Ecosystem Assessment 2005), making the current epidemic of their collapse throughout the western Atlantic (Bertness and Silliman 2008) of paramount concern. Unprecedented consumer control is the common cause of vegetation loss underlying the die-off of marsh ecosystems as diverse as arctic Canada (Jefferies et al. 2006), the Northeastern United States (Holdredge et al. 2009), the Southeastern United States (Silliman et al. 2005), and Argentina (Alberti et al. 2007).

The widespread importance of trophic cascades has become increasingly recognized since they were first identified as a primary determinant of community structure and ecosystem dynamics over a half century

ago (Hairston et al. 1960, Pace et al. 1999). Only recently, however, has it been recognized that trophic cascades can be an important factor limiting the productivity of salt marshes (Silliman and Bertness 2002). Our recent research has identified the native herbivorous crab *Sesarma reticulatum* as the grazer driving die-off in the northeastern United States and suggested that variation in predation could explain elevated *Sesarma* populations and their runaway grazing of the low marsh zone (Holdredge et al. 2009).

These initial observations led us to hypothesize that a trophic cascade is leading to increased grazer populations and the rapid die-off of salt marshes in the northeastern United States (Fig. 1). We further hypothesized that recreational fishing is triggering this trophic cascade because we observed that marsh die-off is highly localized and consistently occurs only where recreational anglers have access to marshes. This line of inquiry is novel because industrialized overfishing has demonstrated that overexploitation of consumers can lead to catastrophic ecosystem collapse through cascading food web interactions; however, similar indirect impacts of recreational fishing likely occur but remain largely unexplored (Post et al. 2002, Cooke and Cowx 2006, Crowder et al. 2008).

We conducted our study in the Cape Cod region, where die-off was first described within the Northeastern United States in 2002 (Smith 2006), and where there is intensive fishing pressure from recreational saltwater anglers, who currently make >377 000 fishing trips

annually (NOAA National Marine Fisheries Service; data *available online*).[3] To test the hypothesis that a trophic cascade associated with recreational fishing pressure is triggering marsh die-off, we conducted a series of surveys and experiments in 14 Cape Cod marshes along >420 km of shoreline, seven of which were "die-off" sites (operationally defined as marshes with >50% of their creekbanks unvegetated) and seven of which were "vegetated" sites (operationally defined as marshes with <20% of their creekbanks unvegetated; see Appendix for list of study sites and locations). To investigate potential links between fishing activity and marsh die-off (Fig. 1), we contrasted the abundance of anglers, top-predator biomass, rates of predation on *Sesarma*, *Sesarma* densities, herbivory rates, and the extent of die-off at all 14 sites. We also reconstructed historical trends across our sites in fishing infrastructure (as a proxy for fishing pressure) and expansion of die-offs from archived aerial images.

Materials and Methods

We quantified whether our study marshes differed in fishing pressure directly by quantifying the number of recreational anglers within each of our study sites with visual surveys in July 2010. Each site was visited at least four times within an hour of sunrise and sunset as well as at mid-morning and mid-afternoon, and we counted all anglers with either fishing rods for finfish or hand lines for blue crabs (*Callinectes sapidus*) and noted whether they were accessing the marsh by boat, by dock, or on foot. Differences in angler numbers per site were analyzed with a one-way ANOVA with site type (die-off or vegetated) as the factor.

Predator populations.—We examined whether the abundance of predators varied between die-off and vegetated sites with a survey in the summer of 2009 that sampled predator populations with traps and nets. Traps were $30 \times 60 \times 90$ cm (height × width × length) with a funnel opening, and were constructed from polyvinyl-chloride-coated galvanized steel mesh (mesh size 2.5 cm). Three baited traps were deployed at each site >100 m apart for one 24-hr period each month in July–September. Nets were 10 m long, constructed from monofilament (mesh size 5 cm), and deployed from the surface to the bottom perpendicular to the shore within a marsh channel. One net was deployed at each site for one overnight 18-h period in August. At the end of each trap or net deployment, the identity and length and/or carapace width of animals were recorded, and the animals were returned to the site. The biomass of each animal was estimated by converting length or carapace width to wet biomass using established conversion equations (Hines 1982, Olmi and Bishop 1983, Sachsse

Fig. 1. Representative photos of (A) vegetated and (B) die-off salt marshes, and (C) recreational fishing at a study site in Cape Cod, Massachusetts, USA. At vegetated marshes without localized fishing pressure, cordgrass, *Spartina alterniflora*, extends to the water's edge at low tide. At marshes with recreational fishing activity, *Sesarma* crabs have consumed vegetation in the low intertidal, leaving expansive die-offs along the marsh margin.

1984, Torchin et al. 2001, Wigley et al. 2003, de Lafontaine et al. 2010). The biomass of predators in traps and nets was pooled for each site. We included all animals that are documented to consume *Sesarma* and other benthic decapods (Ropes 1968, Wenner and Musick 1975, Laughlin 1982, Hines et al. 1990, Rountree and Able 1992, Tucker et al. 1995, Manderson et al. 2000, Harding and Mann 2001, Nelson et al. 2006, Voutier and Hanson 2008). To avoid overrepresentation of trap data in the pooled value, data from the three trap dates at each site were averaged together before being added to the biomass from nets, for a single biomass value for each replicate site. Predator biomass data were analyzed with a one-way ANOVA, with site type (die-off or vegetated) as the factor.

To test the hypothesis that differences in predator biomass found among sites were the consequence of fishing pressure and not other differences in site quality, we quantified nonharvested predator biomass at die-off and vegetated sites in two ways. First, we reanalyzed our trap and net data as before but included only consumers that are not harvested. Second, at each of our study marshes we sampled populations of mummichog fish (*Fundulus heteroclitus*), which are a common fish in New England salt marshes that are not commonly fished recreationally. At each site we deployed four baited traps >100 m apart in marsh channels for four hours spanning a daytime high tide. Mummichog traps were 42×21 cm (length $\times$ diameter), cylindrical in shape, constructed from galvanized steel mesh (6-mm mesh size), and had a funnel-shaped entrance at each end with a 2.5-cm opening. At the end of trap deployment, we measured the total wet biomass of mummichogs in each trap, and the four traps were averaged to get a single biomass value for each replicate marsh. Mummichog biomass data were analyzed with a one-way ANOVA with site type (die-off or vegetated) as the factor.

Sesarma *tethering*

To test the hypothesis that depressed abundances of predators released herbivorous *Sesarma* crabs from predator control, we quantified differences in predation potential on *Sesarma* between die-off and vegetated sites with a tethering experiment. Crabs were fastened to braided fishing line with cyanoacrylic glue and secured with a wire garden staple to marsh creekbank areas where they had access to existing *Sesarma* burrows. Crabs were either left in the open or enclosed in a cage to account for mortality due to tethering artifacts ($n = 15$ per treatment). All crabs were deployed in *Sesarma* burrow areas (unvegetated areas of peat on creekbanks) to minimize potential bias due to interaction with variation in habitat type (Peterson and Black 1994). Following overnight (dusk to dawn) deployment in July 2009, crabs were scored for survivorship. Where crabs did not survive, a portion of broken crab carapace typically remained on the tether, indicating that

predation was the cause of death. Moreover, a high percentage (98% $\pm$ 1%) of crabs were alive and remaining on tethers within cages at the end of the experiment, indicating that there was insignificant mortality attributable to handling stress or tether failure. The proportion of crabs surviving in each treatment at each site was analyzed with a two-factor ANOVA, with caging treatment and site type (die-off or vegetated) as factors.

Sesarma *populations*

We quantified relative differences in *Sesarma* population densities between die-off and vegetated sites with passive pitfall traps. Traps were constructed from 7.5 cm diameter open-top plastic cylinders (empty tennis ball cans with drainage holes drilled in the bottom) sunk flush with the marsh substrate. Twelve traps >2 m apart were deployed overnight in July 2009 along the marsh edge at each site ($n = 12$ per site $\times$ 14 sites). The densities of *Sesarma* in the 12 traps at each site were averaged for a single value representing each replicate marsh for analysis. *Sesarma* populations were analyzed with a one-way ANOVA with site type (die-off or vegetated) as the factor.

Sesarma *grazing rates*

To test the hypothesis that higher crab densities would lead to greater herbivory rates and the subsequent loss of marsh vegetation characteristic of die-off; we conducted experimental crab exclusions and directly observed grazing rates and vegetation loss at each of our study sites. We experimentally manipulated crab access to standardized culms of grass at each of the 14 study sites for a five-week period from May–June 2009. Culms of cordgrass, *Spartina alterniflora*, including 20 cm of belowground material, were collected with a 7.5 cm diameter corer from a common source area to account for potential site differences in plant quality and palatability (Goranson et al. 2004). At each site, 24 culms were randomly assigned to one of three treatments: *Sesarma* exclusion cage, procedural control cage, or no cage ($n = 8$ per treatment $\times$ 14 sites). Exclusion cages consisted of galvanized steel wire mesh (mesh size 6 mm) that extended 20 cm below ground and 40 cm above ground. Control cages were constructed similarly, but had two 7×5 cm (length $\times$ width) windows cut out of the mesh at ground level. At the end of the experiment, we harvested and dried culms to a constant mass at 60°C. Comparison of the aboveground biomass from caged cores not exposed to herbivory was also used to examine the alternative hypothesis that there were physical differences influencing cordgrass performance between die-off and vegetated sites. Aboveground biomass was analyzed with a split-plot ANOVA with site type (die-off or vegetated) as the between-plot factor, site nested within site type, and caging treatment as the within-plot factor.

To avoid interference between sampling and experiments in consumer behavior, we staggered field activities so that they never occurred simultaneously at a given site. In addition to our controlled experiments, we accounted for potential physical differences among die-off and vegetated marshes by measuring substrate hardness and water movement at each of our 14 study sites. Substrate hardness, which can be a determinant of herbivory intensity and die-off extent because it limits the integrity of *Sesarma* burrows, was quantified using a top-loading spring scale with a 10 cm long aluminum rod (1.9 cm diameter) mounted vertically on the weighing pan, which we pushed into the substrate (Bertness et al. 2009). We recorded the mass (kg) required to penetrate to a depth of 5 cm at 20 haphazard locations per site (>5 m apart). We also measured water movement as a proxy for boat wake disturbance and sediment load with a three-week deployment of dissolution blocks ($n = 6$ per site, >5 m apart) at each of the study sites (van Wesenbeeck et al. 2007). Substrate hardness and dissolution loss were analyzed with a one-way ANOVA with site type (die-off or vegetated) as the factor.

To quantify the intensity of *Sesarma* grazing, we developed an average grazing index value for each site in May 2009. A grazing index value was determined for each of eight 1-m^2 plots at each site by multiplying the frequency of stems with grazing damage by the intensity of grazing damage. The frequency of grazing damage was calculated as the proportion of stems with grazing damage out of 50 randomly selected stems in each plot. The intensity of grazing was assessed as the proportion of stems grazed for eight randomly selected stems such that a value of zero signified no grazing and a value of 100 signified that the stems were completely grazed with no green vegetation remaining. The grazing index values for the eight plots at each site were averaged to calculate a single grazing index value representing each replicate marsh for analysis. Grazing index data were analyzed with a one-way ANOVA with site type (die-off or vegetated) as the factor.

Die-off surveys

We surveyed the spatial extent of marsh die-off in May 2009 at each site with a series of six 100-m transects placed randomly along the seaward edge of marshes in the low zone where *Spartina alterniflora* is the dominant vegetation type and die-off is most prominent (Holdredge et al. 2009). Along each transect, we quantified the total length of die-off, and at eight randomly selected points we quantified the width of die-off and the total width of the *S. alterniflora* zone. Die-off was identified as unvegetated peat substrate with remains of *S. alterniflora* belowground structure and characteristic gnawed remnants of stems. We quantified the percentage of the *S. alterniflora* zone that had succumbed to die-off in each transect by first multiplying the average width of die-off × 100 m to get the total area of die-off,

and then dividing that die-off value by the total area of the potential cordgrass zone (average width of cordgrass zone × 100 m). The values for each of the six transects at each site were averaged for a single value of die-off area representing each replicate marsh for analysis. The spatial extent of die-off was analyzed with a one-way ANOVA, with site type (die-off or vegetated) as the factor.

Historical trends in fishing pressure and marsh die-off

We examined the temporal relationship between fishing pressure and the onset of marsh die-off by examining a series of high-quality aerial images of each of our sites from the period spanning 1939–2005 (*available online*: MassGIS, USGS, Cape Cod National Seashore, Town of Mashpee, and Town of Bourne, Massachusetts, GIS databases; *available online*).[4,5,6,7,8] We used fishing infrastructure (e.g., docks and boat slips) as a proxy for fishing pressure through time because (1) records of angling activity on Cape Cod are not available for the same periods as the aerial database; (2) we observed in our contemporary surveys that two-thirds of anglers fished in marshes from either docks or boats, and that no anglers were observed in marshes lacking this infrastructure, indicating a close relationship between fishing pressure and infrastructure availability; and (3) docks and boats slips are large fixed features that are readily identifiable in aerial images. Using ArcGIS (ESRI 2008) we georeferenced each image and then quantified the location and area of marsh vegetation, die-off, and fishing infrastructure. We converted data to raster format to track the fate of individual 1 × 1 m pixels, and thereby quantified the area of each marsh that transitioned between vegetated marsh and marsh die-off. We also counted the total number of docks and boat slips for both die-off and vegetated sites. We examined temporal trends in the extent of marsh die-off and fishing infrastructure with a repeated-measures ANOVA, with time and site type (die-off or vegetated) as factors.

RESULTS

Die-off and vegetated marshes differed dramatically in recreational fishing pressure ($F_{1,12} = 30.16$, $P < 0.001$), as anglers were observed only at die-off sites (Fig. 2A).

Die-off marshes had half the biomass of top-level predators (e.g., striped bass, *Morone saxatilis*; blue crab, *Callinectes sapidus*; smooth dogfish, *Mustelus canis*) found at vegetated sites ($F_{1,11} = 5.14$, $P < 0.05$, Fig.

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[4] http://www.mass.gov/mgis/massgis.htm

[5] http://earthexplorer.usgs.gov/

[6] http://www.nps.gov/caco/index.htm

[7] http://www.mashpeema.gov/pages/mashpeeMA_GIS/index

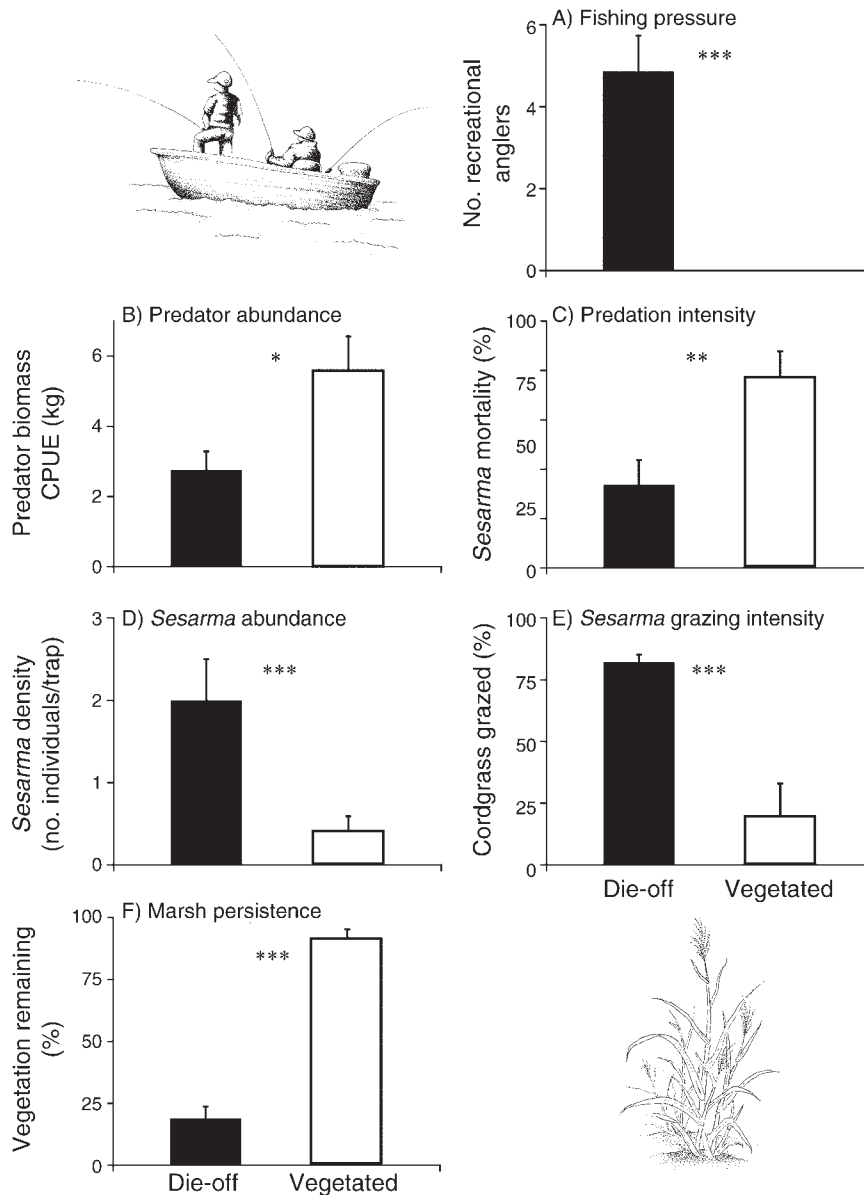[8] http://www.townofbourne.com/Departments/Regulatory/Conservation/tabid/135/Default.aspx

Fig. 2. Results of experiments and surveys that link recreational fishing with die-off of salt-marsh vegetation through a cascade of trophic interactions: (A) fishing pressure, (B) predator abundance (catch per unit effort [CPUE], the biomass of predators caught at a site using standardized gear and deployment durations), (C) predation intensity, (D) density of herbivorous *Sesarma* crab, (E) *Sesarma* grazing intensity, and (F) marsh vegetation persistence. The alternating pattern of abundance and interaction strengths between trophic levels is a hallmark of trophic cascades. Data are means + SE.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

2B). In contrast, the biomass of nonharvested consumers (e.g., spider crabs, *Libinia emarginata*; green crabs, *Carcinus maenas*; diamondback terrapins, *Malaclemys terrapin*) did not differ between die-off and vegetated sites ($F_{1,11} = 0.11$, $P = 0.75$). Likewise, the separate assessment of mummichog fish revealed no difference in biomass between die-off and vegetated marshes ($F_{1,12} = 2.85$, $P = 0.11$).

The predation rate on tethered *Sesarma* at vegetated sites was triple that of die-off sites (caging treatment ×

site type interaction, $F_{1,24} = 9.94$, $P < 0.01$; Tukey's HSD post hoc, no difference between control treatments between sites types; Fig. 2B, C). *Sesarma* abundance varied among marshes in association with these differences in predatory control, with densities over four times higher at the low-predation, die-off marshes than high-predation, vegetated marshes ($F_{1,154} = 59.75$, $P < 0.0001$; Fig. 2D).

Over the course of the five-week grazing experiment, crabs consumed four times more grass at die-off marshes

than at vegetated marshes (caging treatment × site type interaction: $F_{2,317} = 27.14$, $P < 0.0001$; Fig. 2E), in direct proportion to the difference in crab densities between marsh types. That difference in experimental grazing rate was reflected in the observed index of herbivory intensity at our sites, which was an order of magnitude higher at die-off sites than at vegetated sites, with average scores of 2127 ± 406 vs. 205 ± 103 (mean ± SE), respectively ($F_{1,98} = 271.03$, $P < 0.0001$). These higher rates of grazing explain the extensive die-off (>80% of vegetation loss) within the cordgrass zone that was an order of magnitude greater at die-off marshes than at vegetated marshes ($F_{1,12} = 88.02$, $P < 0.0001$; Fig. 2F), in proportion with differences among marshes in grazing intensity index. The biomass of caged cordgrass (i.e., not exposed to herbivory) did not differ between die-off (2.5 ± 0.3 g) and vegetated (2.6 ± 0.2 g; mean ± SE) marshes (Tukey's HSD post hoc, no difference between control treatments between site types). Neither substrate hardness ($F_{1,12} = 0.24$, $P = 0.63$) nor water movement ($F_{1,12} = 0.004$, $P = 0.95$) differed between die-off and vegetated marshes.

Our historical reconstruction from aerial images revealed little net marsh loss (<5%) from 1939 to the end of the archived time-series in 2005 at sites that are currently vegetated (Fig. 3A). In contrast, die-off marshes exhibited the onset of die-off in the mid-1970s, with a persistent trajectory of increasing vegetation loss through 2005, by which point >20% of the total marsh area was lost to die-off (Fig. 3A), and >80% of the cordgrass zone was unvegetated (Fig. 2F). This divergence between die-off and vegetated marshes in vegetation loss coincides with a period of rapid increase in the number of docks and boat slips prior to the mid-1970s that resulted in the establishment of >70% of that fishing infrastructure currently present at die-off marshes (Fig. 3B).

DISCUSSION

Our contemporary experimental work in marshes of the Northeastern United States revealed a sharp contrast between vegetated sites with expanses of intact cordgrass zones, and die-off sites where the cascading effect of top-predator depletion associated with fishing pressure has triggered runaway grazing and the widespread loss of marsh vegetation. Our historical reconstruction of marsh habitats from aerial photographs revealed that the spatial relationship that currently exists between fishing pressure, trophic cascades, and marsh die-off is evident in long-term trends extending back to the first half of the 20th century.

The cascading trophic links between recreational fishing and marsh die-off are further substantiated by four lines of evidence that discount alternative hypotheses related to fishing infrastructure and human activities associated with heavy recreational fishing. First, we found in the present study that populations of unharvested consumers in two separate analyses did
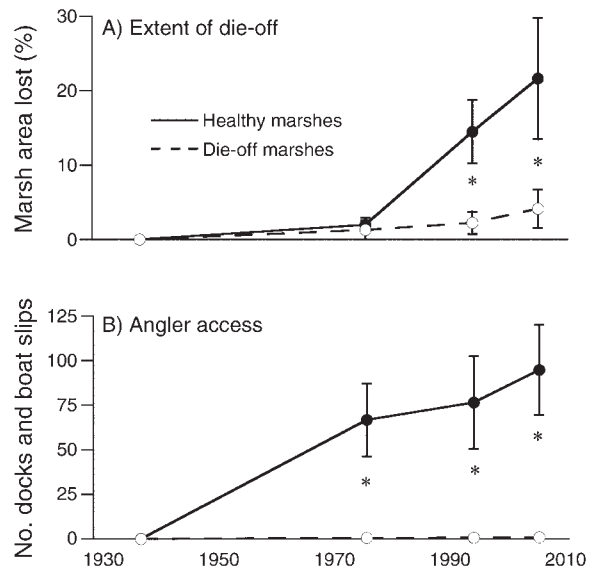

FIG. 3. Historical trends in (A) the increase of salt-marsh die-off and (B) the growth of infrastructure that promotes angler access to marshes. The loss of marsh at die-off sites paralleled increases in the number of docks and slips at the same group of sites following a lag of one time step. We hypothesized that the marginal die-off recently observed at vegetated sites was attributable to a spillover of fishing impacts from die-off sites. Solid lines and circles represent die-off marshes, and dashed lines and open circles represent vegetated marshes. Data are means of replicate marshes ± SE.
* $P \leq 0.05$ for a given time point in post hoc analyses.

not differ between die-off and vegetated sites. Thus differences in predator biomass reflect the absence of recreationally targeted fish and crab species at die-off sites, the signature of selective recreational fishing pressure rather than general habitat degradation. Second, caged controls in our experiments revealed no difference between die-off and vegetated sites in the persistence of tethered *Sesarma* nor biomass of transplanted cordgrass, indicating that differences in survivorship of *Sesarma* and growth of cordgrass was dependent on differences between sites in consumer pressure and not some other aspect of habitat quality. Third, neither substrate hardness, which can be a large-scale determinant of susceptibility to die-off (Bertness et al. 2009), nor water movement as a proxy for boat wake disturbance and sediment load, differed between die-off and vegetated sites. Fourth, previous work in this system has revealed that covariates of human activity and installation of infrastructure, including eutrophication and vegetation disturbance, are not significant triggers of marsh die-off (Bertness et al. 2009). Additionally, the discontinuous distribution of marshes with die-off interspersed with healthy, vegetated marshes suggests that local interactions within fished marshes, rather than regional-scale physical forcing by a factor such as sediment starvation or climate effects, is driving salt-marsh die-off.

PLATE 1. Two recreational anglers fishing from the bank of a marsh that is unvegetated and crumbling at their feet into the creek. A trophic cascade links this fishing activity with the collapse of salt marsh vegetation because the removal of predatory fish and crabs by anglers allows the population of herbivorous *Sesarma* crabs to proliferate, and those crabs in turn clear-cut the marsh vegetation. Photo credit: A. Altieri.

Our results establish a large-scale association between recreational overfishing and salt-marsh die-off and provide the first evidence connecting the local depletion of top predators with salt-marsh die-off. This suggests that overfishing may be a common mechanism underlying trophic-level dysfunction (Steneck et al. 2004), where predator populations are below the functional threshold where they can control herbivores, driving the epidemic of salt-marsh die-off throughout the western Atlantic. More generally, our study is among the first to provide evidence that localized predator depletion can generate shifts in marine community structure and dynamics (Eriksson et al. 2009), and it supports an emerging perspective that predator depletion can lead to rapid collapse of coastal ecosystems and the services they provide (Worm et al. 2006). Our experimental results compliment other studies examining the impacts of predator depletion on coastal marine ecosystems as inferred from either historical trends (Estes et al. 1998, Jackson et al. 2001, Frank et al. 2005, Lotze et al. 2006, Daskalov et al. 2007, Myers et al. 2007) or the implementation of no-take areas where changes in intermediate- and basal-trophic levels are attributed to

consumer interactions (Shears and Babcock 2003, Micheli et al. 2005, Mumby et al. 2006).

The ecological effects of recreational fishing demand increased attention. Although overfishing is recognized as a leading factor in this demise of habitats and ecosystem services (Worm et al. 2009), and the cascading effects of overexploitation are increasingly implicated in the loss and degradation of marine ecosystems around the world, including kelp forests, open oceans, coral reefs, and soft-sediment estuaries (Jackson et al. 2001, Myers and Worm 2003, Pandolfi et al. 2003, Frank et al. 2005, Lotze et al. 2006, Worm et al. 2006, Daskalov et al. 2007, Myers et al. 2007), research on predator depletion in natural ecosystems has focused almost exclusively on the consequences of large-scale commercial overfishing (Worm et al. 2009). Our study reveals the potential impacts of recreational fishing and adds salt marshes to the list of ecosystems impacted by the cascading effects of overexploitation.

Such impacts of angling are likely widespread given that recreational fisheries landings exceed 10 million tons globally (Cooke and Cowx 2004), and their harvests can rival or exceed industrialized fishing in coastal regions (Beal et al. 1998, Schroeder and Love 2002). Moreover, the effects of recreational fishing activities are predicted to be particularly acute because they selectively target top-level predators (Coleman et al. 2004) and are more likely to deplete species to a greater degree and with higher efficiency (Cooke and Cowx 2006, Crowder et al. 2008). Although evidence is emerging that angling can deplete predatory fish populations (Post et al. 2002, Post et al. 2008), the broader ecological impacts of recreational fisheries have remained elusive because they are poorly assessed and fishers are more numerous (Worm et al. 2009). It has been suggested that a perception among the public, managers, and some scientists that recreational fishing is a relatively benign activity has contributed to relative inattention to the impacts of recreational fishing (Kearney 1999, McPhee et al. 2002, Cooke and Cowx 2004, 2006). The tightly coupled association between angler access and marsh die-off that we observed suggests that even small-scale, no-take reserves, comparable in size to inaccessible marshes that functioned as de facto reserves in our study, can have significant management effectiveness.

Our data reveal a surprisingly strong local connection between recreational fishing pressure and its consequences on shoreline community dynamics. This link became apparent in a region where the biomass of many fished species has declined by >50% over the past 25 years (King et al. 2009). We hypothesize that historic, large-scale, industrialized overexploitation of fish in the northwest Atlantic (Steneck et al. 2004, Lotze et al. 2006, King et al. 2009) drove coastal areas to the tipping point, where marshes became vulnerable to the more recent effects of localized recreational fishing, and that resultant localized die-offs could coalesce into complete,

region-wide marsh loss if overharvesting of top consumers continues. We further suggest that other nearshore ecosystems will become increasingly vulnerable to recreational overfishing with continued development of shoreline infrastructure that allows angler access and ongoing depletion by industrialized fishing practices.

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SUPPLEMENTAL MATERIAL

Appendix

A table and map of the study site locations (*Ecological Archives* E093-122-A1).