

Consumer Fronts, Global Change, and Runaway Collapse in Ecosystems

Brian R. Silliman,¹ Michael W. McCoy,²
Christine Angelini,³ Robert D. Holt,³ John N. Griffin,⁴
and Johan van de Koppel^{5,6}

¹Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, Beaufort, North Carolina 28516; email: brian.silliman@duke.edu

²Department of Biology, East Carolina University, Greenville, North Carolina 27858

³Department of Biology, University of Florida, Gainesville, Florida 32611

⁴Department of BioSciences, Swansea University, Swansea, SA2 8PP, Wales, United Kingdom

⁵Spatial Ecology Department, Royal Netherlands Institute for Sea Research, 4401 NT Yerseke, The Netherlands

⁶Community and Conservation Ecology Group, University of Groningen, 9700 AB Groningen, The Netherlands

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Abstract

Consumer fronts occur when grazers or predators aggregate in bands along the edges of a resource. Our review reveals that consumer fronts are a common phenomenon in nature, occur in many different ecosystems, and are triggered by universal mechanisms: External forces locally increase top-down control beyond prey carrying and/or renewal capacity, and resource-dependent movement leads to consumer aggregation along the edge of the remaining prey population. Once formed, consumer fronts move through systems as spatially propagating waves, self-reinforced via intense overexploitation and amplified by density-dependent feedbacks. When consumer fronts are spatially restricted, they generate patchiness. In contrast, when consumer fronts are expansive, they can lead to runaway responses that cause large-scale ecosystem degradation and regime shifts. We conceptualize a synergistic stress hypothesis and model that highlight how coupled intensification of physical stress and enhanced consumer pressure can trigger increased occurrence of consumer fronts and decreased system stability and resilience. With escalating climate change and food-web modification, the physical and biological conditions favoring consumer-front formation will likely become a common feature of many ecosystems.

1. INTRODUCTION: A SHORT HISTORY OF TOP-DOWN CONTROL OF ECOSYSTEMS

For the greater part of the nineteenth and twentieth centuries, most ecologists believed that climate and other physical factors (e.g., sediment type, nutrient availability) ultimately controlled the distribution and primary productivity of vegetation (Warming 1895; Schimper 1898; Odum & Odum 1953; Whittaker 1953, 1970; Teal 1962; Aber & Melillo 1991; Tansley 2010). Across all ecosystems, those dominated by plants (e.g., tundra, grasslands, kelp forest, seagrasses, mangroves, and salt marshes as well as tropical, temperate, and boreal forests) are typically green in appearance during the growing season, and consumer control in these communities was long considered insignificant. Although early suggestions indicated that herbivores could affect plant species composition and/or growth on local scales and in certain situations (Warming 1895, Thomas 1937), the overwhelming consensus remained throughout the 1900s that, relative to physical factors such as precipitation, temperature, and pH, consumers exerted minor influence over large-scale patterns of primary productivity and the long-term persistence and distribution of plant-dominated ecosystems (Odum & Odum 1953, Whittaker 1970, Aber & Melillo 1991, Mitsch & Gosselink 1993).

In 1960, Hairston, Smith, and Slobokin used simple observations and logic to propose an alternative view that consumers play a major role in determining key features of plant-generated ecosystems (Hairston et al. 1960). They hypothesized that the world is green and productive because consumers at higher trophic levels control herbivore abundance and thus allow plant-dominated ecosystems to persist (Hairston et al. 1960). The core tenet of their argument was that, because green plants dominated most natural ecosystems, herbivores must not be food limited, but instead controlled from the top-down by predators. Thus, the world is kept green by trophic interactions where predators reduce herbivore abundance and, in doing so, prevent herbivores from grazing down and eliminating the abundant supply of edible green plants. Such tri-trophic interactions—where predators indirectly facilitate plants by controlling herbivore populations—has since been coined a trophic cascade (Paine 1980). In response to Hairston et al. (1960), other ecologists questioned the basic premise of population stability (Ehrlich & Birch 1967) and further pointed out that what appears to be an abundant supply of green plant biomass is not necessarily edible or of sufficient quality to allow increases in herbivore abundance (Murdoch 1966). This chemically mediated, bottom-up view proposed that most dominant plants, by acquiring heavy defenses and/or exhibiting low nutritional quality, have won the evolutionary arms race against herbivores. With little impact from the top down, plant communities and ecosystems must thus be controlled by resource availability, climate, and other physical factors.

This top-down versus bottom-up debate generated much attention in the field and served as an impetus for ecologists to search and test for examples of grazer control of plant communities (key landmarks and reviews with contrasting opinions include Hunter & Price 1992, Strong 1992, Polis et al. 2000, Shurin et al. 2002, Gruner et al. 2008, Terborgh & Estes 2010). A number of these studies revealed that grazers can control plant growth and species composition in a variety of ecosystems, e.g., tropical forests (Janzen 1970, Connell 1971), rocky shores (Paine 1980), coral reefs (Hay 1984), salt marshes (Smith 1983), and grasslands (Collins 1987; for recent examples, see Terborgh & Estes 2010). Furthermore, in situations where grazer densities are particularly high (e.g., because of the decline of predators and a resultant trophic cascade) (Carpenter et al. 1985; Power 1990; Brett & Goldman 1996; Estes et al. 1998, 2011; Schmitz et al. 2000; Silliman & Bertness 2002; Terborgh & Estes 2010), herbivores can convert lush, green ecosystems into relatively unproductive, barren flats or grazing lawns (Burkepile 2013). In these cases of strong top-down control by grazers, foundation plant species (*sensu* Dayton 1972) can be overgrazed and replaced with unvegetated substrates or functionally inferior, herbivore-resistant species that can

potentially persist as alternative, consumer-driven stable states (Simenstad et al. 1978, Bertness et al. 2002). In terrestrial systems, both invertebrates (e.g., native or introduced beetles and moths) and vertebrates (e.g., introduced possums) can defoliate entire forest canopies (Hard et al. 1983, Holsten et al. 1995, Liebhold et al. 1995), insects can decimate mangrove stands (Anderson & Lee 1995, Feller 2002), ungulates and elephants can convert savannas to sandy deserts (Dublin et al. 1990, Augustine & McNaughton 1998), and small mammal herbivory can constrain the biomass of tundra vegetation (Aunapu et al. 2008). Similar examples emerged from marine systems where super high densities of urchins converted kelp forests and seagrass beds to barren rock beds and sand flats, respectively (Camp et al. 1973, Estes & Palmisano 1974, Estes et al. 1998, Ogden et al. 1973, Rose et al. 1999), and from tundra environments where geese transformed thousands of acres of lush marsh into erosion-prone mudflats (Jefferies 1988). Megaherbivores (e.g., elephants, buffalo) by virtue of their body size can escape regulation by predators, and in east Africa, elephants can convert woodland to grasslands, and hippopotamuses can transform tall tussock grasslands into shortgrass ecosystems (Sinclair et al. 2010). Collectively, these examples and many others support the proposition that whole-ecosystem regulation by consumers is more prevalent and powerful than historically recognized. Such examples demonstrate that consumers, if allowed to overconsume their resource base, can have deleterious impacts on ecosystem structure and function.

2. CONSUMER FRONTS: AN EMERGING FRONTIER IN TOP-DOWN FORCING OF WHOLE ECOSYSTEMS

Recently, work in the field of consumer control of whole ecosystems has also begun to focus on a relatively understudied manifestation of top-down control—the formation, propagation, and ecosystem-level consequences of consumer fronts. Here, we define a consumer front as a super concentration in abundance of mobile grazers or predators that locally overwhelms the carrying and/or renewal capacity of prey, resulting in sharp gradients in resource abundance and the collective movement of consumers from prey-depleted areas to adjacent prey-abundant habitats. Super concentrations of grazers or predators can arise owing to interactions with climatic events such as drought (Silliman et al. 2005) and seasonality (Gueron & Liron 1989), episodic recruitment events (Kayal et al. 2012, Lauzon-Guay et al. 2008, Pratchett 2005), anthropogenic activities such as overfishing (Altieri et al. 2012) and other factors that reduce the impact of top predators that control grazer populations (Osgood & Silliman 2009), and rapid invasions of new species that modify the intensity of bottom-up and top-down regulation of consumers and prey (Hale et al. 2006, Holt 2008). Once formed, fronts locally deplete prey, and the individuals in the fronts collectively move en masse across the ecosystem toward food resources (Silliman et al. 2005, Lauzon-Guay et al. 2008), thereby expanding the zone of depletion. As this process iterates, fronts begin to propagate across ecosystems. The pattern and rate of front movement vary from system to system depending on the behavior, mobility, and nutritional requirements of consumers (Silliman et al. 2005, Lauzon-Guay & Scheibling 2007, Feehan et al. 2012) as well as the abundance, renewal properties, and patchiness of remaining prey (Keller & Segel 1971, Jefferies 1988, Gueron & Liron 1989, Burrows & Balciunas 1997, Silliman et al. 2005, Hale et al. 2006, Lauzon-Guay et al. 2008, Holdredge et al. 2009, Kayal et al. 2012). Factors such as direct density dependence (e.g., Allee effects) and responses of higher-order predators can modulate front formation and the velocity of wave fronts. Whether fronts result in ephemeral or persistent impacts on ecosystem structure and function can depend on the extent of the area impacted as well as the functional role and recovery potential of the prey that has been depleted.

Consumer fronts exhibit inherently transient dynamics (they arise, advance, and then dissipate), and the passing of a front can have impacts that range from seasonal, localized defoliation (Burrows

& Balciunas 1997) to persistent state shifts of the ecosystem (Simenstad et al. 1978, Gueron & Liron 1989). On temperate rocky shorelines, for instance, periwinkle snails form concentrated fronts each spring as they migrate up from subtidal zones where they overwinter to intertidal zones where they graze down mats of fast-growing, competitively dominant green algae. This consumer front persists until the green-algae resource is diminished; in the wake of the snail front, a patchy mosaic of more slowly growing, but less palatable, subordinate algal species is left (Lauzon-Guay & Scheibling 2009). In contrast to this seasonal, consumer-front pulse that only temporarily suppresses plants within a single annual cycle, sea urchin fronts can mow down the giant, canopy-forming algae in kelp beds and maintain barren substrates for extensive periods of time (e.g., at least decades) (Estes & Palmisano 1974, Simenstad et al. 1978).

Theoretical studies suggest that the impact of consumer fronts can also vary depending on the trophic level of the prey (as in the simple food-chain length models of Fretwell 1977). If the prey is a foundation species that generates habitat structure to facilitate whole communities of associated species (Bruno et al. 2003), then the entire ecosystem can be destroyed by a passing consumer front. For example, crown-of-thorns sea stars on the Great Barrier Reef in Australia congregate in consumer fronts following massive recruitment events and move through the ecosystem in consolidated fashion to destroy up to 90% of coral foundation species (Chesher 1969, Pratchett 2005, Kayal et al. 2012). Because corals are slow growing, the imprint of such fronts on ecosystem stability, productivity, and species composition can be profound and linger over long periods. The impacts of this tropical consumer front are not trivial: Grazing-induced loss of corals not only deters ecotourism, with associated economic impacts reaching millions of US dollars (Barbier et al. 2011), but also causes declines in a range of species that rely on live corals for their survival and recruitment (Kayal et al. 2012, Leray et al. 2012). In contrast, when consumer fronts are composed of predators that feed on the grazers of foundation species, plant communities can be enhanced via top-down control of grazers. For example, modeling studies predict that synchronized emergence of metamorphosing frogs can decimate insect grazer abundance and increase plant growth in striking bands around natal ponds to cause temporally and spatially confined “predator shadows” (McCoy et al. 2009) cast by the ponds on the surrounding landscape.

Although the studies referred to above hint that consumer fronts may be widespread (i.e., they come from diverse ecosystems) and elicit both short- and long-term changes in ecosystem structure, function, and stability, relatively little effort has been made to assess and identify the general rules or contingent factors underlying consumer-front formation, maintenance, and extent. What appears inherent to consumer fronts, but has yet to be integrated in a general theory for how top-down control occurs in ecosystems (e.g., in models of food-chain length), is the importance of spatially dependent processes—e.g., variation in recruitment, animal movement, and heterogeneity in the intensity of physical stressors—in determining the creation and impact of these powerful, emergent phenomena.

In this review, we address this intellectual gap in our understanding of top-down control of whole ecosystems and examine the mechanisms behind and implications of moving consumer fronts. Specifically, we ask and address the following questions:

1. Are feeding fronts general across taxa and habitats, and how do these fronts form, move, and impact ecosystems?
2. What are common mechanisms that lead to front formation and propagation, how important is the spatial dimension of these mechanisms, and how powerful are their whole-ecosystem impacts?
3. Do human activities impact the mechanisms that lead to front formation?
4. How do these novel findings and insights about processes and patterns in consumer fronts advance our understanding of top-down control and ecosystem structure and stability?

Our focus is on synthesizing empirical examples of fronts and distilling general messages across these examples, but we also briefly review mathematical models of consumer fronts. We conclude by integrating this information into a cohesive framework for understanding the formation and impacts of consumer fronts that has broad implications for predicting ecosystem stability and resilience. It is increasingly urgent that we refine our abilities to forecast when, where, and to what extent such consumer fronts will emerge. With both accelerating global changes and escalating human-induced modifications of food-web structure, such as increased drought and the loss of top predators, the physical and biological stressors that create conditions favorable for consumer-front formation will likely become a more common and emergent feature of many ecosystems. Thus, this synthesis has substantial implications for understanding interactions between spatial and trophic processes and their emergent community-level impacts and should provide invaluable insights for the management and conservation of many ecosystems.

3. CONSUMER-FRONT FORMATION, MOVEMENT, AND IMPACTS ACROSS DIVERSE ECOSYSTEMS

3.1. Feeding Fronts of Snails and Crabs in Salt Marshes

Although evidence of top-down control of whole ecosystems substantially grew in the 1950s to 1990s, salt marshes continued to be championed as the quintessential system controlled by bottom-up forcing (e.g., Odum & Smalley 1959, Mitsch & Gosselink 2007). This paradigm was turned on its head with the discovery that the most abundant grazer in the southeastern United States, the marsh periwinkle snail (*Littoraria irrorata*)—long thought to be a detritivore specialist—was instead a potent, fungal-farming omnivore that could overwhelm and kill the marsh foundation species, *Spartina alterniflora* (hereafter, cordgrass), if its population was not held in check by predators (Silliman & Zieman 2001, Silliman & Bertness 2002, Silliman & Newell 2003). Further research revealed that snails could become increasingly lethal to cordgrass structure and stability when they congregate in fronts following intensive drought events (Silliman et al. 2005). Specifically, superconcentrated feeding fronts of snails form when drought-induced soil salinity stress and snail grazing act synergistically to kill off cordgrass in localized areas, prompting snails to move from barren mudflats to the border of healthy cordgrass. Field experiments and model analyses reveal snails accumulate on these borders because they display positive taxis toward live cordgrass and because their forward movement slows to near zero once they encounter significant amounts of their resource (i.e., resource-dependent movement rates) (Silliman et al. 2005). Thus, their relative abundance continues to increase as snails leave the barren region and accumulate on the borders. When snail density in the front overreaches the capacity of the cordgrass to compensate via growth ($\sim 2,000$ snails/m²), the front overgrazes the plants underneath it. This belt of superconcentrated snails subsequently begins to propagate across the marsh as snails follow the plant-availability resource gradient that they themselves are creating. The snail fronts generated by these processes can reach more than 1 km in length, span 4–5 m in width, contain more than 10,000,000 individuals (**Figure 1**) (Silliman et al. 2005), and have been observed in locations across 4,000 km of southeastern US coastline.

Multiple snail fronts can occur in one marsh and last more than one year. The end result of this runaway consumption in salt marshes is widespread devastation of cordgrass and loss of dependent components of biodiversity as well as key ecosystem services, such as carbon sequestration, commercial fishery production, and shoreline protection (Silliman et al. 2005, Bertness & Silliman 2008, Angelini & Silliman 2012). Although this system experiences runaway impacts for a time, there are negative feedbacks that ultimately cause fronts to dissipate. Fronts begin to disband

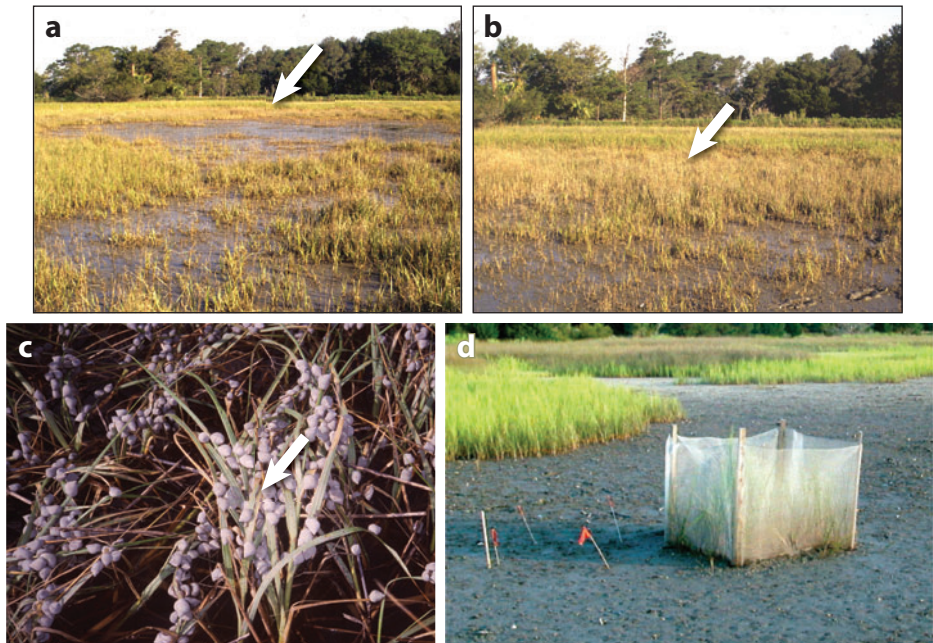


Figure 1

(a) Marsh die-off area on Sapelo Island, Georgia. (b) Close-up of snail front ($>2,200$ individuals/ m^2 and >400 -m long) overgrazing cordgrass at the edge of the die-off area. Arrows denote same location in panels *a* and *b*. (c) Representative snail density on the leading edge of front. (d) Effect of removal of snails in grazer front on cordgrass biomass after 3 months; uncaged control areas were barren, whereas cordgrass in caged areas was robust, green, and without grazer damage. Photos by Brian R. Silliman.

when cordgrass renewal capacity increases as drought subsides (Angelini & Silliman 2012). Fronts also disband when they hit open-water areas, or they break up during cold winter months when snails become inactive and are exposed to abiotic stress (B.R. Silliman, personal observations). A key question that still needs to be answered is how climate change and declines in predators (i.e., blue crabs) will impact the persistence, abundance, and interaction of snail fronts across the marsh landscape (Angelini & Silliman 2012). This issue must be addressed if managers and researchers hope to understand the long-term stability of this valuable coastal ecosystem.

In northeastern US salt marshes from Long Island, New York, to Cape Cod, Massachusetts, extensive consumer fronts have begun forming similarly in recent decades (Holdredge et al. 2009). These fronts are composed of thousands of burrowing purple marsh crabs and initiate on the marsh creek bank in the tall cordgrass zone—the preferred and natural habitat of these crabs (Figure 2). The key force driving local population increases is the human-induced depletion of predators (i.e., fish and predatory crabs) that would otherwise consume the crabs (Altieri et al. 2012). As crabs accumulate in their preferred creek-bank habitat, they soon overreach the carrying capacity of sympatric marsh grasses and subsequently denude the substrate, devouring both above- and belowground plant material during nighttime feeding activities (Holdredge et al. 2009, Coverdale et al. 2012). Once plants have been depleted locally, marsh crabs maintain front formation, moving higher into the marsh toward the remaining vegetation and away from eroding creek banks that are no longer capable of supporting their burrows (Altieri et al. 2013). Although more mobile than marsh periwinkle snails, and thus capable of diffusing the intensity of their

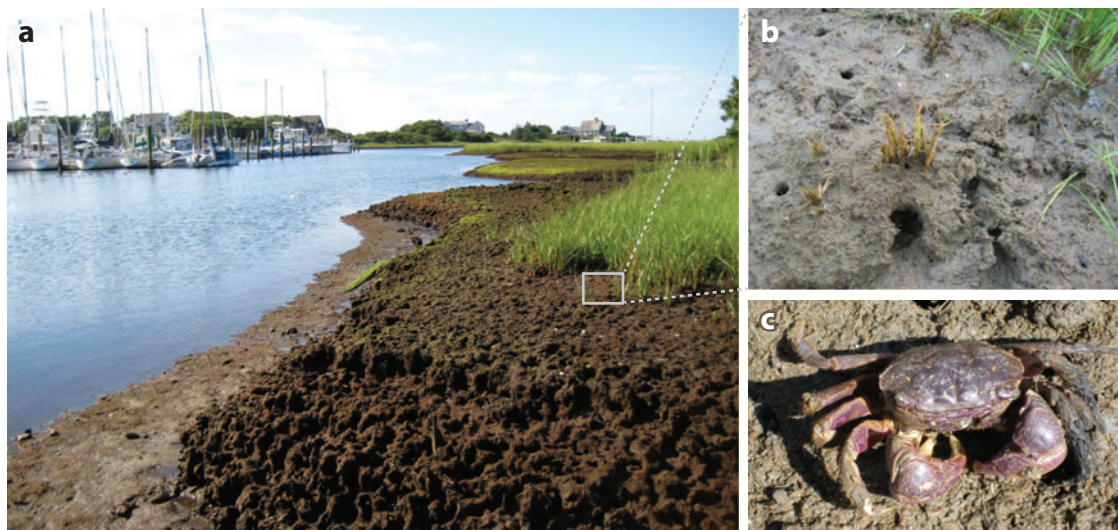


Figure 2

(a) Extensive die off of cordgrass along the creekbanks of Cape Cod, Massachusetts, salt marshes. (b) Close-up of cordgrass chewed by (c) the purple marsh crab, *Sesarma reticulatum*, the culprit of marsh die off. Photos by Christine Angelini.

top-down impacts via rapid movement away from conspecifics, these crabs are social (i.e., they live in communal burrows) and persist at high densities for multiple years as they move through the marsh and devour nearly all available cordgrass (Altieri et al. 2012). In their wake, these crab fronts leave mudflats characterized by reduced biodiversity, decreased carbon storage and nursery benefits, and increased shoreline erosion rates (Altieri et al. 2013). Although these fronts have decimated dozens of marshes throughout the northeastern United States over the past decade, surprisingly some fronts are now breaking up and marshes are recovering (Bertness & Coverdale 2013). The suggested stabilizing mechanism now leading to front decay is density-dependent predation by an invasive predator—the green crab, *Carcinus maenas*.

A key component of these two salt marsh consumer fronts is that grazer-induced scars facilitate fungal (Ascomycetes) infection in live plant tissue (**Figure 3**). These fungi are ubiquitous in the marsh and typically break down dead plant material, but they can switch to live cordgrass when intensive grazing provides a substrate for opportunistic infection (Silliman & Newell 2003, Daleo et al. 2009). Field experiments have revealed that both crabs and snails increase fungal biomass in live plant tissue and that this infection can account for 40–90% of the top-down effect of marsh consumers (Silliman & Newell 2003, Daleo et al. 2009). Because grazer scarring increases with increasing grazer density (Silliman et al. 2005, Holdredge et al. 2009), fungi likely play an important, but understudied, role in propagating crab and snail fronts. Acknowledging that consumer fronts involve grazer-disease-plant interactions improves our understanding not only of when and where consumer fronts are initiated (i.e., disease can lower the grazer-density threshold needed to overconsume plants), but also of how long they last in different environmental and biotic contexts, given the differential metabolic demands and susceptibility of grazers and disease to stress (Silliman & Newell 2003, Silliman et al. 2005). Abiotic stressors could also induce front formation initially by enhancing the vulnerability of plants to overgrazing and infection, hampering the impacts of higher-level predators, and altering the rate of plant recovery after a front has passed (Silliman et al. 2005).

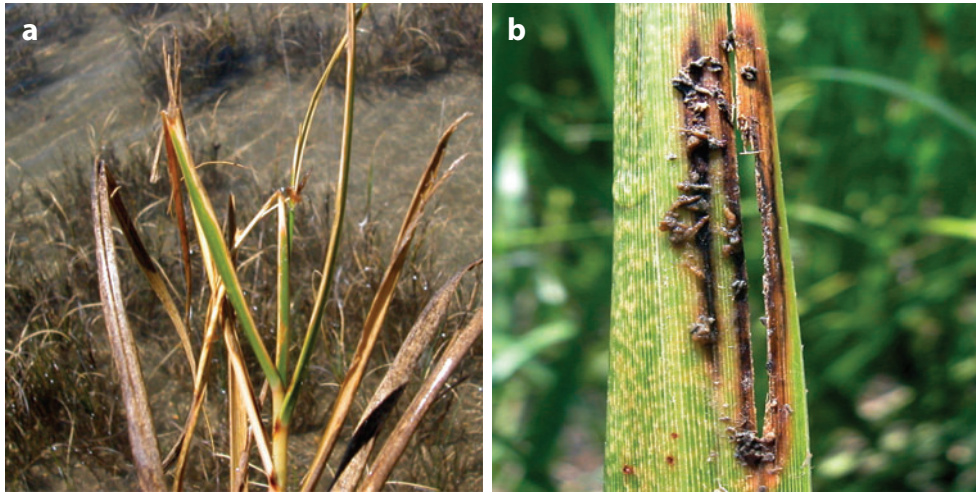


Figure 3

(a) Crab-induced wound on cordgrass heavily infected with fungi. (b) Snail-induced wound on cordgrass heavily infected with fungi. Photos by Brian Silliman.

3.2. Snail Fronts in the Rocky Intertidal Zones

In the rocky intertidal zone of North Atlantic shores, periwinkle snails (*Littorina littorea*) can form feeding fronts at the boundary of their preferred resource—the poorly defended green macroalgae *Ulva* spp. (Lauzon-Guay & Scheibling 2009). *Ulva* often form extensive intertidal mats when grazer densities are naturally low, such as following large-scale disturbances (e.g., ice-scour events or intense storm wave action) or when *Littorina* migrates to subtidal areas during the winter. As periwinkles move back into these areas and detect their preferred food, their movement slows dramatically, causing them to pile up on the periphery of *Ulva* mats (Figure 4). As periwinkles overconsume *Ulva*, a forward-propagating front is formed because periwinkles exhibit resource-dependent movement (Lauzon-Guay & Scheibling 2009). Chemotaxis toward edible algae may

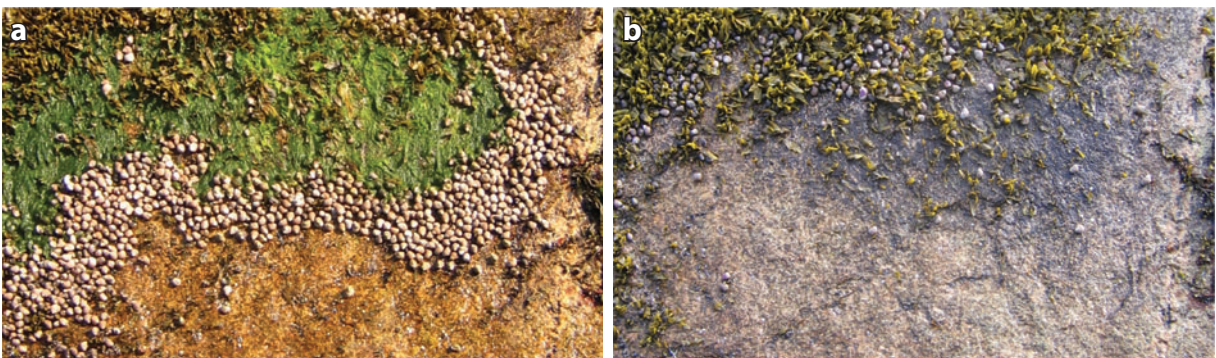


Figure 4

(a) Snail (*Littorina littorea*) grazing front on the North Atlantic coast that has formed on the edge of a mat of highly edible green algae. (b) Removal of the algal mat by the front and the resulting new dominant heavily defended brown algae. Photos by Jean-Sébastien Lauzon-Guay.

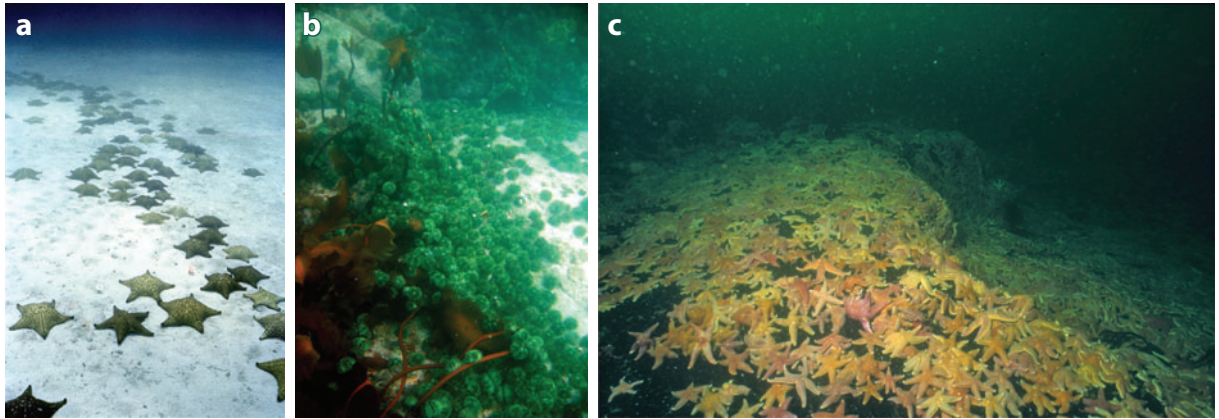


Figure 5

Echinoderm consumer fronts of (a) cushion stars in the Caribbean, (b) urchins in North Atlantic kelp beds, and (c) sea stars in the Gulf of Maine. Photo a by Jean-Sébastien Lauzon-Guay; photos b and c by Jon Witman.

also act to increase the rate of front formation and forward movement, but this has not been experimentally tested.

Observations from an experimentally created snail front suggest that periwinkle density is a key factor determining front speed, as movement rates increase with increasing densities within the front—the same observation was made for snail fronts in marshes (Silliman et al. 2005, Lauzon-Guay & Scheibling 2009). In turn, periwinkle density on fronts may be inversely related to wave action: Higher numbers and thus faster front movement occur under calmer conditions (Lauzon-Guay & Scheibling 2009). Once green algal mats are depleted, the periwinkle fronts break up. The ecosystem impacts of these fronts often include the suppression of fast-growing, competitively dominant algae and more rapid development of later-successional communities that have greater resistance to herbivory (Lauzon-Guay & Scheibling 2009).

3.3. Sea Star Fronts on Sandy and Rocky Shores

Fronts of sea stars amassing on the edge of beds of their preferred food, i.e., mussels, have been observed at many sites across the world (**Figure 5**), including in the Pacific (Paine 1966) and Atlantic oceans (Witman et al. 2003). Sea stars can concentrate on or just adjacent to mussel beds via adult migration into these areas (Paine 1966) as well as via the preferential recruitment of larvae to areas covered by mussels (Witman et al. 2003). As with snails, sea star movement is characterized as resource dependent: Sea stars move quickly over barren areas and then decelerate to a near halt once they encounter prey. This process leads to a pileup of sea stars on the edges of mussel beds, and if densities are high enough, aggregations are formed (Witman et al. 2003). As the sea stars completely consume the mussels at the edge, the front moves forward with sea stars in the back “leap frogging” to the leading edge of the front where mussels are still present. This process moves the consumer fronts forward at speeds of 1–20 m/year (depending on sea star density in the front) and can result in complete demolition of mussel beds (up to hundreds of square kilometers) (Witman et al. 2003) and the biodiversity hot spots that mussel beds facilitate (Silliman et al. 2011). Once mussel resources are extinguished from a region, the movement speed and direction of the sea stars are no longer coordinated by spatial gradients in the resources, and

fronts break up as sea stars migrate to other areas in search of food (Paine 1966) or turn on each other in cannibalistic feeding (Witman et al. 2003).

In subtidal sand flats in the Caribbean, the cushion sea star (*Oreaster reticulatus*) has also been observed forming fronts at the boundary of its primary food resource—microalgal and detrital films (**Figure 5a**) (Scheibling 1980). Key to the formation of cushion star fronts is spatial heterogeneity in the abundance of food resources; this pattern is often generated by the release of top-down control on algal growth (e.g., due to storms). Field observations and individual-based models (Scheibling et al. 1999, Lauzon-Guay et al. 2008) suggest that, following local increases in algae on the ocean floor, sea star fronts form on the edges of these microalgal mats as a result of food-dependent dispersal (i.e., fast movement when there is no food, but markedly slower movements when food is available). Importantly, fronts will form and persist only at high consumer population densities of sea stars, as large numbers are needed to deplete local resources and because high densities maintain spatial heterogeneity in the resource. Impacts of these fronts include significantly depressed primary production and decreased stability of the substrate due to loss of sediment-binding algal mats.

3.4. Crown-of-Thorns Sea Stars

Throughout the tropical Indo-Pacific, *Acanthaster planci*, or crown-of-thorns starfish (**Figure 6**), roam shallow waters and consume scleractinian (stony) corals, the reef-building foundation species that support hyperdiverse associated communities. At low densities (~0.06 individuals/ha) (Endean 1974), *Acanthaster* can promote coral diversity and reef heterogeneity by selectively feeding on fast-growing species (De'ath & Moran 1998). Similar to many echinoderms, *Acanthaster* experience episodic population outbreaks (Uthicke et al. 2009, Timmers et al. 2012). Although there is no consensus on the proximate causes of these outbreaks, the most commonly cited hypothesis proposes that *Acanthaster* larvae experience unusually high survival during pulses of nutrient-enriched runoff that fuels blooms of their phytoplankton prey (Brodie et al. 2005, Fabricius et al. 2010).

In contrast to snail, sea star, and crab fronts that form along the margins of concentrated prey (see above), superconcentrations of *Acanthaster* form patchy fronts at local spatial scales (tens of meters) because their coral prey typically occur in spatially heterogeneous, mixed-species assemblages. In addition, *Acanthaster* sequentially feed on preferred, and then nonpreferred, coral species (Ormond et al. 1973, Pratchett 2007, Kayal et al. 2011), leading to localized heterogeneity in the direction of *Acanthaster* movements. Yet, at larger scales (hundreds to thousands of meters), however, *Acanthaster* fronts exhibit linear formations and strong directional movement, as they migrate across reef complexes from coral-depleted to adjacent, unimpacted regions (Chesher 1969, Ormond et al. 1973, Laxton 1974, Kayal et al. 2012). In Moorea, for example, annual surveys show that *Acanthaster* fronts initiated at a single origin and were then methodical in their forward propagation across the island's 110 km of fringing reef (Kayal et al. 2012). Given their relatively slow movement, *Acanthaster* fronts can persist for months to years (Pratchett 2005, Leray et al. 2012), depending on the density of individuals and the distribution and cover of live coral. The fronts are thought to dissipate because of starvation, disease, and *Acanthaster's* strong aversion to traversing deeper waters or sandy substrates to reach healthy reefs (Chesher 1969, Ormond et al. 1973, Uthicke et al. 2009). Fronts necessarily disappear when they have devastated the entirety of a patch of reef.

By systematically removing live coral (**Figure 6**), *Acanthaster* outbreaks are causally linked with marked declines in reef fish and invertebrates (Sano et al. 1987, Kayal et al. 2012, Leray et al. 2012) and, thus, rank below only cyclones as the most devastating disturbance impacting Indo-Pacific

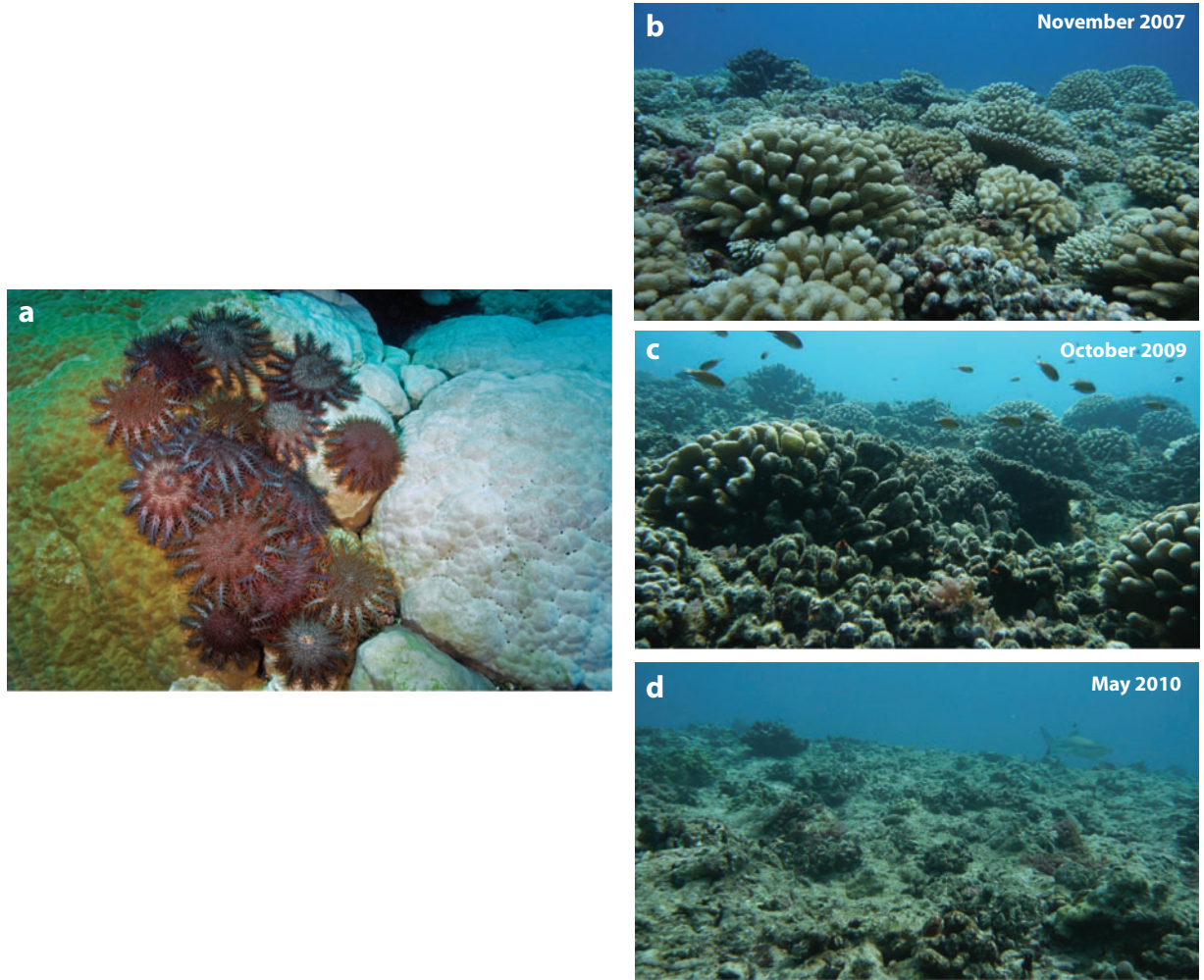


Figure 6

(a) Section of an extensive consumer front composed of crown-of-thorns sea stars, *Acanthaster planci*. (b) High coral cover in a reef in Moorea, French Polynesia, before an *Acanthaster* front moves through. (c) Massive decline in coral cover and colonization by algae after the front, and (d) the same area after the consumer front and then cyclone passed. Photo a copyright Brian Skerry; photos (b–d) by Mohsen Kayal.

reef communities. Although a recent meta-analysis suggested that systems impacted by *Acanthaster* are faster to recover than those degraded by other types of disturbance (e.g., bleaching, cyclones) (Graham et al. 2011), it remains unclear whether coral reefs will be able to withstand the more frequent *Acanthaster* outbreaks that are predicted to arise as a result of anthropogenic changes that increase *Acanthaster* survival (i.e., nutrient pollution and depletion of predators), particularly in conjunction with other forms of disturbance.

3.5. Microbes (Coral Disease) on Coral Reefs

In addition to outbreaks of *Acanthaster* feeding fronts, reef-building scleractinian corals are also vulnerable to consumer fronts generated by microbes (e.g., bacteria, fungi, helminthes, and/or

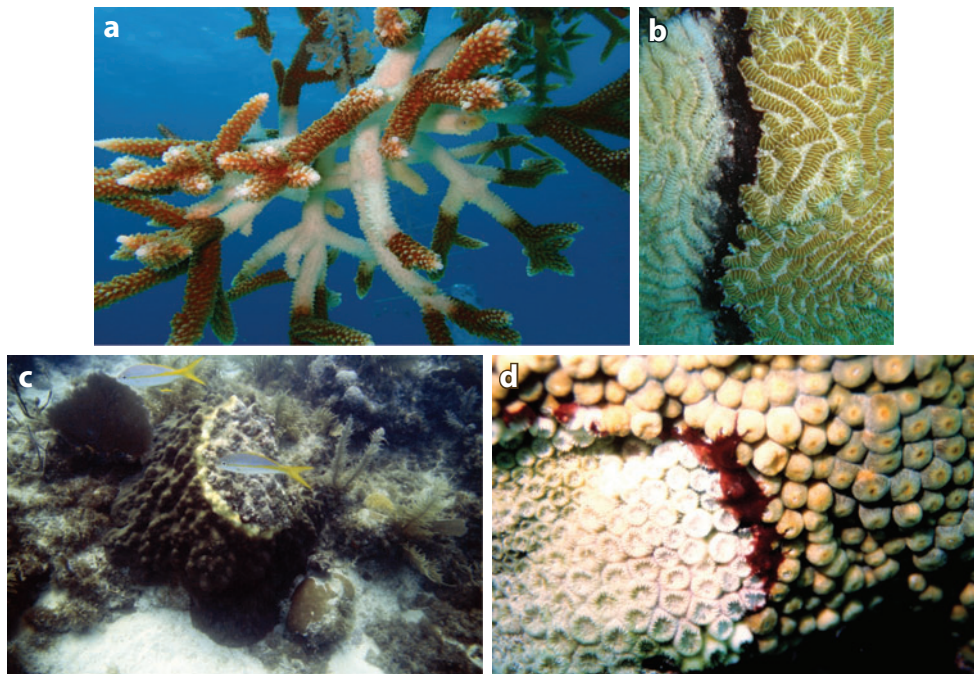


Figure 7

Microbial consumer fronts on coral colonies: (a) white-band disease, (b) black-band disease, (c) yellow-band disease, and (d) red-band disease. Photos *a–b* by Liz Schrack; photos *c–d* by Craig Quirolo, Reef Relief/Marine Photobank.

viruses), including the disease agents that cause black-band disease, white-band disease, yellow blotch, and white plague, all of which consume live coral (Muller & Woesik 2012). Incidences of coral disease are typically associated with abnormal, heightened environmental conditions, namely high summer temperatures and pulses of nutrient enrichment that stress corals, facilitate the growth of disease-causing microbes, or both (Jones et al. 2004, Bruno et al. 2007, Muller & Woesik 2012). Although coral diseases differ widely in their host specificity, transmission mode (e.g., direct contact, waterborne, or facilitation by corallivorous snails and fish) (Williams & Miller 2005, Aeby & Santavy 2006), spatiotemporal dynamics (e.g., seasonality) (Sato et al. 2009), and rate of propagation, most are consistent in forming consumer fronts on their host colony and advancing in distinct linear bands across individual coral colonies. As such, although coral diseases have yet to be studied as actual consumer fronts, they appear to exhibit striking directional (resource-dependent) movement and/or differentially higher replication from the point of initial infection, such as a bite wound, toward adjacent live coral polyps (Figure 7). The net impact of disease fronts interacting with other stressors on corals, the organisms they support, and ecosystem services they provide can be dramatic. For example, an outbreak of white-band disease in the Florida Keys, coinciding with high temperatures in 2001–2002, caused live elkhorn and staghorn coral cover to plummet from 96% to 12% (Williams & Miller 2005). To date, elkhorn and staghorn reefs have not fully recovered, resulting in lower fish and invertebrate biomass and biodiversity as well as reduced provision of shoreline protection.

3.6. Urchin Fronts

Urchins form consumer fronts in a variety of habitats, including seagrasses (Rose et al. 1999), mussel beds composed of recently settled bivalves (Witman et al. 2003), and kelp beds around the world (Estes & Palmisano 1974, Scheibling et al. 1999, Brady & Scheibling 2005, Lauzon-Guay & Scheibling 2007). A crucial element in the formation of urchin fronts is movement behavior (Lauzon-Guay & Scheibling 2010). Urchin movement can, in large part, be described as random (perhaps with a slight taxis toward kelp), but when encountering a dense kelp stand (or other prey resource such as mussels), their movement speed reduces dramatically. As a consequence, urchins accumulate at the edge of the kelp stand and can form a consumer front if local urchin densities are high enough. Locally elevated urchin abundance can occur for a variety of reasons, including loss of top-down control by large predators (Estes & Palmisano 1974) or disease (Estes & Palmisano 1974, Scheibling et al. 1999, Brady & Scheibling 2005), massive migration of adult urchins into a local area, or episodic recruitment (Witman et al. 2003). Once a front forms, model analyses and field observations highlight the fact that negative density dependence of movement speed (urchins move less when their density is high) also plays a key role in front persistence, maintaining movement of a consolidated front on the rock barren-kelp bed edge and preventing the urchins from individually dispersing into the kelp bed. Hence, simple movement characteristics (resource and density dependence) play defining roles in the development and persistence of urchin grazing fronts.

Some of the most well-studied urchin fronts occur along the Atlantic coast of Nova Scotia where transitions between dense kelp beds and barren rock covered by encrusting coralline algae occur on a decadal scale. In this ecosystem, kelp beds emerge when urchins suffer from disease outbreak, which decimates their numbers and releases kelp from top-down control. Urchins often regain their dominance over these areas in a spectacular fashion. Deep-living sea urchins, unaffected by disease, form feeding aggregations (fronts) (**Figure 5b**) at the lower margin of regenerating kelp beds (Mann 1982, Scheibling et al. 1999, Brady & Scheibling 2005, Lauzon-Guay & Scheibling 2007). These dense fronts can number more than 1,000 individuals/m² (Foreman 1977). Once urchins have consumed kelp holdfast at the barren-kelp bed ecotone, the fronts destructively move forward through the remaining kelp stand at up to 4 m/month (Mann 1982, Scheibling et al. 1999), removing all fleshy seaweeds and leaving rock barrens dominated by encrusting coralline algae. The implications of such high grazing pressure on the kelp beds are dramatic. Coalescence of multiple bare patches into large-scale barrens can transform large sections of the subtidal coastline into an urchin barren with little macrophyte growth. The landscape that remains is characterized by reduced biodiversity and habitat complexity (Rose et al. 1999). In the absence of these grazing fronts, kelp beds can persist for prolonged periods (Chapman & Johnson 1990), suggesting that the barrens reveal a long-lasting signature of past consumer front(s).

3.7. Ungulates in Grassland Systems

Some of the most expansive and ecologically important grazing fronts occur among large herbivorous mammals. In fact, the earliest recognized grazer front and one of the most spectacular examples of consumer-front formation occurs on the African Serengeti, where the congregation of wildebeest during their annual migration leads to striking wavelike front propagation (Sinclair 1977, Mloszewski & Mloszewski 1983).

The Serengeti supports the largest herds of migrating ungulates in the world (Mloszewski & Mloszewski 1983, McNaughton 1985, Mduma & Hopcraft 2008), including more than a million

wildebeest (Nkwabi et al. 2011) that amass in herds of 100,000 or more individuals (Sinclair 1977). During the rainy season, these large grazers forage primarily in the expansive short-grass plains that are characteristic of much of the eastern Serengeti ecosystem. However, as rains dissipate in the early summer months, a distinctive rainfall gradient is created across the Serengeti. This gradient is characterized by a drying pattern in the east as prevailing winds blow offshore over the Indian Ocean and by a continued wet pattern in the west as a result of the climatic effects of Lake Victoria. The short-grass plains preferred by the wildebeest (Sinclair et al. 1985, Mduma et al. 2001) are farthest from Lake Victoria and typically dry out first. As these plains dry, grass growth and carrying capacity decrease, leading to local overgrazing by wildebeest. In response to decreased food availability, wildebeest move off the overgrazed lands in search of ungrazed lands with abundant and nutrient-rich grasses (Hopcraft et al. 2010, 2012). The movement of individual wildebeest dramatically slows once they encounter ungrazed lands. This cessation of movement is doubtless augmented by the “selfish-herd” effect; there is protection in sheer numbers against predation by, e.g., lions, so any wildebeest that wanders far ahead of the crowd is more vulnerable to predation (a kind of trophically mediated Allee effect) (e.g., Boukal et al. 2007, McLellan et al. 2010). This resource- and predator-dependent behavior results in a concentration of large herds of wildebeest in massive grazer fronts that then move westward out of the short-grass plains and into tall grasses, following a spatial gradient of food availability (Sinclair 1977; Gueron & Levin 1993; Gueron et al. 1996; Holdo et al. 2009; Hopcraft et al. 2010, 2012) and escaping top-down predator control (Fryxell et al. 1988; Hopcraft et al. 2010, 2012). Although the wildebeest move rapidly through the tall-grass areas, they arrive in such dense and expansive waves (**Figure 8**) that they can graze down as much as 50% of the plant biomass, changing the structure of the community from a predominantly tall-grass into a predominantly short-grass system (Sinclair 1977, Sinclair et al. 1985). Consequently, wildebeest grazing fronts have keystone effects in these ecosystems, affecting the diversity of small herbaceous flowering plants, herbivorous insects, and birds (Sinclair 2003, Sinclair et al. 2007).



Figure 8

Massive consumer front of wildebeest on grasslands in Africa extending tens of kilometers in length and commonly more than 1 km in width. Photo by Joe Scherschel at National Geographic Creative.

3.8. Insects in Forests and Other Ecosystems

Though not widely documented, the development of consumer fronts among herbivorous insects is likely common (Feeny 1970, Price et al. 1990, Hunter & Price 1992). Insects that are specialists on rare, patchy plants are a priori less likely to form fronts, compared with generalists that feed on homogeneous resource bases or most members of a plant community. Here we highlight two examples of consumer fronts that have enormous ecological and socioeconomic consequences: plague locusts and gypsy moths.

Locust plagues can have such profound effects on natural and agricultural landscapes that they were chronicled in the Old Testament of the Bible as acts of God. They have also been the causes of famine and economic loss around the globe for centuries. A locust plague is characterized by the merging of multiple swarms of migrating winged locusts and bands of wingless nymphs into vast swarms that consume all edible vegetation as they move across a landscape. These outbreaks occur in response to specific climatic events and arise through the movements of breeding adults (Krall et al. 1997). The locusts' phenotype is plastic—individuals can develop into either solitary or gregarious morphs (Simpson et al. 2002). Plague-forming locusts typically develop into nongregarious morphs, but following intense rain events and subsequent increases in both plant growth and locust population densities, individuals develop into gregarious morphs (Hunter 2004). These gregarious adults then take flight and migrate in swarms from areas where they have depleted the local edible vegetation toward areas that have recently received rainfall. After several generations of this positive feedback, multiple swarms can converge and begin to exhibit plague-like outbreak dynamics (Hunter 2004). Although winged adult locusts consume biomass and can devastate vegetation, their ability to move large distances results in cloud-like formations that travel rapidly across the landscape and makes them less prone to create the more concentrated front formations highlighted in this review.

In contrast to the highly mobile winged adults, the wingless locust nymphs associated with these swarm-forming outbreaks lack the ability to move great distances. Instead, these nymphs will often congregate in grazing fronts sometimes more than 1 km in length, often 1–3 m in width, and potentially consist of billions of individuals (**Figure 9**). Mid- to late-instar nymphs of single mass cohorts of eggs deposited by the gregarious adults come together and form a line or front that moves as a rolling wave as individuals on the front edge eat and those behind leap forward to the ungrazed shoots ahead (i.e., resource-dependent movement). We conjecture that the sharp edges revealed in **Figure 9** could also reflect an emergent Allee effect of predator satiation, where individuals who wander too far ahead may be subject to bird predation, for example, whereas those in the front are protected by the sheer ability of their vast numbers to overwhelm local insect predators.

Similar to locusts, gypsy moths are dietary generalists, and their populations can persist at low densities for many years (Wallner 1987) before erupting into massive outbreaks that in as few as two generations result in rapid defoliation of forests (Elkinton & Liebhold 1990). The conditions that drive the conversion of low-density populations of gypsy moths into outbreaks are not fully understood, but outbreaks are associated with warm, dry weather patterns in summer, changes in forage quality, and relaxation of density-dependent mortality (Elkinton & Liebhold 1990). When at low density, gypsy moth populations are thought to be primarily controlled by small mammals, parasitoids, birds, and viral infections (Elkinton & Liebhold 1990) that kill off late-instar larvae and pupae (Campbell & Sloan 1977). Indeed, an abundance of alternative foods for small mammals, such as high yields of blueberries or acorn masts, reduces predation on gypsy moths and is associated with population outbreaks. But a surge in gypsy moth numbers can allow them to satiate local predator populations, a form of positive density dependence that can foster continued population growth and predator escape.



Figure 9

An extensive front of late-instar locust nymphs in Australian croplands. These 2–10-m wide consumer fronts, the dark line in this image, can stretch multiple kilometers and turn thousands of square kilometers of healthy crops (*green vegetation on right*) into barren fields (*brown landscape on left*). Photo copyright New South Wales Department of Primary Industries.

Early-instar gypsy moth larvae are relatively stationary, spending much of their time foraging in the lower canopy of host trees. Later instars, however, become highly mobile, moving into the litter to rest during the day and into the lower and upper canopy at night to forage, often in different trees. The circadian movements of these late-instar moth larvae can lead to accumulations of individuals on some trees (Mauffette & Lechowicz 1984, Lance et al. 1986, Rossiter 1987). Because adult female gypsy moths are flightless, they often move only a few meters from their birth sites before depositing their eggs (Odell & Mastro 1980), leading to high egg densities at sites where moths have begun to accumulate. As the population densities increase locally and reach outbreak proportions over multiple generations, the late-instar larvae defoliate their host trees. Moth larvae then move in search of food and pile up on adjacent healthy trees, governed by resource-dependent movement and satiation of local predators. This leads to the formation of an insect front that rapidly defoliates this new host tree and continues to radiate outward from the focal site (Elkinton & Liebhold 1990). These consumer fronts can be greater than 1 km in length, last almost a year, and defoliate almost entire forest ecosystems stretching for hundreds of kilometers (**Figure 10**), resulting in the loss of the ecosystem services those forests provide.

3.9. Invasive Consumers

Introduction of alien consumers into novel landscapes can lead to massive increases in their numbers owing to a variety of causes, including competitive parasite or predator release as well as increased availability of food (Lockwood 2006). When invasive consumers both rapidly increase in numbers and aggregate, they can locally overwhelm their prey and generate consumer fronts that propagate through novel habitats. Invasion fronts may have arisen following the introduction of many animals, including pigs, goats, fire ants, and yellow crazy ants (Lockwood 2006). Many of these, however, do not fit the type of front dynamics we focus on here, i.e., a tight band of



Figure 10

Massive defoliation of temperate forests in North America generated by multiple waves of consumer fronts composed of gypsy moths. Photo by Mark Robinson, USDA Forest Service, <http://www.Bugwood.org>.

superconcentrated consumers. Two examples involving invasive species that do fit this dynamic include European worms in North American temperate forests and the rusty crayfish in northern, temperate US lakes.

Across northern Minnesota and the Great Lakes region there are many leading edges demarking the ongoing European earthworm invasion. These leading edges can be classified as consumer fronts because they are well-defined linear bands (~6–10-m wide) of high concentrations of earthworms (biomass is ~20–100 times higher than in areas just behind the front) that overconsume their local prey (Wilson et al. 2004). As the front passes, earthworm densities drop off rapidly, most likely because food resources have been severely depleted. These fronts can stretch for hundreds of kilometers, move ~5 m/year, and leave a massive mark on the forest ecosystem in their wake, drastically changing nutrient and leaf-litter availability, soil fungal and bacterial composition, and the understory plant community that depends on the native soil's character for its persistence (**Figure 11**) (Wilson et al. 2004). Before an earthworm invasion, plant understories are dense and diverse. After the front passes, however, plant diversity and biomass drastically decline, most likely because earthworms overgraze mycorrhizal fungi on which many of these plants depend (Wilson et al. 2004). Although earthworms are generally thought to be beneficial to plants because they enhance nutrient availability and sediment porosity, the cascading impacts of these consumer fronts are dramatically negative and diverse, including decreased primary production and declines in understory mammal, bird, and reptile abundances and diversity (Wilson et al. 2004). In the longer term, these invasive earthworm fronts may affect future tree composition in the forest because they act as a filter to suppress the sapling densities of many of the currently dominant adult trees (e.g., sugar maples).

In a similarly powerful example, invasive rusty crayfish formed a consumer front in the littoral zone of a large temperate lake and left a markedly different ecosystem as they passed over the substrate (Wilson et al. 2004). This consumer front had crayfish densities 5–10 times higher

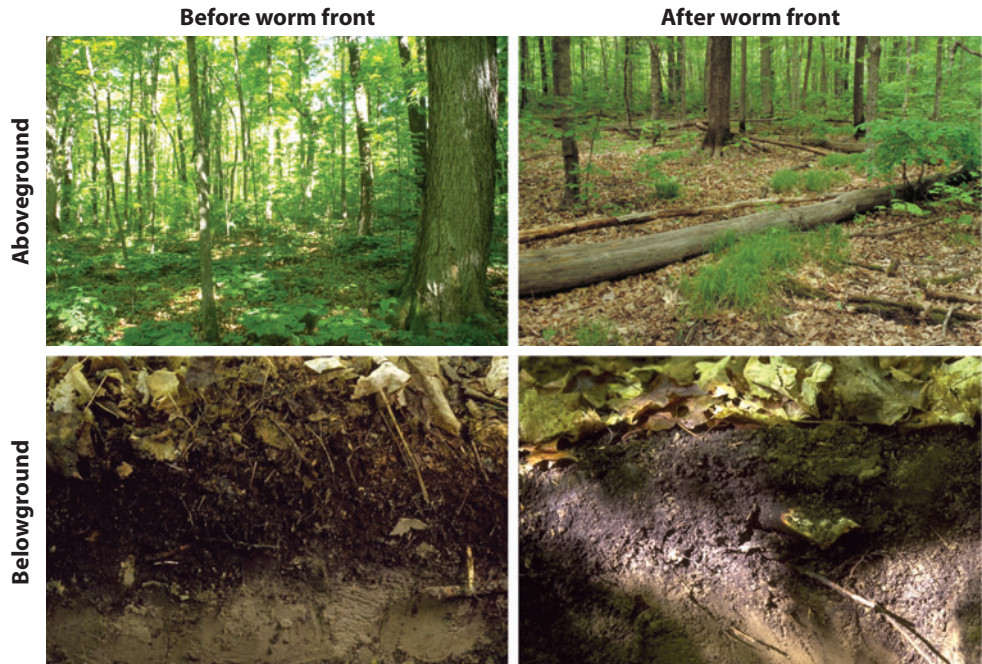


Figure 11

An understory plant community and soil composition in a temperate forest before and after an earthworm consumer front. Earthworms significantly suppress understory plant growth and alter soil chemistry and composition as well as the organic content of soils. Photos by Ryan Huffmeier and Cindy Hale.

than those of nearby adjacent areas behind the front, and few or no invasive crayfish occurred ahead of the front. Crayfish are voracious omnivores and ecosystem engineers; thus, at such high numbers, overconsumption and habitat modification by crayfish resulted in dramatic declines in snail and other invertebrate densities as well as the loss of once-abundant macrophyte cover (Wilson et al. 2004). Simple models predicted that these fronts could move as fast as 3 km/year, but measurements from the field showed that real-world speeds were slower at ~ 0.7 km/year, a difference attributed to the suppression of crayfish movement by predatory fish (Wilson et al. 2004). We conjecture that this reflects positive density dependence in the crayfish emerging from localized predator satiation. This powerful front of consumers persisted for multiple years until it had circled the entire lake, leaving the entire littoral zone devoid of almost all emergent vegetation. The indirect effects of this consumer front were strong and varied from ecosystem-level to food-web alterations, as plant production and density of sunfish was drastically reduced in its wake (Wilson et al. 2004).

4. ECOSYSTEM IMPACTS OF CONSUMER FRONTS AND COMMON MECHANISMS UNDERLYING THEIR FORMATION AND MOVEMENT

Our survey of the literature reveals that consumer fronts occur in a wide variety of ecosystems as disparate as African savannas and subtidal mussel beds (**Table 1**). Proliferation of these extensive fronts, often repeated across vast spatial scales, is a dramatic phenomenon. Fronts can last months, multiple years, or even decades and can lead to wholesale loss of foundation species and dramatic

diversity declines over massive spatial scales, with consequences that may extend into centuries or millennia (**Tables 1** and **2**). Most fronts eventually break up owing to resource extinction, physical heterogeneity in the resource base, suppression of the original force(s) that amplified top-down impacts, amplification of predation pressure from above, migration, or metamorphosis (**Table 2**). The lone exception so far is earthworm fronts, which may require another Ice Age to get knocked back. Otherwise, consumers that once comprised the front either fan out into dramatically less dense units, are eaten, migrate away, or die of starvation.

Despite the fact that most fronts eventually break up, many fronts can be long lasting and spatially extensive, and the considerable habitat loss generated by these fronts leads to cascading, negative impacts that affect important ecosystem services that the habitats supply, including carbon sequestration, nutrient uptake, shoreline protection, and water purification. The damage caused by these fronts also leads to the loss of millions of US dollars in revenue from decreased tourism, crops, and other services (**Table 2**). The dynamics of front breakup, however, have received considerably less attention and are thus ripe for further empirical and modeling research.

Wave and front formations in ecological systems have been studied extensively in the theoretical and mathematical literature (Noble 1974, Chow & Tam 1976, Dwyer 1992, Murray 1993, Lewis 1994, Holt et al. 2011). Even the simplest predator-prey and host-pathogen models with passive predator dispersal can reveal traveling wave fronts when a predator or pathogen is introduced into a landscape where its prey or host is present homogeneously at carrying capacity. Predator numbers surge locally because of ample food, then they collapse when prey abundance is depleted by high predator abundance. Diffusive moment of predators to nearby locations leads to a new population explosion at that locality, again followed by local population collapse and thus forming a front of predation. Adding an Allee effect can alter the rate of advance of the consumer front and sharpen the wave front (Lewis & Kareiva 1993). Underlying these models, however, is an unstable, cyclic interaction between the predator and its prey, and empirical examples of this process have been relatively limited (Rohani 1997, but see Kaitala & Ranta 1998).

Our review discusses an additional suite of key processes that can drive front formation in consumers, with dramatic consequences for community structure and ecosystem function. The case studies we have sketched above reveal that these processes facilitate front formation in consumers worldwide. Across the kingdoms of life, there is a striking similarity in the mechanisms that generate consumer fronts and then propel their destructive waves through nature (**Table 2**). In all cases, an external force that locally increases top-down control by consumers must first be added to the system, such that consumer pressure must increase to a point that it exceeds prey carrying capacity and/or renewal capabilities. These external forces must do one of the following: (a) increase prey susceptibility to predation (such as drought with marsh snails, locusts, or wildebeest), (b) increase the local density of the consumer (such as eutrophication with sea stars; high rainfalls with moths; predator or disease release with urchins, marsh crabs, and moths; or human introduction with earthworms and crayfish), or (c) increase both prey susceptibility to predation and local consumer density (such as with marsh snails, for which drought both weakens plants on which snails feed and suppresses predators that control their densities). Following this threshold disturbance, consumers overgraze their prey and severely deplete them locally, creating a spatial void of resources. In all cases (except fungi that are facilitated by snails and crabs), front-forming consumers then exhibit resource-dependent movement and move off these prey-depleted areas at relatively high speeds and slow to a near halt once they reach healthy prey, leading to a pileup of consumers on the border between a barren and a healthy ecosystem. Propagation of the front continues because of two characteristics common to all these species: continued local overconsumption of the prey species within the consumer front and resource-dependent movement. In most cases, the addition

Table 1 Classification, distribution, and aggregation morphometrics of consumer fronts that can drastically transform whole ecosystems

Kingdom	Phylum	Scientific name	Common name	Ecosystem	Length of front	Multiple fronts	Width	Density ^a	Duration	Range
Animalia	Mollusca	<i>Littoraria irrorata</i>	Marsh periwinkle	Salt marsh	10–500 m	Yes	1–4 m	1,000–4,000	0.5–2 years	Southeastern and gulf USA
Animalia	Athropoda	<i>Seseria reticulatum</i>	Purple marsh crab	Salt marsh	10–300 m	Yes	1–2 m	30–100	Up to 5 years	Northeastern USA
Animalia	Athropoda	<i>Locusta migratoria</i>	Migratory locust	Grassland and agro-systems	Up to 1 km	Yes	~1–3 m	300	Days to weeks	Africa, Asia, Australia
Animalia	Athropoda	<i>Schistocerca gregaria</i>	Desert locust	Grassland and agro-systems	Up to 1 km	Yes	NR	> 1,000	Days to weeks	North Africa, Middle East, Asia
Animalia	Athropoda	<i>Chortioctetes terminifera</i>	Australian plague locust	Grassland and agro-systems	Up to 1 km	Yes	NR	> 1,000	Days to weeks	Australia, New Zealand
Animalia	Athropoda	<i>Schistocerca americana</i>	American desert locust	Grassland and agro-systems	Up to 1 km	Yes	NR	> 1,000	Days to weeks	North America
Animalia	Athropoda	<i>Lymnaea dispar</i>	Gypsy moth	Deciduous forest	Up to 1 km	Yes	5–10 m	> 1,000	0.5–1 year	North America and Europe
Animalia	Athropoda	<i>Orconectes rusticus</i>	Rusty crayfish	Lakes	Littoral zone	Potentially	< 1–4 m	~5–10 × > in front	Up to 3 years	North America
Animalia	Annelida	Multiple species	European earthworm	Forests, grasslands	Kilometers	Yes	Yes	20–100 × > in front	Tens of years	North America
Animalia	Echinodermata	<i>Oreaster reticulatus</i>	Cushion star	Subtidal sand patches	10–30 m	Yes	< 1 m	2–7	2–3 months	Caribbean

(Continued)

Table 1 (Continued)

Animalia	Echinodermata	<i>Asterias</i> spp.	Common sea star	Inter- and subtidal rocks	10–50 m	Yes	1–5 m	5–25	0.5–3 years	Temperate global areas
Animalia	Echinodermata	<i>Acanaster planci</i>	Crown-of-thorns sea star	Coral reefs	NR	Yes	NR	0.004–0.025	Up to 3 years	Indo-Pacific
Animalia	Echinodermata	<i>Strongylocentrotus droebachiensis</i>	Green sea urchin	Kelp and seagrass beds	Hundreds of meters	No	NR	400	Decadal	Circumpolar regions
Animalia	Mollusca	<i>Littorina littorea</i>	Edible periwinkle	Intertidal rocks	NR	Likely	NR	1,300–2,300	2–8 weeks	North Atlantic
Animalia	Vertebrata	<i>Comachaetes gnou</i>	Wildebeest	Grassland	1–5 km	Potentially	> 100 m	~0.5	~0.25 years	Africa
Fungi	Ascomycete	<i>Phaeosphaeria spartanicola</i>	Salt marsh fungus	Salt marsh	10–500 m	Yes	1–4 m	1,000–4,000	0.552 years	US Atlantic Coast
Fungi	Ascomycete	<i>Aspergillus sydowii</i>	Aspergillosis sea fan disease	Coral reefs	0.01–0.1 m	Yes	0.001–0.02 m	NR	2–3 years	Caribbean
Bacteria	Proteobacteria	<i>Serratia marcescens</i>	White pox disease	Coral reefs	0.01–5 m	Yes	0.001–0.03 m	NR	Weeks	Caribbean
Protista	Ciliophora	<i>Halofolliculina corallista</i>	Skeletal eroding band	Coral reefs	0.01–5 m	Yes	0.001–0.03 m	190–660 ciliates cm ⁻²	Weeks	Indo-Pacific
Bacteria	Proteobacteria	<i>Vibrio cholerae</i>	White-band disease Type II	Coral reefs	0.01–5 m	Yes	0.001–0.03 m	NR	1–2 years	Caribbean

^aDensity measured in individuals per square meters. Abbreviation: NR, not reported.

Table 2 Mechansims underlying consumer front formation, persistence, impacts, and breakup^a

Common name	Formation	Persistence	Whole-ecosystem impacts	Breakup
Marsh periwinkle	Climatic stress	Strong resource-dependent movement	Massive ecosystem die-off, decreased biodiversity	Cold weather
	Predator depletion	Weak or no positive density-dependent movement	Loss of carbon sequestration, loss of nursery habitat	Climatic stress cessation
	Local overconsumption/ patch formation	Addition of new individuals to front		Resource extinction
	Resource-dependent movement			
Purple marsh crab	Predator depletion	Strong resource-dependent movement	Massive ecosystem die-off, loss of shoreline protection	Restoration of predation
	Local overconsumption/ patch formation	Weak or no positive density-dependent movement	Loss of carbon sequestration, loss of nursery habitat	Resource extinction
	Resource-dependent movement	Addition of new individuals to front	Decreased biodiversity	
		Gregarious		
Migratory locust	Climatic stress	Strong resource-dependent movement	Dieback/-off of massive agricultural fields or grasslands	Resource extinction
	Density-dependent phase polyphenism (solitary to gregarious)	Weak or no positive density-dependent movement	Decreased biodiversity and carbon sequestration	Metamorphosis
	Correlated reproduction	Addition of new individuals to front	Millions of US\$ lost in decreased crop revenue	Potentially compensatory predation
	Local overconsumption/ patch formation	Gregarious		Migration
	Resource-dependent movement			
Desert locust	Climatic stress	Strong resource-dependent movement	Dieback/-off of massive agricultural fields or grasslands	Resource extinction
	Density-dependent phase polyphenism (solitary to gregarious)	Weak or no positive density-dependent movement	Decreased biodiversity and carbon sequestration	Metamorphosis
	Correlated reproduction	Addition of new individuals to front	Millions of US\$ lost in decreased crop revenue	Potentially compensatory predation
	Local overconsumption/ patch formation	Gregarious		Migration
	Resource-dependent movement			

(Continued)

Table 2 (Continued)

Common name	Formation	Persistence	Whole-ecosystem impacts	Breakup
Australian plague locust	Climatic stress	Strong resource-dependent movement	Dieback/-off of massive agricultural fields or grasslands	Resource extinction
	Density-dependent phase polyphenism (solitary to gregarious)	Weak or no positive density-dependent movement	Decreased biodiversity and carbon sequestration	Metamorphosis
	Correlated reproduction	Addition of new individuals to front	Millions of US\$ lost in decreased crop revenue	Potentially compensatory predation
	Local overconsumption/patch formation	Gregarious		Migration
	Resource-dependent movement			
American desert locust	Climatic stress	Strong resource-dependent movement	Dieback/-off of massive agricultural fields or grasslands	Resource extinction
	Density-dependent phase polyphenism (solitary to gregarious)	Weak or no positive density-dependent movement	Decreased biodiversity and carbon sequestration	Metamorphosis
	Correlated reproduction	Addition of new individuals to front	Millions of US\$ lost in decreased crop revenue	Potentially compensatory predation
	Local overconsumption/patch formation	Gregarious		Migration
	Resource-dependent movement			
Gypsy moth	High rainfalls increasing plant quality	Taxis movement toward food/habitat	Massive defoliation of deciduous forest	Resource extinction
	Predator depletion	Addition of new individuals to front	Decreased biodiversity and carbon sequestration	Metamorphosis?
	Local overconsumption/patch formation	Weak, positive density-dependent movement	Millions of US\$ lost in decreased forestry revenue	Potentially compensatory predation
	Resource-dependent movement	Gregarious		Introduction
Rusty crayfish	Introduction	Strong resource-dependent movement	Complete loss of macrophytes from the littoral zone	Resource extinction
	Local overconsumption/patch formation	Weak or no positive density-dependent movement	Decreased biodiversity and carbon sequestration	
	Resource-dependent movement	Addition of new individuals to front	Decreased production of game fish (sunfish)	
		Gregarious		

(Continued)

Table 2 (Continued)

Common name	Formation	Persistence	Whole-ecosystem impacts	Breakup
European earthworm	Introduction	Strong resource-dependent movement	Drastic reductions in understory plant biomass	Still going
	Local overconsumption/patch formation	Weak or no positive density-dependent movement	Decreased biodiversity	
	Resource-dependent movement	Addition of new individuals to front	Long-term changes in evenness of adult tree dominance	
Cushion star	Spawning aggregation	Strong resource-dependent movement	Reduced primary production	?
	Local overconsumption/patch formation		Decreased sediment stabilization	
	Resource-dependent movement			
Crown-of-thorns sea star	Eutrophication-driven high recruitment	Strong resource-dependent movement	Die-off of reef ecosystem, algae proliferation	Resource extinction
	Predator depletion	Addition of new individuals to front	Decreased biodiversity and carbon sequestration	
	Local overconsumption/patch formation		Millions of US\$ lost in decreased tourist revenue	
	Resource-dependent movement			
Common sea star	Habitat-specific recruitment	Strong resource-dependent movement	Complete removal of extensive mussel beds	Resource extinction
	Local overconsumption/patch formation	Weak or no positive density-dependent movement	Millions of US\$ lost in decreased fishery revenue	
	Resource-dependent movement	Addition of new individuals to front		
Green sea urchin	Immigration	Strong resource-dependent movement	Removal of all macrophytes, loss of habitat structure and habitat	Disease or predator emergence
	Predator depletion	Weak or no positive density-dependent movement	Decreased biodiversity and carbon sequestration	
	Patch creation by storms	Addition of new individuals to front	Decreased production of game fish (e.g., rock fish)	
	Local overconsumption/patch formation			
	Resource-dependent movement			

(Continued)

Table 2 (Continued)

Common name	Formation	Persistence	Whole-ecosystem impacts	Breakup
Edible periwinkle	Disturbance allowing bloom of edible algae	Strong resource-dependent movement	Suppression of competitively dominant fast-growing algae	Resource extinction
	Taxis movement toward preferred food	Weak or no positive density-dependent movement	Facilitation of later successional species	
	Overconsumption	Addition of new individuals to front		
	Resource-dependent movement			
Wildebeest	Climatic stress	Strong resource-dependent movement	Conversion of tall-grass ecosystem into short grass	Climatic stress cessation
	Local overconsumption/patch formation	Weak or no positive density-dependent movement	Decreased biodiversity and carbon sequestration	Migration
	Resource-dependent movement	Gregarious		
Salt marsh fungus	Climatic stress	Facilitation by front-forming consumers	Massive ecosystem die-off, loss of shoreline protection	Climatic stress cessation
	Consumer facilitation		Loss of carbon sequestration, loss of nursery habitat	Resource extinction
	Local overconsumption/patch formation		Decreased biodiversity	Cold weather
Aspergillois sea fan disease	Climatic stress	Resource-dependent movement	Regional die-off of sea fans	Resource extinction
	Consumer facilitation	Weak or no positive density-dependent movement		
	Local overconsumption/patch formation	Addition of new individuals to front		
	Resource-dependent movement			
White pox disease	Climatic stress	Resource-dependent movement	Regional die-off of <i>Acropora palmata</i> , foundation species	Resource extinction
	Eutrophication	Weak or no positive density-dependent movement	Decreased biodiversity	
	Consumer facilitation	Addition of new individuals to front	Millions of US\$ lost in decreased tourist and fisheries revenue	

(Continued)

Table 2 (Continued)

Common name	Formation	Persistence	Whole-ecosystem impacts	Breakup
	Local overconsumption/ patch formation		Decreased shoreline protection	
	Resource-dependent movement			
Skeletal eroding band	Climatic stress	Resource-dependent movement	Regional mortality of multiple foundation species corals	Resource extinction
	Eutrophication	Weak or no positive density-dependent movement	Decreased biodiversity	
	Consumer facilitation	Addition of new individuals to front	Millions of US\$ lost in decreased tourist and fisheries revenue	
	Local overconsumption		Decreased shoreline protection	
	Resource-dependent movement			
White-band disease Type II	Climatic stress	Resource-dependent movement	Regional die-off <i>Acropora cervicornis</i> , foundation species	Resource extinction
	Consumer facilitation	Weak or no positive density-dependent movement	Decreased biodiversity	
	Local overgrazing	Addition of new individuals to front	Millions of US\$ lost in decreased tourist and fisheries revenue	
	Resource-dependent movement		Decreased shoreline protection	

^aText in red denotes the force that locally increases top-down control by consumers. Text in green denotes front-facilitating mechanisms that occur for all or almost all consumers.

of new animals to the front, through either reproduction (e.g., moths, locusts, bacteria, viruses, worms) or assimilation from the healthy area that is being consumed (e.g., marsh snails), also helps maintain front integrity for long periods of time (one year for snails, tens of years for urchins and earthworms).

Beyond the aggregation of consumers at vegetation edges, the impact that consumers have on their resource builds strongly on three forms of Allee effects. First, if a top predator of the consumer has a saturating functional response, but its population density is kept in check by processes other than the availability of this particular consumer, then a sufficient increase in consumer abundance will reduce the rate of mortality per prey, permitting even higher net consumer growth rates. This can permit outbreaks of a consumer that can then decimate its own resource. Second, if resources have defenses that can be disproportionately overwhelmed by increased consumer abundance, then consumption pressure may increase as resource abundance declines. Third, if resource growth is reduced at low resource density (for instance, because environmental conditions deteriorate when

resource abundance declines), then the resource may collapse. These positive, density-dependent effects can also, we suggest, enhance the sharpness of both sides of the front's borders and may also contribute to the often striking linearity of the front formation.

A mathematical model presented in Silliman et al. (2005) illustrates the result of combining resource-dependent consumer movement with an Allee effect (often stress dependent) in the resource. Here, reduced aeration of the soil, caused by the decline of vegetation, is presumed to reduce vegetation regrowth in a salt marsh when a snail front has drastically reduced vegetation density. Both processes have large impacts on the shape and velocity of the wave front. Although the formal mathematical work has yet to be done, our intuition is that this will further reveal how aggregative movement of consumers into fronts, in combination with increasing abiotic stress negatively affecting resource growth, influences front formation and drives runaway ecosystem collapse.

Other factors promoting consumer fronts and their impacts are suggested by the examples we have surveyed. First, consumer-front formation is most likely to occur and impacts are strongest when the prey resource is almost a continuum in space, with little patchiness or dramatic spatial heterogeneity (e.g., see **Figures 1, 2, 8, and 9**). In species-rich plant communities, specialist herbivores are likely to encounter their resource plants in a patchy and heterogeneous way, so they may be less prone to generating dramatic consumer fronts. Second, local population densities of the consumer must neither experience strong demographic effects of the local decline of the resource (e.g., starve) nor experience amplified predation pressure, which would break up the front. In many of the examples discussed above, the consumers solve both local resource depletion and local predator buildup either by moving toward a higher resource concentration or by outrunning predators, as with the wildebeest in the Serengeti (Sinclair 1977).

Taken together, these convergent mechanisms across divergent systems reveal that the phenomena of consumer fronts represent a unique manifestation of top-down control that is an emergent property of interactions among consumer-strengthening stressors, organism movement behavior, and spatial processes. Consumer fronts form after external forces have locally increased top-down control by consumers beyond prey carrying and/or renewal capacity, and resource-dependent movement leads to consumer aggregation along the edge of the remaining prey population. Consumer waves then spatially propagate through ecosystems due to continued overexploitation and density-dependent feedbacks. Although there are many reasons fronts subside (**Table 2**), their spatial and temporal extent are often large enough to commonly lead to massive loss and/or transformation of ecosystems and the services they provide.

5. HUMAN ACTIVITIES LIKELY AMPLIFY CONSUMER FRONTS

Research has definitively shown that human activities directly impact the mechanisms leading to front formation. Nearly all of the external forces identified in our survey that stimulate local increases in the top-down strength of consumers, including predator depletion, drought, excess rainfall, temperature increases, and nutrient enrichment, are impacted by human activities (Halpern et al. 2009). Because anthropogenic forces globally increase the intensity and frequency of these top-down strengthening forces through amplification of climate change, watershed development, and killing of predators, our study warns that ecosystem-destroying consumer fronts will likely become more frequent and more destructive. Currently, this possibility is not often considered in ecological and conservation models and theory. Our study, however, shows that it should be broadly incorporated, as feeding-front intensity and occurrence have already been increasing at alarming rates over the past 1–2 decades both on coral (Ormond et al. 1973, Laxton 1974, Kayal et al. 2012) and in salt marshes (Silliman et al. 2005, Angelini & Silliman 2012).

6. ADVANCES IN OUR THEORETICAL UNDERSTANDING OF TOP-DOWN CONTROL OF ECOSYSTEM STRUCTURE AND RESILIENCE

6.1. Consumer Fronts Are Not Rare, but Common Across Taxa and Ecosystems

Though often mentioned in ecology textbooks, consumer fronts are widely considered to be unusual, spectacular events that are not general across taxa or ecosystems (e.g., mention of locusts as powerful, but rare, events). This review challenges this notion and shows that consumer fronts occur across diverse ecosystems (up to 11), including rocky intertidal, subtidal sand flats, salt marshes, kelp beds, mussel beds, coral reefs, seagrasses, grasslands, forests, and agricultural fields (**Table 1**), and can be driven by a wide array of consumer species spanning freshwater, terrestrial and marine realms, and all kingdoms, including 10 phyla. Affected taxa include bacteria, fungi, viruses, molluscs, annelids, echinoderms (sea stars, sea urchins), crustacea, insects, amphibians, and mammals (wildebeests) (**Table 1**). Given the widespread taxonomic and geographic extent of front-forming consumers and the fact that they share key characteristics (strong resource dependency and negative or weak positive density-dependent movement) with many other organisms (e.g., other species of snails, crabs, insects, ungulates), the potential for consumer fronts is more widespread than previously thought and increases with amplifying consumer impacts. It is essential that these novel insights be incorporated and further tested in future ecological and conservation research.

6.2. Predicting Ecosystem-Level Impacts of Consumer Fronts Is Primarily Dependent on Prey Functional Type, Not Trophic Level

Food-web theory posits that the number of trophic levels in a food chain is a good predictor of whether foundation species (and thus ecosystem stability) will be facilitated or depressed by cascading consumer impacts. For example, the presence of three-level food chains such as the sea otter–urchin–sea kelp system should protect basal, habitat-forming species (Hairston et al. 1960, Estes & Palmisano 1974, Fretwell 1977), whereas four-level chains such as the killer whale–sea otter–urchin–sea kelp system should lead to high grazer stocks and a consumption-controlled ecosystem (Fretwell 1977, Estes et al. 2010). Our review suggests that, when consumers aggregate, food-chain length alone is likely not the best predictor of the susceptibility of a foundation species to wholesale reduction of ecosystems. Instead, the key predictor of consumer impact in these types of systems will likely be whether the prey functional group is a foundation species and if it can be replaced by an unpalatable species (which may even facilitate the consumer by providing refuge) (see Orrock et al. 2010). If the prey is a foundation species that cannot be quickly replaced, as can be the case in coral reefs, salt marshes, mussel beds, kelps, and forests, then the whole-ecosystem impacts of the consumer fronts will be strong, long lasting, and devastating to biodiversity and ecosystem services.

6.3. Physical Stress Often Stimulates Consumer-Front Formation and Amplifies Top-Down Control

Current environmental stress (ES) models predict that increases in physical stress will lead to decreased top-down control of community structure (Menge & Sutherland 1976, 1987; Bruno et al. 2003). Challenging this view, we predict that amplification of top-down control of ecosystems by physical stress is much more common in nature than currently appreciated and occurs when habitat-forming prey are relatively more susceptible to physical stress. We term this new idea

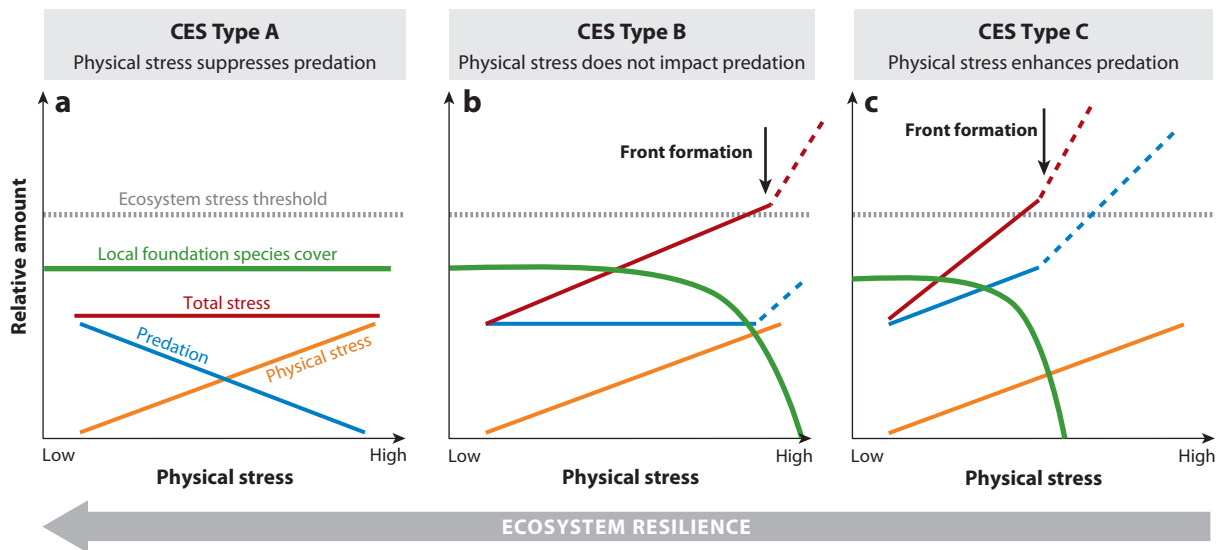


Figure 12

Consumer–environmental stress (CES) model. (a) Type A consumer–stress functional relationship. This relationship is presented in the traditional Menge–Sutherland environmental stress model wherein the relative strength of predation decreases with increasing physical stress. Foundation species cover is predicted not to change because total stress does not eclipse stress thresholds. (b) Type B consumer–stress functional relationship. Predation does not change as physical stress increases, so total stress increases and eclipses ecosystem threshold stress at high physical stress levels. Foundation species cover is predicted to collapse but only at high physical stress levels, leading to consumer–front formation (*dashed lines*) and further escalation of stress. (c) Type C consumer–stress functional relationship. Predation increases as physical stress increases, resulting in total stress levels increasing at the fastest rate. Consequently, total stress is predicted to eclipse ecosystem thresholds and drive the collapse of foundation species cover and formation of consumer fronts at moderate abiotic stress levels.

the synergistic stress hypothesis (SSH). To begin integrating the SSH into theory, we expand the current ES model to incorporate positive functional responses of consumers to physical stress. We then discuss implications of the SSH for predicting ecosystem stability and resilience, especially in relation to cases where climate change is predicted to amplify physical stressors.

Traditional ES models predict that consumer pressure and control of community structure will decrease with increasing environmental stress (Menge & Sutherland 1976, Menge & Sutherland 1987). According to a major assumption of the qualitative model, this negative relationship occurs because consumers are more susceptible than their prey are to physical stress. Such a functional relationship between physical and consumer stress in the ES model means that the total of these two stressors (i.e., the sum of consumer stress and physical stress) should remain approximately equal as physical stress increases (**Figure 12a**). Support for this model has been mixed and reveals that it can break down when its major assumption (prey are more susceptible to stress) is violated (Menge & Farrell 1989).

In contrast, our broad survey suggests that the ES model does not break down under these conditions, but instead that the functional relationship between consumer and physical stress is often reversed (**Figure 12b,c**). In more than half of our examples, increasing physical stress increases top-down control of prey and the ecosystem (**Table 2**). Incorporation of this positive, functional relationship between consumer and physical stress leads to completely different predictions. For example, when consumer stress increases with increasing physical stress, total ecosystem stress increases in an additive or possibly multiplicative way—a relationship that can rapidly lead to an

eclipse of threshold stress levels for ecosystems (**Figure 12b,c**) and the subsequent local collapse of foundation species. Combining the SSH with the ES model leads to a consumer–environmental stress (CES) model generating three different functional relationships that can occur between consumer and physical stress: As physical stress increases, consumer stress can either decrease, as in the traditional ES model (Type A), stay the same (Type B), or increase (Type C) (**Figure 12**). Lafferty & Holt (2003) explored comparable issues regarding the impacts of stress and infectious disease on hosts, and they likewise suggested that this range of possibilities may arise.

The CES model also predicts that, at threshold stress levels for foundation species, consumers can locally overconsume their prey and, if conditions are ripe (see **Table 2**), trigger consumer–front formation and subsequent runaway consumption in adjacent habitats (**Figure 12b,c**). In this scenario (e.g., in southern US salt marshes), the consumer front starts in the area of highest physical stress, but once initiated and local overconsumption has occurred, it moves to areas of lower physical stress where prey resources still occur, causing further ecosystem loss over a larger landscape owing to greatly increased consumer stress (Silliman et al. 2005). The CES model thus predicts that ecosystems characterized by Type B and Type C consumer–stress functional relationships are both less stable and less resilient because of their propinquity for additive or synergistic effects between abiotic and consumer forces and the potential for subsequent consumer–front formation.

Collectively, this review reveals that many natural systems are characterized by Type B and Type C consumer–stress functional relationships (**Table 2**). If this finding is general across more ecosystems, then increasing climate stress that amplifies physical stressors (e.g., increased drought, increased water or air temperatures) is likely to generate more, stronger, and longer-lasting consumer fronts. As a result, the impact of consumers on ecosystems during the current stage of accelerated global change may occur more quickly and to more devastating effects than is currently predicted.

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