Ecology of harvest-driven trait changes and implications for ecosystem management

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Running heads:

Harvest of wild animals and plants is pervasive, exerts ecological and evolutionary pressure on populations, and is known to drive rapid changes in organismal traits. Although the factors that lead to rapid trait changes have received increased attention, the ecological consequences of harvest-driven trait changes are less appreciated. We review recent evidence that harvest-driven trait changes can affect community and ecosystem processes. Growing experimental evidence, modeling studies, and field observations have revealed that common responses to harvest include changes in life-history and behavioral traits, which have the potential to reshape the ecology of harvested systems. On the basis of existing evidence, we propose a set of general mechanisms that link harvest-driven trait changes to ecological processes, including trophic cascades, nutrient dynamics, keystone interactions, ecosystem stability, and habitat use. Managing harvested ecosystems sustainably may require strategies that account for harvest-driven trait changes. We recommend that trait changes be monitored closely as part of ecosystem-based

management plans, especially in cases where targeted traits are known to affect important aspects of ecosystem function.

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In a nutshell:

- Humans harvest a large percentage of the wild animal and plant species on Earth
- Hunting, fishing, and collecting are known to change the traits of wild populations, but the ecological consequences of these changes are not well understood
- Life-history and behavioral traits are particularly responsive to harvest and underlie many important aspects of ecosystem function
- As the number of species affected by harvest continues to rise, conservation and management strategies should account for trait responses and their potential impacts on critical ecosystem functions

The harvest of wild animal and plant populations is pervasive and represents a principal driver of contemporary trait change (Darimont *et al.* 2009). According to the International Union for Conservation of Nature (IUCN), over two thousand species of plants and animals are endangered or critically endangered as a result of overharvesting (IUCN 2015). We consider harvest to include the taking from the wild of any non-domesticated organisms intended for human consumption or other uses. Motivations and methods of harvest are diverse; they include legal hunting and fishing, and illegal poaching for subsistence, recreational, and commercial uses. Harvest also involves the removal from the wild of live organisms for a variety of purposes, most notably the international pet trade. Our definition of harvest is intended to be broad, given that any removal of individuals from wild populations has the potential to drive trait changes.

The ecological effects of harvesting wild animals and plants have traditionally been viewed through the lens of reduced abundance. For example, harvest-driven reductions in the abundance of top predators have been shown to drive trophic cascades in freshwater, marine, and terrestrial ecosystems worldwide (Estes *et al.* 2011). However, harvest can also cause rapid phenotypic changes in wild populations (Darimont *et al.* 2009). Importantly, the phenotypic responses of these populations to harvest often involve traits with known importance for ecological dynamics, such as body size and feeding behavior (Heino *et al.* 2015). The existing

literature has focused primarily on assessing rates of observed phenotypic changes, distinguishing evolution from phenotypic plasticity, and assessing consequences for population dynamics (Dunlop *et al.* 2015; Eikeset *et al.* 2016). The impact of harvest-induced trait changes for communities and ecosystems has received considerably less attention, despite emerging evidence that contemporary human-driven evolution can be an important driver of community and ecosystem dynamics (Palkovacs *et al.* 2012; Fraser 2013).

Current information supports harvest as a strong driver of trait change via a combination of demographic (age structure), evolutionary (genetic), and plastic (non-genetic) changes (Heino *et al.* 2015). Experimental harvests in guppies (*Poecilia reticulata*) and zebrafish (*Danio rerio*) were found to cause shifts in phenotypic traits and at functional genetic loci (van Wijk *et al.* 2013). Evolutionary effects in real-world harvested populations have been more difficult to isolate. Recent work on Atlantic cod (*Gadus morhua*) supports an important role for evolution in shifting age and size at maturation, with demographic and phenotypic contributions varying depending on density-dependent growth (Eikeset *et al.* 2016). Likewise, research on bighorn sheep (*Ovis canadensis*) reveals that declines in male horn length were accompanied by genetic changes indicative of evolution (Pigeon *et al.* 2016). Although both genetic and phenotypic changes can have important ecological consequences (Lundsgaard-Hansen *et al.* 2014), no studies have isolated these effects in the context of harvest. The rate at which traits recover after the cessation of harvest may depend on the causal mechanisms, with demographic and plastic changes recovering more quickly than genetic changes (Salinas *et al.* 2012). Here we focus our attention on the ecological consequences of overall changes in phenotypes because this is what field studies have generally documented and what is most immediately relevant for management.

The efficiency of modern human harvesting methods leads to rapid rates of trait change (Darimont *et al.* 2009). However, these effects are not new and are not restricted to modern harvesting technologies. Declines in body size have been attributed to harvest by indigenous hunter-gatherer groups in a variety of ecosystems. For instance, the early indigenous people of Caribbean Panama drove declines in the size of the edible conch (*Strombus pugilis*) (O'Dea *et al.* 2014). Similarly, the native people of the San Francisco Bay area caused declines in the size of white sturgeon (*Acipenser transmontanus*) (Broughton *et al.* 2015). Selective forces caused by indigenous harvest practices may have produced changes over spans of centuries, whereas

modern harvest has accelerated rates of change and expanded their geographic scope (Roy *et al.* 2003).

Harvest can alter traits that are directly targeted by harvesters (eg body size) and associated traits (eg fecundity, egg size) (Walsh *et al.* 2006). A wide variety of traits may be subject to selection, but in terms of their importance for ecological interactions, two sets of traits that commonly respond to harvest may be particularly important – life-history traits and behavioral traits. For life-history traits, there is strong evidence that harvest drives decreased age and size at maturity (Heino *et al.* 2015). This shift in age and size aligns with classic predictions from life-history theory based on the effects of increased mortality rates (Stearns 1992). In terms of behavioral traits, harvest tends to remove the boldest, most active individuals, thereby selecting for shyness and inactivity (Biro and Post 2008; Uusi-Heikkila *et al.* 2008; Arlinghaus *et al.* 2017). Such a behavioral shift is in general accordance with the classic trade-off between acquiring resources and avoiding predation (Lima and Dill 1990).

Changes in life-history and behavioral traits may affect a wide variety of harvested species and ecosystems (Figure 1). Behavioral responses have been widely observed in both aquatic and terrestrial species, whereas life-history shifts have been primarily documented in aquatic species (Kuparinen and Festa-Bianchet 2017). This disparity may be due to a combination of factors, including differences in growth strategies, harvest methods, and exploitation rates. Harvested aquatic species exhibiting strong life-history shifts typically display indeterminate growth (continuous growth throughout life) and have been subject to high exploitation rates in size-selective commercial fisheries. In contrast, examples from terrestrial species come primarily from species with determinate growth (growth ceases at maturation) that have been subject to recreational hunting at much lower, but still highly selective, levels. Nonetheless, evidence is emerging that recreational harvest of terrestrial mammals can cause life-history shifts (Kuparinen and Festa-Bianchet 2017). Trait changes in terrestrial species that have been subject to high rates of commercial exploitation, such as the near-extermination of bison (*Bison bison*) and beavers (*Castor canadensis*) from large portions of North America, have not been evaluated for evidence of trait change. The multitude of species affected by historical and current hunting undoubtedly include many undocumented and unexplored cases of trait change.

Ecosystem consequences

Studies to date indicate that harvest-driven trait changes may affect community and ecosystem processes (Figure 2) in various ways, including the (1) strength of trophic cascades, (2) rates of nutrient recycling and translocation, (3) activities of keystone species and ecosystem engineers, (4) ecosystem stability, and (5) patterns of habitat use. For each potential mechanism, our reference point is the unharvested state of the system, and our predictions are based on expected trait changes and resulting ecological changes. In harvest scenarios, evolution can prevent extinction (Dunlop *et al.* 2015), thereby maintaining community structure. The effect of evolution on population persistence has been explored in detail elsewhere (Carlson *et al.* 2014). Here we focus on the effects of trait changes on ecological interactions. We review evidence from theoretical models, experiments, and observational studies of harvested ecosystems and explore implications for managing these ecosystems.

Theoretical models

Modeling studies have explored the potential effects of trait change on the strength of trophic cascades and the stability of ecosystem processes (Figure 2). Ecogenetic models have played a major role in improving our understanding of the consequences of fishing for the evolution of life-history traits and for population dynamics under harvest and recovery (Dunlop *et al.* 2015). Despite their widespread use in fisheries ecology, ecosystem models are just beginning to be applied to examine ecological responses to harvest-induced trait changes. Several recent studies suggest that even modest rates of decline in body size can have ecosystem effects comparable to the direct effects of fishing on population size (Audzijonyte *et al.* 2014). Modeled food web interactions suggest that trait changes may amplify the effects of fishing on targeted stocks. Smaller body size increases vulnerability to predators and can therefore increase natural mortality rates, which can further reduce population abundance and hinder post-fishing recovery (Audzijonyte *et al.* 2014). Reduced body size can also affect the strength of trophic cascades by reducing per-capita consumption rates of harvested predators (Audzijonyte *et al.* 2014). Food web models also suggest that evolution of smaller size and earlier age of maturation may destabilize ecosystems, leading to large population and biomass fluctuations at multiple trophic levels (Figure 3) (Kuparinen *et al.* 2016). However, by increasing population size, adaptation can also support the presence of more, larger fish even under high fishing mortality. These larger fish

often occupy a higher trophic position, leading to increased variation or trophic scope of the population, which may have important consequences for food web dynamics (Kindsvater and Palkovacs 2017). At the same time, harvesting may change behavioral traits, for example by reducing boldness and inducing prey switching that may further amplify the strength of trophic cascades. These types of changes can lead to ecosystem state shifts if, for example, a prey species released from predation increases in abundance and begins to consume large numbers of juvenile predators (Audzijonyte *et al.* 2014). Importantly, models suggest that the ecological changes caused by harvest-induced downsizing amplify the effects of fishing, perhaps making ecosystems more vulnerable to the effects of overfishing than previously thought (Kuparinen *et al.* 2016).

Experimental evidence

Experimental studies have revealed important effects of trait change on the strength of trophic cascades and rates of nutrient recycling (Figure 2). Experimental work in Trinidadian guppies (*P reticulata*) shows that, when translocated from streams with predators to streams without predators, these fish underwent rapid evolutionary change, maturing at a later age and larger size (Reznick *et al.* 1990). These introduction experiments can serve as a useful analogy for understanding the evolution of life-history traits under harvest (Reznick and Ghalambor 2005). Experiments in captive guppy populations demonstrate that body size and associated genetic markers respond to size-selective harvest over four generations, where the removal of large individuals rapidly decreased mature body size in the population (van Wijk *et al.* 2013).

Recent experiments extend this work on guppy evolution to examine consequences for communities and ecosystems (Palkovacs *et al.* 2009; Bassar *et al.* 2010; El-Sabaawi *et al.* 2015). In addition to exhibiting shifts in life-history traits, guppy populations that have adapted to the presence of predators display differences in feeding behavior and nutrient excretion rates. Consistent with a trade-off between acquiring resources and avoiding predation, guppies from high predation localities exhibit reduced feeding rates as compared to guppies from low predation sites (Palkovacs *et al.* 2011). Perhaps because of lower population densities and reduced intraspecific competition, high predation guppies are more selective for high-quality food items, in particular invertebrate prey high in phosphorus content (Zandonà *et al.* 2011). Due to their smaller size, high predation guppies also recycle nitrogen and phosphorus at higher rates

(on a per gram basis) than do guppies from low predation sites (Palkovacs *et al.* 2009). This combination of traits leads to a suite of ecosystem changes; ecosystems with high predation guppies consistently show lower invertebrate biomass and higher algal biomass (Palkovacs *et al.* 2009; Bassar *et al.* 2010; El-Sabaawi *et al.* 2015). The ecosystem shift caused by guppy evolution is not subtle. The effects of guppy trait change on ecosystem properties are equivalent to other "classic" ecological drivers such as guppy invasion (Palkovacs *et al.* 2009), guppy density (Bassar *et al.* 2010), and light availability (El-Sabaawi *et al.* 2015).

Observational evidence

Studies of harvested ecosystems show that harvest-driven trait changes can impact trophic cascades, nutrient recycling and translocation, the activities of keystone species and ecosystem engineers, and patterns of habitat use (Figure 2). Perhaps the best-studied example of fisheries-induced evolution of life-history traits and body size in the wild comes from Atlantic cod. Populations from across the North Atlantic have experienced substantial shifts in age and size at maturation indicative of fisheries-induced evolution (Heino *et al.* 2015). Reduced body size in cod releases planktivorous prey fishes from predation pressure, leading to large-scale trophic cascades (Shackell *et al.* 2010). The effects of life-history evolution for population recovery have received some attention; evolutionary responses are predicted to slow population recovery after the cessation of fishing (Dunlop *et al.* 2015). However, food web changes that result from reduced body size may further impede population recovery if predators increasingly become prey. Such ecological changes may be contributing to the failure of cod stock recovery (Swain 2011).

Nutrient dynamics can be affected by changes in the body size of harvested fishes. Anadromous fishes migrate from the ocean into fresh water to spawn and, in doing so, move marine-derived nutrients into coastal freshwater ecosystems (Schindler *et al.* 2003). Anadromous species – including sockeye salmon (*Oncorhynchus nerka*), Chinook salmon (*Oncorhynchus tshawytscha*), and alewife (*Alosa pseudoharengus*) – show evidence of harvest-driven changes in life-history traits and body size (Davis and Schultz 2009; Kendall *et al.* 2014; Lewis *et al.* 2015). Reductions in body size for these species decrease phosphorus imports into freshwater ecosystems (Twining *et al.* 2016). Harvested fishes not only translocate nutrients between ecosystems, but also recycle nutrients within ecosystems. In the tropical rivers of Venezuela, the

flannelmouth caracin (*Prochilodus mariae*) is the principal fish species shaping nutrient dynamics. Size-selective harvest has reduced body size of this species markedly, with important consequences for detrital processing and nutrient recycling (Taylor *et al.* 2006).

Ecosystem impacts of harvest-driven trait changes are particularly strong when they disrupt interactions involving keystone species and ecosystem engineers. The maintenance of diverse ecosystem processes depends on keystone interactions involving harvested species. In the seasonally flooded forests of South America, frugivorous fish species are the principal vectors for seed dispersal, structuring the plant community of the forest itself. Seed dispersal effectiveness increases with body size; larger fish disperse greater numbers of seeds from a wider diversity of plant species (Anderson *et al.* 2011; Correa *et al.* 2015). Thus, harvest-induced reduction in body size has the potential to alter the diversity and structure of flooded forests.

In the marine environment, keystone predators and ecosystem engineers can maintain the structure of the ecosystem. In kelp forests, predation on urchins is critical for maintaining habitat structure. In California, larger California sheephead (*Semicossyphus pulcher*) consume greater numbers and larger sizes of urchins (*Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*), exerting more top-down control on urchin populations (Hamilton and Caselle 2015). Harvest-driven reductions in sheephead size release urchins from top-down control, potentially leading to the loss of kelp. Likewise, in eastern Tasmania, harvest-driven reductions in the body size of spiny lobsters (*Jasus edwardsii*) release urchins from predation (Ling *et al.* 2009). Kelp forest ecosystems display alternative stable states, and the loss of large lobsters has led to an ecosystem state shift from kelp beds to urchin barrens (Ling *et al.* 2009) (Figure 4). On coral reefs, large parrotfish (*Bolbometopon* spp) act as dominant grazers and bioeroders, reducing algal accumulation on coral polyps and creating sediment for reef flat habitats (Bellwood *et al.* 2012). Heavy fishing in parts of the Australian Great Barrier Reef has reduced parrotfish size, decreasing algal consumption rates and contributing to a transition from a coral-dominated to an alga-dominated ecosystem (Hoey and Bellwood 2008).

Harvesting can shift behavior in ways that not only affect habitat use and feeding patterns but also induce trophic cascades. In temperate forests in North America and Europe, selection on elk (*Cervus canadensis*) and red deer (*Cervus elaphus*) from trophy hunting targets bolder and more active individuals (Ciuti *et al.* 2012; Lone *et al.* 2015). Changes in behavior and habitat use by elk and other mammalian herbivores may, in turn, influence patterns of plant regeneration.

Brown bears (*Ursus arctos*) in Scandinavia change their habitat use to avoid encounters with hunters and, in doing so, may change interactions with their own prey species (Ordiz *et al.* 2012) as well as with humans (Steyaert *et al.* 2016). Harvest also affects migratory behavior in some ungulate species, thereby redistributing herbivory across the landscape (Loe *et al.* 2016). For mesocarnivores that are hunted and harassed, the fear of humans and domestic dogs changes vigilance and feeding behavior in ways that can lead to trophic cascades (Clinchy *et al.* 2016; Suraci *et al.* 2016). It would be worthwhile to explore similar effects in other species – for example, the potential for humans to change the ecosystem engineering behavior of beavers in ways that might change aquatic and riparian ecosystems.

Implications for conservation and management

To maintain selected aspects of ecosystem function, resource managers may be required to reduce trait changes or restore trait values in harvested species. This will necessitate implementing management strategies – including decreasing harvest rates and harvest selectivity, as well as creating refuges – that maintain plasticity and genetic variation within populations. Such approaches will be important for integrating harvest-induced trait change into ecosystem-based management (EBM).

Decreasing harvest rates and selectivity

When natural selection acts in opposition to harvest selection, managing trait changes can be achieved by decreasing harvest mortality (Edeline *et al.* 2007). Balanced exploitation, in which harvest is distributed across many species, can reduce the selective pressure on a few of the targeted species without decreasing the overall harvested biomass (Garcia *et al.* 2012). This strategy may be effective when applied to communities of harvested species that all contribute to a shared ecosystem function, such as grazers that consume algae on coral reefs or frugivores that disperse seeds in tropical forests.

In combination with reducing harvest rates, decreasing harvest selectivity can substantially slow trait change. Reducing selectivity can be achieved by switching or rotating through different gear types or harvesting methods, each of which targets individuals with different sets of traits (Martinez *et al.* 2005; Pauli *et al.* 2015). To combat the truncation of size distributions, many recreational fisheries rely on slot limits, which specify both a minimum and

maximum legal size at which an individual can be harvested. While minimum size limits alone tend to impose strong size selection on exploited populations, slot limits protect the largest individuals, thereby reducing the strength of directional selection (Matsumura *et al.* 2011). In sequential hermaphrodites and species characterized by marked sexual dimorphism with respect to body size, size-selective harvest can skew sex ratios, which can have its own effects on ecosystem processes (Fryxell *et al.* 2015). Slot limits can be used to maintain balanced sex ratios for such species.

Establishing refuges and protected areas

Protected areas can be effective tools for maintaining genetic variation in populations connected by gene flow. Inside reserves, the natural selection regime is maintained. Gene flow out of the reserve can slow the rate of trait changes in nearby harvested populations. This strategy is analogous to the agricultural practice of deliberately avoiding the application of pesticides on selected fields adjacent to crops to prevent the fixation of genes conferring pesticide resistance in crop pests. Various implementations of marine protected areas (MPAs) have shown that reserves can reverse shifts in size distribution imposed by selective harvest. MPAs have been effective at restoring large lobsters, allowing them to once again control sea urchins and shift the state of the ecosystem from urchin barrens back to kelp beds (Ling *et al.* 2009) (Figure 4). Analyses of global case studies have demonstrated that even long-lived, slow-growing species can recover to sustainable size distributions within 5 years of enacting no-take zones (Babcock *et al.* 2010). However, reserves alone may be ineffective at reversing evolutionary changes, necessitating their use in combination with other strategies for managing the magnitude and selectivity of harvest outside of the reserve (Dunlop *et al.* 2009).

Spatial restrictions are less effective for managing the harvest of wide-ranging species or species that make long-distance migrations (Miethe *et al.* 2011). For migratory species, harvest may drive changes in movement patterns, favoring individuals that either do not move through harvested areas or that move during times when harvest pressure is low. For such species, care should be taken to avoid harvest selection that would change migratory behavior, given that such behavior can be a major driver of community and ecosystem processes. It is important to protect the migratory species' life stages that are most evolutionarily responsive to harvest. Specifically, protecting areas where both adults and juveniles feed and grow may be more effective at

reducing harvest-driven trait changes than protecting adults alone in spawning areas (Dunlop *et al.* 2009; Miethe *et al.* 2011). Non-static refuge types such as dynamic protected areas and time–area closures in fisheries have received little attention from the standpoint of managing trait change, but may be an effective approach for highly migratory species.

Integrating trait changes into ecosystem-based management

EBM has emerged as a holistic alternative to single-species management (Laugen *et al.* 2014). Broadly defined, EBM seeks to maintain an ecosystem's biodiversity and function. While management actions used in this approach vary, ecosystem-based approaches focus on maintaining target levels for various physical and biological indicators of ecosystem health. Integrating trait change into EBM is likely important for maintaining sustainable harvests and other ecosystem services (Laugen *et al.* 2014). Species-specific targets for trait values could be considered in EBM plans, and traits of harvested populations could be monitored as early warning signs of ecological regime shifts. For instance, rapid changes in the life-history traits of Atlantic cod were observed prior to the collapse of the fishery (Olsen *et al.* 2004). Had these changes been detected earlier, the effects of the collapse might have been lessened or avoided. For some traits, such as predator body size, changes can cause major shifts in ecosystem state (Ling *et al.* 2009; Shackell *et al.* 2010). Therefore, management limits for allowable trait changes could be considered, based on ecological information, such as empirical predator–prey body size relationships and the propensity of harvested ecosystems to exhibit non-linear behavior such as threshold dynamics or alternative stable states.

Despite recent progress toward understanding the ecological impacts of harvest-driven trait changes, some important knowledge gaps remain. First, there is limited direct evidence from terrestrial ecosystems linking trait changes to ecological outcomes. In addition to behavioral changes, harvest in terrestrial species often affects sexually selected traits such as horns, antlers, and tusks (Chiyo *et al.* 2015; Pigeon *et al.* 2016). Such traits can serve as defensive weapons against predators, and their reduction or loss may have implications for predator–prey interactions, which deserve further study. Second, existing evidence for harvest-driven trait changes comes primarily from regulated commercial and recreational harvests. These harvest systems often rely on modern technology and are closely monitored by fishery and wildlife managers. The many other forms of harvest, which may rely on traditional technologies and

informal management, warrant monitoring for evidence of such changes and their ecological consequences. Finally, the interacting effects of harvest and climate change on traits and ecosystems are largely unknown. Many traits that respond to harvest are also expected to respond to climate change. For example, both harvest and climate warming are predicted to select for reduced body size, but the magnitude of such shifts is expected to differ between organisms and ecosystem types (Forster *et al.* 2012). How harvesting and climate change will interact to shape traits and ecological processes across a range of climate and harvest scenarios deserves detailed attention.

Conclusions

As the number of harvested species continues to rise, scientists and resource managers need to update ecosystem management strategies with current ecological and evolutionary knowledge. Existing evidence suggests that harvest is causing rapid changes to the traits of individuals within wild populations. Many of these traits play an important role in community and ecosystem processes. The use of adaptive management strategies may enable scientists and resource managers to examine key aspects of how harvest-driven trait changes are reshaping community and ecosystem processes. We propose that contemporary trait change and its ecosystem consequences be considered in the development and implementation of conservation and management plans.

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Supporting Information

Additional, web-only material may be found in the online version of this article at

*Figure 1. Examples of changes in the traits of harvested species that alter abiotic or biotic conditions, influencing community interactions and ecosystem functions. (a) Decreased body size of Atlantic cod (*Gadus morhua*) affects the strength of marine trophic cascades. (b) Decreased body size of Chinook salmon (*Oncorhynchus tshawytscha*) reduces rates of nutrient transport between marine and freshwater ecosystems. (c) Altered habitat use by red deer (*Cervus elaphus*) influences the ability of plant communities to regenerate.*

Credits:

    (a) NOAA

    (b) M Humling/USFWS

    (c) License: CC0/Pixabay

Figure 2. Potential mechanisms determining the impacts of harvest-driven trait changes on community and ecosystem processes. These mechanisms derive from a variety of types of evidence (theoretical models, experiments, and observational studies of harvested ecosystems) and include examples from various organisms and ecosystem types.

Figure 3. *Evolution caused by fishing can lead to large fluctuations in population densities across multiple trophic levels (adapted from Kuparinen* et al. *2016). Fisheries-induced changes in size and maturation age for Eurasian perch (*Perca fluviatilis*) and European whitefish (*Coregonus lavaretus*) in central Europe's Lake Constance are predicted to increase the magnitude of variation in total ecosystem biomass (black line represents the case with no evolution; red line represents the case with evolution).*

Figure 4. *Harvest-driven trait changes can cause major ecosystem state shifts, such as the transition between alternative stable states – in this case from kelp beds to urchin barrens when spiny lobster (*Jasus edwardsii*) body size is reduced (adapted from Ling* et al. *2009). Knowledge of trait-dependent ecological interactions, ongoing trait monitoring, and management limits for trait change may be useful for preventing undesirable ecosystem state shifts, which can be difficult to reverse*.
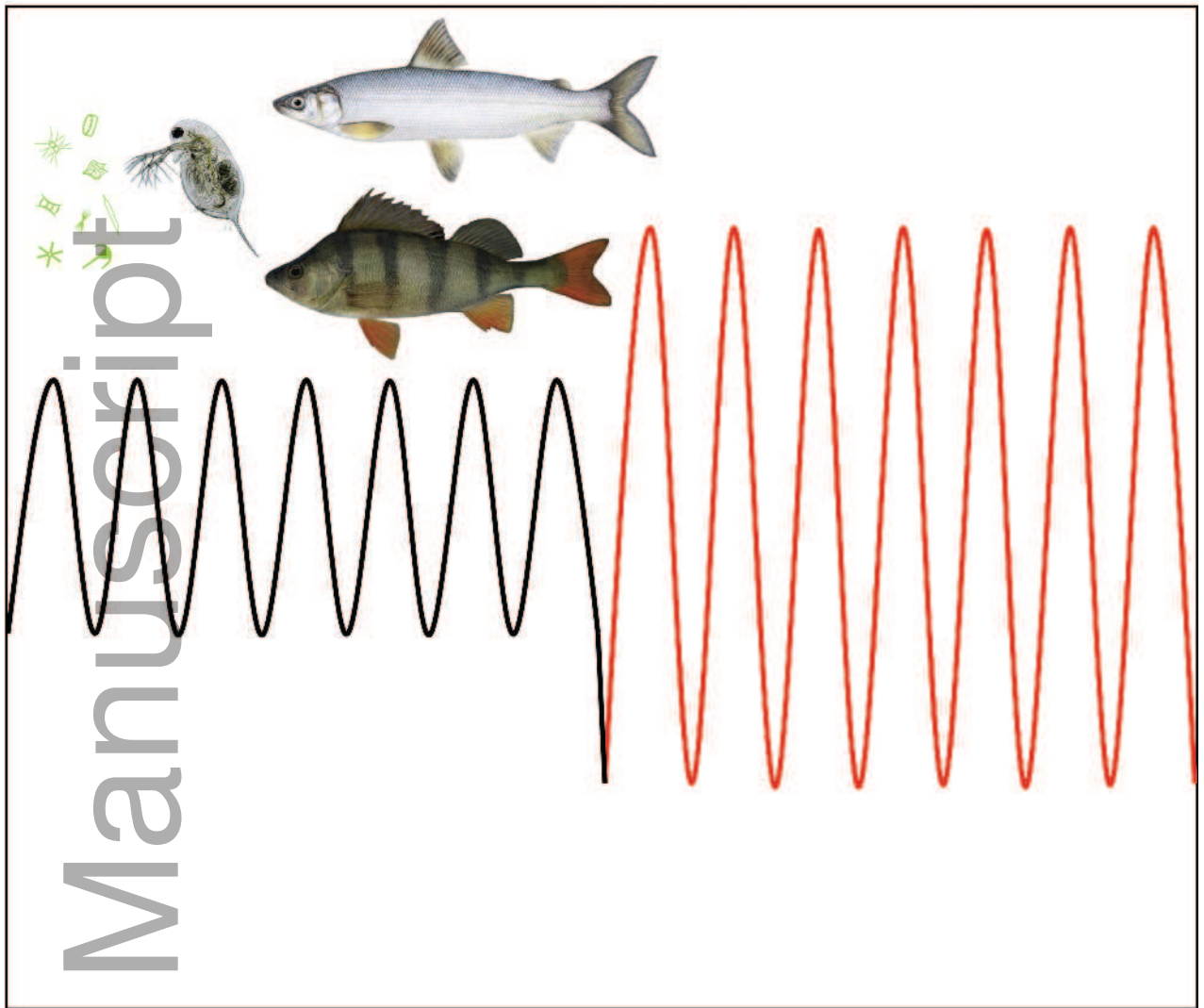
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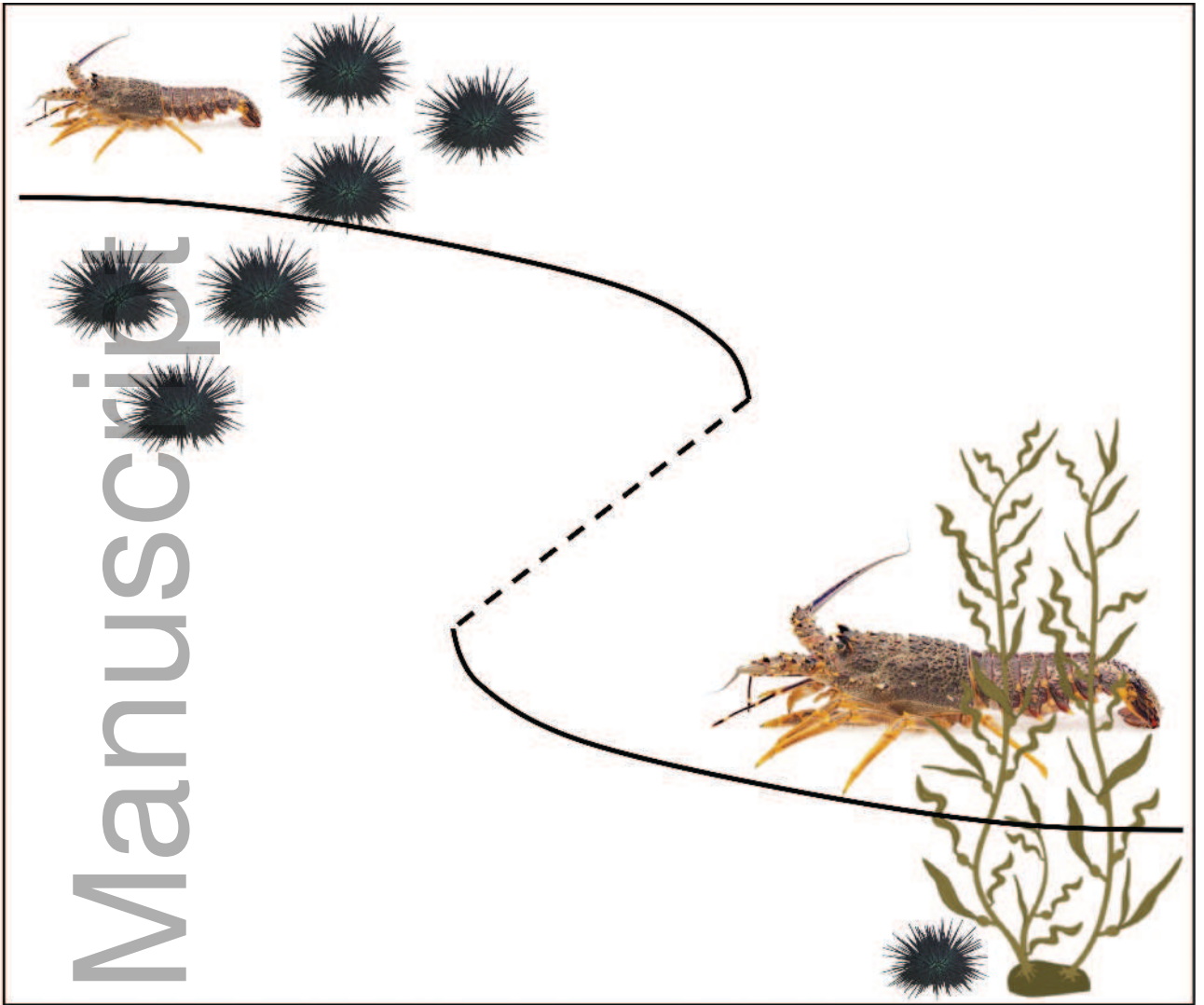
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Time

Total ecosystem biomass

fee_1743_f3.tif

Urchin density (y-axis)

Spiny lobster size (x-axis)

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