Marine top predators as climate and ecosystem sentinels

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The rapid pace of environmental change in the Anthropocene necessitates the development of a new suite of tools for measuring ecosystem dynamics. Sentinel species can provide insight into ecosystem function, identify hidden risks to human health, and predict future change. As sentinels, marine apex (top) predators offer a unique perspective into ocean processes, given that they can move across ocean basins and amplify trophic information across multiple spatiotemporal scales. Because use of the terms "ecosystem sentinel" and "climate sentinel" has proliferated in the scientific literature, there is a need to identify the properties that make marine predators effective sentinels. We provide a clear definition of the term "sentinel", review the attributes of species identified as sentinels, and describe how a suite of such sentinels could strengthen our understanding and management of marine ecosystems. We contend that the use of marine predators as ecosystem sentinels will enable rapid response and adaptation to ecosystem variability and change.

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In an era of unprecedented environmental change, developing a suite of tools for ecosystem monitoring is critical. This need is particularly urgent in marine ecosystems, given the rapid, climate-driven changes in marine populations and communities (Poloczanska *et al.* 2013). Comprehensive monitoring in marine ecosystems presents a challenge due to difficulties inherent in observing the highly dynamic ocean environment at relevant timescales. Traditional ship-based surveys are expensive, autonomous floats and underwater vehicles are still sparsely distributed, and remote sensing fails to capture three-dimensional ocean structure. Furthermore, ecological monitoring in the open

In a nutshell:

- Marine top predators are often conspicuous and wide ranging, and integrate information from the bottom to the top of the food web
- Such predators could act as "sentinels" of an ecosystem's response to climate variability and change
- We define the terms "climate sentinel" and "ecosystem sentinel", and describe the features of marine predators that would make them useful in these roles
- Choosing one or more appropriate sentinels can provide insight into ecosystem processes and help to manage changing ecosystems into the future

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"Sentinel" species have been proposed as a means to provide information about unobserved components of the ecosystem (Zacharias and Roff 2001). Classic examples of sentinels include a domesticated variety of the canary (Serinus canaria), which was formerly used to monitor air quality in coal mines, and invertebrates, whose diversity has been used as an indicator of aquatic ecosystem health (Wilhm and Dorris 1968; Barry 2013). More recent studies show that vertebrate species can serve as sentinels of human health and environmental pollution (Bossart 2006; Smits and Fernie 2013), as well as coupled climate-ecosystem processes (Moore 2008). Useful sentinel species should integrate broader processes into rapidly interpretable metrics that reflect underlying ecosystem processes. Marine top predators (including certain species of predatory fish, seabirds, sea turtles, and marine mammals) have been proposed as ecosystem sentinels based on their conspicuous nature and capacity to indicate or respond to changes in ecosystem structure and function that would otherwise be difficult to observe directly (Figure 1; Bossart 2006; Boersma 2008; Moore 2008). Many marine top predators possess key characteristics of sentinel species, including (1) exhibiting clear responses to environmental variability or change (Sydeman et al. 2015; Fleming et al. 2016), (2) playing important roles in shaping marine food webs (Estes et al. 2016), and (3) indicating anthropogenic impacts on ecosystems (Sergio et al. 2008). Given these characteristics, there is a strong argument for using marine predators as ecosystem sentinels.

Despite the contemporary use of marine predators as sentinels (relevant examples are listed in WebTable 1), the absence of a standardized framework for identifying sentinel



Figure 1. Sampling methods and measurements of select predators: (a) collection of penguin chick morphometrics, (b) leatherback sea turtle (*Dermochelys coriacea*) with a satellite tag, (c) blue whale (*Balaenoptera musculus*) morphometrics via unmanned aircraft system, and (d) weight measurements of a female elephant seal (*Mirounga angustirostris*) carrying a biologging tag.

species limits consistent application of this concept in both scientific and management realms. Clearly, not all top predators make for good sentinel species. For instance, a species may be affected by environmental change but with a lagged response, which diminishes its value as a sentinel where rapid monitoring is required. Indeed, "sentinel species" may now face the same problem that "indicator species" faced nearly two decades ago: the choice of a particular species is often based on the popularity of that species, or reflects single-species conservation goals rather than broad scientific rationale (Zacharias and Roff 2001; Sergio *et al.* 2008). Here, we describe how marine top predators can provide insight into important ecological processes that are difficult to observe directly, identify the attributes of effective sentinel species, and outline key metrics that can be derived from top predators for long-term monitoring (Figure 2). Finally, we discuss the future of sentinel science and how the use of sentinels can inform management.

What is an ecosystem sentinel?

We define an "ecosystem sentinel" as a species that responds to ecosystem variability and/or change in a timely, measurable, and interpretable way, and can indicate an otherwise unobserved change in ecosystem structure or function (Panel 1). The term "climate sentinel" refers to an ecosystem sentinel that responds specifically to climate variability or change (Mallard and Couderchet 2019). Here, we use the term ecosystem sentinel with the understanding that it includes climate sentinels. A sentinel does not necessarily measure environmental conditions directly but rather indicates an ecosystem response to changing environmental conditions. On the basis of this definition, sentinel species can be used to monitor the ecosystem in two ways: as indicators of past or ongoing ecosystem changes that would otherwise be unobserved ("elucidating sentinels"), or as leading indicators of future ecosystem change ("leading sentinels"). We discuss both classifications below, and provide select examples in WebTable 1.

Lavage Diet Scat analysis Blubber Whisker / Feather Stable isotopes Blood biologging **Movement** acoustic telemetry photo ID / citizen science growth rates Life History body condition size-at-age breeding phenology **Reproduction** breeding success juvenile survival population counts Demography metapopulation dynamics Hours to Days Months to Years

Figure 2. Timescales of various sampling methods. Multiple measurements can provide insights about diets at varying spatial and temporal scales. The timescales represented here (hours to days versus months to years) indicate the scale at which an ecological process is measured by a particular method, not the length of a particular time-series. Lavage and scat provide information about recent meals, while stable isotopes or fatty acids can provide measures integrated over broader spatial scales and longer temporal scales.

Elucidating sentinels

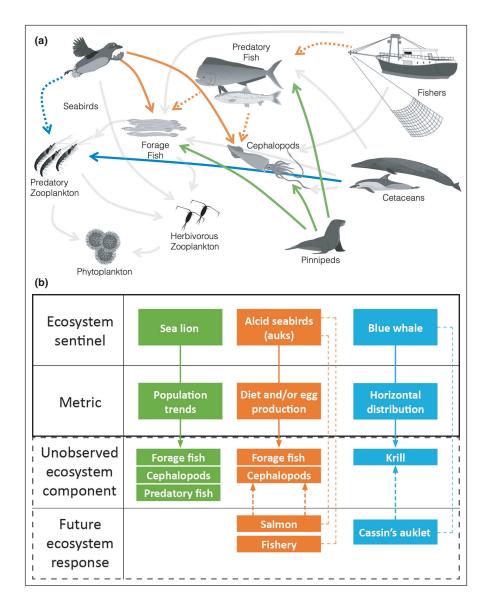
Traditional observing systems - including ship- and shorebased sampling, satellite-borne sensors, moorings, autonomous floats, and underwater vehicles - are capable of monitoring a wide range of physical and environmental properties (Constable et al. 2016; Miloslavich et al. 2018; Harcourt et al. 2019). But understanding how and when physical changes cascade through ecosystems remains difficult, and ecosystem sentinels can play an important role in elucidating ecosystem responses. These responses include oceanographically driven changes in ecosystem function; changes in the distribution, abundance, and composition of the prey community; and changes in food-web dynamics. These ecological factors influence trophic transfer, and in turn can affect ecosystem productivity. While one can hypothesize how and when environmental changes (eg a delay in upwelling or an increase in temperature) will affect the ecosystem more broadly, top predator sentinels can indicate when and where these broad-scale impacts occur, and can help identify physical thresholds or tipping points when physical processes translate to broad-scale implications for the ecosystem (WebTable 1). For this reason, metrics derived from monitoring top predators have been proposed as essential ocean variables that can contribute to the Global Ocean Observing System (Miloslavich *et al.* 2018; www. goosocean.org).

Elucidating sentinels therefore provide an observable link between physical processes and biological responses, and can be used to monitor processes that are difficult to observe directly. For example, the elegant tern (*Thalasseus elegans*) is a trophic generalist, and monitoring its diet composition has been proposed as a feasible way of monitoring changes in the forage fish community off southern California (Horn and Whitcombe 2015). Rhinoceros auklets (*Cerorhinca monocerata*) carry prey visibly in their beak, allowing direct observa-

Panel 1. Sentinel definition and characteristics

Ecosystem sentinel: a species that responds to ecosystem variability and/or change in a timely and measurable way, and can indicate an otherwise unobserved change in ecosystem function. There are two types of ecosystem sentinels: an *elucidating sentinel* indicates past or ongoing changes in components of the ecosystem that are otherwise unobserved, whereas a *leading sentinel*

presages future change in the marine environment (see WebTable 1 for examples). Regardless of the type, ecosystem sentinels are conspicuous, easily accessible, and observable; provide ecosystem information across spatiotemporal scales; reveal unobserved ecosystem component(s); and are mechanistically linked to ecosystem component(s).



tion of changes in prey between cold-water and warm-water periods that go undetected by traditional sampling techniques (Cunningham et al. 2018). Changes in the distribution and migration phenology of specialist foragers such as blue whales (Balaenoptera musculus) and North Atlantic right whales (Eubalaena glacialis) can indicate relative changes in the distribution and abundance of prey populations (Croll et al. 2005; Piatt et al. 2007). Dietary specialists may also serve as sentinels for other predators that feed on the same prey type but that are more difficult to observe (Lyday et al. 2015). A sentinel species can also signal an integrated ecological effect of climate forcing; for instance, the first indication of a strong ecosystem response to unusually delayed upwelling in the California Current system in 2005 was the widespread colony abandonment by Cassin's auklet (Ptychoramphus aleuticus; Sydeman et al. 2006). In that case, anomalous atmospheric and oceanographic conditions ultimately affected the entire ecosystem, from phytoplankton to sea lions and whales (Weise et al. 2006; Barth et al. 2007).

Figure 3. Climate variability and change can result in ecosystem response via trophic pathways. (a) Trophic linkages (gray and colored arrows) in a generic pelagic food web; (b) the sentinel species and the metric being measured (black rectangle) to reveal the unobserved or future response of ecosystem components (dashed gray rectangle). In the food web, gray arrows represent a trophic linkage outside of the sentinel relationship, with colors referring to a specific example. Solid colored lines represent a direct relationship between a sentinel via the metric measured and an ecosystem component; dashed colored lines represent the capacity of an organism to function as a leading sentinel, which can be used to predict a future ecosystem response; and dotted colored arrows represent the ecosystem link that is heralded by a leading sentinel. In (b), examples illustrate how ecosystem sentinels can function: (1) a generalist predator, the California sea lion (Zalophus californianus), feeds on a broad forage base (solid green arrow), and sea lion population declines can therefore be indicative of unobserved broad ecosystem changes in the forage fish, cephalopod, and predatory fish communities. (2) Many alcid seabirds (auks) feed upon the same prey species as commercially important salmon (solid orange arrow); alcid dietary changes and egg production can therefore act as leading indicators of the strength of future salmon runs and fisheries (dotted orange arrows). (3) Blue whales (Balaenoptera musculus) and Cassin's auklets (Ptychoramphus aleuticus) are specialist krill predators (solid and dotted blue arrows, respectively); measuring the horizontal distribution and corresponding changes in foraging patterns of these whales could potentially indicate whether localized krill resources will support a strong year class of auklets (hypothesized; dotted blue arrows).

Leading sentinels

Sentinel species can be used in a predictive capacity when they have a lower threshold for responding to changes in the environment than other ecosystem components, or when they are exposed to changes earlier than other ecosystem components (Figure 3). In the Gulf of California, for example, the diets of several seabird species (eg Heermann's gull [Larus heermanni], elegant tern, and brown pelican [Pelecanus occidentalis]) are used to predict sardine and anchovy (Sardinops sagax and Engraulis mordax) fisheries landings (Velarde et al. 2015). Because these seabirds feed on juvenile fish that have yet to enter the fishery due to their size, their diets forecast changes in the older fish targeted by the fishery months later. In addition, poor harvest rates of sooty shearwater (Ardenna grisea) chicks in the Southern Hemisphere may foreshadow El Niño events by up to 12 months in advance (Humphries and Möller 2017). While there are fewer examples of leading sentinels

relative to elucidating sentinels, the increased exploration of sentinels in general as monitoring tools will offer opportunities to identify other leading sentinels that will act like the canary in the coal mine.

What makes a good sentinel species?

Several key characteristics are common to species that are well suited for use as ecosystem sentinels. These include conspicuousness, sensitivity to ecosystem processes, and timeliness in their responses, as well as offering the ability to collect multiple indicators from a single individual or population that will provide information about ecological processes over multiple scales (Figure 1). The relative importance of these characteristics depends on the ecosystem process and timescale of interest. For example, detecting impacts of shortterm climate variability may require measurements in a relatively short timeframe, while impacts of decadal variability may be monitored effectively with less frequent sampling.

Although predators can be useful for observing changes in marine ecosystems, not all predators make good sentinels, and a particular species may be an appropriate sentinel for certain processes but not others. Some species have intrinsic variability in their movement patterns at individual and population scales, which can make observing clear responses to changing conditions more difficult (Abrahms et al. 2017). Moreover, the same benefits that top predators convey in integrating ecosystem processes may mean they exhibit a delayed response compared with other ecosystem components. For example, long-lived species are evolutionarily equipped to cope with variable food availability, potentially making adult survival of these species a poor proxy for adverse ocean conditions in a given year. Furthermore, multiple stressors often affect organisms in multiplicative or synergistic ways that could confound sentinel responses. Species that are subject to commercial harvest (or recovering from exploitation) may have differing population-level responses to environmental variability than species at carrying capacity, making the former taxa potentially less reliable as sentinels of ecosystem change than the latter. The importance of scale highlights the need to consider a suite of metrics from multiple ecosystem components to obtain a more holistic view of ecosystem response to ocean and climate variability (Levin et al. 2009).

Conspicuousness

As compared with the species they feed on, many marine predators are relatively easy to observe, due to their dependence on land for reproduction (eg central-place foragers such as seabirds, pinnipeds, and sea turtles) or their need to come to the surface to breathe air (eg cetaceans). Being conspicuous facilitates measurement and monitoring of multiple attributes (Panel 2). Seabirds and pinniped colonies are particularly amenable to sampling on land, and as such they provide some of the best information on changes in ecosystem structure and function over multiple timescales (Parsons *et al.* 2008; Sydeman

et al. 2015). The near-shore distribution of gray whales (*Eschrichtius robustus*) facilitates monitoring their migration and helps to improve estimates of their population size (Moore 2008). They also respond to changes in the ecosystem by delaying their southbound migration when favorable Arctic foraging conditions persist due to late ice formation (Moore 2008).

Sensitivity and timeliness

An effective sentinel species must be sensitive to the underlying processes of interest, and should respond to change in a timely and detectable manner. Species that respond faster than other components to a change in the ecosystem make for better sentinels. The collapse of breeding success for Cassin's auklets was a rapid and timely response to a lack of prey in 2005, which was one of the first indicators that delayed upwelling resulted in a broader ecosystem response (Sydeman et al. 2006). Predators with a specialized diet, or those with highly restricted ranges, are likely to be more sensitive to ecosystem change, such as variation in prey availability (Furness and Tasker 2000); Antarctic penguins are sensitive to environmentally mediated changes in the abundance or distribution of krill (Euphausia superba) (Trivelpiece et al. 2011). Using specialist species as ecosystem sentinels has the advantage of demonstrating a clear link between the sentinel's response and the underlying process; conversely, the diet of generalist predators may be indicative of broad changes in the prey community (Weise and Harvey 2008; Horn and Whitcombe 2015; Fleming et al. 2016). However, prey switching may buffer generalists from being affected by resource variability, which could limit their usefulness as sentinels.

Multiple indicators

A particularly useful sentinel species may be one that supplies information about multiple processes, or the same process over multiple spatial and temporal scales. It is often possible to collect a suite of measurements from multiple individuals or even species at a single site, such as mammal or seabird breeding colonies and fish spawning aggregations. These can be combined to give a more complete picture of ecosystem changes (Figure 4). Breeding success data have been synthesized across six sympatric seabird species to better infer changes in prey communities in the North Sea (Frederiksen et al. 2007). In addition, measurements of multiple parameters - such as movement patterns (Weise et al. 2006), juvenile survival (McClatchie et al. 2016), and adult population size (Laake et al. 2018) - from a single sentinel species like the California sea lion (Zalophus californianus; Figures 1 and 3) can be used to extend inference across multiple spatiotemporal scales (Panel 2; Figure 2). An expert elicitation exercise found that foraging trip duration was the best metric for detecting climate effects on marine predators but that additional indicators could provide inferences at broader timescales (Wilcox et al. 2018).

Panel 2. Measurable attributes from sentinels

Diet: animal diet and diet variability provide direct information on trophic position, as well as the trophodynamics of an ecosystem. Derived metrics can capture multiple temporal scales of trophic transfer from hours (eg lavage and scat analysis) to days (eg stable isotope analysis of blood and/or tissue) to years (eg stable isotope analysis of whiskers) (Newsome *et al.* 2010).

Movement: animal movement summarizes a diverse suite of ecological processes, ranging from energetic activity to migration phenology to foraging effort. Metrics derived from biotelemetry or sightings data can reveal changes in spatial distribution, habitat use or residency, and foraging behavior in response to anomalous ecosystems conditions (Payne *et al.* 1986; Weise *et al.* 2006; Harwood *et al.* 2015).

Morphometrics: animal morphometrics involves examining the size and shape of an animal as an indicator of its health, condition, fitness, and growth rate. Such metrics often integrate over timescales of days

Discussion

Relevance of ecosystem sentinels to marine management and governance

Monitoring ecosystem sentinels can help guide ecosystem science and conservation efforts. Relevant data from ecosystem sentinels can be integrated into adaptive, ecosystem-based, or co-management strategies to help support fisheries adaptation (Ogier et al. 2016) and increase socioeconomic resilience to climate variability and change. Sentinels are most beneficial when used alongside other physical and biological time-series to help describe the state of the ecosystem and detect ecological thresholds (Samhouri et al. 2017). Juvenile mortality in California sea lions in 2013 (McClatchie et al. 2016) may have been the first indication of ecosystem effects from a marine heatwave developing in the northeastern Pacific Ocean (Cavole et al. 2016; Jacox et al. 2018); as prey became increasingly scarce, weaning juvenile sea lions were unable to find food, resulting in high mortality (Cavole et al. 2016). In the future, metrics such as sea lion juvenile mortality could flag unobserved variability in fish stocks, supporting changes to fisheries quotas in anomalous years.

Sentinels have also been used to identify when other anthropogenic stressors have major ecosystem-level effects, thereby initiating management responses. Southern resident killer whales (*Orcinus orca*) have been negatively affected by human activities in the Pacific Northwest. In combination with stressors such as marine noise and contaminants, competition with the Chinook salmon (*Oncorhynchus tshawytscha*) fishery is believed to contribute to the continued poor health, breeding performance, and population decline of these killer whales (Chasco *et al.* 2017). Concerns about this population led to closures of multiple Canadian salmon fisheries in 2018, and to proposals for reducing future Chinook salmon fisheries quotas to years (Figure 4) and can indicate changes to foraging conditions (Weimerskirch *et al.* 2012; Harwood *et al.* 2015).

Reproduction: reproductive attributes like breeding success, breeding phenology, clutch size, and juvenile survival are generally easier to measure in central-place foragers that rely on land. Changes in these attributes often reflect some of the most severe ecosystem responses, such as auklet colony abandonment and juvenile sea lion die-offs in response to the 2013–16 marine heatwave in the Northeast Pacific Ocean (Cavole *et al.* 2016).

Demography: demography can include counts of adults or specific life-history stages, often integrating prey quality over large periods and areas. Juvenile and adult population assessments for California sea lions (*Zalophus californianus*) have been important in diagnosing how ecosystem patterns affect a recovering population (Laake *et al.* 2018).

by up to 35%. Similarly, polar bears (*Ursus maritimus*) have become the "public face" of climate change, as declines in their health and increased instances of bear–human conflict have been linked to declines in the solid pack ice on which their seal prey are found (Regehr *et al.* 2016). Polar bears are highly sensitive sentinels that have captured public attention and provide a tangible impetus for changes in governance to address the global impacts of climate change (Friedrich *et al.* 2014; Lescroël *et al.* 2016).

Large-scale migration is a hallmark of many marine top predators, with animals capable of moving across national "exclusive economic zones" and through international waters (Block et al. 2011; Harrison et al. 2018). Although crossjurisdictional movements of animals often present management challenges, sentinels could offer opportunities to further support marine management and ocean observation (Hays et al. 2016). Tagging efforts could be concentrated in easily accessible and well-observed regions, with subsequent broadscale animal movements gathering data on the ecosystem in unobserved or remote locations (Roquet et al. 2013), or in regions without ecosystem monitoring programs (Harrison et al. 2018). Tracking animals across remote, undersampled areas can provide novel oceanographic measurements from animal-borne sensors, and migration and foraging patterns of tagged species may help to reveal underlying ecosystem conditions (Weise et al. 2006; Roquet et al. 2013).

Sentinel monitoring could be funded from alternate sources (eg non-governmental organizations, private trusts, citizen science) to assist ecosystem monitoring in countries, regions, or communities that may not have the resources to self-fund holistic sampling programs (Lodi and Tardin 2018). Many existing (WebTable 1) and potential ecosystem sentinels can serve to leverage support for biodiversity conservation by capturing the public's interest (Friedrich *et al.* 2014). The perhaps unintended but positive corollary of such attention could be the creation of an "ecological umbrella", whereby management approaches for iconic sentinel species also help to protect non-sentinel species and habitats.

The future of sentinel science

Over time, technological advances in tools for field investigations and data analysis will provide opportunities for the identification of sentinel species and interpretation of sentinelobtained data. Furthermore, automated sampling (eg with Argo floats [www.argo.net], underwater gliders, and so forth) will enable additional physical and biological measurements of the world's oceans, reducing the number of unobserved components. Our capacity to use marine predators as sentinels will also improve as technology progresses. Advances in biologging technology will permit studies on individuals encompassing a range of sizes, ontogenies, habitats, and lifehistory characteristics (Hazen et al. 2012). One example is the International Cooperation for Animal Research Using Space (ICARUS) Initiative, which could provide a lower-cost and smaller-sized satellite tag, allowing for substantially more deployments that would ultimately improve population-level inferences from animal movements (Wikelski and Tertitski 2016). Biologging data can provide metrics of ecosystem change when movement patterns are anomalous but can also directly sample the physical environment (Bograd et al. 2010). This suite of data collected by animal-borne sensors can improve our understanding of how environmental conditions are changing, and how these changes affect both the sentinel and the broader ecosystem (Harcourt et al. 2019). Continuing advancements in the dissemination of real-time data are characterized by reduced transmission costs and higher bandwidth speeds. Such improvements could also lessen our dependence on central-place foragers as sentinels, if animals no longer need to be recaptured to retrieve data.

Increases in remote-sensing capacity also have major implications for sentinel science. For instance, satellite imagery has been used to document both the recovery of gray seal (*Halichoerus grypus*) populations in New England (Moxley *et al.* 2017) and an 88% decline in the world's largest king penguin (*Aptenodytes patagonicus*) colony (Weimerskirch *et al.* 2018). Consequently, population estimates of animals in remote locales can be obtained more frequently and more broadly than is possible through traditional survey methods. Technologies that are increasingly being used in marine research, such as unmanned aerial vehicles, can also provide non-invasive monitoring of population size, health, and reproductive status of individuals: for example, by collecting samples from whale blows (exhaled breath) (Burgess *et al.* 2018; Johnston 2019).

In addition to their capacity to signal climate-driven changes to ecosystem function, marine predators are useful as sentinels for other forms of anthropogenic disturbance. In one prominent example, northern fulmars (*Fulmarus glacialis*) have been used as indicators of microplastic pollution in the

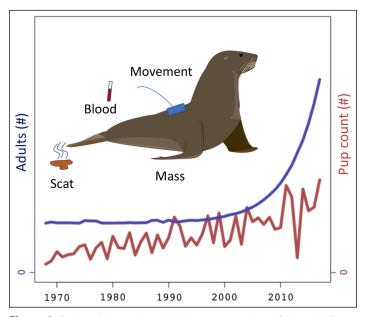


Figure 4. Scales of data collectable from a top predator. Schematic figure on the suite of measurements that can be collected to understand varying scales of a single top predator response to climate-induced ecosystem change. Hypothetical time-series were drawn to highlight scales of variability and are not based on actual data. Blood samples can measure stable isotopes, fatty acids, or hormones integrated over the past week of foraging, whereas samples of whiskers or blubber can reflect broader timescales. Scat contents can identify diet composition and prey items over the period of time from digestion to excretion. High-resolution archival tags can measure individual foraging events and response to local ocean processes. At seasonal to interannual scales, mass gain, pup counts, and long-term archival tags can be used to measure foraging success of adults, as well as changes in distribution due to alterations in prey dynamics and migration phenology. At annual to decadal scales, adult population growth or mortality events can indicate unfavorable prey regimes that may lead to multiple ecosystem responses.

High Arctic (Van Franeker *et al.* 2011); Pacific bluefin tuna (*Thunnus orientalis*) help scientists track the transfer of radioactive material from the Fukushima Daiichi nuclear disaster across the Pacific Ocean (Madigan *et al.* 2012); and feathers from museum specimens of black-footed albatross (*Phoebastria nigripes*) provide indications of mercury levels in the North Pacific over the past 120 years (Vo *et al.* 2011). Changes in the diets of sentinel species over time may reflect an ecosystem response to fishing pressure overlooked by traditional stock assessments (Velarde *et al.* 2015).

Conclusions

Identifying an appropriate suite of ecosystem sentinels will improve our ability to monitor and predict environmental change, a capability that is particularly important as we move farther into the Anthropocene and encounter novel physical and ecological conditions that reflect the cumulative impacts of multiple anthropogenic stressors. Sentinels have historically been used primarily as harbingers of ecosystem change rather than as direct inputs into management decision making, but continued observations of top predators create an opportunity to define ecosystem thresholds and adjust management accordingly (Samhouri *et al.* 2017).

Our definition of ecosystem sentinels can help refine existing research and direct future efforts to identify sentinels. We have presented examples of marine predators that can act as sentinels of unobserved ecosystem change and have developed a framework for identifying useful ecosystem sentinels - one that could also be adapted to aquatic and terrestrial systems. Species that either exhibit a clear mechanistic link to unobserved ecosystem processes (Scopel et al. 2017) or act as sentinels across multiple spatial or temporal scales (Boersma 2008; Moore 2008) should be the subject of long-term monitoring programs, and the data derived from such programs then need to be translated into management action (Samhouri et al. 2017; Hays et al. 2019). Where possible, future studies should focus on identifying the mechanistic links between sentinels and the broader ecosystem. Marine predators have already demonstrated their utility as sentinels of ecosystem processes, and can further improve our capacity to monitor and predict otherwise unobservable changes in the complex and dynamic ocean environment.

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Supporting Information

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Frontiers EcoPics

Lizard pollination: the stigma of having food on your face

Solution Still, you've got something on your nose!" There is only one *stigma* (that of plants, the pollen-receiving organ!) associated with having food on your face, at least where pollen and island-dwelling lizards are concerned.

Lizards are important pollinators, in some cases replacing birds and insects in many island systems. This ornate day gecko (*Phelsuma ornata*) on Round Island, Mauritius, hopped from plant to plant, enthusiastically feeding on the nectar of endemic plants, and transporting pollen in the process. In fact, it was not unusual to see pollen grains sprinkled across the face of these attractive geckos during feeding forays. Just out of reach of a lapping tongue, the settled pollen grains were in an ideal position for transfer to the stigma of the next plant(s). Lizards play a seemingly sizable, yet largely underappreciated and understudied, role in pollination in island ecosystems.

Round Island, the last remnant of endemic Mauritian lowland palm forest, has been saved following the eradication of non-native herbivores and intensive replanting of endemic plants. However, island restoration has been dogged by the persistence of exotic plants. Do these pollinating lizards influence the interplay of native and exotic plants? How large is the role of this little gecko in reconnecting and strengthening ecological connections in this community? Plant–animal interactions, such as pollination, have broad ecological and conservation implications, especially on islands.

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