Keystone predators govern the pathway and pace of climate impacts in a subarctic marine ecosystem

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TROPHIC CASCADES

Keystone predators govern the pathway and pace of climate impacts in a subarctic marine ecosystem

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Predator loss and climate change are hallmarks of the Anthropocene yet their interactive effects are largely unknown. Here, we show that massive calcareous reefs, built slowly by the alga *Clathromorphum nereostratum* over centuries to millennia, are now declining because of the emerging interplay between these two processes. Such reefs, the structural base of Aleutian kelp forests, are rapidly eroding because of overgrazing by herbivores. Historical reconstructions and experiments reveal that overgrazing was initiated by the loss of sea otters, *Enhydra lutris* (which gave rise to herbivores capable of causing bioerosion), and then accelerated with ocean warming and acidification (which increased per capita lethal grazing by 34 to 60% compared with preindustrial times). Thus, keystone predators can mediate the ways in which climate effects emerge in nature and the pace with which they alter ecosystems.

Predator loss and climate change are defining features of the Anthropocene (*1*–*6*). However, these processes have mostly been explored independently even in well-studied ocean ecosystems where the impacts of predator loss and climate change are both pronounced (*5*, *7*). Because the interplay between these processes and their combined impacts are largely unknown, our ability to predict the mode and pace of ecosystem change in the Anthropocene is limited. Here, we address this limitation by revealing how keystone predator loss and climate change are together reshaping kelp forests of the remote Aleutian archipelago (*8*, *9*) (Fig. 1A).

Aleutian kelp forests are built upon a vast framework of *Clathromorphum nereostratum*, a long-lived red alga that forms massive limestone structures covering 50 to 100% of the shallow seafloor (Fig. 1B). These living reefs, assembled slowly (~0.35 mm of vertical growth/year) over centuries to millennia (*10*), serve as a habitat to many other species (*11*). They dominate the seafloor when kelp forests prevail (*12*) and have persisted through recent centuries when this ecosystem was deforested by herbivores, principally because the alga's calcified morphology makes it especially resistant to grazing (*13*). Like tropical corals (*14*), however, this calcifying reef builder may be especially sensitive to climate-induced changes in seawater temperature and acidity (*15*), and the alga's skeleton indeed appears to have weakened in recent decades (*16*). Moreover, sea otters (*Enhydra lutris*), which maintain Aleutian kelp forests through a trophic cascade (*8*), have rapidly disappeared from southwest Alaska over the past 30 years (table S1) perhaps because of increased predation by killer whales (*9*), which ostensibly shifted their diet in response to industrial whaling (*17*). With this collapse, the sea otter's main prey, the herbivorous sea urchin *Strongylocentrotus polyacanthus*, proliferated and denuded the region of kelp (table S2). We thus hypothesized that *C. nereostratum* reefs may now be susceptible to rapid destruction through overgrazing, given that (i) sea urchins, the system's only major herbivore, are now hyperabundant; (ii) the alga's skeleton weakened rapidly in the early 2000s (*16*), which could have increased the intensity (depth/bite) with which sea urchins can graze (*13*) and thus the lethality of grazing in recent time; and (iii) warming is postulated to elevate herbivore grazing rates in the ocean (*18*). To evaluate this hypothesis, we surveyed multiple islands across >700 km of the archipelago (Fig. 1A), quantifying the impacts of sea urchin grazing on *C. nereostratum* from 2014 to 2017; reconstructed the history of sea urchin grazing frequency on *C. nereostratum* (through grazing scars archived in the alga's skeleton) and modeled the putative drivers of change through time; and used controlled experiments to isolate the manner and degree to which present-day seawater conditions have altered the net impacts of sea urchin grazing relative to the preindustrial era.

Lethal grazing of *C. nereostratum* [i.e., repeated grazing of tissues to a depth of >0.25 mm, far below the regenerative cell layer (*10*, *13*); hereafter referred to as "bioerosion"] was severe and widespread. At each study site in 2014, 40 to 85% of every colony was bioeroded, establishing that much of each colony had lost its living tissue and in turn the capacity to generate new growth (Fig. 1C). Sea urchin grazing scars were up to 2.5 mm deep (Fig. 1D), revealing that up to 7 years of prior algal growth (*10*) can be removed by a single sea urchin bite. Destructive overgrazing was further evidenced by the presence of 40- to 60-mm-deep excavation pits (Fig. 1E) and a relatively reduced algal abundance (Fig. 1F) at Attu and the Semichi Islands, suggesting that decades to centuries of algal growth had already been lost in certain places by 2014. After these observations, we discovered that coralline algal abundance (virtually all *C. nereostratum*) declined across the archipelago during the next 3 years (Fig. 1F) (2014 versus 2017; 25 reefs among $n = 6$ islands, $n = 4$ to 6 sites/island; paired t test: $t = 6.178$, $df = 24$; $P < 0.0001$) such that among all 6 islands, reefs lost on average 24% (± 4 SE; median: 17%) and up to 64% of their total calcified reef framework over the 3-year period. Although marine heat waves occurred across the North Pacific in 2014 and 2015 (*19*), they did not produce local temperatures that would trigger algal mortality (*10*). Overgrazing, but not algal bleaching, was seen during each of our annual surveys, indicating that the most parsimonious driver of the observed reef decline was intense bioerosion.

When sea otters are present at ecologically effective densities (*20*) [six or more individuals per kilometer of coastline (*21*)], they greatly suppress the size and abundance of sea urchins in the ecosystem (*8*). The severe bioerosion of *C. nereostratum* that we are now observing (Fig. 1) is therefore at least partially caused by the functional extinction of this keystone predator (table S1) and the resultant proliferation of large sea urchins (tables S2 and S3), the principal agents of bioerosion (fig. S1). However, unlike in past centuries, when sea otters went functionally extinct because of the maritime fur trade (*22*), their recent population collapse occurred in tandem with rapid ocean warming and acidification due to rising atmospheric $P\text{CO}_2$ (*23*). This region has also experienced several ocean heat waves during recent decades (*24*), including in 2014 and 2015 (*19*). The lethal bioerosion that is currently unfolding (Fig. 1) could thus be a function of the interplay among trophic cascades, ocean warming, and ocean acidification. We therefore sought to establish how the process of bioerosion has changed through time and to determine the contributions of each putative driver to that

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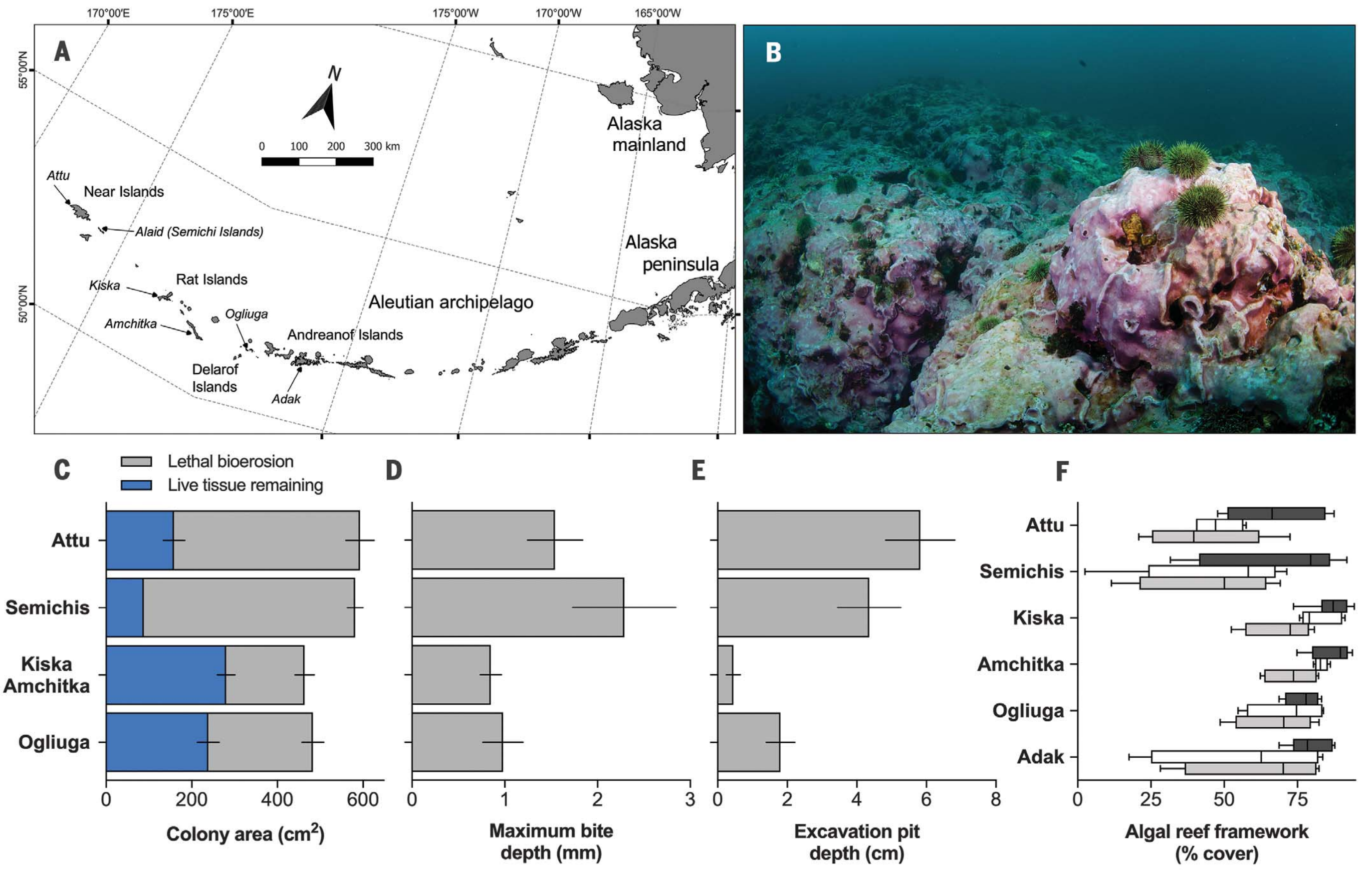

Fig. 1. Erosion of long-lived coralline algal reefs across the Aleutian archipelago. (**A**) Over centuries to millennia, *C. nereostratum* formed massive reefs that structurally underpinned Aleutian kelp forests. (**B**) However, these reefs are now eroding because of overgrazing by sea urchins. (**C**) Area (in square centimeters) of each colony that was grazed to a depth below its regenerative layer (gray bar) versus the area that persisted as living tissue (blue bar). (**D**) Maximum depth (in millimeters) of individual sea urchin bites on each colony. (**E**) Depth (in centimeters) of grazing "excavation pits" on the reef. Bars in (C) to (E) are global means ± SE from each island in 2014 (n = 10 surveys/site; n = 2 sites/island or group; n = 8 sites total). (**F**) Spatial coverage of the coralline algal framework (median and quartiles; whiskers indicate 95% confidence intervals) when assessed at n = 6 islands (n = 20 quadrats/site; n = 4 to 6 sites/island) in 2014 (dark gray bars), 2015 (white bars), and 2017 (light gray bars).

change. To do so, we reconstructed the annual frequency of bioerosion over a 40-year period (1965–2004) through sea urchin grazing scars archived in the skeletons of *C. nereostratum* at Attu, Alaid, Amchitka, and Ogliuga, locations that experienced differing levels of sea otter recovery after cessation of the fur trade but before the recent collapse (*22*). We then modeled the degree to which bioerosion rates were predicted through space and time by the coinciding abundance of sea urchins and by summer sea surface temperatures (SSTs) [note: we focus here on SST because although both seawater temperature and pH are changing because of rising atmospheric $P\mathrm{CO}_2$, only local reconstructions of SST are available (*25*)].

As expected, bioerosion rates through space and time (Fig. 2, A and B, and table S4) were predicted by sea urchin biomass, and thus by sea otter density (*21*). At Amchitka and Ogliuga, islands where sea otters had recovered to near carrying capacity and kelp forests had correspondingly returned by 1965, bioerosion was negligible from 1965 to 1995 (Fig. 2A) but then abruptly increased to high levels thereafter when sea otter populations synchronously collapsed across the region (*22*). At Attu, bioerosion was frequent from 1965 to 1970, when sea otters were absent. Rates then declined over the next 20 years in concert with Attu being repopulated by sea otters (*12*) but returned again to high levels after the aforementioned collapse. Bioerosion at Alaid, an island functionally devoid of sea otters since at least 1912, was frequent throughout the 40-year period. Further, after statistically controlling for the cascading influence of sea otters and sea urchins (Fig. 2B), we discovered that bioerosion covaried positively with SST from 1965 to 2004 (Fig. 2C and table S4). Aleutian SSTs have increased on average 0.5°C since 1965, and this region experienced several warming anomalies during the 20th century (*24*, *25*). Thus, whereas bioerosion was initiated by the loss of sea otters and the resulting trophic cascade, seawater warming appears to have markedly accelerated this process in recent times.

To further establish whether sea urchin grazing has become more lethal to *C. nereostratum* in recent years and to identify the respective roles of seawater temperature versus $P\mathrm{CO}_2$ in this process, we cultured *C. nereostratum* and large *S. polyacanthus* for 3 months under an appropriate suite of temperature and $P\mathrm{CO}_2$ treatments and then measured the effect of each on the structural integrity of *C. nereostratum* and its susceptibility to sea urchin grazing. Certain treatment combinations mirrored preindustrial, present-day, and predicted near-future mean summer conditions specific to the Aleutians (table S5). Elevating seawater $P\mathrm{CO}_2$ reduced the skeletal density of *C. nereostratum*, particularly when temperature was also increased [Fig. 3A and table S6; linear mixed-effects (LME) interaction term: P = 0.007]. Notably, a similar

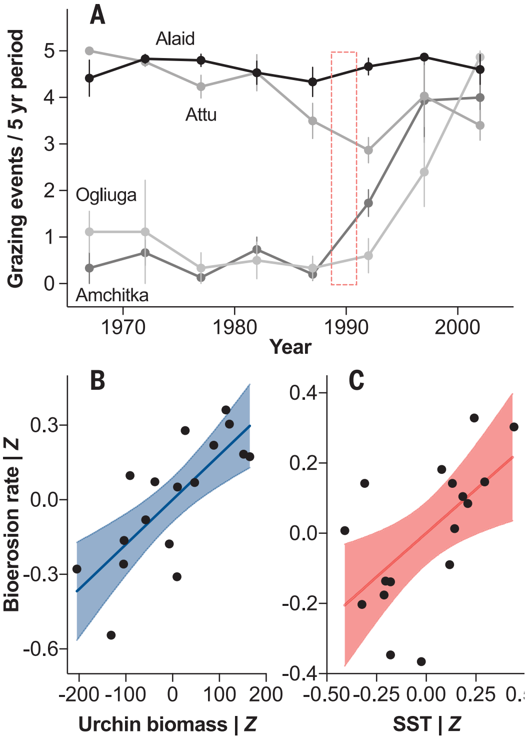

Fig. 2. Historical patterns and causes of bioerosion. (**A**) Annual frequency of sea urchin grazing scars on *C. nereostratum* (mean/5-year period ± SE) from 1965 to 2004 at Attu, Alaid, Amchitka, and Ogliuga (n = 5/island). Rectangle depicts the onset of the recent sea otter decline hindcasted from surveys (*22*). Partial effects plots of (**B**) sea urchin biomass and (**C**) SST reveal their independent effect on bioerosion rate (given the other covariates Z) in the associated model.

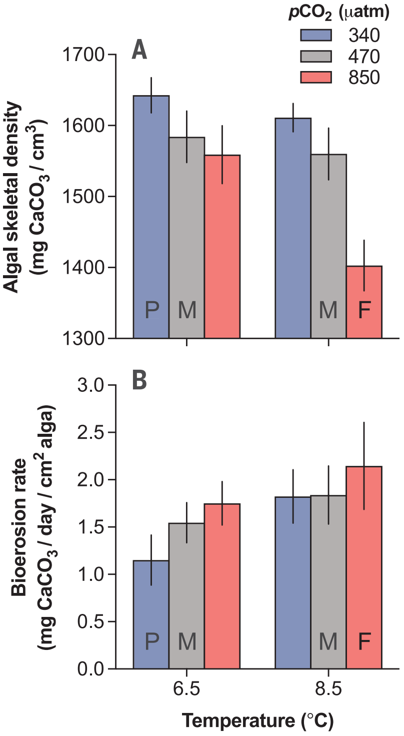

Fig. 3. Effects of seawater temperature and $P\mathrm{co}_2$ on algal integrity and bioerosion rate. (**A**) Skeletal density (in milligrams of CaCO$_3$ per cubic centimeter) of *C. nereostratum* when cultured for 4 months under various temperatures and $P\mathrm{co}_2$ levels, including pairs that represent preindustrial (P), modern (M), and predicted near-future (F) conditions specific to the Aleutian Islands (n = 3/treatment). (**B**) Rate at which large *S. polyacanthus* consumed *C. nereostratum* (in milligrams of CaCO$_3$ per day per square centimeter of alga) during a 20-day grazing assay plotted as a function of the treatments that both experienced for 3 months before and during the assay (n = 9 to 13/treatment). Bars in (A) and (B) are means ± SE.

inverse relationship between skeletal density and seawater temperature has been evident in wild *C. nereostratum* since 1914 (*16*). Elevating temperature increased per capita rates of lethal grazing (LME: $P < 0.001$) irrespective of $P\mathrm{co}_2$ ($P = 0.467$) (Fig. 3B and table S7). Net rates of bioerosion under present-day seawater conditions (470 µatm $P\mathrm{co}_2$; 6.5 to 8.5°C) were 34 to 60% higher than those seen under preindustrial conditions (340 µatm $P\mathrm{co}_2$; 6.5°C), suggesting that per capita rates of sea urchin–induced bioerosion are much higher (and thus more lethal) today than they were in the 18th century, a time when sea otters were hunted to near extinction but societies had yet to fully industrialize. Our experiment also suggests that marine heat waves in 2014 and 2015 likely triggered particularly intense bioerosion during those years (i.e., at rates similar to or above those seen at 470 µatm $P\mathrm{co}_2$; 8.5°C, a 60% increase from preindustrial). Finally, our experiment predicts that without rapid adaptive evolution in *C. nereostratum*, an unlikely event given that it is long-lived and rarely reproduces sexually (*10*), per capita bioerosion will increase another 17 to 39% by the year 2100 with the additional seawater warming (+2°C) and acidification (+360 to 400 µatm $P\mathrm{co}_2$) projected for this region (*26*, *27*).

Our study reveals that long-lived *C. nereostratum* reefs, which underpin the diversity and stability of Aleutian kelp forests, are in rapid decline. This decline, initiated by a trophic cascade and accelerated by ocean warming and acidification, would have gone undiscovered had we focused solely on the direct effects of climate change on *C. nereostratum* (*15*). Our study reveals that the pathways and pace with which climate change is affecting *C. nereostratum* have been, and will continue to be, contingent upon the outcomes of species interactions, a general dependency that heretofore has neither been widely recognized nor well documented in nature. In the near term, the recovery of Aleutian sea otter populations would effectively buffer this system against a climate-induced decline of its structural foundation. Without sea otter recovery, subtle temperature- and pH-induced changes in *C. nereostratum* and *S. polyacanthus* will continue to amplify "interaction strengths" within the cascade, likely causing *C. nereostratum* reefs to collapse sooner than expected from the direct effects of climate change alone. Studying climate change through an ecological lens is therefore necessary (*28*, *29*) to properly identify its emergent effects and to predict its future impacts.

Our study also highlights the power of trophic cascades in nature (*7*) and the potential for large predators to ameliorate some of the effects of climate change in the near term. Keystone predators are generally thought to act as "biotic multipliers" of climate change (*30*). Our study expands on this view, indicating that in some cases, keystone predators may instead serve as "biotic attenuators" of change and that these predators will amplify or attenuate change only in the places on Earth where they remain at ecologically effective densities (*1*–*3*).

REFERENCES AND NOTES

1. W. J. Ripple *et al.*, *Science* **343**, 1241484 (2014).
2. R. Dirzo *et al.*, *Science* **345**, 401–406 (2014).
3. D. J. McCauley *et al.*, *Science* **347**, 1255641 (2015).
4. G. T. Pecl *et al.*, *Science* **355**, eaai9214 (2017).
5. T. P. Hughes *et al.*, *Science* **359**, 80–83 (2018).
6. C. M. Free *et al.*, *Science* **363**, 979–983 (2019).
7. J. A. Estes *et al.*, *Science* **333**, 301–306 (2011).

8. J. A. Estes, J. F. Palmisano, *Science* **185**, 1058–1060 (1974).
9. J. A. Estes, M. T. Tinker, T. M. Williams, D. F. Doak, *Science* **282**, 473–476 (1998).
10. W. Adey, J. Halfar, B. Williams, *Smithson. Contrib. Mar. Sci.* **40**, 1–41 (2013).
11. H. Chenelot, S. C. Jewett, M. K. Hoberg, *Mar. Biodivers.* **41**, 413–424 (2011).
12. J. A. Estes, D. O. Duggins, *Ecol. Monogr.* **65**, 75–100 (1995).
13. R. S. Steneck, *Annu. Rev. Ecol. Syst.* **17**, 273–303 (1986).
14. R. Albright *et al*., *Nature* **531**, 362–365 (2016).
15. K. J. Kroeker *et al*., *Glob. Change Biol.* **19**, 1884–1896 (2013).
16. P. T. W. Chan *et al*., *Geology* **48**, 226–230 (2020).
17. A. M. Springer *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **100**, 12223–12228 (2003).
18. I. Nagelkerken, S. D. Connell, *Proc. Natl. Acad. Sci. U.S.A.* **112**, 13272–13277 (2015).
19. E. Di Lorenzo, N. Mantua, *Nat. Clim. Chang.* **6**, 1042–1047 (2016).
20. M. E. Soulé, J. A. Estes, J. Berger, C. M. Del Rio, *Conserv. Biol.* **17**, 1238–1250 (2003).
21. J. A. Estes, M. T. Tinker, J. L. Bodkin, *Conserv. Biol.* **24**, 852–860 (2010).
22. A. M. Doroff, J. A. Estes, M. T. Tinker, D. M. Burn, T. J. Evans, *J. Mammal.* **84**, 55–64 (2003).
23. J. Fietzke *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **112**, 2960–2965 (2015).
24. E. C. J. Oliver *et al*., *Nat. Commun.* **9**, 1324 (2018).
25. B. Huang *et al*., Extended Reconstructed Sea Surface Temperature (ERSST), version 4 (2015); https://10.7289/V5KD1VVF.
26. R. K. Pachauri, L. A. Meyer, "Climate change 2014: Synthesis report" (Geneva, 2014).
27. B. I. McNeil, T. P. Sasse, *Nature* **529**, 383–386 (2016).
28. C. D. G. Harley, *Science* **334**, 1124–1127 (2011).
29. J. L. Blois, P. L. Zarnetske, M. C. Fitzpatrick, S. Finnegan, *Science* **341**, 499–504 (2013).
30. P. L. Zarnetske, D. K. Skelly, M. C. Urban, *Science* **336**, 1516–1518 (2012).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Fig. S1
Tables S1 to S8
References (*31*–*45*)

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A lethal combination

It is well established that predators are essential for the structuring and maintenance of biotic communities. One of the first demonstrations of this importance came from studies of the importance of sea otters to the maintenance of kelp forests. Rasher *et al.* now show that the effects caused by the absence of this predator can be further exacerbated by climate warming. In North Pacific kelp forests, otter absence led to a decline of slow-growing calcareous algae through sea urchin herbivory, and this pattern was amplified by warming temperatures. Keystone predators are thus essential not only for trophic structure but also for mitigating the impacts of climate change.

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