BIOLOGY LETTERS

royalsocietypublishing.org/journal/rsbl

Research

Cite this article: Hammerschlag N, Fallows C, Meÿer M, Seakamela SM, Orndorff S, Kirkman S, Kotze D, Creel S. 2022 Loss of an apex predator in the wild induces physiological and behavioural changes in prey. *Biol. Lett.* **18**: 20210476.
https://doi.org/10.1098/rsbl.2021.0476

Received: 7 September 2021
Accepted: 20 December 2021

Subject Areas:
ecology, ecosystems

Keywords:
predation risk, predation release, ecology of fear, predation stress, apex predator, landscape of fear

Author for correspondence:
Neil Hammerschlag
e-mail: nhammerschlag@miami.edu

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5809158.

THE ROYAL SOCIETY PUBLISHING

Global change biology

Loss of an apex predator in the wild induces physiological and behavioural changes in prey

Neil Hammerschlag[1], Chris Fallows[2], Michael Meÿer[3], Simon Mduduzi Seakamela[3], Samantha Orndorff[1], Steve Kirkman[3,4], Deon Kotze[3] and Scott Creel[5,6]

[1]Department of Environmental Science and Policy, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA
[2]Apex Shark Expeditions, Shop 3 Quayside Center, Simonstown, Cape Town 7975, South Africa
[3]Department of Forestry, Fisheries and the Environment, Oceans and Coasts Branch, 2 East Pier Road, Waterfront, Cape Town 8000, South Africa
[4]Marine Apex Predator Research Unit (MAPRU), Department of Zoology and Institute for Coastal and Marine Research, Nelson Mandela University, Port Elizabeth 6031, South Africa
[5]Department of Ecology, Montana State University, Bozeman, MT 59717, USA
[6]Institutionen för Vilt, Fisk och Miljö, Sveriges lantbruksuniversitet, 90183 Umeå, Sweden

NH, 0000-0001-9002-9082; MM, 0000-0002-9486-5448; SMS, 0000-0002-7873-208X; SK, 0000-0001-5428-7375; SC, 0000-0003-3170-6113

Predators can impact prey via predation or risk effects, which can initiate trophic cascades. Given widespread population declines of apex predators, understanding and predicting the associated ecological consequences is a priority. When predation risk is relatively unpredictable or uncontrollable by prey, the loss of predators is hypothesized to release prey from stress; however, there are few tests of this hypothesis in the wild. A well-studied predator–prey system between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) in False Bay, South Africa, has previously demonstrated elevated faecal glucocorticoid metabolite concentrations (fGCMs) in seals exposed to high levels of predation risk from white sharks. A recent decline and disappearance of white sharks from the system has coincided with a pronounced decrease in seal fGCM concentrations. Seals have concurrently been rafting further from shore and over deeper water, a behaviour that would have previously rendered them vulnerable to attack. These results show rapid physiological and behavioural responses by seals to release from predation stress. To our knowledge, this represents the first demonstration in the wild of physiological changes in prey from predator decline, and such responses are likely to increase given the scale and pace of apex predator declines globally.

1. Background

Apex predators can alter food webs through direct mortality on prey [1] and via risk effects that can induce plastic and/or genetic alterations in prey traits, including changes in prey behaviour [2,3], morphology [4], life history [5] and physiology [6]. Such risk effects can also initiate trophic cascades [7]. Understanding and predicting the ecological consequences of apex predator declines are central to ecology and important for conservation management given widespread apex predator declines globally, coupled with significant efforts to restore their numbers [8,9].

The control of risk hypothesis [10] predicts that proactive responses by prey to predictable and controllable aspects of risk will generally result in prey forfeiting food for safety, while reactive responses to unpredictable or uncontrollable aspects of predation risk will generally result in prey suffering physiological stress. Thus, the loss of apex predators is expected to release prey from predator-induced stress (i.e. predation stress release) in some (but not all) circumstances, but no prior empirical evidence of such a phenomenon exists in the wild. Predator–prey interactions involving white sharks *Carcharodon carcharias* and Cape fur seals *Arctocephalus pusillus pusillus* have been extensively studied in the waters off Southwestern Africa (e.g. [11–13]). More than two decades of monitoring shark–seal interactions at Seal Island in False Bay have revealed unusually clear-cut spatial and temporal variation in predation risk to seals from white sharks [14–18]. Here, seals exhibit a pronounced stress response to high levels of unpredictable and relatively uncontrollable risk of attack from white sharks as measured through elevated faecal glucocorticoid concentrations (fGCMs) ([19], see electronic supplementary material). These physiological stress responses have been detected in both adults and juvenile seals, with a strong positive correlation between fGCM levels and weekly variation in white shark attack rate [19]. While white shark abundance at Seal Island was relatively stable for a long period, their numbers began to precipitously decline after 2015 [20]. While the reasons for the decline are still unknown, this provides an unparalleled opportunity to test the physiological responses of seals to the loss of their predator.

Here, we tested for hypothesized predation stress release in seals at Seal Island, following the decline and disappearance of white sharks from the system. First, we evaluated white shark relative abundance and predatory activity at Seal Island from 2000 to 2020 (including 5 years after the decline: [20]). Second, we collected seal scat samples and compared fGCMs in the years prior to and following the decline of white sharks. Third, we tested if seal faecal cortisol levels, inclusive of the years following shark decline, were correlated with attack rates on seals. Furthermore, we tested whether fGCM concentrations were associated with spatial and temporal variation in environmental factors measured at the site. Finally, we evaluated for potential changes in seal antipredator behaviour following the decline of white sharks from the system that would also be indicative of predation stress release.

2. Methods

(a) Study system

Seal Island (34.1374° S, 18.5825° E) is an island rookery in False Bay, South Africa, that is inhabited by over 60 000 Cape fur seals exhibiting high site fidelity [21,22]. During colder months (winter: May through September), white sharks patrol the waters around Seal Island to actively hunt Cape fur seals that leave and return to the island to forage [15,23].

Around the island's perimeter, seals often enter the water to cool down and/or play in large groups, which is referred to as rafting behaviour [24]. During high predation risk periods, rafting seals remain close to the island's edge [17], where depths are shallow, and thus seals are relatively safe from attack from below [14,25] and can also quickly exit the water if a white shark is detected.

(b) Boat-based surveys

Between 2000 and 2020, white shark relative abundance and predatory activity during winter months at Seal Island were monitored from standardized boat-based observation surveys (described in [20]; electronic supplementary material). Water temperatures (°C) were recorded using the vessel's onboard temperature sensor, and the following environmental variables were estimated: percentage cloud cover, wind speed (kt) and direction, swell height (m) and water visibility (m). Additionally, the relative distances of rafting seal groups from the Island's perimeter were estimated according to one of three distance categories: (i) seals rafting less than 5 m from the island, (ii) seals rafting more than 5 m and less than 10 m from the island and (iii) seals rafting more than 10 m from the island perimeter.

Between 07.00 and 09.30 h, instances of predation by white sharks on Cape fur seals were recorded following the approach outlined in [18] (see also electronic supplementary material). The duration of each observational period along with the number of predatory attacks by sharks on seals during this period were recorded to calculate white shark predation rates (i.e. number of predation events per hour). After 09.30 h, the vessel anchored and conducted standardized boat-based baited surveys of white sharks (following [20]; see electronic supplementary material). The number of different individual sharks observed per hour during these baited surveys was calculated as a metric of relative white shark abundance.

(c) Seal faecal sample collection and immunoassay

Seal faecal samples were collected from Seal Island during 2014 and 2015 prior to the onset of shark decline (see [19]) and during the decline and eventual disappearance of white sharks from the study site in 2016, 2017 and 2019 (see electronic supplementary material). Steroid hormone metabolites were extracted from faecal samples by drying the scat and boiling a known mass of dry faeces in ethanol following [26]. Glucocorticoid metabolite concentrations in faecal extracts (fGCM) were analysed as detailed in [19] and measured using an enzyme-linked immunoassay with a cortisol antibody (Enzo Life Sciences ADI-900-071; see electronic supplementary material for procedural validation).

(d) Statistical analysis

Previous analyses applied to annual trends in white shark relative abundance data at the study site, collected between 2000 and 2018, revealed a significant change point in 2015, after which (2016 onwards) white shark relative abundance began to decline precipitously [20]. Therefore, we classified the period prior to shark decline as the years 2000 to 2015 and the post-decline period as years 2016 through 2020.

To examine annual trends in white shark relative abundance and predation rates across the 2000–2020 time series, we calculated the mean number of white sharks sighted per hour and the mean number of shark predations per hour, for each year, following the approach of [20]. To compare changes in seal behaviour in relation to white shark relative abundance and predatory activity, we evaluated annual trends in seal rafting distance from the island by calculating the mean daily rafting category for each year.

To compare seal stress responses to annual trends in white shark relative abundance and predatory activity, we calculated mean fGCM concentrations by sampling year and by period (pre-decline versus post-decline of white sharks).

Previous laboratory studies that have subjected sea lions (*Eumetopias jubatus*) to an adrenocorticotropic hormone (ACTH) challenge found a lag of up to 4 days between ACTH injection and peak fGCM [27]. Accordingly, here we considered that measured fGCM values reflected hormone values in seals based on stress experienced within the week prior. Indeed, Hammerschlag *et al.* [19] found a very strong correlation between seal fGCM concentrations and mean predation rates (attacks/h) measured within the week prior to scat collections. Accordingly, here we used Spearman correlation to test for a correlation between weekly shark attack rates and associated fGCM concentrations spanning the pre- and post-decline period. We also separately tested for correlations of seal fGCM levels against water temperature, wind speed, swell height, water visibility and cloud cover. As in our analysis of the correlation between fGCM with predation rates, we used mean values of the environmental variables recorded during the previous week and up to the day of scat sampling in this analysis.

Because white sharks only actively prey on seals at Seal Island during winter months, we restricted analyses to data collected from May to September, such that all data reflected seal behaviour and physiology during the season in which seals historically experienced high predation risk. All statistical analyses were performed in SAS with $p < 0.05$ used as a threshold for strong evidence of an effect.

3. Results

Between 2000 and 2020, a total of 4351 white shark sightings were made during 2790.2 h of standardized observational surveys that occurred during cold months (May through September). Extension of the previous time series from 2018 to 2020 demonstrated that the decline in white shark numbers at Seal Island that began in 2016 continued through 2020 (figure 1*a*). The last white shark sighting at Seal Island during this survey occurred on 7 August 2018; since then, there have been 78 trips to Seal Island in which no white sharks were seen in 181.3 h of standardized observations. Between 2000 and 2020, a total of 8007 predations by white sharks on Cape fur seals were recorded during 3006.1 h of standardized observation. Consistent with the trend in shark abundance, the predation rate continued to decline through 2020 (figure 1*b*). The last predation event at Seal Island during this survey was recorded on 23 July 2018. Annual trends in seal rafting distance to the Island exhibited relatively little variation in the pre-decline period (2000–2015), with rafting generally restricted to within 5 m of the Island perimeter (rafting category 1); however, in 2016, seals rafting distance from the Island began to increase during the post-decline period, peaking in the most recent years coinciding with the disappearance of white sharks in our surveys (figure 1*c*).

One-hundred twenty-five scat samples were collected during the period of shark decline and disappearance, with individual fGCM concentrations in scats ranging from a maximum value of 3372.1 ng g^{-1} (recorded during the pre-decline period) to a minimum value of 87.8 ng g^{-1} (recorded during the post-decline period). Annual mean fGCM concentrations measured during the pre-decline period were between 6.3 and 2.3 times higher than annual mean concentrations measured in the post-decline period (figure 2*a*). Mean (±s.e.) fGCM concentration during the pre-decline period was 1864.8 ± 82.9 ng g^{-1} ($N = 66$), 4.2 times higher than the post-decline period (445.5 ± 51.6 ng g^{-1}, $N = 59$). On six occasions in which scat samples were collected from Seal Island, white shark predatory activity was also monitored during the week prior. Mean weekly predation rates ranged from a maximum of 3.76 attacks/h (pre-decline period) to a minimum of 0 attacks/h (post-decline period). Spearman correlation revealed a strong linear correlation between mean fGCM concentrations and mean weekly predation rates ($r = 0.94$, $p = 0.005$; figure 2*b*). By contrast, mean fGCM concentrations were not correlated with mean weekly values of water temperature ($r = -0.54$, 0.27), wind speed ($r = 0.35$, $p = 0.5$), swell height ($r = -0.54$, $p = 0.27$), water visibility ($r = 0.26$, $p = 0.62$) and cloud cover ($r = 0.03$, $p = 0.96$).

4. Discussion

Historically, Cape fur seals exposed to risk of white shark attack at Seal Island in False Bay exhibited a pronounced physiological stress response, as measured by fGCM concentrations ([19]; electronic supplementary material). However, numbers of white sharks began to decline precipitously in 2016, leading to the complete disappearance of this apex predator from the site. Here, we found that physiological stress levels in seals have since diminished more than fourfold on average. Following the disappearance of white sharks, fGCM concentrations are now closely comparable to levels at seal colonies that are not subjected to white shark predation [19].

The decline in white shark numbers and associated decline in seal stress levels have coincided with seal behavioural changes indicative of predation stress release, including seals rafting over deeper water, further from the Island, a behaviour that would have historically exposed seals to risk of shark attack. Taken together, these results suggest relatively rapid physiological and behavioural responses in seals due to release from risk of predation.

Chronic glucocorticoid secretion has been found to negatively impact reproduction and survival [28–30]. Indeed, previous research has revealed that acute and chronic physiological stress experienced by fur seals can result in death [31]. Therefore, the drop in fGCM levels and changes in behaviour may have positive fitness consequences, which could in turn have consequences for their population dynamics, though such effects are notoriously difficult to parse out from the concurrent decrease in direct predation.

High population density or crowding can impact glucocorticoid stress responses in animals. In theory, changes in the seal population size may contribute to some of the variation in glucocorticoid secretion measured here; for example, if there was a yet undocumented decline in seal population size at Seal Island. However, such a decline in recent years would be incongruous with the release of predation pressure reported here; moreover, changes in seal population size would not explain the strong correlation found between measured seal fGCM levels and weekly shark predation rates. Our previous research has also found no correlations between seal colony density or population size and fGCM levels [19]. While we cannot rule out that some unmeasured variable could be contributing in part to the pre- versus post-decline differences in seal stress levels, various environmental factors measured here (swell height, water temperature, visibility, cloud cover) were not correlated with fGCM concentrations. Our findings and interpretations are strengthened by coherency among results over time, scale and types of data, inclusive of seal rafting distance from the Island.

The reasons for the white shark decline from Seal Island remain unknown [20]. Regardless, the data presented here suggest a physiological response in seals due to predator release. In the absence of white sharks, sevengill sharks (*Notorynchus cepedianus*) have taken up residency at Seal

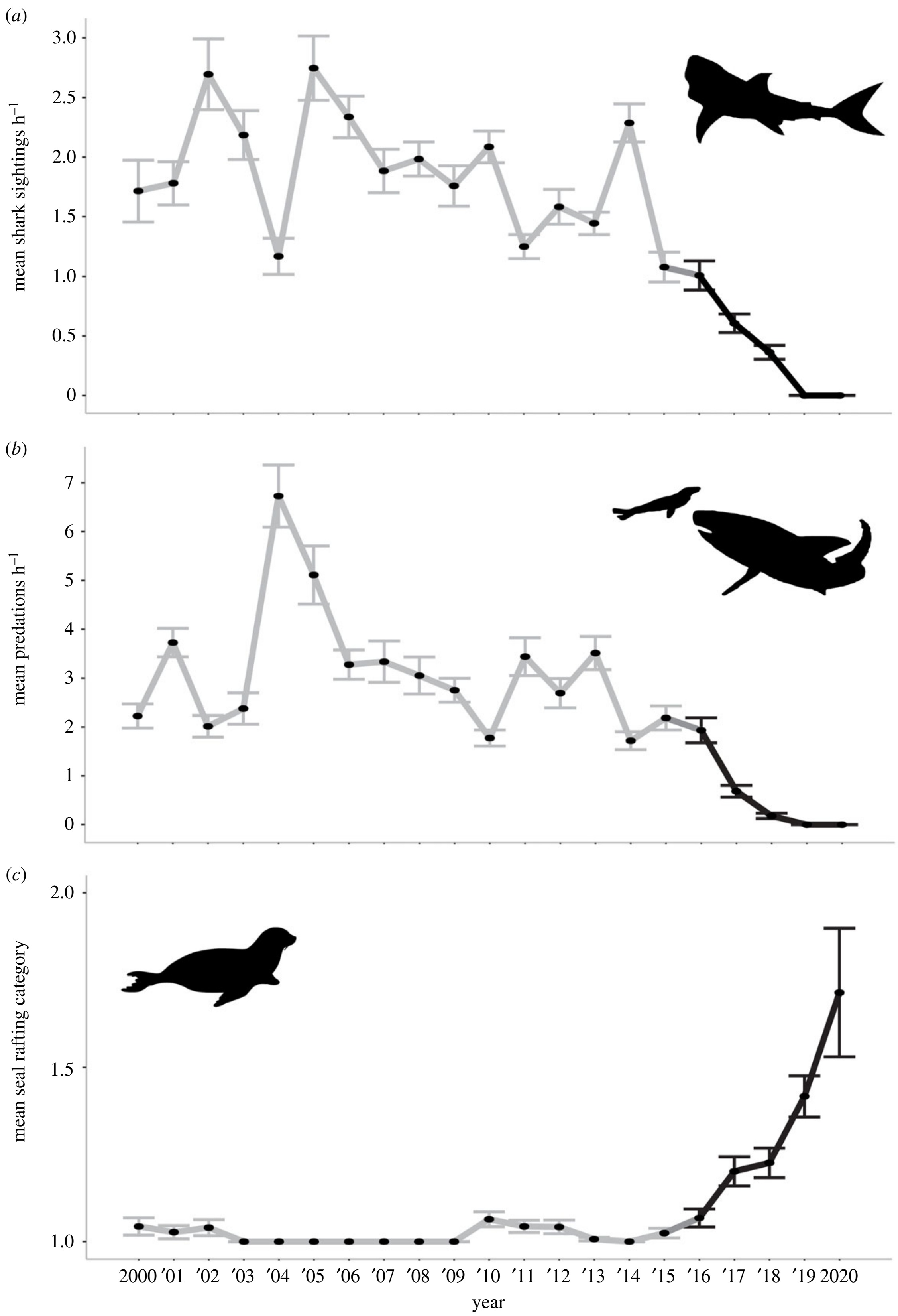

Figure 1. Annual trends in (*a*) white shark relative abundance, (*b*) predatory attacks on seals and (*c*) seal rafting proximity to Seal Island prior to (grey) and following the decline (black) of white sharks. Data are mean ± standard error of (*a*) white shark sightings per hour, (*b*) white shark predations per hour and (*c*) seal rafting distance category, averaged across sampling days for each year. Seal rafting distance was estimated according to one of three categories: (i) seals rafting <5 m from the island; (ii) seals rafting >5 m and <10 m from the island and (iii) seals rafting >10 m from the island perimeter.

Island [20]. Sevengill sharks are known to scavenge on seal carcasses [32]. While there has been a single observation of a sevengill shark attacking a sick seal at Seal Island [20], the emergence of this shark species does not appear to have induced a physiological stress response in seals, as might be expected if they were frequently attacking healthy seals. Thus, from an ecological standpoint, this suggests a lack of functional trophic redundancy between white sharks and sevengill sharks, despite both being apex predators in the region.

royalsocietypublishing.org/journal/rsbl *Biol. Lett.* **18**: 20210476

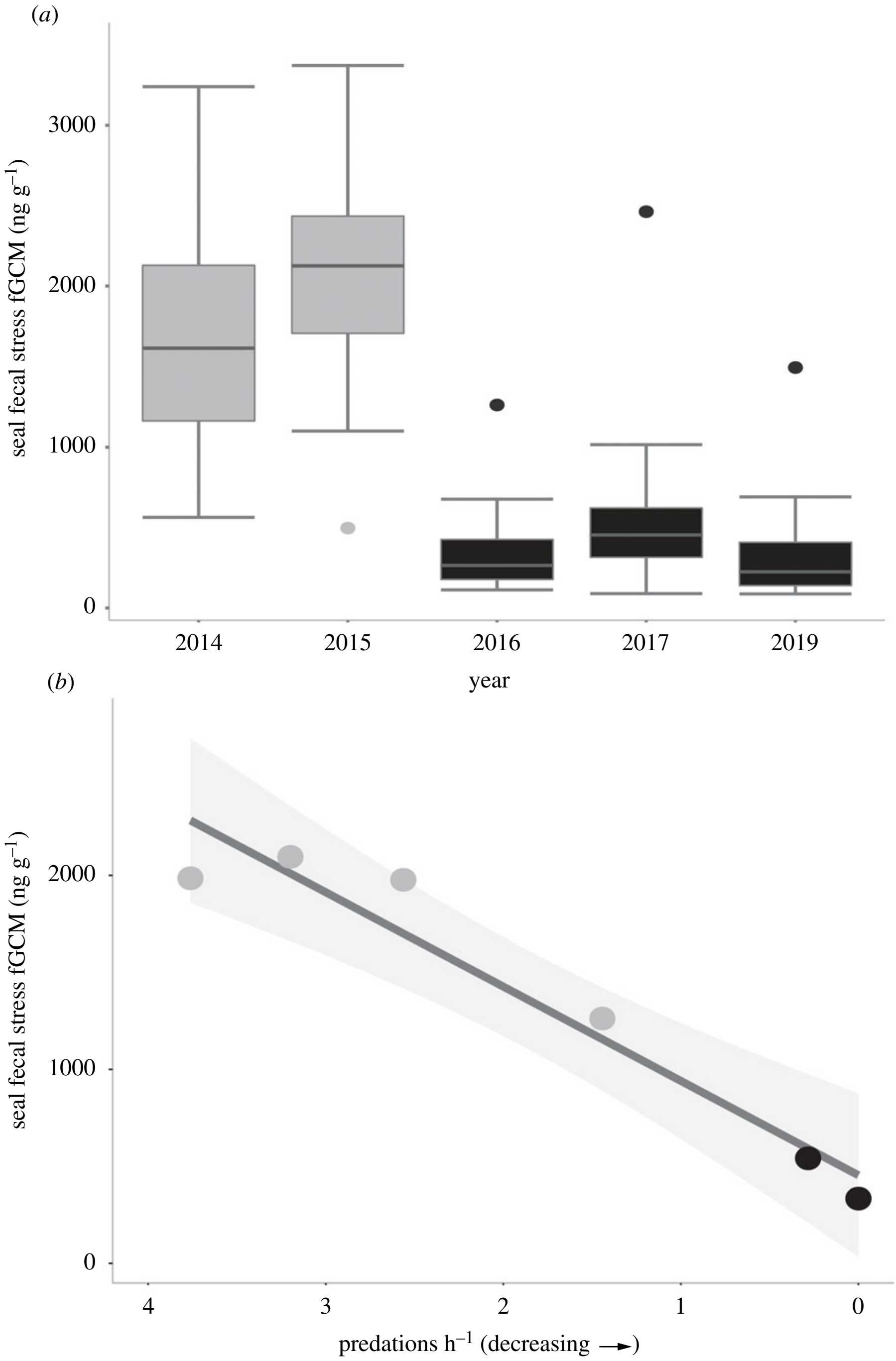

Figure 2. Seal faecal glucocorticoid metabolite concentrations (fGCMs) measured at Seal Island prior to (grey) and following the decline (black) of white sharks. (*a*) Boxplots of fGCM measurements by year; upper and lower box edges are the inter quartile ranges (25th and 75th percentiles), the line within each box is the median, whiskers are the minimum and maximum values and circles indicate outliers. (*b*) Correlation between fGCM values and mean weekly predation rates. The shaded areas represent the 95% CIs around a linear trend line. Values are fGCM means for each sampling day; does not include data from faecal collections in 2016 (post-decline period), which were included in (*a*), because corresponding surveys of shark predation rates were not conducted. Note: to facilitate interpretation in (*b*), predation data on the *x*-axis are constructed with values decreasing from left to right.

5. Conclusion

Here, we found that the rapid decline and disappearance of white sharks from Seal Island have led to physiological and behavioural responses in seals, probably due to predation release, including a pronounced decrease in seal fGCM concentrations. To our knowledge, this represents the first demonstration in the wild of a physiological response by prey to the loss of an apex predator. However, such physiological responses are likely pervasive as apex predators are among the most threatened vertebrates on the planet [8,9]. Given that changes in glucocorticoids can have fitness and reproductive consequences [28–30], understanding how alterations in these and other stress responses manifest in prey due to widespread declines of apex predators is an important area of future research.

Ethics. Observational surveys and seal faecal sample collections were conducted under authorization and permits from the Department of Forestry, Fisheries and the Environment (DFFE), South Africa.

Data accessibility. The data and description of the data associated with this study are available from the Dryad Digital Repository [33]: https://doi.org/10.5061/dryad.jwstqjq9r// https://datadryad.org/stash/share/_Y_Rjs_DdmKxor3N_VMBIWGvi1Bu7ZEv2qxCNzJSHo0.

The data are provided in electronic supplementary material [33].

Authors' contributions. N.H.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing; C.F.: conceptualization, data curation, investigation, methodology, resources, writing—review and editing; M.M.: investigation, project administration, resources, writing—review and editing; S.M.S.: investigation, resources, writing—review and editing; S.O.: data curation, writing—review and editing; S.K.: investigation, writing—review and editing; D.K.: investigation, methodology, writing—review and editing; S.C.: data curation, investigation, methodology, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. We received no funding for this study.

Acknowledgements. A special thanks to the crew of Apex Shark Expeditions for help with data collection through the years, especially Monique Fallows, Poenas Jacobs and Ryan Miller. For assisting with collection and organization of faecal samples, we are grateful to Steven McCue and Lieze Swart and several DFFE interns. We are thankful to Patricia Albano, who helped with sample transport. We also thank the reviewers, whose comments helped improve the manuscript.

References

1. Estes JA, Tinker MT, Williams TM, Doak DF. 1998 Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**, 473–476. (doi:10.1126/science.282.5388.473)
2. Werner EE, Peacor SD. 2003 A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**, 1083–1100. (doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2)
3. Peckarsky BL *et al.* 2008 Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology* **89**, 2416–2425. (doi:10.1890/07-1131.1)
4. Hammerschlag N, Barley SC, Irschick DJ, Meeuwig JJ, Nelson ER, Meekan MG. 2018 Predator declines and morphological changes in prey: evidence from coral reefs depleted of sharks. *Mar. Ecol. Prog. Ser.* **586**, 127–139. (doi:10.3354/meps12426)
5. Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U. 2004 Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**, 932–935. (doi:10.1038/nature02430)
6. Zanette LY, Clinchy M, Suraci JP. 2014 Diagnosing predation risk effects on demography: can measuring physiology provide the means? *Oecologia* **176**, 637–651. (doi:10.1007/s00442-014-3057-9)
7. Trussell GC, Matassa CM, Ewanchuk PJ. 2017 Moving beyond linear food chains: trait-mediated indirect interactions in a rocky intertidal food web. *Proc. R. Soc. B* **284**, 20162590. (doi:10.1098/rspb.2016.2590)
8. Myers RA, Worm B. 2003 Rapid worldwide depletion of predatory fish communities. *Nature* **423**, 280–283. (doi:10.1038/nature01610)
9. Ripple WJ *et al.* 2014 Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484. (doi:10.1126/science.1241484)
10. Creel S. 2018 The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. *Ecol. Lett.* **21**, 947–956. (doi:10.1111/ele.12975)
11. Martin RA, Hammerschlag N. 2012 Marine predator–prey contests: ambush and speed versus vigilance and agility. *Mar. Biol. Res.* **8**, 90–94. (doi:10.1080/17451000.2011.614255)
12. Wcisel M, O'Riain MJ, de Vos A, Chivell W. 2015 The role of refugia in reducing predation risk for Cape fur seals by white sharks. *Behav. Ecol. Sociobiol.* **69**, 127–138. (doi:10.1007/s00265-014-1825-5)
13. Towner AV, Leos-Barajas V, Langrock R, Schick RS, Smale MJ, Kaschke T, Jewell OJ, Papastamatiou YP. 2016 Sex-specific and individual preferences for hunting strategies in white sharks. *Funct. Ecol.* **8**, 1397–1407. (doi:10.1111/1365-2435.12613)
14. Hammerschlag N, Martin RA, Fallows C. 2006 Effects of environmental conditions on predator–prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environ. Biol. Fishes.* **76**, 341–350. (doi:10.1007/s10641-006-9038-z)
15. Martin RA, Hammerschlag N, Collier RS, Fallows C. 2005 Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J. Mar. Biol. Assoc. UK* **85**, 1121–1136. (doi:10.1017/S002531540501218X)
16. Martin RA, Rossmo DK, Hammerschlag N. 2009 Hunting patterns and geographic profiling of white shark predation. *J. Zool.* **279**, 111–118. (doi:10.1111/j.1469-7998.2009.00586.x)
17. De Vos A, Justin O'Riain M, Meyer MA, Kotze PG, Kock AA. 2015 Behavior of Cape fur seals (*Arctocephalus pusillus pusillus*) in response to spatial variation in white shark (*Carcharodon carcharias*) predation risk. *Mar. Mammal. Sci.* **31**, 1234–1251. (doi:10.1111/mms.12208)
18. Fallows C, Fallows M, Hammerschlag N. 2016 Effects of lunar phase on predator–prey interactions between white shark (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*). *Environ. Biol. Fishes.* **99**, 805–812. (doi:10.1007/s10641-016-0515-8)
19. Hammerschlag N, Meÿer M, Seakamela SM, Kirkman S, Fallows C, Creel S. 2017 Physiological stress responses to natural variation in predation risk: evidence from white sharks and seals. *Ecology* **98**, 3199–3210. (doi:10.1002/ecy.2049)
20. Hammerschlag N, Williams L, Fallows M, Fallows C. 2019 Disappearance of white sharks leads to the novel emergence of an allopatric apex predator, the sevengill shark. *Sci. Rep.* **9**, 1908. (doi:10.1038/s41598-018-37576-6)
21. Rand R. 1959 The Cape fur seal (*Arctocephalus pusillus*): distribution, abundance and feeding habits off the south western coast of the Cape Province. *Investigational Report No. 34, South African Division of Fisheries, South Africa*.
22. Oosthuizen WH. 1991 General movements of South African (Cape) fur seals *Arctocephalus pusillus pusillus* from analysis of recoveries of tagged animals. *S. Afr. J. Mar. Sci.* **11**, 21–29. (doi:10.2989/025776191784287772)
23. Kock A, O'Riain MJ, Mauff K, Meÿer M, Kotze D, Griffiths C. 2013 Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PLoS ONE* **8**, e55048. (doi:10.1371/journal.pone.0055048)
24. David JH. 1987 South African fur seal, *Arctocephalus pusillus pusillus*. In *Status, biology, and ecology of fur seals: proceedings of an international symposium and workshop, Cambridge, UK, 23–27 April 1984* (eds JP Croxall, RL Gentry), pp. 65–71. Beaufort, NC: National Marine Fisheries Service.
25. Fallows C, Martin RA, Hammerschlag N. 2012 Comparisons between white shark-pinniped interactions at Seal Island (South Africa) with other sites in California. In *Global perspectives on the biology and life history of the white shark* (ed. ML Domeier), pp. 105–117. Boca Raton, FL: CRC Press.
26. Creel S, Winnie JA, Christianson D. 2009 Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proc. Natl Acad. Sci. USA* **106**, 12 388–12 393. (doi:10.1073/pnas.0902235106)
27. Hunt KE, Trites AW, Wasser SK. 2004 Validation of a fecal glucocorticoid assay for Steller sea lions (*Eumetopias jubatus*). *Physiol. Behav.* **80**, 595–601. (doi:10.1016/j.physbeh.2003.10.017)
28. Bonier F, Martin PR, Moore IT, Wingfield JC. 2009 Do baseline glucocorticoids predict fitness? *Trends Ecol. Evol.* **24**, 634–642. (doi:10.1016/j.tree.2009.04.013)
29. Romero M, Wingfield JC. 2016 *Tempests, poxes, predators and people: stress in wild animals and how they cope*. Oxford, UK: Oxford University Press.
30. Dulude-de Broin F, Hamel S, Mastromonaco GF, Côté SD. 2019 Predation risk and mountain goat reproduction: evidence for stress-induced breeding suppression in a wild ungulate. *Funct. Ecol.* **34**, 1003–1114. (doi:10.1111/1365-2435.13514)

31. Seguel M, Paredes E, Pavés H, Gottdenker NL. 2014 Capture-induced stress cardiomyopathy in South American fur seal pups (*Arctophoca australis gracilis*). *Mar. Mamm. Sci.* **30**, 1149–1156. (doi:10.1111/mms.12079)
32. Ebert DA. 1991 Diet of the seven gill shark *Notorynchus cepedianus* in the temperate coastal waters of Southern Africa. *S. Afr. J. Mar. Sci.* **11**, 565–572. (doi:10.2989/025776191784287547)
33. Hammerschlag N, Fallows C, Meÿer M, Seakamela SM, Orndorff S, Kirkman S, Kotze D, Creel S. 2022 Loss of an apex predator in the wild induces physiological and behavioural changes in prey. FigShare.