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Long-term decline in survival and reproduction of dolphins following a marine heatwave

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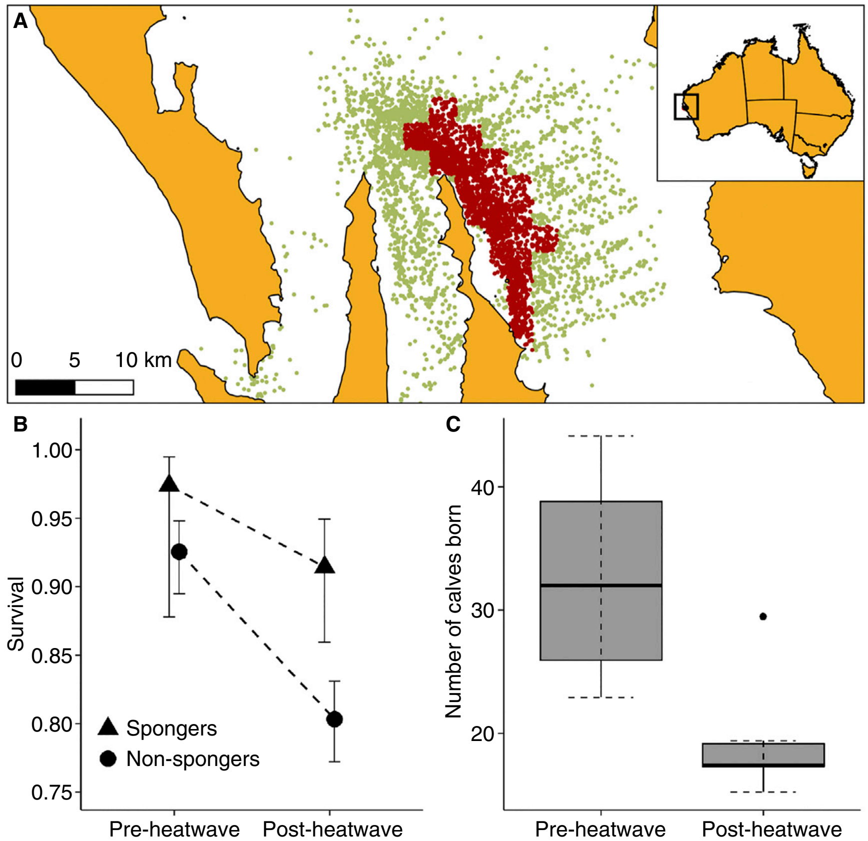

Figure 1. Dolphin vital rates in western Shark Bay before and after the 2011 marine heatwave.
(A) The study area in the western gulf of Shark Bay, Western Australia, encompassing approximately 1,500 km^2. Over 5,000 dolphin group encounters have been documented between 2007 and 2017 (all points). To account for unequal survey effort in each field season, the study area was overlaid with a grid of 2 x 2 km cells. Only encounters within grid cells covered in all seasons ('core' study area) were considered for capture–recapture analyses (red points). (B) While both spongers and non-spongers experienced declines in survival from pre- to post-heatwave, spongers were less affected than non-spongers (5.9% decline versus 12.2% decline, respectively). (C) The number of calves detected (controlled for number of known mothers observed each field season) was significantly higher pre- compared to post-heatwave, suggesting that female dolphin reproductive success was also negatively impacted by habitat degradation and prey species loss following the heatwave.

One of many challenges in the conservation of biodiversity is the recent trend in the frequency and intensity of extreme climatic events [1]. The Shark Bay World Heritage Area, Western Australia, endured an unprecedented marine heatwave in 2011. Catastrophic losses of habitat-forming seagrass meadows followed [2], along with mass mortalities of invertebrate and fish communities [3]. Our long-term demographic data on Shark Bay's resident Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population revealed a significant decline in female reproductive rates following the heatwave. Moreover, capture–recapture analyses indicated 5.9% and 12.2% post-heatwave declines in the survival of dolphins that use tools to forage and those that do not, respectively. This implies that the tool-using dolphins may have been somewhat buffered against the cascading effects of habitat loss following the heatwave by having access to a less severely affected foraging niche [4]. Overall, however, lower survival has persisted post-heatwave, suggesting that habitat loss following extreme weather events may have prolonged, negative impacts on even behaviourally flexible, higher-trophic level predators.

In the 2011 Austral summer, Western Australian coastal water temperatures rose 2–4°C above long-term averages for more than two months [5]. In the shallow, subtropical embayment of Shark Bay, an estimated 36% of seagrass meadows were damaged [2]. Wide-ranging effects associated with the heatwave were documented across lower trophic levels, while those on large vertebrates have remained more elusive. We investigated the vital rates (survival and reproduction) of dolphins in Shark Bay's western gulf, using long-term demographic and behavioural data collected between 2007 and 2017 (Figure 1A; see also Supplemental Information).

We assessed changes in apparent survival of dolphins over time using capture–recapture analyses (Data S1). Using Akaike weights as approximate model probabilities, there was a considerable decrease in survival after the heatwave. We suggest this was due to the well-documented losses of prey during the heatwave [3]. We also found that, on average, survival remained lower in the seven years after the heatwave than before. Again, having support from Akaike weights, we interpret this as evidence that dolphin mortality was impacted over a protracted period, rather than a single peak following the temperature anomaly (which had much lower support by Akaike weights). As such, the catastrophic reduction in seagrass coverage [2], which shows little sign of recovery [6], appears to be responsible for preventing fish stock recovery, since established seagrass meadows represent important breeding grounds and refuge habitat for numerous species [7].

We also tested for differences in survival between dolphins occupying different habitats, and those that use marine sponges as foraging tools ('spongers') versus those that do not ('non-spongers') [4]. Interestingly, while there was an overall decline in dolphin survival post-heatwave, survival of spongers was not as adversely impacted as that of non-spongers (5.9% versus 12.2% declines in survival from pre- to post-heatwave, respectively; Figure 1B). Sponge use is restricted to deeper channel habitats with no seagrass cover. While both spongers and non-spongers use these channels for foraging, sponge use allows access to a foraging niche which dolphins without the tool-using know-how cannot access [4], implying that the spongers' foraging niche may have been less severely impacted by the heatwave (Figure 1B).

A significantly greater number of calves per female per year was detected pre-heatwave compared with post-heatwave (Poisson generalized linear model (GLM); $z = -2.579$; effect size = 31.6%; 95% C.I. = [7.5%, 55.7%]; $p < 0.010$; Figure 1C), while no significant differences were found when comparing reproductive success for females from different habitat types (Poisson GLM; $z = 1.468$; $p = 0.142$), or using different foraging techniques (Poisson GLM; $z = -0.673$; $p = 0.501$) (Data S1). This result suggests that the spongers' access to a different foraging niche may have led to less severe effects on survival, but not reproduction. Reduced reproductive success as a consequence of significant ecological changes is not surprising, since a decline in food availability is expected to affect the most vulnerable members of a population, such as the young and those with high nutritional demands, like pregnant or lactating females [8].

There are several plausible explanations for this reduced reproductive success. First, lower prey availability may have forced female dolphins to spend more time foraging, leading to reduced vigilance and, ultimately, greater shark predation on calves. Second, reduced food availability can lead to either increased rates of abortion during pregnancy or increased neonate mortality, when both the mother's and the offspring's nutritional needs cannot be sustained [8]. Both abortions and increased mortality of young calves would effectively appear as lower reproductive success in the demographic data. Third, suppressed ovulation or delayed sexual maturity may have occurred when females did not reach a certain threshold of body weight [9]. Indeed, along with juvenile survival, fertility is the vital rate most sensitive to changes in resource availability in marine mammals [10].

Western Australia's 2011 marine heatwave negatively impacted habitat-forming and lower-trophic level organisms [2,3,5], and our results suggest cascading effects through to a behaviourally flexible, top-order predator. Long-lived taxa, such as some birds, great apes and cetaceans, are likely to experience changing ecological conditions throughout their lifetimes and, hence, may display behavioural plasticity in adapting to such changes. However, our findings suggest that the ecological consequences of extreme weather events may be too sudden or disruptive for even highly adaptable, animals to respond, leading to negative impacts on population viability. Such impacts may persist if ecosystems fail to recover. Further, our study adds to research illustrating that extreme events can drive biodiversity patterns and cause shifts in community structure toward more depauperate states [5]. These findings raise concerns over the long-term viability of the dolphin population, given that marine heatwaves are occurring with greater frequency in association with anthropogenic climate change [1].

SUPPLEMENTAL INFORMATION

Supplemental information includes two figures, one data file, supplemental experimental procedures and supplemental references and can be found at https://doi.org/10.1016/j.cub.2019.02.047. A video abstract is available at https://doi.org/10.1016/j.cub.2019.02.047#mmc3.

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AUTHOR CONTRIBUTIONS

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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