Nothing Goes to Waste: Perspectives from Sea Star Wasting Synthesis

J. P. Wares[1,*], L. M. Schiebelhut[2], and M. N Dawson[2]

[1] Odum School of Ecology and Department of Genetics, University of Georgia, Athens, Georgia 30602
[2] Life and Environmental Sciences, University of California, Merced, 5200 North Lake Road, Merced, California 95343

The global biodiversity crisis unfurling around us often requires that we have more complete information to predict how emerging threats will affect ecosystems. We must be able to derive mechanisms from events that we were not prepared to study before they happened. Biologists have learned from undesirable outcomes many times before; the tremendous impacts of species translocations to new localities through human activities are unfortunate—but informative—"experiments" from which we could gain new insights into changing organismal interactions and distributions (Sax *et al.*, 2005. *Species Invasions: Insights into Ecology, Evolution, and Biogeography*). Similarly, major disruptions to ecosystems have been a source of new understanding when experiments of similar magnitude are not possible, such as new models for community assembly following the massive volcanic eruption that wiped the Krakatau Islands clean of life (MacArthur and Wilson, 1963. *Evolution* 17: 373–387).

These massive "natural experiments" far exceed what is ethically acceptable or feasible but often invite conceptual novelty. The multispecies mass-mortality event known as "sea star wasting" (SSW) along the west coast of North America beginning in 2013 (Eisenlord *et al.*, 2016. *Philos. Trans. R. Soc. B* 371: 20150212) was immediately recognized as an opportunity to assess Paine's (1966. *Am Nat.* 100: 65–75) classical "keystone" hypothesis on such a massive scale, with greater variation in spatial and ecological contexts (Gravem and Morgan, 2017. *Ecology* 98: 1006–1015). From this massive perturbation we also gained novel information about growth and maturation, recruitment and repopulation, and other aspects of diversity in sea stars (*e.g.*, Menge *et al.*, 2016. *PLoS One* 11: e0157302; Miner *et al.*, 2018. *PLoS One* 13: e0192870; Moritsch and Raimondi, 2018. *Ecol. Evol.* 8: 3952–3964; Jaffe *et al.*, 2019. *PLoS One* 14: e0225248).

Because of the scale and impact to ecosystems, numerous studies have developed around this syndrome: how SSW associates with environmental anomalies (Held and Harley, 2009. *Invertebr. Biol.* 128: 381–390; Eisenlord *et al.*, 2016. *Philos. Trans. R. Soc. B* 371: 20150212; Aalto *et al.*, 2020. *Sci. Rep.* 10: 5975), the spatial context of disease response (Menge *et al.*, 2016. *PLoS One* 11: e0157302), how genomic diversity relates to disease (Ruíz-Ramos *et al.*, 2020. *Mol. Ecol.* 29: 1087–1102), and associations with microbial assemblages (Lloyd and Pespeni, 2018. *Sci. Rep.* 8: 16476; Aquino *et al.*, 2021. *Front. Microbiol.* 11: 3278; McCracken *et al.*, 2023. *Front. Mar. Sci.* 10: 1130912). The flurry of studies since the outbreak of SSW on the Pacific coast of North America have highlighted that there is still much to learn, whether SSW is a single phenomenon with common mechanisms across diverse observations (Hewson *et al.*, 2019. *Front. Mar. Sci.* 6: 406; *e.g.*, Smith *et al.*, 2022. *Biol. Lett.* 18: 20220197) or how strong selection has changed the very animals we study (Schiebelhut *et al.*, 2018. *Proc. Natl. Acad. Sci. U.S.A.* 115: 7069–7074). In short, SSW stimulated a massive and coordinated response among researchers, community scientists, and resource managers alike.

What has been less appreciated is that open questions about massive perturbations may be addressed, in part, using large amounts of data collected for reasons unrelated to the events themselves. Importantly, in these cases, baseline data or data predating the event are often available. Decades-old monitoring efforts along the coasts of Mexico, California,

Received 18 January 2024; Accepted 18 January 2024; Published online 21 February 2024.
* Corresponding author; email: jpwares@uga.edu.

The Biological Bulletin, June 2023, volume 244, number 3: 139–142. https://doi.org/10.1086/729512

Oregon, Washington, British Columbia, and Alaska—about sea star distribution, condition, and interactions—suddenly gained additional relevance. Such survey data provided observations of how quickly some species disappeared and in some cases the pattern of relative abundance during reappearance (Kay *et al.*, 2019. *Proc. R. Soc. B* 286: 20182766). Long-term data put these most recent mass-mortality events into the context of historical variation and previously unlinked observations (Hewson *et al.*, 2019. *Front. Mar. Sci.* 6: 406). Tissues collected for basic exploration gained new value for questions about evolutionary responses and experimental insights into how the unusual body architecture of asteroids itself may promote differential mortality (Aquino *et al.*, 2021. *Front. Microbiol.* 11: 3278). Public contributions through platforms such as iNaturalist have been adapted to better visualize the distribution of incidence and recovery (Michonneau and Paulay, 2015. *Reef Encount.* 30: 29–31). These are just a few examples of many efforts to understand the problem more thoroughly.

In a series of collaborative papers (Oulhen *et al.*, 2022. *Biol. Bull.* 243: 50–75; Schiebelhut, Giakoumis, *et al.*, 2023a. *Biol. Bull.* 243: 328–338; Schiebelhut, Giakoumis, *et al.*, 2023b. *Biol. Bull.* 243: 315–327; Dawson *et al.*, 2023. *Biol. Bull.* 244: 143–163), we further leveraged preexisting data and samples from varied perspectives—*via* an international consortium of early- to late-career researchers in evolutionary biology and genomics, ecology and environment, and whole-organism integrative biology—to revisit and revise baseline knowledge of asteroids affected by the diverse events often considered under the auspices of SSW. Our intent was both to learn more about the biology, ecology, and evolution of these organisms from the event and to learn more about the event from the organisms. In the end, it is clear that our overall understanding has been improved by these legacy data, and a key lesson—put into perspective for us by the endeavor as a whole—is that urgent action is necessary for our coastal ecosystems.

As a key example, consider Schiebelhut, Giakoumis *et al.* (2023a. *Biol. Bull.* 243: 328–338; hereafter, SG2023a), which explored the demographic and evolutionary responses to SSW in the canonical keystone species *Pisaster ochraceus*. The study would have been impossible without tissues archived since 2006 and 2012 that were then complemented by post-SSW collections by a large team of collaborators covering large spatial scales in the Pacific. The findings remind us that major mortality events can have limited effects on overall genomic diversity in the short term, particularly if the bottleneck is quite brief (Nei, 1987. *Molecular Evolutionary Genetics*, pp. 198–201), as seen in many coastal sites for *P. ochraceus*. Yet such events also may impact the distribution of genomic diversity on the landscape (SG2023a) and lead to rapid shifts in allele frequencies, including loss of rare diversity. The lesson learned is that while we can capture demographic changes through traditional ecological monitoring, we can only capture genomic consequences through continued molecular monitoring of change and loss in natural populations; coupling both is necessary to document short- and long-term impacts of mass mortalities. We need such monitoring across more regions of the world to better understand mechanisms of change.

Questions also have arisen about potential roles of organismal phenotype and variation across sea stars as factors influencing wasting response. Exploration of whether the dermal color of polymorphic sea stars like *P. ochraceus* have varying SSW incidence (Menge *et al.*, 2016. *PLoS One* 11: e0157302) have led to observations that orange *P. ochraceus* individuals are more likely to develop lesions but have greater survival (Work *et al.*, 2021. *Dis. Aquat. Org.* 145: 21–33). Such observations bring new relevance to historical patterns of color morph distribution (Harley *et al.*, 2006. *Biol. Bull.* 211: 248–262; Raimondi *et al.*, 2007. *Pac. Sci.* 61: 201–210) and raise questions about how variation in appearance may also have structural, physiological, developmental, or other implications related to individual fitness (Fig. 1). Thus, our consortium also focused on the mechanistic cell- and tissue-organized responses as sea stars twisted, autotomized, and disappeared during these outbreaks. Oulhen and colleagues (2022. *Biol. Bull.* 243: 50–75) started with a straightforward premise: to summarize how a sea star operates under normal conditions across cellular, tissue, and whole-organism levels and then identify the ways in which these systems seem to break or contribute to the process of degradation in SSW. This paper should be a useful starting resource for those new to asteroid biology, and it sparked deliberations into how neuronal or behavioral responses to SSW are generated, how reproductive maturity is involved, and what changes at the surface boundary seem to rapidly affect the dermal tissues (often the first sign of wasting in an individual). The surface rugosity of sea stars alone appears to be a predictive factor in SSW (Aquino *et al.*, 2021. *Front. Microbiol.* 11: 3278); Oulhen *et al.* (2022. *Biol. Bull.* 243: 50–75) additionally explored variation in immune response, disease signs, histology, and the unique structures of asteroids as components of understanding the mechanisms of SSW. In the end, so much is biologically unusual about sea stars that the SSW events end up repainting them as more environmentally sensitive than apex predators are often presumed to be.

The SSW outcomes across species were further explored by Schiebelhut, Giakoumis *et al.* (2023b. *Biol. Bull.* 243: 315–327; hereafter, SG2023b), exploring the phylogenetic distribution of SSW across time and trait space. Observations of SSW-like symptoms are phylogenetically extremely broad, and so SG2023b evaluated whether traits shared across species corresponded to shared wasting outcomes. Testing for a number of trait-specific associations with wasting observations, they found that stars with a shallower minimum depth distribution and earlier seasonal peak reproductive period experienced more severe wasting impacts. The

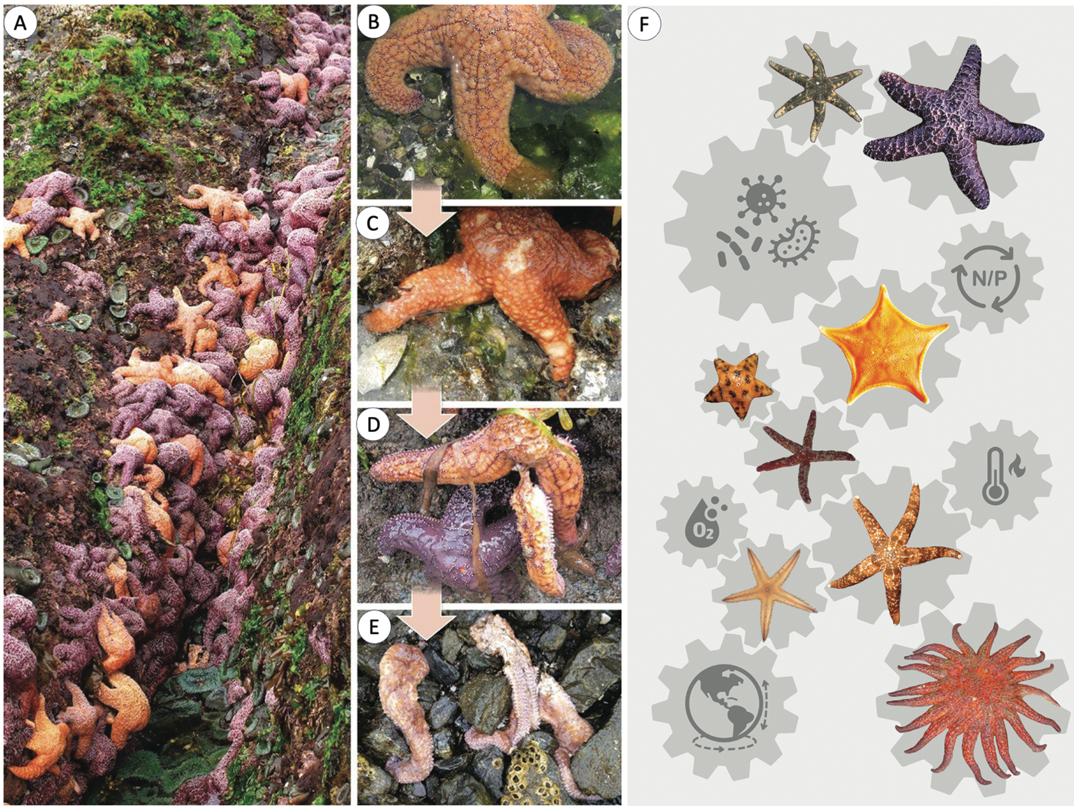

Figure 1. Single and multispecies examples of perspectives on sea star wasting (SSW). Photographs (A–E), adapted from Eisenlord *et al.* (2016. *Philos. Trans. R. Soc. B* 371: 20150212), represent common pre-SSW abundance of *Pisaster ochraceus* (A) and contrasts of individuals ranging from asymptomatic (B) to symptomatic (C, D) prior to death (E). (F) Schematic for ecosystem and community change mediated *via* many factors and interactions, including microbial feedbacks, eutrophication, and changes in dissolved oxygen and temperature, that influence sea star health and abundance in varying ways—and over varying timescales. Broad spatial and dense monitoring for environmental conditions, patterns of within-species and community-level diversity, and opportunities for restoration are necessary to slow or reverse ecosystem degradation.

results of this new synthetic phylogeny and analysis hint at some intrinsic traits that do contribute to species' vulnerability toward SSW. Yet both the review of Oulhen *et al.* (2022. *Biol. Bull.* 243: 50–75) and SG2023b also point toward the environmental context of sea star–dominated ecosystems in the past decade as an important, if often circumstantial, means to gain insight into these die-offs.

The final paper in the series, Dawson *et al.* (2023. *Biol. Bull.* 244: 143–163), aggregated assemblage and environmental data from diverse monitoring projects spanning depth, latitudinal, and temporal frames to explore the broadest contexts for SSW. While refining the temporal and taxonomic extents of SSW, their work also highlighted basic uncertainties—such as how to distinguish new recruits—and raised questions about how to interpret environmental variance in the context of mass mortality. For example, when a wasting outbreak precedes a massive marine heat wave by a year, it has tempted dismissal of temperature as a causal factor—but following decades of chronic sea surface warming, a minor heat wave that coincided with the outbreak could be the straw that broke the sea star's back. Given the recognized boom-bust cycles of echinoderms, can population and community dynamics under "normal" conditions predict dynamics during mass-mortality events? What *are* the relationships among multiple stressors—whether abiotic environmental changes and/or the emergence of pathogenic interactions? And how much effort should we invest in following partial and counterintuitive lines of evidence, such as that surface dysoxia might be important in the intertidal zone and varying levels of wave exposure? Clearly, the data needed for understanding SSW are still far beyond what we have in hand. That almost all the data summarized here arise from one of the best studied coastlines on the planet (Leslie *et al.*, 2019. *Oceanography* 32: 12–15) and yet we still do not know what precipitated SSW and how it propagated through sea star assemblages is itself a warning about how we need to approach ongoing exploration and management of a rapidly changing world (Orr *et al.*, 2020. *Proc. R. Soc. B* 287: 20200421).

And therein lies the concern. Although our scientific community can gather more precise and more comprehensive data, collectively glean more insights (*e.g.*, Hewson *et al.*, 2018. *Front. Mar. Sci.* 5: 77; Wares and Duffin, 2019. *bioRxiv*: 10.1101/584235v1), and continue to reevaluate what we have seen and will see in the years to come, what will such efforts achieve? We already have enough evidence that—whether sea stars died as a result of heat, dysoxia, and/or pathogen(s) or some additional combination—this event was the most extreme on record and an illustration of a decline in resilience (*e.g.*, Menge *et al.*, 2021. *Proc. Natl. Acad. Sci. U.S.A.* 119: e2114257119). To avoid another decade of death, it is time to focus on pathways toward recovery of threatened species (Hamilton *et al.*, 2021. *Proc. R. Soc. B* 288: 20211195) and ecosystem feedback loops (Aquino *et al.*, 2021. *Front. Microbiol.* 11: 3278) that can rebalance how and where sea stars can thrive, remembering that these animals are typically important consumers that drive diversity in marine ecosystems (Fig. 1F). One way or another, this massive SSW "experiment" is a component of a global problem that we must urgently resolve how to address.

The effort to synthesize so much available data inevitably requires difficult choices on how to represent the scale of the problem, the disciplinary breadth required to understand it, and the tremendous gaps in information from poorly monitored coasts of the world (see Dawson Suppl. 7). These basic components of natural history are needed as we prepare for new observations of decline—whether in the same form or not, in new locations around the world, driven by the force of anthropogenic changes (Dudgeon and Petraitis, 2020. *Commun. Biol.* 3: 591). Nonetheless, what has been learned in recent years points to actions that can be taken even while details of organismal responses are being refined. As temperature, eutrophication, and extreme weather events—elements of our climate and environmental emergencies—have been implicated multiple times as factors in SSW (Held and Harley, 2009. *Invertebr. Biol.* 128: 381–390; Menge *et al.*, 2016. *PLoS One* 11: e0157302; Eisenlord *et al.*, 2016. *Philos. Trans. R. Soc. B* 371: 20150212; Aquino *et al.*, 2021. *Front. Microbiol.* 11: 3278; Dawson *et al.*, 2023. *Biol. Bull.* 244: 143–163), we have to imagine that continued extirpations may ratchet toward extinctions (Gravem *et al.*, 2021. IUCN Red List of Threatened Species; Hamilton *et al.*, 2021. *Proc. R. Soc. B* 288: 20211195; Dawson *et al.*, 2023. *Biol. Bull.* 244: 143–163). Even with gained knowledge, perspectives, and approaches, unless we take additional actions to change the trajectory for the planet, all we will have are better ways to document the decline. As Steinbeck (1951. *Log from the Sea of Cortez*, p. 179) noted, "it is advisable to look from the tide pool to the stars and then back to the tide pool again." And in the devastation in the tidepool, we must see our own reflection. Steinbeck referred to a whole cosmology in that phrase, yet imagine a sea without stars.

Acknowledgments

Our collaboration was supported through National Science Foundation awards OCE-1737091 to JPW and OCE-1737381 to MND. P. J. Duffin generated the schematic in Figure 1. Images in Figure 1 are from Eisenlord *et al.* (2016. *Philos. Trans. R. Soc. B* 371: 20150212) (CC BY 4.0), and individual sea star images in the schematic from Schiebelhut, Giakoumis, *et al.* (2023b. *Biol. Bull.* 243: 315–327), except the *Pisaster ochraceus* in top right corner, are from a photo taken by Jerry Kirkhart (https://www.flickr.com/photos/jkirkhart35/2132256087) (CC BY 2.0).