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Perspective: Something Old, Something New? Review of Wasting and Other Mortality in Asteroidea (Echinodermata)

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Asteroids (Echinodermata) experience mass mortality events that have the potential to cause dramatic shifts in ecosystem structure. Asteroid wasting describes a suite of body wall abnormalities that can ultimately result in animal mortality. Wasting in Northeast Pacific asteroids has gained considerable recent scientific attention due to its geographic extent, number of species affected, and effects on overall population density in some affected regions. However, asteroid wasting has been observed for over a century in other regions and species. Asteroids are subject to physical injury and adverse environmental conditions, which may result in very similar external manifestations to wasting, making identification of causative processes sometimes problematic. Here we review asteroid health abnormalities reported in years prior to the 2013–present Northeast Pacific wasting mass mortality, and report two additional geographically disparate wasting events that occurred concomitantly with the recent wasting outbreak.

Keywords: sea star wasting, disease, syndrome, asteroid, echinoderm

INTRODUCTION

Marine disease events can have profound influences on ecosystem structure, causing shifts in species dominance, biodiversity, and function. Sea stars (Echinodermata: Asteroidea) are ecologically significant constituents of benthic communities worldwide, where some species can exert significant influence on the population structure and composition of sympatric organisms (Paine, 1966; Menge and Sanford, 2013). Asteroid diseases have been reported for over a century (Mead, 1898; Christensen, 1970; Menge, 1979; Dungan et al., 1982; Jangoux, 1987; Eckert et al., 1999; Bates et al., 2009).

The term “sea star wasting disease (SSWD)”, first used to describe a common suite of clinical signs that affected Asteroidea in Southern California asteroids in the early 1980s (Dungan et al., 1982) and late 1990s (Eckert et al., 1999), has more recently been used to describe the mass mortality of asteroids on the Pacific coast of North America beginning in 2013 (Hewson et al., 2014) and in the North Atlantic Ocean beginning in 2012 (Bucci et al., 2017). The sea star wasting outbreak [also referred to as “Asteroid Idiopathic Wasting Syndrome” (Hewson et al., 2018)] widely reported

from 2013 to present is amongst the most geographically extensive marine mass mortality events ever observed (Hewson et al., 2014), leading to catastrophic declines in some species of sea stars in affected areas (Montecino-Latorre et al., 2016; Schultz et al., 2016) and increased abundance of prey urchins (Schultz et al., 2016). Whereas mass-mortalities of asteroids in the northeast Pacific Ocean prior to 2013 represented mostly endemic events with local impacts on ecosystem structure, wasting since 2013 is currently described as an epidemic and is hypothesized to result in continental-scale changes in coastal habitats (Harvell et al., 2019).

Generally, asteroid wasting is described as a progression of clinical signs whereby lesions appear on their surface tissues, followed by tissue decay around lesions, limb autotomy and death. Wasting can be rapid, leading to animal mortality in a few days (Miner et al., 2018). In the Northeast Pacific, apparently asymptomatic individuals that were collected and transported to the laboratory and housed in flow-through sea tables (i.e., ambient seawater conditions) showed very rapid (within hours) disintegration (Eisenlord et al., 2016; Kohl et al., 2016). Signs of wasting are similar to those produced by environmental stressors (e.g., desiccation) or physical injury, hence wasting occurrence is only recorded when large numbers of individuals in a population display extensive wasting signs (Miner et al., 2018) during systematic surveys of wasting (Eisenlord et al., 2016; Menge et al., 2016; Schultz et al., 2016). As with many invertebrate diseases, sea star wasting is not pathognomic (i.e., no defining disease signs) since echinoderms possess a limited repertoire of abnormal gross characteristics.

The purpose of this perspective is to summarize reported asteroid disorders recorded before 2013, and report two geographically disparate wasting events in 2015. It will also review physical injury and mortality due to predation and abnormalities induced by abiotic causes. Here we show that grossly apparent disease signs reported in the current Northeast Pacific sea star wasting outbreak share similarity with those caused by non-pathogenic factors, and are also similar to reported asteroid mass mortalities since at least 1898.

Abiotic Causes of Mass Mortality

Physical injury to asteroids may cause clinical signs similar to wasting and other health conditions (Figure 1). A treatise on abiotic health conditions in echinoderms, including asteroids, was prepared by Lawrence (1996). Abiotic factors that cause health abnormalities in asteroids include burial (obration; Schaefer and Craig, 1972), dislodgement by storms and currents (Sieling, 1960; Tiffany, 1978; McClintock, 2013) leading to mass strandings [Sheehan and Cousens, 2017; see **Supplementary Table 1** for stranding events in the popular press recorded in the last decade (2008–2018)], temperature excursions (Crisp, 1964; Moyses and Nelson-Smith, 1964; Staehli et al., 2008), desiccation during emersion (Hodgkin, 1959), salinity variation (Smith, 1940), hypoxia (Osborne, 1979), and exposure to anthropogenic toxins (Smith, 1968). Abiotic conditions generally present as density-independent occurrences, and normally also include sympatrics. Individuals experiencing the effects of abiotic abnormalities typically show either no gross morphological

change prior to death, show lesions consistent with abrasion (in the case of current scouring), or may show signs of advanced decay (which is unrelated to the cause of death) when found (McClintock, 2013). For example, Waldichuk (1990) reported a highly localized mass mortality of deep water asteroids in southern British Columbia, where hundreds of individuals were found “broken into pieces” and attributed the event to fishing by-catch. Similarly, a mass mortality of asteroids, mostly intact, occurred near the Powell River in British Columbia, which was accompanied by mortality of conspecifics and therefore likely due to adverse environmental condition or pollutants (Anon, 1990). Abiotic mass mortalities of asteroids is observed in the fossil record, where thousands of individuals in a single strata (i.e., occurring at the same geological time and within a former shallow sea) occurred in a single region (Gale and Villier, 2013).

While physical injuries may be caused by predation, they are subject to predation by relatively few animals, presumably due to feeding deterrents in their tissues. Specifically, asteroids possess a suite of saponins, which are not palatable by many predators (Hashimoto and Yasumoto, 1960; Lucas et al., 1979). Despite these defenses, sea stars can be subject to predation by sympatrics, fish, seabirds (notably gulls) (Suraci and Dill, 2011; Rogers and Elliott, 2013) and otters (Estes et al., 2003; Vicknair and Estes, 2012; reviewed in Robles, 2013 and Pearse et al., 2010). Specifically, there are examples of predation on sea stars by birds (Verbeek, 1977) and otters when food is limited (Larsen, 1984). It is worthwhile noting that the physical injuries (bites/pecks) from predation are similar to lesions seen in sea star wasting.

Wasting Syndromes

While the 2013–present asteroid wasting event has attracted considerable recent attention, wasting as a phenomenon affecting asteroids is not new, and similar wasting signs described in previous events (Mead, 1898; Christensen, 1970; Menge, 1979; Pratchett, 1999; Staehli et al., 2008) are highly similar to those observed today.

The earliest known account of asteroid wasting was in *Asterias forbesi* more than 120 years ago (Mead, 1898). In a report on fisheries by the Harvard Professor A.D. Mead addressing a wide suite of starfish biology, they noted “on certain lots of star-fish, dredged from different localities, what appears to be a disease, attacking the skin first and not infrequently eating its way through the body. This disease attacks both the common star and the purple star. Some of the star-fish in my cars at Kickemuit river were so seriously affected that some of the arms were entirely eaten through and the ends dropped off. Later some of them recovered”. The author suggested that this disease could be of service in mitigating starfish impacts on the shellfish fishery, since “There seems to be no doubt but that, with the development of the oyster beds, the star-fish has become more numerous along our New England coast”.

Christensen (1970) reported that *Astropecten irregularis* was subject to wasting by a fungal infection of the epidermis, however, no specific pathogen was identified. During feeding experiments, Christensen (1970) also reported that one individual had an “unknown skin disease” which caused mortality several months after it first showed signs of wasting – the animal “burst with

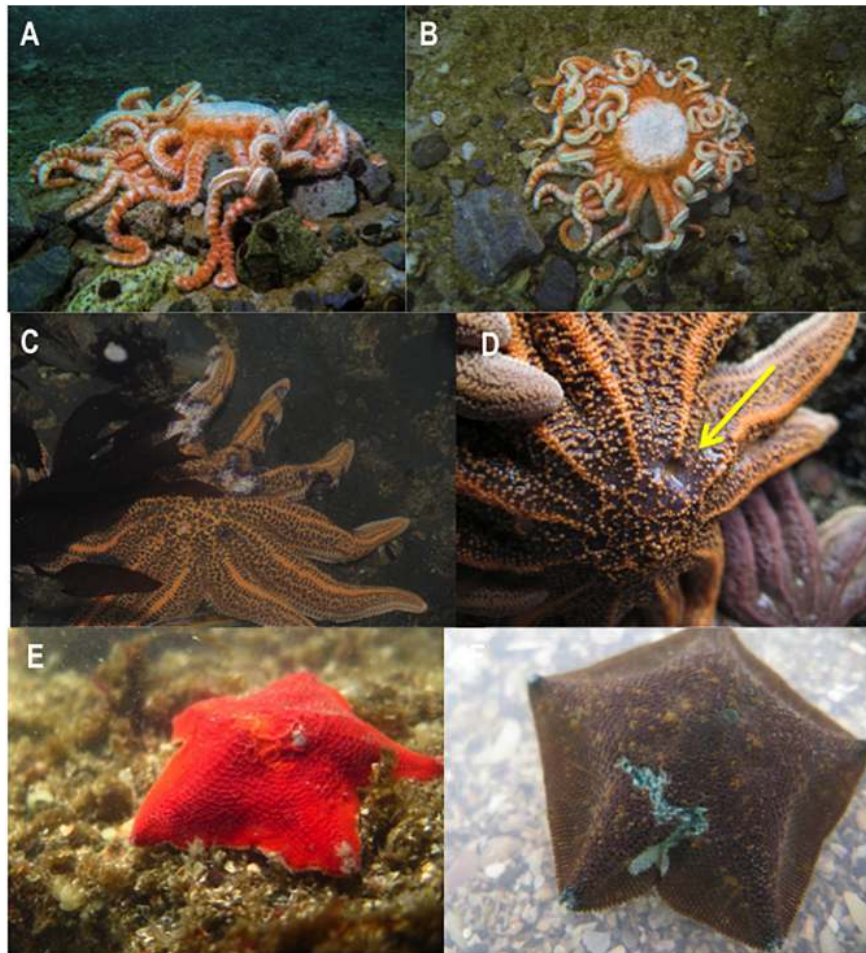


FIGURE 1 | Unidentified disorders in asteroids. **(A,B)** *Labidiaster* sp. From Antarctica showing wasting signs. The individual was the sole example demonstrating abnormalities amongst hundreds of individuals (Photo credit Shaylyn Potter). **(C)** Lesions on *Stichaster australis* from Muriwai, Auckland, New Zealand in June 2015. The individual was the sole example of affected stars amongst hundreds. Subsequent surveys in the area later in 2015 revealed no additional stars (Photo credit Richard Taylor). **(D)** Degraded madreporite in *S. australis* from Piha, Auckland, New Zealand (madreporite indicated by yellow arrow) **(E,F)** Lesions on *Patiriella regularis* from the North Island of New Zealand, in December 2017 and January 2018, respectively. The individuals were one of a small handful with lesions which may indicate physical injury.

parts of at least 2 gonads piercing through the body wall". It is unclear if wasting resulted in the eventual death of the animal.

Menge (1979) reported a wasting event in *Asterias* spp. in the Gulf of Maine, which bears similarities to the 2013–2016 Northeast Pacific wasting event. He reported that animals experienced necrotic areas on their epidermis, which progressed to erosions through their body walls. Wasting first appeared in late autumn 1972 and was followed by disappearance of most large *Asterias*, causing a shift in the size range of individuals to smaller animals (and juveniles) in subsequent surveys.

Dungan et al. (1982) reported extensive wasting in the predatory sun star *Heliaster kubiniji*, in the Gulf of California during 1977 and 1978. Reported wasting signs included the appearance of white lesions on the aboral surface of affected individuals, which rapidly enlarged to encompass the whole animal and resulted in limb autotomy. The wasting onset corresponded with a period of higher-than-15 year average water

temperatures and led to the functional extirpation of the species in the region (Dungan et al., 1982). Populations of *H. kubiniji* have not recovered as of 2008 (Sagarin et al., 2008).

A wasting-like disease was reported by Prestedge (1998) in the asterinid *Patiriella vivipara* in Tasmania. The condition – known as “brown spot” disease elicited small brown areas on the aboral and sometimes oral epidermis. The disease appeared to have a high prevalence in both natural and aquarium-housed individuals, and was present year-round over 8 years. The author indicated that brown spot may persist for months, clear up in some individuals, and in severe cases cause skin necrosis which over several weeks resulted in animal mortality (Prestedge, 1998).

Stahli et al. (2008) reported the presence of wasting in the sand star *Astropecten johnstoni* in Sardinian waters. Wasting manifested with the appearance of white lesions and loss of turgor, followed by swelling on one side, eversion of stomach through the mouth and erosions in body wall tissues, the spread

of lesions over the entire body wall and finally animal death and disintegration within 48 h of appearance of first lesions. The authors found that enhanced temperature (+8–13°C above ambient) significantly accelerated the progress of wasting signs, and also observed the presence of several genera of bacteria, for which there are known pathogenic representatives (e.g., *Vibrio* spp.), in skin swabs of affected tissues.

Wasting was also reported by Pratchett (1999), where a single *Acanthaster planci* “was found with numerous lesions of the dermal tissue, collapsed spines, and a completely debilitated water-vascular system”. An experiment where affected tissues were placed into aquaria with healthy individuals resulted in identical wasting signs (epidermal lesions and collapsed spines) in 3 of 6 challenged individuals, resulting in mortality 6–9 days after challenge. Further investigation of wasting in *A. planci* revealed that wasting with the same signs could be induced by injection with thiosulfate-citrate-bile-sucrose (TCBS) (Rivera-Posada et al., 2011a; Rivera-Posada et al., 2012). TCBS media is used to selectively culture *Vibrio* spp. and other Proteobacteria (Lotz et al., 1983). Wasting was associated with dysbiosis and presence of bacterial genera with pathogenic representatives, notably *Vibrio* spp. (Rivera-Posada et al., 2011b,c). Interestingly, similar wasting, attributed to an unidentified sporozoan parasite, were observed in 1984 and 1986 in Suva, Fiji, which led to the extirpation of cohorts (Zann et al., 1990).

Bates et al. (2009) observed wasting in *Pisaster ochraceus* in Barkley Sound, Vancouver, British Columbia in 2008. Affected stars demonstrated the appearance of small white lesions (especially in inter-radial tissue), edema of epidermal tissues (a “mushroom”-like swelling) which spread to the whole individual, followed by spread of lesions across the body and ultimately animal death. There was a higher prevalence of wasting in field populations in presumably cooler waters of June than in August. Interestingly, wasting was also more prevalent in protected waters, which typically experience stronger diel temperature shifts than exposed shores.

An epidermal disease was reported in the circum-Antarctic asteroid *Odontaster validus* near the volcanic Deception Island (South Shetland Islands, near Antarctica) from 2012 to 2013 and again in 2016 (Núñez-Pons et al., 2018). The disease presented as focal epidermal depigmentation, anorexia, and limb autotomy, affecting ~10% of the population. The disease concurred with unprecedented geothermal anomalies (increased water temperature and seismic events). The authors found no evidence of disease transmission from affected to healthy individuals. Histopathological investigation revealed ulceration (edema), epidermal necrosis, and infiltration by hemocytes, accompanied by cleft formation between outer epidermis and ossicle-rich body wall tissues. Analyses of microbial communities on lesion fronts revealed decreased bacterial richness relative to unaffected tissues, and communities were different between lesions and healthy tissues. Fungal communities, however, were not different between lesions and clinically normal tissues. No etiological agent could be identified from analysis of the disease (Núñez-Pons et al., 2018).

Asteroid wasting in the northeast Pacific (Bates et al., 2009; Hewson et al., 2014) and northwest Atlantic (Bucci et al., 2017)

from 2013 onward manifested with similar wasting signs to those reported previously (Christensen, 1970; Menge, 1979; Dungan et al., 1982; Pratchett, 1999; Staehli et al., 2008). Affected individuals demonstrated various wasting signs, including loss of turgor, appearance of body wall lesions on their aboral surfaces, which enlarged to permit internal organs (i.e., gonads and pyloric caeca) to protrude, tissue loss and limb autotomy. A more subjective wasting sign, limb twisting and folding, was also reported (Hewson et al., 2014). The etiology of the northeast Pacific and northwest Atlantic wasting events remains poorly resolved (Miner et al., 2018). While the Sea Star Associated Densovirus (SSaDV) was the best candidate microorganism associated with wasting in one species of asteroid (Hewson et al., 2014), no candidate pathogenic microorganism has been identified for the remaining 19 species of sea star affected in the region (Hewson et al., 2018). Furthermore, while increased temperature (Eisenlord et al., 2016; Kohl et al., 2016), decreased temperature (Menge et al., 2016), and shifts in temperature and precipitation (Hewson et al., 2018) corresponded with SSWD at some locations, there remains no parsimonious explanation for wasting occurrence across the event's geographically wide distribution.

Here we report the occurrence of two significant asteroid wasting events that occurred elsewhere in 2015 that have hitherto been undocumented. Beginning in April 2015 and continuing until at least September 2015, asteroid wasting was observed in the Yellow Sea, China. Wasting was first observed in the field in Dongjiakou Bay in April, followed by Haizhou Bay in May, and further North in Qingdao in subsequent months, affecting three species of asteriid sea stars, *Asterias amurensis*, *Aphelasterias japonica*, and *Distolasterias nipon* (Figures 2A–F). In Haizhou Bay, most surviving sea stars were small individuals with armlength shorter than 3 cm. A collection of >130 apparently healthy adult *A. amurensis* with well-developed gonads was performed from Rongcheng, Weihai, in June 2015 for use in experiments aimed to determine the etiology of field-observed wasting. After collection and maintenance in aquaria, 80% of collected individuals died within 7 days. Individuals demonstrated wasting-like signs consistent with wasting in the northeast Pacific, including limb twisting and autotomy, appearance of lesions and protrusion of internal organs, and finally death.

A sea star wasting event was observed in Port Phillip Bay, Victoria, Australia from September–December 2015 (Figures 2G,H) concomitant with the wasting epidemic on the North American West Coast from 2013 to 2016. The Port Phillip Bay event occurred at the same time as the longest and most intense marine heat wave ever recorded in the region (Oliver et al., 2017). The first observations were made in individuals transferred from wild populations to the Victorian Marine Science Consortium (VMSC) in Queenscliff, Victoria in September 2015. Signs of wasting presented in two species transferred to the lab, including the invasive *A. amurensis*, and the native *Coscinasterias muricata*. Symptoms were much more pronounced in the *C. muricata*, which dominated the study site and were most frequently observed. The signs presented were typical of wasting elsewhere, including loss of turgor, swelling,

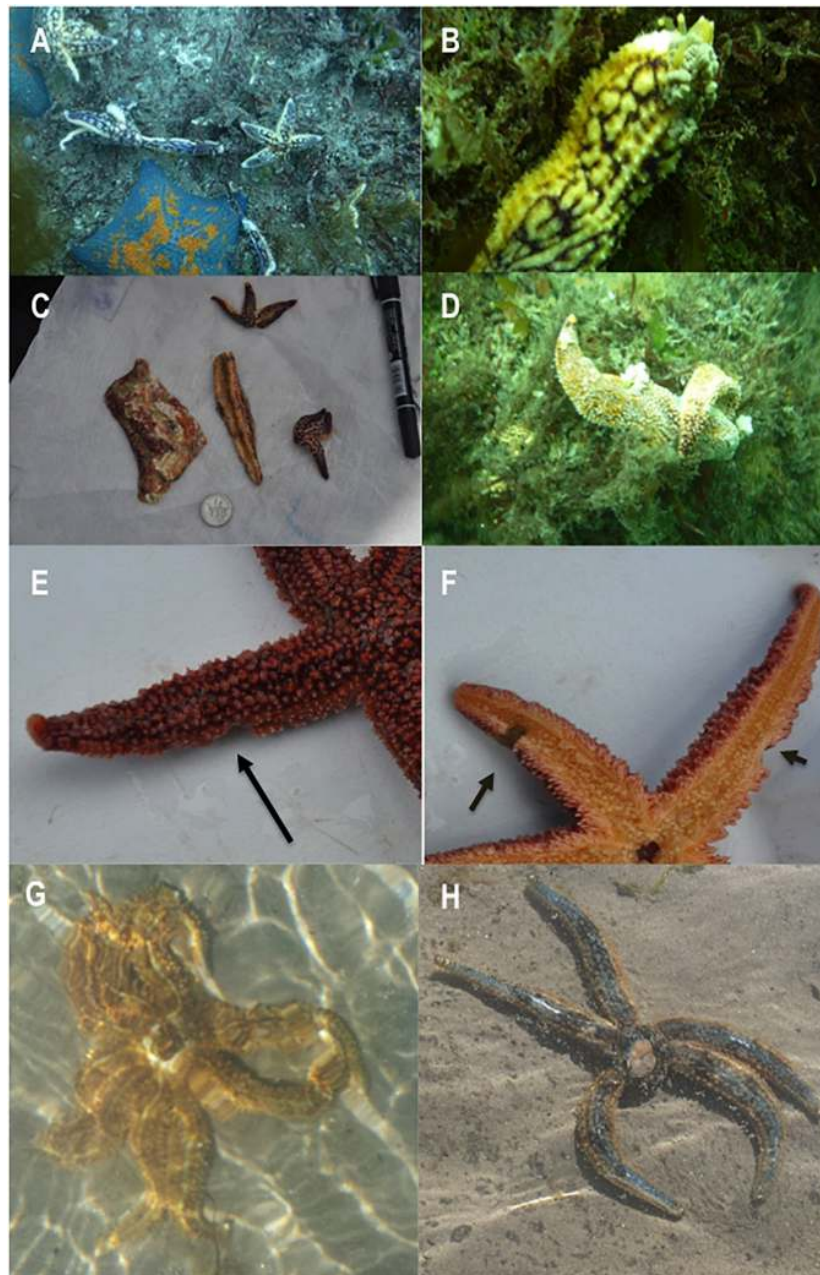


FIGURE 2 | Wasting signs in four species of asteroid. **(A)** *Asterias amurensis* with sympatric *Patria pectinifera* from the Yellow Sea, April–June 2015; **(B)** Autotomized limb of *A. amurensis*; **(C)** *A. amurensis* recovered in the lab; **(D)** *Distolasterias nipon*; **(E,F)** *Aphelasterias japonica* showing arm lesions (denoted by black arrows); **(G,H)** *Coscinasterias muricata* inhabiting Port Phillip Bay, Australia, September–October 2015.

lesion formation, tissue decay and limb autotomy, resulting eventually in animal mortality. In total 18 *A. amurensis* and 12 *C. muricata* died within 3 days of arriving at the research center. Upon first observation of wasting at the VMSC aquaria, field observations of asteroid health were performed by a snorkeler over the same 5 transects on two dates (4 October 2015 and 27 October 2015). A population decline of >75% (of $n = 146$ individuals on 4 October 2015) was estimated from the surveys, and asteroid rays and other detached parts were

observed on adjacent beaches and washing up with the tides. These semi-quantitative and anecdotal observations suggest that the asteroid population in Queenscliff experienced a widespread die-off. Photographs and videos were taken both of captive and wild asteroids to document their health state using the wasting scale (0–4)¹. A total of 155 individuals were assessed for wasting category. This analysis indicated that there was no significant

¹www.seastarwasting.org

change (t -test, $df = 128$) in mean wasting category between 4 October 2015 and 27 October 2015, with most individuals having limb autotomy and body wall lesions (mean category = 3.0 ± 0.3 on 4 October and = 2.2 ± 0.1 on 27 October). Since there had been no accounts of large asteroid losses previously in Port Phillip Bay, there was little support or resources available to researchers for further investigation. In addition, the study site was destroyed (buried) during pier improvements in 2016 and the populations have not been observed since.

Priorities for Future Research

As of June 2019, the cause of most echinoderm health conditions remain unknown; however, there are several lines of evidence to suggest association with either putative pathogens or environmental stressors. The mass mortality of *Diadema antillarum* in the early 1980s was almost certainly transmissible, but few specimens of affected individuals were collected, and those that were collected were in an advanced state of degradation for histopathology (Peters, 1992). Hence, scientists may never learn the cause of that wasting event. Early wasting asteroids from southern California (*H. kubiniji*) and from the Mediterranean (Christensen, 1970) were likewise not preserved. Future efforts to elucidate the causes of asteroid wasting should ensure adequate long-term preservation and archiving of samples for future analyses that may not be possible with contemporary technologies. In veterinary medicine, case studies of infectious diseases are typically made to provide an up-to-date summary for field-practitioners and clinicians to help guide them toward best practices for diagnosis. No case study currently exists for wasting, which could be of great value to guide researchers and veterinarians toward a standardized approach for field-sampling, reporting and documentation. Wasting is currently an umbrella term to describe any and all signs of an affected sea star, which may not be appropriate since these signs are not pathognomic. The signs of wasting that have been categorized into progressive stages require greater detail and attention for each species. For instance, there might exist subtleties among lesions or signs that have important biological significance that would help distinguish between two or more diseases.

CONCLUSION

Asteroid wasting events exhibit similarity in clinical signs, which are most notably characterized by appearance of lesions which may enlarge over time to allow internal organs to protrude. These

REFERENCES

- Anon, A. (1990). Mysterious starfish mortality near Powell river, British Columbia. *Mar. Poll. Bull.* 21:462. doi: 10.1016/0025-326x(90)90056-e
- Bates, A. E., Hilton, B. J., and Harley, C. D. G. (2009). Effects of temperature, season and locality on wasting disease in the keystone predatory sea star *Pisaster ochraceus*. *Dis. Aquat. Org.* 86, 245–251. doi: 10.3354/dao02125
- Bucci, C., Francoeur, M., McGreal, J., Smolowitz, R., Zazueta-Novoa, V., Wessel, G. M., et al. (2017). Sea star wasting disease in *Asterias forbesi* along the Atlantic coast of North America. *PLoS One* 12:20. doi: 10.1371/journal.pone.0188523
- Christensen, A. M. (1970). Feeding biology of the sea-star *Astropecten irregularis* Pennant. *Ophelia* 8, 1–134.
- Crisp, D. J. (1964). Mortalities in marine life in north Wales during the winter of 1962–1963. *J. Anim. Ecol.* 33, 190–197.
- Dungan, M. L., Miller, T. E., and Thomson, D. A. (1982). Catastrophic decline of a top carnivore in the Gulf of California rocky intertidal zone. *Science* 216, 989–991. doi: 10.1126/science.216.4549.989
- Eckert, G., Engle, J. M., and Kushner, D. (1999). “Sea star disease and population declines at the Channel Islands,” in *Proceedings of the 6th California Islands Symposium*, Ventura, CA, 435–441.

events can have significant impacts on the population density of their hosts (Menge, 1979; Dungan et al., 1982; Zann et al., 1990; Menge et al., 2016), and shift population structure from large individuals (presumably adults) to juveniles (Menge, 1979; Menge et al., 2016). However, distinguishing between wasting diseases is difficult since they demonstrate consistent suites of clinical signs but may represent different etiologies (Hewson et al., 2018). The apparent “emergence” of wasting disease in the Northeastern Pacific in 2013 is perhaps not a new phenomenon but a more geographically widespread, and within-population intensive, phenomenon that has been observed for over a century.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

All authors wrote the manuscript. QX, HL, CL, and BS performed field observations and laboratory analysis of wasting events in the China and Australia.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00406/full#supplementary-material>

- Eisenlord, M. E., Groner, M. L., Yoshioka, R. M., Elliott, J., Maynard, J., Fradkin, S., et al. (2016). Ochre star mortality during the 2014 wasting disease epizootic: role of population size structure and temperature. *Philos. Trans. R. Soc. B* 371:20150212. doi: 10.1098/rstb.2015.0212
- Estes, J. A., Riedman, M. L., Staedler, M. M., Tinker, M. T., and Lyon, B. E. (2003). Individual variation in prey selection by sea otters: patterns, causes and implications. *J. Anim. Ecol.* 72, 144–155. doi: 10.1046/j.1365-2656.2003.00690.x
- Gale, A., and Villier, L. (2013). Mass mortality of an asteriid starfish (Forcipulatida, Asteroidea, Echinodermata) from the late Maastrichtian (Late Cretaceous) of Morocco. *Palaeontology* 56, 577–588. doi: 10.1111/pala.12002
- Harvell, C. D., Montecino-Latorre, D., Caldwell, J. M., Burt, J. M., Bosley, K., Keller, A., et al. (2019). Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*). *Sci. Adv.* 5:eaau7042. doi: 10.1126/sciadv.aau7042
- Hashimoto, Y., and Yasumoto, T. (1960). Confirmation of saponin as a toxic principle of starfish. *Nippon Suisan Gakkaishi* 26, 1132–1138. doi: 10.2331/suisan.26.1132
- Hewson, I., Bistolas, K. S. I., Quijano Carde, E. M., Button, J. B., Foster, P. J., Flanzenbaum, J. M., et al. (2018). Investigating the complex association between viral ecology, environment and Northeast Pacific Sea Star Wasting. *Front. Mar. Sci.* 5:77. doi: 10.3389/fmars.2018.00077
- Hewson, I., Button, J. B., Gudenkauf, B. M., Miner, B., Newton, A. L., Gaydos, J. K., et al. (2014). Densovirus associated with sea-star wasting disease and mass mortality. *Proc. Nat. Acad. Sci. U.S.A.* 111, 17276–17283.
- Hodgkin, E. P. (1959). Catastrophic destruction of the littoral fauna and flora near Fremantle January 1959. *West Aust. Nat.* 7, 6–11.
- Jangoux, M. (1987). Diseases of echinodermata. I. agents microorganisms and protists. *Dis. Aquat. Org.* 2, 147–162. doi: 10.3354/dao002147
- Kohl, W. T., McClure, T. I., and Miner, B. G. (2016). Decreased temperature facilitates short-term sea star wasting disease survival in the keystone intertidal sea star *Pisaster ochraceus*. *PLoS One* 11:e0153670. doi: 10.1371/journal.pone.0153670
- Larsen, D. N. (1984). Feeding habits of river otters in coastal southeastern Alaska. *J. Wildlife Manag.* 48, 1446–1452.
- Lawrence, J. M. (1996). “Mass mortality of echinoderms from abiotic factors,” in *Echinoderm Studies*, eds M. Jangoux and J. M. Lawrence (Rotterdam: A.A. Balkema), 103–137.
- Lotz, M. J., Tamplin, M. L., and Rodrick, G. E. (1983). Thiosulfate-citrate-bile sucrose agar and its selectivity for clinical and marine *Vibrio* organisms. *Ann. Clin. Lab. Sci.* 13, 45–48.
- Lucas, J. S., Hart, M. E., and Salathe, H. R. (1979). Saponins in eggs and larvae of *Acanthaster planci* (L.) (Asteroidea) as chemical defenses against planktivorous fish. *J. Exper. Mar. Biol. Ecol.* 40, 155–165. doi: 10.1016/0022-0981(79)90042-x
- McClintock, J. (2013). Mass mortality of the sea stars *Luidia clathrata* and *Luidia alternata alternata* on the Alabama Coast, December 2013. *Gulf Mexico Sci.* 2013, 74–78.
- Mead, A. D. (1898). *Twenty-Eighth Annual Report of the Commissioners of Inland Fisheries, Made to the General Assembly at Its January Session, 1898*, eds J. M. K. Southwick, H. T. Root, C. W. Willard, W. M. P. Morton, A. D. Roberts, and H. C. Bumpus (Freeman and Sons, Printers to the State), 112.
- Menge, B. A. (1979). Coexistence between the seastars *Asterias vulgaris* and *Asterias forbesi* in a heterogeneous environment—nonequilibrium explanation. *Oecologia* 41, 245–272. doi: 10.1007/bf00377430
- Menge, B. A., Cerny-Chipman, E. B., Johnson, A., Sullivan, J., Gravem, S., and Chan, F. (2016). Sea star wasting disease in the keystone predator *Pisaster ochraceus* in Oregon: insights into differential population impacts, recovery, predation rate, and temperature effects from long-term research. *PLoS One* 11:e0153994. doi: 10.1371/journal.pone.0153994
- Menge, B. A., and Sanford, E. (2013). “Ecological role of sea stars from populations to meta-ecosystems,” in *Starfish: Biology and Ecology of the Asteroidea*, ed. E. Sanford (Washington, DC: John Hopkins University Press), 67–80.
- Miner, C. M., Burnaford, J. L., Ambrose, R. F., Antrim, L., Bohlmann, H., Blanchette, C. A., et al. (2018). Large-scale impacts of sea star wasting disease (SSWD) on intertidal sea stars and implications for recovery. *PLoS One* 13:e0192870. doi: 10.1371/journal.pone.0192870
- Montecino-Latorre, D., Eisenlord, M. E., Turner, M., Yoshioka, R., Harvell, C. D., Pattengill-Semmens, C. V., et al. (2016). Devastating transboundary impacts of sea star wasting disease on subtidal asteroids. *PLoS One* 11:e0163190. doi: 10.1371/journal.pone.0163190
- Moyle, J., and Nelson-Smith, A. (1964). Effects of the severe cold of 1962–1963 upon shore animals in south Wales. *J. Anim. Ecol.* 33, 183–190.
- Núñez-Pons, L., Work, T. M., Angulo-Preckler, C., Moles, J., and Avila, C. (2018). Exploring the pathology of an epidermal disease affecting a circum-Antarctic sea star. *Sci. Rep.* 8:12. doi: 10.1038/s41598-018-29684-0
- Oliver, E. C. J., Benthuyens, J. A., Bindoff, N. L., Hobday, A. J., Holbrook, N. J., Mundy, C. N., et al. (2017). The unprecedented 2015/16 tasman sea marine heatwave. *Nat. Commun.* 8:16101. doi: 10.1038/ncomms16101
- Osborne, S. W. (1979). *The Seasonal Distribution of Luidia Clathrata (Say) in Charlotte Harbor with Reference to Various Physical-Chemical Parameters*. Master of Science, Florida State University, Florida.
- Paine, R. T. (1966). Food web complexity and species diversity. *Am. Nat.* 100, 65–75. doi: 10.1086/282400
- Pearse, J. S., McIntock, J. B., Vicknair, K. E., and Feder, H. M. (2010). “Long-term population changes in sea stars at three contrasting sites,” in *Echinoderms: Durham*, ed. L. G. Harris (London: Taylor & Francis), 633–640.
- Peters, E. C. (1992). “Diseases of other invertebrate phyla: Porifera, cnidaria, ctenophora, annelida, echinodermata,” in *Pathobiology of Marine and Estuarine Organisms*, ed. J. A. Couch (Gulf Breeze, FL: CRC press), 393–449.
- Pratchett, M. S. (1999). An infectious disease in crown-of-thorns starfish on the Great Barrier Reef. *Coral Reefs* 18, 272–272. doi: 10.1007/s003380050192
- Prestdige, G. K. (1998). The distribution and biology of *Patriella vivipara* (Echinodermata: asteroidea: Asterinidae) a sea star endemic to southeast Australia. *Rec. Aust. Mus.* 50, 161–170. doi: 10.3853/j.0067-1975.50.1998.1277
- Rivera-Posada, J., Owens, L., Caballes, C. F., and Pratchett, M. S. (2012). The role of protein extracts in the induction of disease in *Acanthaster planci*. *J. Expert Mar. Biol. Ecol.* 429, 1–6. doi: 10.1016/j.jembe.2012.06.008
- Rivera-Posada, J. A., Pratchett, M., Cano-Gomez, A., Arango-Gomez, J. D., and Owens, L. (2011a). Injection of *Acanthaster planci* with thiosulfate-citrate-bile-sucrose agar (TCBS). I. Disease induction. *Dis. Aquat. Org.* 97, 85–94. doi: 10.3354/dao02401
- Rivera-Posada, J. A., Pratchett, M., Cano-Gomez, A., Arango-Gomez, J. D., and Owens, L. (2011b). Refined identification of *Vibrio* bacterial flora from *Acanthaster planci* based on biochemical profiling and analysis of housekeeping genes. *Dis. Aquat. Org.* 96, 113–123. doi: 10.3354/dao02389
- Rivera-Posada, J. A., Pratchett, M., and Owens, L. (2011c). Injection of *Acanthaster planci* with thiosulfate-citrate-bile-sucrose agar (TCBS). II. Histopathological changes. *Dis. Aquat. Org.* 97, 95–102. doi: 10.3354/dao02400
- Robles, C. (2013). “*Pisaster ochraceus*,” in *Starfish Biology and Ecology of the Asteroidea*, ed. J. M. Lawrence (Baltimore, MD: The John Hopkins University Press), 161–173.
- Rogers, T. L., and Elliott, J. K. (2013). Differences in relative abundance and size structure of the sea stars *Pisaster ochraceus* and *Evasterias troschelii* among habitat types in Puget Sound, Washington, USA. *Mar. Biol.* 160, 853–865. doi: 10.1007/s00227-012-2139-7
- Sagarin, R. D., Gilly, W. F., Baxter, C. H., Burnett, N., and Christensen, J. (2008). Remembering the Gulf: changes to the marine communities of the Sea of Cortez since the Steinbeck and Ricketts expedition of 1940. *Front. Ecol. Environ.* 6, 372–379. doi: 10.1890/070067
- Schaefer, W., and Craig, G. Y. (1972). *Ecology and Palaeoecology of Marine Environments*. Edinburgh: Oliver and Boyd.
- Schultz, J. A., Cloutier, R. N., and Cote, I. M. (2016). Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia. *PeerJ* 4:19. doi: 10.7717/peerj.1980
- Sheehan, E. V., and Cousens, S. L. (2017). “Starballing”: a potential explanation for mass stranding. *Mar. Biodiv.* 47, 617–618. doi: 10.1007/s12526-016-0504-3
- Sieling, F. W. (1960). Mass mortality of the starfish, *Asterias forbesi*, on the Atlantic Coast of Maryland. *Chesapeake Sci.* 1, 73–74. doi: 10.1007/bf02688260
- Smith, G. F. M. (1940). Factors limiting distribution and size in starfish. *J. Fish Res. Board Can.* 5, 84–103. doi: 10.1139/f40-010
- Smith, J. E. (1968). *Torrey Canyon Pollution and Marine Life*. New York, NY: Plymouth Laboratory of the Marine Biological Association of the United Kingdom.
- Stahli, A., Schaefer, R., Hoelzle, K., and Ribi, G. (2008). Temperature induced disease in the starfish *Astropecten jonstoni*. *Mar. Biodiv. Rec.* 2:e78.

- Suraci, J. P., and Dill, L. M. (2011). Energy intake, kleptoparasitism risk, and prey choice by glaucous-winged gulls (*Larus glaucescens*) foraging on sea stars. *Auk* 128, 643–650. doi: 10.1525/auk.2011.11105
- Tiffany, W. J. (1978). Mass mortality of *Luidia senegalensis* (Lamarck, 1816) on Captiva Island, Florida, with a note on its occurrence in Florida Gulf coastal waters. *Florida Sci.* 41, 63–64.
- Verbeek, N. A. M. (1977). Comparative feeding behavior of immature and adult herring gulls. *Wilson Bull.* 89, 415–421.
- Vicknair, K., and Estes, J. A. (2012). Interactions among sea otters, sea stars, and suspension-feeding invertebrates in the western Aleutian archipelago. *Mar. Biol.* 159, 2641–2649. doi: 10.1007/s00227-012-2021-7
- Waldichuk, M. (1990). Mysterious starfish deaths in coastal British Columbia. *Mar. Poll. Bull.* 21:222. doi: 10.1016/0025-326x(90)90331-2
- Zann, L., Brodie, J., and Vuki, V. (1990). History and dynamics of the crown-of-thorns starfish *Acanthaster planci* (L) in the suva area, Fiji. *Coral Reefs* 9, 135–144. doi: 10.1007/bf00258225

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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