**The effect of a simulated marine heat wave on giant California sea cucumbers (*Parastichopus* californicus)**

Introduction and Methods, 29 October 2021

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**Introduction:**

Over the past two centuries, unchecked human development and greenhouse gas emissions have profoundly impacted the biosphere and the climate (Steffen et al., 2018; Walther et al., 2002). One effect of this is a rising frequency of extreme climatic and weather events, including marine heatwaves (MHWs) and warm water anomalies (Allan et al., 2021). MHWs are occurrences of anomalously warm seawater temperatures for a discrete duration of time in a specific locality (Oliver et al., 2021). Anthropogenic climate change is increasing the intensity, duration, size, and frequency of MHWs with consequences across the globe (Allan et al., 2021; Frölicher et al., 2018; Oliver et al., 2021).

Marine heatwaves have damaging and potentially catastrophic effects on marine ecosystems and human economies (Di Lorenzo & Mantua, 2016). They have bottom-up trophic impacts on ecosystems, driving sudden and large-scale die-offs at all trophic levels from thermal stress, starvation, toxicity, and hypoxia (Cavole et al., 2016; Di Lorenzo & Mantua, 2016; Suryan et al., 2021; von Biela et al., 2019). For example, the 2014-2015 warm water anomaly in the Northeast Pacific Ocean (nicknamed “the Blob”) drastically reduced both the nutritional value and abundance of subarctic copoepods, krill, and sand lace, which caused huge starvation-induced die-offs of species from salmon to sea birds (Cavole et al., 2016; von Biela et al., 2019). The Blob significantly harmed commercial, recreational, and subsistence fisheries, and triggered the closures of open water fisheries such as salmon and tuna (Cavole et al., 2016; Di Lorenzo & Mantua, 2016). It also triggered a large harmful algal bloom which resulted in closures of economically important shellfish fisheries (Cavole et al., 2016; Di Lorenzo & Mantua, 2016; Frölicher et al., 2018). The Blob has had multi-year lasting impacts (Suryan et al., 2021); this warm water anomaly, and others of comparable severity, have driven sudden and significant change as they can push ecosystem resilience past ecological tipping points (Harley & Paine, 2009; von Biela et al., 2019; Wernberg et al., 2015).

At an individual level, MHWs directly impact marine organisms in a myriad of ways. Certain species already close to their thermal tolerances are killed directly (Dong et al., 2011; Oliver et al., 2017). Thermal stress can have negative but sub lethal impacts on an organism’s fitness by modifying their behaviour, feeding patterns, and food/nutrient requirements (Kühnhold et al., 2017). Marine heat waves also exert indirect effects on marine organisms, modifying natural processes including disease dynamics. For example, temperature has been shown to regulate the virulence of marine diseases in corals and algae (Case et al., 2011). In the NE Pacific, sea star wasting disease (SSWD) epidemics have decimated populations of several sea star species over the last decade. Wasting is assumed to be infectious (Work et al., 2021), with epidemics being exacerbated or triggered by environmental factors including warm temperatures (Aquino et al., 2021; Bates et al., 2009; Eisenlord et al., 2016; Harvell et al., 2019; Hewson et al., 2018, 2020). SSWD is an ambiguous set of usually-lethal symptoms including twisted arms, lesions, deflation/loss of turgor, lost arms, lack of grip strength in tube feet, and disintegration (Bates et al., 2009; Hewson et al., 2018; Menge et al., 2016). Recent reports have indicated that wasting may affect more than just sea stars: giant California sea cucumbers (*Parastichopus californicus)* displaying wasting symptoms have been reported in small numbers throughout the Salish Sea and the Northwest Coast of British Columbia and Alaska since 2014 (Hewson et al., 2020; Schroeder, 2017).

The direct and indirect effects of MHWs on giant California sea cucumbers are unknown. This is concerning given the potentially devastating impacts of heat-induced disease outbreaks. The most recent sea cucumber wasting (SCW) event occurred in Nanoose Bay, B.C., from August – October 2021 (Em Lim, *personal communication*). This event followed several severe regional heat waves (Kotyk, 2021). There is insufficient evidence to confirm that wasting-like symptoms were *not* caused by direct heat stress, as reported in farmed *Holothuria scabra* (Delroisse et al., 2020), or a heat-unrelated viral or bacterial disease as observed in farmed *Apostichopus japonicus* (Deng et al., 2008; Liu et al., 2010). However, based on our knowledge of SSWD, warm water anomalies could plausibly play an etiological role though heat stress interactions with disease dynamics, as reported above corals, algae, oysters, and sea stars (Case et al., 2011; Hewson et al., 2018; Oliver et al., 2017). Understanding whether giant California sea cucumber wasting is linked to MHWs is important for informing management efforts seeking to protect this important species.

Sea cucumbers, often underappreciated, provide several important ecological and economic services. As benthic detritivores, sea cucumbers break down organic matter and are thus important for nutrient recycling (Wheeling et al., 2007). Sea cucumbers maintain sediment health for bacteria and other detritivores through bioturbation and sediment cleaning (Purcell et al., 2016). There is also evidence that sea cucumbers may provide localized buffering against ocean acidification by releasing alkaline ammonia compounds which facilitate the calcification of corals and calcareous algae (Schneider et al., 2011). North America is also seeing a growing sea cucumber harvest industry (Hannah et al., 2013; van Dam-Bates et al., 2016); in British Columbia alone the total industry is worth 10.2 million dollars (Fisheries and Oceans Canada, 2021). Recent studies have also been investigating the use of giant California sea cucumbers for multi-trophic aquaculture and sea cucumber ranching (Hannah et al., 2013; van Dam-Bates et al., 2016). Given their importance, evaluating how marine heat waves may impact sea cucumbers is a pressing concern, especially considering recent heat stress events that have devastated marine invertebrates across the NE Pacific Ocean (Harvell et al., 2019).

This paper seeks to assess the direct lethal and sublethal effects of marine heat waves on giant California sea cucumbers, and to enhance our understanding of the etiology of sea cucumber wasting. Evaluating how marine heat waves affect giant California sea cucumbers is important to understand the risks facing the sea cucumber harvesting industry and to inform future research into the impacts of marine heat waves on sea cucumbers. We simulated a MHW in a controlled laboratory setting to test three hypotheses. First, we hypothesized that prolonged exposure to temperatures outside the normal range of sea cucumbers will cause direct mortality because of extreme physiological stress. Second, we hypothesized that warming will affect sea cucumber movement and behaviours because of heat-induced stress responses. Third, we hypothesized that we would observe wasting symptoms due to direct physiological or indirect disease responses caused by extreme heat stress. Based on our hypotheses, we make three predictions: 1) we will observe greater mortality with higher temperatures; 2) we will observe changes in movement rates and stress responses as temperature increases; and 3) we will observe wasting symptoms only in warmer temperature treatments.

**Methods:**

*Study organisms*

We collected 63 *Parastichopus californicus* from in Scott’s Bay and the entrance to Bamfield Inlet in Barkley Sound, British Columbia (48°50'02"N, 125°08'45"W) in July 2021. All were gathered from the shallow subtidal, between {NUMBER} and {NUMBER} depth. We placed the cucumbers in deep flow-through sea tables at the Bamfield Marine Sciences Centre, which had a constant input of water from 9m depth in Barkley Sound. We also provided the sea cucumbers with an abundant supply of kelp and supplemented their diet with plankton culture and bloodworms. The cucumbers remained in the lab for {NUMBER} days prior to the start of the experiment. As part of a separate study, individuals were tagged with several types of tags and monitored; the results of this study indicated that the tags did not affect the sea cucumbers’ behaviour (Lim et al., unpublished data). One sea cucumber developed injuries around its T-tag, so we removed it from our experiment.

We measured sea cucumber size to account for potential confounds in our experiments, as some studies have shown that body size can affect the thermal tolerance of marine organisms (Di Santo & Lobel, 2017; Kelley et al., 2011). The metrics we measured were the total length from mouthparts to anus, circumference at widest point, wet weight, and volume (which was measured by measuring volume water displacement). We also conducted a pilot study before the start of our experiment to determine how many cucumbers had their internal organs. Giant California sea cucumbers seasonally lose their internal organs in a poorly understood process that may be caused by absorption of the internal organs or expulsion by evisceration (Fankboner & Cameron, 1985; Swan, 1961). This loss of internal organs is hypothesized to be part of a seasonal senescence that could affect their behaviour and therefore confound our experiment (Brothers et al., 2015). We isolated cucumbers into individual containers for 24 hours to determine if they were defecating. Sea tables were then divided by a coarse plastic mesh to allow for plankton and water to flow through, and to prevent the mixing of cucumbers with and without internal organs.

*Experimental Design*

Marine heatwaves have been observed in the Northeast Pacific Ocean year-round, with subtidal November temperatures reaching similar extremes as those recorded in summer months (Chen et al., 2021a). We chose temperature treatments to mimic low (8ºC), high (16ºC), and extreme (24ºC) heat events. The 8ºC treatment represents the average seawater temperature 50 meters below surface in Barkley Sound during November (Pawlowicz, 2017). Sixteen degrees Celsius mimics a high, but realistic, subtidal temperature (Xuereb et al., 2018). Twenty-four degrees represents an extreme heat event that is unlikely to occur under natural circumstances (Chen et al., 2021b; Pawlowicz, 2017; Xuereb et al., 2018), but we expected would induce a severe heat stress response in sea cucumbers.

We separated *N*=60 sea cucumbers into the three temperature treatments. Each treatment had a total of *N*=20 sea cucumbers in 10 bins. We used a water permeable divider to separate cucumbers within bins to allow for individual identification throughout the experiment. We did not provide sea cucumbers with food during the experiment. We placed bins in sea tables, which acted as temperature control water baths with either a chiller (8ºC treatment) or 2 heaters per sea table (16ºC and 24ºC treatments). 50% water changes were required at 24h intervals to keep nitrate and ammonium levels low. We acclimatized seawater to room temperature for 6 hours. We exposed sea cucumbers to treatments for 96 hours and monitored them for 10 days afterwards for mortality and wasting symptoms.

*Measuring Response to Simulated Marine Heat Wave*

We measured several response variables to capture direct lethal, sublethal, and wasting thermal impacts on giant California sea cucumbers (Table 1). The first of these was the time until direct mortality. We considered cucumbers to be dead if their tube feet were unresponsive to stimulus and all movement had ceased for over 60 minutes.

Sea cucumbers stiffen as a defense mechanism and for posture maintenance (Motokawa & Tsuchi, 2003). We measured stiffness using two different ordinal scales. First, we gently poked the cucumber with one finger and then poked them again after 3 seconds to measure their defense response. We assigned the cucumber a score of 0 if it failed to stiffen when initially poked, a score of 1 if it stiffened but was not still stiff when poked a second time, and a score of 2 if the cucumber got hard and stayed hard. Secondly, we removed each cucumber from their tank and placed them on a 5 cm x 5 cm elevated platform to measure their ability to maintain their posture. We assigned the cucumber a score of 0 if it failed to stiffen at all, a score of 1 if it failed to remain stiff when placed on the platform, a score of 2 if it maintained its posture for less than 2 seconds, and a score of 3 if it maintained its posture for more than 5 seconds. Each stiffness test was performed before, once during, and after the heat wave.

The cucumbers and their tanks were checked every 12 hours to see if a cucumber had eviscerated, an act where they partially expulse their inner organs. We also checked for symptoms of wasting and whether cucumbers spawned, since heat-stress induced spawning has been reported in other sea cucumber species (Battaglene et al., 2002). Finally, we recorded if cucumbers were defecating to determine if there was a change in the status of their organ reabsorption throughout the course of the experiment.

To measure movement rates and dispersal distances we removed each cucumber from their aquaria, placed them in a large tank that had been heated to match the temperature of their heat treatment, and then recorded their activity for 30 minutes using a GoPro camera. In a previous movement trial, sea cucumbers consistently moved from the center to the container walls for shelter (Em Lim*, personal communication*). To analyze movement, we replayed the video and laid 4x5 grid over the screen. We recorded the number of times the cucumber crossed a gridline, and the duration of time it took for a cucumber to reach the sidewall of the container. We measured movement before the experiment, on the second of four days of the heat treatment, and one day after the heat treatment.

*Statistical Analyses*

To determine whether survival differed across temperature treatments we used a cox proportional hazards model (Cox, 1972). We included several covariates in the model that we hypothesized could have also affected survival: intestinal status (reabsorbed Y/N), initial movement rates, and body size metrics. We assessed whether our qualitative scales (stiffness scales) for sublethal responses varied across temperature treatments using ordinal logistic regression, a model designed for use on qualitative scaled data (McCullagh, 1980). For qualitative values measured as binary response variables we used logistic regression. We determined if movement varied significantly across treatments using a linear regression model with dispersal distance or time until reaching the container wall as the response variables and temperature as the explanatory variable. Finally, we used a binary logistic regression model to determine if wasting (yes/no) was temperature dependent.

**Table** **1**. The response variables measured to quantify the effect of a marine heat wave on giant California sea cucumbers (*Apostichopus californicus*).

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| --- | --- | --- | --- |
| Category | Response Variables | Measurement Method | Variable Type |
| Direct lethal | Mortality | Time to Death | Continuous |
| Direct sublethal | Stiffening (antipredator defense) | Repeated poke test | Ordinal (3 level) |
| Stiffening (posture maintenance) | Platform test | Ordinal (4 level) |
| Evisceration | Inner organs observed | Binary |
| Spawning | Sperm or eggs observed | Binary |
| Movement | Dispersal distance | Continuous |
| Disease (indirect or direct) | Wasting | Presence of wasting lesions | Binary |

**Literature Cited**

Allan, R. P., Arias, P. A., Berger, S., Canadell, J. G., Cassou, C., Chen, D., Cherchi, A., Connors, S. L., Coppola, E., Cruz, F. A., Diongue-Niang, A., Doblas-Reyes, F. J., Douville, H., Driouech, F., Edwards, T. L., Engelbrecht, F., Eyring, V., Fischer, E., Flato, G. M., … Zickfeld, K. (2021). IPCC: Climate Change 2021: The Physical Science Basis. *Cambridge University Press. In Press.*, 42. https://www.ipcc.ch/report/ar6/wg1/

Aquino, C. A., Besemer, R. M., DeRito, C. M., Kocian, J., Porter, I. R., Raimondi, P. T., Rede, J. E., Schiebelhut, L. M., Sparks, J. P., Wares, J. P., & Hewson, I. (2021). Evidence That Microorganisms at the Animal-Water Interface Drive Sea Star Wasting Disease. *Frontiers in Microbiology*, *11*. https://doi.org/10.3389/fmicb.2020.610009

Bates, A. E., Hilton, B. J., & Harley, C. D. G. (2009). Effects of temperature, season and locality on wasting disease in the keystone predatory sea star Pisaster ochraceus. *Diseases of Aquatic Organisms*, *86*(3), 245–251. https://doi.org/10.3354/dao02125

Battaglene, S. C., Seymour, J. E., Ramofafia, C., & Lane, I. (2002). Spawning induction of three tropical sea cucumbers, Holothuria scabra, H. fuscogilva and Actinopyga mauritiana. *Aquaculture*, *207*(1–2), 29–47. https://doi.org/10.1016/S0044-8486(01)00725-6

Brothers, C. J., Lee, R. W., & Nestler, J. R. (2015). The uptake of dissolved organic material by the sea cucumber Parastichopus californicus (Stimpson) and its potential role in visceral regeneration. *Journal of Experimental Marine Biology and Ecology*, *469*, 69–75. https://doi.org/10.1016/J.JEMBE.2015.04.016

Case, R. J., Longford, S. R., Campbell, A. H., Low, A., Tujula, N., Steinberg, P. D., & Kjelleberg, S. (2011). Temperature induced bacterial virulence and bleaching disease in a chemically defended marine macroalga. *Environmental Microbiology*, *13*(2), 529–537. https://doi.org/10.1111/j.1462-2920.2010.02356.x

Cavole, L. M., Demko, A. M., Diner, R. E., Giddings, A., Koester, I., Pagniello, C. M. L. S., Paulsen, M. L., Ramirez-Valdez, A., Schwenck, S. M., Yen, N. K., Zill, M. E., & Franks, P. J. S. (2016). Biological impacts of the 2013–2015 warm-water anomaly in the northeast Pacific: Winners, Losers, and the Future. *Oceanography*, *29*(2), 273–285. https://doi.org/10.5670/oceanog.2016.32

Chen, Z., Shi, J., Liu, Q., Chen, H., & Li, C. (2021a). A Persistent and Intense Marine Heatwave in the Northeast Pacific During 2019–2020. *Geophysical Research Letters*, *48*(13). https://doi.org/10.1029/2021GL093239

Chen, Z., Shi, J., Liu, Q., Chen, H., & Li, C. (2021b). A Persistent and Intense Marine Heatwave in the Northeast Pacific During 2019–2020. *Geophysical Research Letters*, *48*(13). https://doi.org/10.1029/2021GL093239

Cox, D. R. (1972). Regression Models and Life-Tables. *Journal of the Royal Statistical Society: Series B (Methodological)*, *34*(2), 187–202. https://doi.org/10.1111/J.2517-6161.1972.TB00899.X

Delroisse, J., Van Wayneberghe, K., Flammang, P., Gillan, D., Gerbaux, P., Opina, N., Todinanahary, G. G. B., & Eeckhaut, I. (2020). Epidemiology of a SKin Ulceration Disease (SKUD) in the sea cucumber Holothuria scabra with a review on the SKUDs in Holothuroidea (Echinodermata). *Scientific Reports*, *10*(1). https://doi.org/10.1038/S41598-020-78876-0

Deng, H., Zhou, Z. C., Wang, N. Bin, & Liu, C. (2008). The syndrome of sea cucumber (Apostichopus japonicus) infected by virus and bacteria. *Virologica Sinica*, *23*(1), 63–67. https://doi.org/10.1007/S12250-008-2863-9

Di Lorenzo, E., & Mantua, N. (2016). Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change*, *6*(11), 1042–1047. https://doi.org/10.1038/nclimate3082

Di Santo, V., & Lobel, P. S. (2017). Body size and thermal tolerance in tropical gobies. *Journal of Experimental Marine Biology and Ecology*, *487*, 11–17. https://doi.org/10.1016/J.JEMBE.2016.11.007

Dong, Y. wei, Yu, S. shan, Wang, Q. lin, & Dong, S. lin. (2011). Physiological responses in a variable environment: Relationships between metabolism, hsp and thermotolerance in an intertidal-subtidal species. *PLoS ONE*, *6*(10). https://doi.org/10.1371/journal.pone.0026446

Eisenlord, M. E., Groner, M. L., Yoshioka, R. M., Elliott, J., Maynard, J., Fradkin, S., Turner, M., Pyne, K., Rivlin, N., Van Hooidonk, R., & Harvell, C. D. (2016). Ochre star mortality during the 2014 wasting disease epizootic: Role of population size structure and temperature. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1689). https://doi.org/10.1098/rstb.2015.0212

Fankboner, P. V., & Cameron, J. L. (1985). Seasonal atrophy of the visceral organs in a sea cucumber. *Canadian Journal of Zoology*, *63*(12), 2888–2892. https://doi.org/10.1139/Z85-432

Fisheries and Oceans Canada. (2021). *Integrated Fisheries Management Plan Summary, Sea Cucumber (Apostichopus californicus) By Dive, Pacific Region*. https://www.pac.dfo-mpo.gc.ca/fm-gp/mplans/sea-cucumber-holothurie-ifmp-pgip-sm-eng.pdf

Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. *Nature*, *560*(7718), 360–364. https://doi.org/10.1038/s41586-018-0383-9

Hannah, L., Pearce, C. M., & Cross, S. F. (2013). Growth and survival of California sea cucumbers (Parastichopus californicus) cultivated with sablefish (Anoplopoma fimbria) at an integrated multi-trophic aquaculture site. *Aquaculture*, *406*–*407*, 34–42. https://doi.org/10.1016/J.AQUACULTURE.2013.04.022

Harley, C. D. G., & Paine, R. T. (2009). Contingencies and compounded rare perturbations dictate sudden distributional shifts during periods of gradual climate change. *PNAS*, *106*(27), 11172–11176. www.pnas.org/cgi/content/full/

Harvell, C. D., Montecino-Latorre, D., Caldwell, J. M., Burt, J. M., Bosley, K., Keller, A., Heron, S. F., Salomon, A. K., Lee, L., Pontier, O., Pattengill-Semmens, C., & Gaydos, J. K. (2019). Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (Pycnopodia helianthoides). *Science Advances*, *5*(1), 1–9. https://doi.org/10.1126/sciadv.aau7042

Hewson, I., Bistolas, K. S. I., Quijano Cardé, E. M., Button, J. B., Foster, P. J., Flanzenbaum, J. M., Kocian, J., & Lewis, C. K. (2018). Investigating the complex association between viral ecology, environment, and northeast Pacific Sea Star Wasting. *Frontiers in Marine Science*, *5*(MAR). https://doi.org/10.3389/fmars.2018.00077

Hewson, I., Johnson, M. R., & Tibbetts, I. R. (2020). An Unconventional Flavivirus and Other RNA Viruses in the Sea Cucumber (Holothuroidea; Echinodermata) Virome. *Viruses*, *12*(1057). https://doi.org/10.3390/v12091057

Kelley, A. L., de Rivera, C. E., & Buckley, B. A. (2011). Intraspecific variation in thermotolerance and morphology of the invasive European green crab, Carcinus maenas, on the west coast of North America. *Journal of Experimental Marine Biology and Ecology*, *409*(1–2), 70–78. https://doi.org/10.1016/J.JEMBE.2011.08.005

Kotyk, A. (2021, August 13). More than a dozen weather records broken in B.C. in latest heat wave. *CTV News Vancouver*. https://bc.ctvnews.ca/more-than-a-dozen-weather-records-broken-in-b-c-in-latest-heat-wave-1.5546239

Kühnhold, H., Kamyab, E., Novais, S., Indriana, L., Kunzmann, A., Slater, M., & Lemos, M. (2017). Thermal stress effects on energy resource allocation and oxygen consumption rate in the juvenile sea cucumber, Holothuria scabra (Jaeger, 1833). *Aquaculture*, *467*, 109–117. https://doi.org/10.1016/j.aquaculture.2016.03.018

Liu, H., Zheng, F., Sun, X., Hong, X., Dong, S., Wang, B., Tang, X., & Wang, Y. (2010). Identification of the pathogens associated with skin ulceration and peristome tumescence in cultured sea cucumbers Apostichopus japonicus (Selenka). *Journal of Invertebrate Pathology*, *105*(3), 236–242. https://doi.org/10.1016/J.JIP.2010.05.016

McCullagh, P. (1980). Regression Models for Ordinal Data. *Journal of the Royal Statistical Society: Series B (Methodological)*, *42*(2), 109–127. https://doi.org/10.1111/J.2517-6161.1980.TB01109.X

Menge, B. A., Cerny-Chipman, E. B., Johnson, A., Sullivan, J., Gravem, S., & 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*(5). https://doi.org/10.1371/journal.pone.0153994

Motokawa, T., & Tsuchi, A. (2003). Dynamic Mechanical Properties of Body-Wall Dermis in Various Mechanical States and Their Implications for the Behavior of Sea Cucumbers. *Biological Bulletin*, *205*(3), 261–275. https://doi.org/10.2307/1543290

Oliver, E. C. J., Benthuysen, J. A., Bindoff, N. L., Hobday, A. J., Holbrook, N. J., Mundy, C. N., & Perkins-Kirkpatrick, S. E. (2017). The unprecedented 2015/16 Tasman Sea marine heatwave. *Nature Communications*, *8*(May), 1–12. https://doi.org/10.1038/ncomms16101

Oliver, E. C. J., Benthuysen, J. A., Darmaraki, S., Donat, M. G., Hobday, A. J., Holbrook, N. J., Schlegel, R. W., & Sen Gupta, A. (2021). Marine Heatwaves. *Annual Review of Marine Science*, *13*, 313–342. https://doi.org/10.1146/annurev-marine-032720-095144

Pawlowicz, R. (2017). Seasonal Cycles, Hypoxia, and Renewal in a Coastal Fjord (Barkley Sound, British Columbia). *Atmosphere - Ocean*, *55*(4–5), 264–283. https://doi.org/10.1080/07055900.2017.1374240

Purcell, S., Conand, C., Uthicke, S., & Byrne, M. (2016). Ecological Roles of Exploited Sea Cucumbers. *Oceanography and Marine Biology: An Annual Review*, *54*, 367–386. https://doi.org/10.1201/9781315368597-8

Schneider, K., Silverman, J., Woolsey, E., Eriksson, H., Byrne, M., & Caldeira, K. (2011). Potential influence of sea cucumbers on coral reef CaCO3 budget: A case study at One Tree Reef. *Journal of Geophysical Research: Biogeosciences*, *116*(G4). https://doi.org/10.1029/2011JG001755

Schroeder, L. (2017). Wasting-like lesions occurring on California Sea Cucumbers. *The Dredgings*, *57*(3), 3. www.PNWSC.org

Steffen, W., Rockström, J., Richardson, K., Lenton, T. M., Folke, C., Liverman, D., Summerhayes, C. P., Barnosky, A. D., Cornell, S. E., Crucifix, M., Donges, J. F., Fetzer, I., Lade, S. J., Scheffer, M., Winkelmann, R., & Schellnhuber, H. J. (2018). Trajectories of the Earth System in the Anthropocene. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(33), 8252–8259. https://doi.org/10.1073/PNAS.1810141115

Suryan, R. M., Arimitsu, M. L., Coletti, H. A., Hopcroft, R. R., Lindeberg, M. R., Barbeaux, S. J., Batten, S. D., Burt, W. J., Bishop, M. A., Bodkin, J. L., Brenner, R., Campbell, R. W., Cushing, D. A., Danielson, S. L., Dorn, M. W., Drummond, B., Esler, D., Gelatt, T., Hanselman, D. H., … Zador, S. G. (2021). Ecosystem response persists after a prolonged marine heatwave. *Scientific Reports*, *11*(1), 1–17. https://doi.org/10.1038/s41598-021-83818-5

Swan, E. F. (1961). Seasonal evisceration in the sea cucumber, Parastichopus californicus (Stimpson). *Science*, *133*(3458), 1078–1079. https://doi.org/10.1126/science.133.3458.1078

van Dam-Bates, P., Curtis, D., Cowen, L., Cross, S., & Pearce, C. (2016). Assessing movement of the California sea cucumber Parastichopus californicus in response to organically enriched areas typical of aquaculture sites. *Aquaculture Environment Interactions*, *8*, 67–76. https://doi.org/10.3354/AEI00156

von Biela, V., Arimitsu, M. L., Piatt, J. F., Heflin, B. M., & Schoen, S. (2019). Extreme reduction in condition of a key forage fish during the Pacific marine heatwave of 2014–2016. *Marine Ecology Progress Series*, *613*, 171–182.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *419*. www.nature.com

Wernberg, T., Bennett, S., Babcock, R. C., Bettignies, T. De, Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C. J., Hovey, R. K., Harvey, E. S., Holmes, T. H., Kendrick, G. A., Radford, B., Santana-garcon, J., Saunders, B. J., Smale, D. A., Thomsen, M. S., Tuckett, C. A., & Tuya, F. (2015). Climate-driven regime shift of a temperate marine ecosystem. *Science*, *353*(6295), 169–172. https://doi.org/10.1126/science.aad8745

Wheeling, R. J., Verde, E. A., & Nestler, J. R. (2007). Diel cycles of activity, metabolism, and ammonium concentration in tropical holothurians. *Marine Biology*, *152*(2), 297–305. https://doi.org/10.1007/S00227-007-0683-3

Work, T. M., Weatherby, T. M., DeRito, C. M., Besemer, R. M., & Hewson, I. (2021). Sea star wasting disease pathology in Pisaster ochraceus shows a basal-to-surface process affecting color phenotypes differently. *Diseases of Aquatic Organisms*, *145*, 21–33. https://doi.org/10.3354/DAO03598

Xuereb, A., Kimber, C. M., Curtis, J. M. R., Bernatchez, L., & Fortin, M.-J. (2018). Putatively adaptive genetic variation in the giant California sea cucumber (Parastichopus californicus) as revealed by environmental association analysis of restriction-site associated DNA sequencing data. *Molecular Ecology*, *27*(24), 5035–5048. https://doi.org/10.1111/MEC.14942