

Shifts in intertidal zonation and refuge use by prey after mass mortalities of two predators

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Appendix S1

Methods: Monitoring sea star mortality events

We documented mass mortality events of *Leptasterias* spp. and *Pisaster ochraceus* as part of long-term experiments at two study sites. We tracked trends in *Leptasterias* and *Tegula funebris* populations as part of a manipulative experiment on trait-mediated indirect effects of *Leptasterias* on tidepool algal communities (Gravem 2015). We estimated *Leptasterias* population size (Fig. 1) by counting and removing them in 8 small mid to high intertidal tidepools (~1.3 m² total surface area) approximately weekly from July 24, 2009 to December 21, 2011 in Horseshoe Cove, Bodega Head, California (38°18'59.4"N, 123° 4'16.3"W). *Leptasterias* were placed in nearby non-experimental tidepools after removal. We tracked *Pisaster* population size (Fig. 1) as part of a separate study where we counted and removed *Pisaster* from 12 mid intertidal boulders approximately every two weeks from October 29, 2009 to October 15, 2014 at Schoolhouse Beach (38°22'28.4"N, 123° 4'44.9"W), which is 6.4 km north of Horseshoe Cove. *Pisaster* were placed in the low intertidal after removal. The mortality events affected this *Pisaster* population similarly to the population in Horseshoe Cove where the focal study was performed. Though these removal experiments do not precisely quantify population density, we are able to track changes in relative population size (Fig. 1).

Shortly after the mass mortality of *Leptasterias*, we searched nearby locations to establish its extent. We searched the south and north shores of Horseshoe Cove (~170 m apart) for remaining sea stars in the low zone for 30 - 90 minutes each on December 29, 2010 and January 15, February 15, February 28, May 4, and June 2, 2011. We found only a single unhealthy *Leptasterias* missing an arm on May 4, 2011, and a single healthy *Leptasterias* on June 2, 2011. On June 7, 2011 we also searched the mid to low zone ~100 m alongshore to the south of the Bodega Harbor jetty (38°18'14.0"N, 123° 3'12.2"W), and on June 8, 2011 we searched ~200 m alongshore just north of Windmill Cove, Bodega Head (38°17'55.4"N, 123° 3'31.9"W) and found only 2 survivors. We are confident that many more *Leptasterias* would have been located if present, since we searched in their preferred habitat (crevices, cobble and coralline algae) where we had easily located them in the past. We also noted an absence of *Leptasterias* while searching for *Pisaster* at Schoolhouse Beach, indicating *Leptasterias* died there too. *Leptasterias* were moderately abundant (~15 sea stars per person per hour) 17 km north of Horseshoe Cove at Twin Coves near Jenner, California (38°27'28.8"N, 123° 8'42.9"W) on May 13, 2011 and June 15, 2011. Though we did not sample this location before the mortality event, the mortality event did not appear to extend there.

To investigate the cause of the *Leptasterias* mortality event, we queried the Bodega Ocean Observing Node (BOON) database (<http://bml.ucdavis.edu/boon>) for average hourly conditions from September 1, 2010 to Jan 31, 2011. Rainfall was measured ~100 m onshore from the experimental tidepools. Seawater temperature, salinity, and fluorescence were recorded ~60 m offshore from the tidepools at ~4 m depth. pH was recorded hourly ~1 km offshore using a submersible autonomous moored instrument (SAMI, Sunburst Sensors) from November 19, 2010 to January 11, 2011. To investigate abundances of potentially harmful phytoplankton species, we obtained data from water samples taken monthly during 2010 at the US Coastguard

Station just inside Bodega Harbor (38°18'46.0"N, 123° 3'5.7"W) by the California Department of Public Health Marine Biotoxin Monitoring Program.

Results: Timing and locations of sea star mortality events

Leptasterias were nearly eradicated between November 8 and December 3, 2010 (Fig. 1) and did not recover over 4 years later. Large rain events occurred in late November 2010, but decreases in salinity were not apparent 4 m deep in Horseshoe Cove (Fig. S1a). Unusually low pH also was not evident from November 19, 2010 to January 11, 2011 (data not shown). An algal bloom occurred from November 20 to 24, 2010 (Fig. S1b) within the window of the *Leptasterias* mortality event (Fig. 1). Fluorescence was not particularly high, peaking at 47.0 $\mu\text{g L}^{-1}$ (peak not shown in hourly averages). Though overall densities of phytoplankton were not high, the harmful algal species, *Gonyaulux spinifera* was the most abundant species (36%) on November 18, 2010, 2 days before the bloom developed (Fig. S1c).

A sharp decrease in the population size of *Pisaster* occurred between August 17, 2011 and August 31, 2011 (Fig. 1), which coincided with a harmful algal bloom in the last days of August 2011 (Rogers-Bennett et al. 2012, Jurgens et al. 2015) which killed *Pisaster*, *Leptasterias* and other species over 100km of coastline. *Pisaster* briefly recovered at Schoolhouse Beach in the summer of 2013, but the population crashed again between August 21 and November 19, 2013 (Fig. 1). Many sea stars looked shriveled on July 25, 2013, and by September 21, 2013, they were observed with white lesions, missing arms, and “melting”, consistent with sea star wasting disease (Hewson et al. 2014). These symptoms continued into the summer of 2014, and adult *Pisaster* continues to be much less abundant than before the mortality events.

Discussion: Extent and possible causes of Leptasterias mortality

Leptasterias suffered nearly 100% mortality between November 8 and December 3, 2010 on Bodega Head and has yet to recover at time of publication. Mortality may have been localized near Bodega Head, because *Leptasterias* was unaffected 17 km north, though the southern extent is unknown. A moderate algal bloom occurred from November 20 to 24, 2010 with relatively high concentrations of the dinoflagellate *Gonyaulux spinifera* occurring 2 days prior. Since a poisonous yessotoxin released by *G. spinifera* is strongly suspected as the cause of the second mortality event in August 2011 that killed *Leptasterias*, *Pisaster* and many other species (Rogers-Bennett et al. 2012, Jurgens et al. 2015), it is possible that the 2010 mortality of *Leptasterias* was also caused by a smaller, weaker bloom of *G. spinifera*. Though we did not observe mortality of any other species, *Leptasterias* may be particularly susceptible to the yessotoxin due to their small size. However, the 2010 bloom occurred in the late fall, after rain events and under normal water temperatures (~12°C), whereas the 2011 bloom occurred in midsummer during abnormally warm (~14°C), calm conditions (Rogers-Bennett et al. 2012, Jurgens et al. 2015).

Disease also could have been responsible for the 2010 *Leptasterias* mortality event since the mortality event was abrupt, fairly localized, and specific to *Leptasterias*. Though symptoms of sea star wasting disease were not detected, the disease could have progressed swiftly in this small sea star with bodies being hard to see. However, other species were not affected and *Leptasterias* appeared to be more resistant to the disease than *Pisaster* on the open coasts of Oregon during the outbreak in fall 2013 (Jenna Sullivan, *pers. comm.*). We detected no other anomalous seawater or weather conditions that could have caused the mortality event. Strong rain events in November 2010 did not form a freshwater lens deep enough to kill subtidal *Leptasterias*, though some intertidal *Leptasterias* could have been killed. Low pH and anoxia

also were unlikely culprits since animals held in the flow-through seawater system at BML did not die.

LITERATURE CITED

- Gravem, S. A. 2015. Linking antipredator behavior of prey to intertidal zonation and community structure in rocky tidepools. PhD. University of California, Davis, CA.
- Hewson, I., J. B. Button, B. M. Gudenkauf, B. Miner, A. L. Newton, J. K. Gaydos, J. Wynne, C. L. Groves, G. Hendler, M. Murray, S. Fradkin, M. Breitbart, E. Fahsbender, K. D. Lafferty, A. M. Kilpatrick, C. M. Miner, P. Raimondi, L. Lahner, C. S. Friedman, S. Daniels, M. Haulena, J. Marliave, C. A. Burge, M. E. Eisenlord, and C. D. Harvell. 2014. Densovirus associated with sea-star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences of the United States of America* **111**:17278-17283.
- Jurgens, L. J., L. Rogers-Bennett, P. T. Raimondi, L. M. Schiebelhut, M. N. Dawson, R. K. Grosberg, and B. Gaylord. 2015. Patterns of mass mortality among rocky shore invertebrates across 100 km of Northeastern Pacific Coastline. *Plos One* **10**:e0126280.
- Rogers-Bennett, L., R. Kudela, K. Nielsen, A. Paquin, C. O'Kelly, G. Langlois, D. Crane, and J. Moore. 2012. Dinoflagellate bloom coincides with marine invertebrate mortalities in Northern California. *Harmful Algae News* **46**:10-11.

Supplemental figure

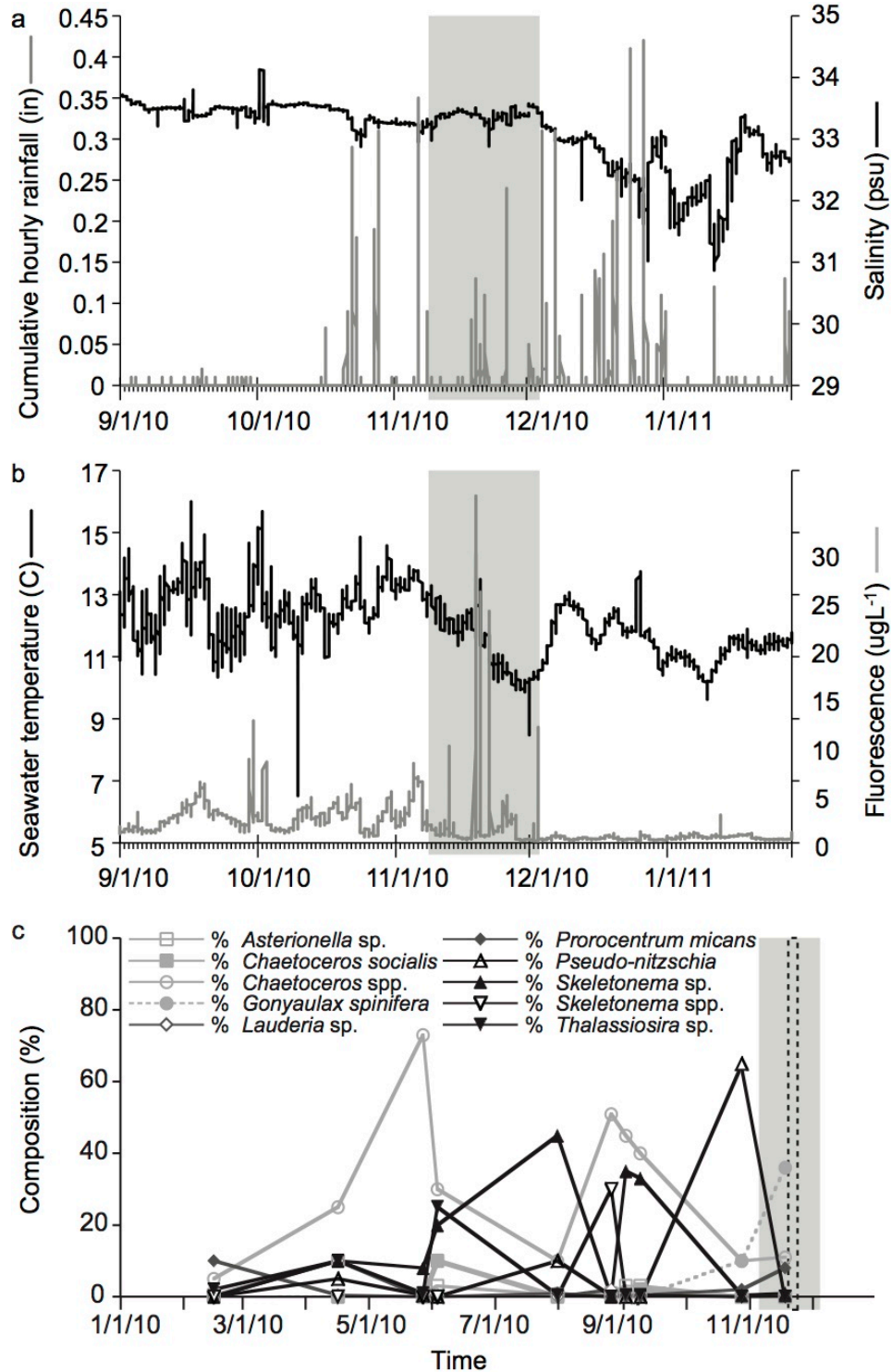


Figure S1. Time series of ocean conditions and precipitation (a & b) on Bodega Head, California from September 2010 through January 2011 and common phytoplankton in water samples (c) taken by the California Department of Public Health in Bodega Harbor during 2010 (note

different time scales). Gray boxes in each panel indicate the time frame of a mass mortality of *Leptasterias* spp. on Bodega Head (November 8 to December 3, 2010). Panel a shows hourly cumulative rainfall (gray lines) and salinity (black lines). Panel b shows hourly seawater temperature (black lines) and chlorophyll-*a* fluorescence (gray lines), which approximates phytoplankton concentration. Panel c shows the percent composition of common harmful algal species relative to total phytoplankton plus detritus. Note increase of *Gonyaulux spinifera* (dashed line) just before an algal bloom (dashed box). Salinity was recorded at 4 m depth in Horseshoe Cove and temperature and fluorescence were recorded 60 m offshore. Rainfall was measured onshore adjacent to Horseshoe Cove.