



Sunflower Sea Star (*Pycnopodia helianthoides*)

Red List Category: Critically Endangered

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***Pycnopodia* Populations in the Literature**

Historical abundance

Literature on *Pycnopodia helianthoides* abundance before the 2013-2017 sea star wasting syndrome (SSWS) outbreak suggests that it was common throughout its range, with higher densities from the Salish Sea to the Aleutian Islands, Alaska. In the Gulf of Alaska, Konar *et al.* (2019) assessed rocky intertidal populations starting in 2012 and showed that it was common toward the northwest part of its range in the Katmai National Park and Preserve near Kodiak Island, Alaska (0.038 m^{-2} in 2012 and 0.048 m^{-2} in 2016, respectively, both before the local outbreak in 2016). Moving east along the Gulf of Alaska, they were less common in Kachemak Bay in the Cook Inlet ($<0.005 \text{ m}^{-2}$), fairly common in the Kenai Fjords National Park ($\sim 0.075/\text{m}^{-2}$), and quite common in western Prince William Sound (average $0.233/\text{m}^{-2}$) (Konar *et al.* 2019). In subtidal rocky reefs near Torch Bay, southeast Alaska, densities were high ($0.09 \pm 0.055 \text{ m}^{-2}$) in the 1980s (Duggins 1983). In subtidal rocky reefs along the central coast of British Columbia, *Pycnopodia* biomass ranged from 0.57 to $0.93 \text{ kg}/10 \text{ m}^2$ in 2010–2014 (Harvell *et al.* 2019). In Howe Sound, near Vancouver, British Columbia, densities were high at $0.43 \pm 0.76 \text{ m}^{-2}$ in 2009–2010 before the SSWS outbreak (Schultz *et al.* 2016). Montecino-LaTorre *et al.* (2016) found that *Pycnopodia* abundance averaged 6–14 individuals per roving diver survey throughout much of the Salish Sea from 2006–2013. In deep water habitats off the coasts of Washington, Oregon, and California 2004–2014 pre-outbreak biomass averaged 3.11, 1.73, and $2.78 \text{ kg}/10 \text{ ha}$, respectively (Harvell *et al.* 2019). Along the north and central California coastline, average population densities were $0.01\text{--}0.12 \text{ m}^{-2}$ prior to 2013 (Rogers-Bennett and Catton 2019). The oldest density records come from kelp forests near Monterey, California where densities were 0.03 per m^{-2} in 1980–81 (Herrlinger 1983). Populations in the Channel Islands off Southern California have been studied extensively, and from 1982–2014 densities ranged from $0\text{--}0.25 \text{ m}^{-2}$ (Bonaviri *et al.* 2017), from 1996–1998 they were $0\text{--}0.02 \text{ m}^{-2}$ (Eckert 2007), from 2003–2007 they were $0\text{--}0.07 \text{ m}^{-2}$ (Rassweiler *et al.* 2010), and from 2010–2012 they were $\sim 0.10\text{--}0.14 \text{ m}^{-2}$ (Eisaguirre *et al.* 2020).

SSWS-related declines in the literature

The outbreak of SSWS that began in 2013 resulted in high mortality and precipitous declines of *Pycnopodia* in shallow and deep waters throughout most of its range. Harvell *et al.* (2019) is the most spatially comprehensive analysis published, and shows severe declines coincident with the 2013–2017 SSWS outbreak. In deep-water trawl surveys, they detected a 100% decline in Oregon and California (from an average of $1.73 \text{ kg}/10 \text{ ha}$ and $2.78 \text{ kg}/10 \text{ ha}$ from 2004–2012, respectively, to none seen in 2015–2016) and a 99.2% decline in Washington (from an average of $3.11 \text{ kg}/10 \text{ ha}$ in 2004–2012 to $0.02 \text{ kg}/10 \text{ ha}$ in 2015-2016). In 2016, no *Pycnopodia* individuals were collected across the 1,264 ha area covered by 692 trawl surveys. Harvell *et al.* (2019) also showed similar dramatic declines in shallow subtidal populations from California to Alaska.

Local and regional studies also documented declines due to SSWS. In the Gulf of Alaska, Konar *et al.* (2019) showed a 67–94% decline in density of *Pycnopodia* in rocky intertidal habitats in the Gulf of Alaska coincident with the outbreak. In British Columbia, Burt *et al.* (2018) detected a decline of up to $\sim 92\%$ in *Pycnopodia* biomass on subtidal rocky reefs and Schultz *et al.* (2016) recorded an 86% decline in *Pycnopodia* densities in Howe Sound between 2009/2010 and 2015 (from [Mean \pm SD] $430,000 \pm 760,000 \text{ km}^{-2}$

to $60,000 \pm 220,000 \text{ km}^2$). In the Salish Sea, Montecino-LaTorre *et al.* (2016) showed divers averaged only 0–3 sunflower star sightings per dive after the outbreak compared to 6–14 before.

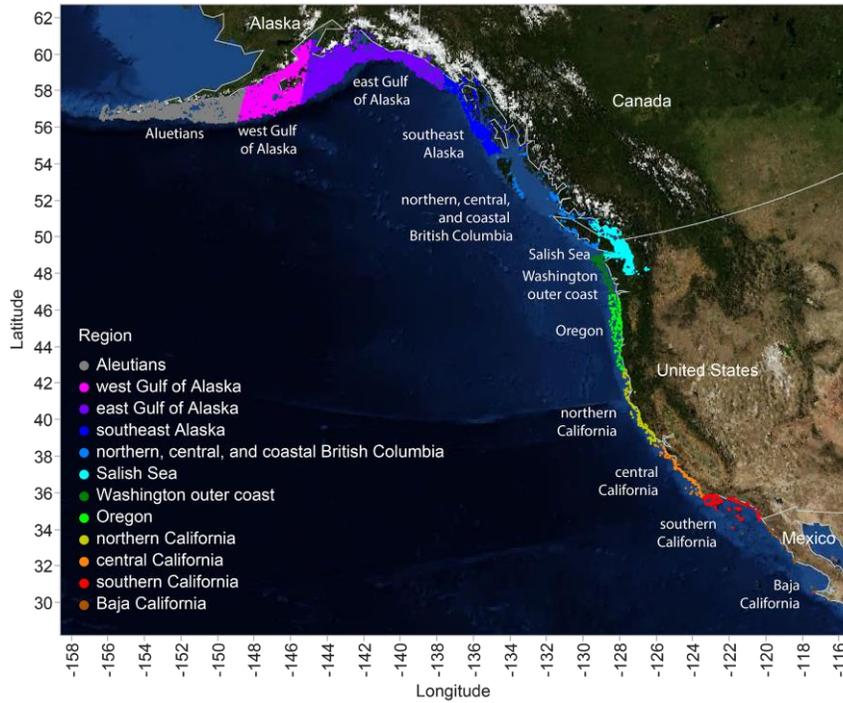
The most severe declines occurred along the outer coastline of the contiguous United States and Baja California, Mexico. During extensive surveys along the northern and central California coastlines, the California Department of Fish and Wildlife detected one *Pycnopodia* in 2014–2015 and none in 2016–2019 (Rogers-Bennett and Catton 2019). *Pycnopodia* also appeared to be locally extinct in California’s Channel Islands, where none were found from 2014–2017 (Eisaguirre *et al.* 2020). Because *Pycnopodia* is a broadcast spawner that does not appear to migrate to find mates, there is substantial concern that these sparse populations will neither successfully fertilize eggs during spawning nor see successful juvenile recruitment in the near future.

Population Data and Methods for IUCN Assessment

Data

Twenty-nine research groups from Canada, the United States, Mexico and First Nations shared 31 datasets containing field surveys of *Pycnopodia* for this effort ([Fig. 1](#) and [Table 1](#)). The data included 61,043 surveys spanning 1967 to 2020 ([Fig. 1b](#)). We utilized multiple types of surveys including trawls, ROV Dives, SCUBA dives, intertidal surveys, and community science observations. They ranged from presence-only identifications by community scientists (e.g., iNaturalist) to quantitative estimates of density, size, and disease presence (e.g., Hakai Institute, Simon Fraser University-Salomon). We compiled all observations into a standardized format and included at minimum the latitude and longitude, date, depth, area surveyed, and *Pycnopodia* count. When datasets contained more than one survey on a site and date (e.g., multiple transects at the same location), we summed the count of *Pycnopodia* and the area searched, and averaged the latitude and longitude (if necessary). To determine densities, we divided the total count by the total area searched for each site and date. We then re-assigned presence and absence as 1 and 0, respectively, so that extent of occurrence and area of occupancy maps would reflect whether *Pycnopodia* was detected at a given site and date.

a) Dataset Map



b) Dataset Temporal Coverage

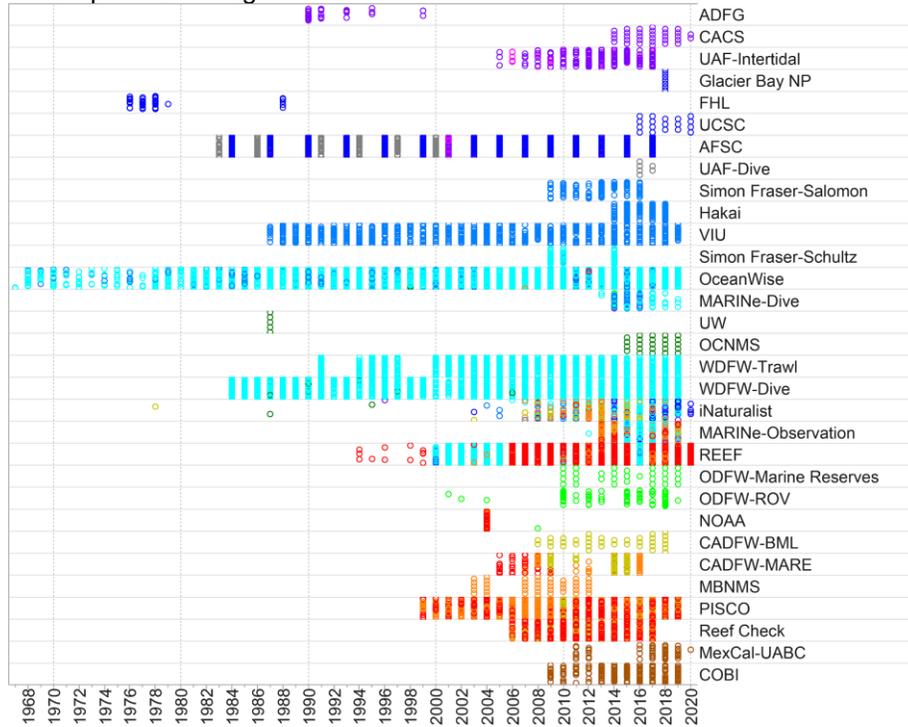


Figure 1. a) Map and b) temporal coverage of the 31 datasets used to assess the global populations of *Pycnopodia helianthoides*. Colours match the 12 regional designations used in the assessment. Datasets in (b) are listed approximately north to south.

Table 1. Datasets used for the IUCN Red List assessment.

Dataset	Institution	Contact	Region(s)	Survey Type	Years	References / websites
ADFG	Alaska Dept of Fish and Game	Tom Dean	east Gulf of Alaska	SCUBA Dive	1990-1999	Jewett <i>et al.</i> 1995
AFSC	Alaska Fisheries Science Center	Nancy Roberson	Aleutians, west and east Gulf of Alaska, southeast Alaska	Trawl	1983-2018	www.fisheries.noaa.gov/region/alaska
CACS	Center for Alaskan Coastal Studies	Katie Gavenus	east Gulf of Alaska	Intertidal Survey	2014-2020	www.akcoastalstudies.org
CDFW-BML	California Dept of Fish and Wildlife & Bodega Marine Laboratory	Laura Rogers-Bennett	northern California	SCUBA Dive	2008-2018	https://marinescience.ucdavis.edu
CDFW-MARE	California Dept of Fish and Wildlife & Marine Applied Research & Exploration	Mike Prall, Dirk Rosen, Andy Lauermann	northern, Central, southern California	ROV Dive	2005-2016	www.maregroup.org
COBI	Comunidad y Biodiversidad	Eduardo Diaz	Baja California	SCUBA Dive	2009-2019	https://cobi.org.mx/en/
FHL	Friday Harbor Labs	David Duggins	southeast Alaska	SCUBA Dive	1976-1988	Duggins 1983
Glacier Bay NP	Glacier Bay National Park and Preserve	George Esslinger, Ben Weitzman	southeast Alaska	SCUBA Dive	2018-2018	Donnellan <i>et al.</i> 2002
Hakai	Hakai Institute	Alyssa Gehman	north, central and coastal BC	SCUBA Dive	2014-2018	www.hakai.org
iNaturalist	iNaturalist	California Academy of Sciences	all	Community Science Observation	1978-2020	www.inaturalist.org
MARINe-Dive	Multi-Agency Rocky Intertidal Network	Melissa Miner	east Gulf of Alaska, north, central and coastal BC, Salish Sea, Oregon	Community Science; SCUBA Dive	2013-2019	https://marine.ucsc.edu/data-products/collaborative-monitoring/index.html

Dataset	Institution	Contact	Region(s)	Survey Type	Years	References / websites
MARINE-Observation	Multi-Agency Rocky Intertidal Network	Melissa Miner	all except Aleutians	Community Science Observation	2012-2019	http://data.piscoweb.org/marine1/seastardisease.html
MBNMS	Monterey Bay National Marine Sanctuary	Steve Lonhart	Central California	SCUBA Dive	2003-2012	https://sanctuarysimon.org/dbtools/project-database/index.php?ID=100312
MexCal-UABC	Universidad Autónoma de Baja California	Rodrigo Baes	Baja California	SCUBA Dive	2009-2020	Beas-Luna <i>et al.</i> in prep
NOAA	NOAA- National Marine Fisheries Science	Aimee Keller	Washington outer coast, Oregon, northern, Central, southern California	Trawl	2004-2008	Harvell <i>et al.</i> 2019; https://www.nwfsc.noaa.gov/data/map
OceanWise	Oceanwise - Vancouver Aquarium	Donna Gibbs	all except Aleutians, west Gulf of Alaska, northern California, Baja California	Community Science SCUBA Dive	1967-2019	https://ocean.org/
OCNMS	Olympic Coast National Marine Sanctuary	Ole Shelton	Washington outer coast	SCUBA Dive	2015-2019	https://olympiccoast.noaa.gov/
ODFW-Marine Reserves	Oregon Dept of Fish and Wildlife	Lindsay Aylesworth, Cori Kane	Oregon	SCUBA Dive	2010-2019	https://oregonmarinereserves.com/
ODFW-ROV	Oregon Dept of Fish and Wildlife	Scott Marion	Oregon	ROV Dive	2001-2018	https://www.dfw.state.or.us/MRP/habitat/
PISCO	University of California Santa Cruz & Santa Barbara	Dan Malone	Oregon, northern, Central, southern California	SCUBA Dive	1999-2019	http://www.piscoweb.org/kelp-forest-study
REEF	Reef Environmental Education Foundation	Christy Pattengill-Semmens	all except Aleutians, west and east Gulf of Alaska	SCUBA Dive	1994-2020	Harvell <i>et al.</i> 2019; https://www.reef.org/reefs-invertebrate-and-algae-monitoring-program

Dataset	Institution	Contact	Region(s)	Survey Type	Years	References / websites
Reef Check	Reef Check	Jan Friewald	northern, Central, southern California	SCUBA Dive	2006-2017	https://www.reefcheck.org/california-program/
Simon Fraser-Salomon	Simon Fraser University	Anne Salomon	north, central and coastal BC	SCUBA Dive	2009-2013	Burt <i>et al.</i> 2018
Simon Fraser-Schultz	Simon Fraser University & Vancouver Aquarium	Jessica Schultz	north, central and coastal BC, Salish Sea	SCUBA Dive	2009-2014	Schultz <i>et al.</i> 2016
UAF-Dive	University of Alaska Fairbanks	Brenda Konar	Aleutians	SCUBA Dive	2016-2016	www.uaf.edu/cfos/people/faculty/detail/brenda-konar.php
UAF-Intertidal	University of Alaska Fairbanks	Brenda Konar	west and east Gulf of Alaska	Intertidal Survey	2005-2017	Konar <i>et al.</i> 2019
UCSC	University of California Santa Cruz	Kristy Kroeker	southeast Alaska	SCUBA Dive	2016-2020	kristy-kroeker.squarespace.com
UW	University of Washington	none	Washington outer coast	SCUBA Dive	1987-1987	Kvitek <i>et al.</i> 1989
VIU	Vancouver Island University	Jane Watson	north, central and coastal BC	SCUBA Dive	1987-2019	https://scitech.viu.ca/biology/faculty/jane-watson-phd
WDFW-Dive	Washington Dept of Fish and Wildlife	Taylor Frierson and Henry Carson	Salish Sea, Washington outer coast	SCUBA Dive	1984-2019	https://wdfw.wa.gov/
WDFW-Trawl	Washington Dept of Fish and Wildlife	Taylor Frierson and Henry Carson	Salish Sea	Trawl	1991-2019	https://wdfw.wa.gov/

Data Analysis

Regional Designations

To analyse how *Pycnopodia* varied over space, we first assigned the data to 12 regions that include: the Aleutian Islands; the west Gulf of Alaska; the east Gulf of Alaska; southeastern Alaska; northern, central and coastal British Columbia; the Salish Sea; the Washington outer coast; Oregon; northern California; central California; southern California; and the Pacific coast of Baja California, using ArcGIS 10.8 ([Fig. 1a](#) and [Table 1](#)). From west to east, then north to south, we used the following regional border cutoffs: the Aleutians began at Samalga Pass/Umnak Island at -169.5°W ; the west Gulf of Alaska began at -157.7°W ; the east Gulf of Alaska began at the eastern edge of Kodiak Island around -152.2°W ; southeast Alaska began at -138.1°W ; central British Columbia began at the United States-Canada border at 54.7°N ; the Salish Sea began at the Campbell River around 50.0°N and included the strait of Juan de Fuca and the Puget Sound; the Washington outer coast began near Neah Bay around 48.4°N ; -124.8°W , Oregon began at its northern border around 46.3°N ; Northern California began at California's northern border at 42.0°N ; central California began at the San Francisco Bay at 37.8°N ; southern California began at Point Conception at 34.5°N ; Baja California began at the United States-Mexico border around 32.5°N ; and Baja California ended at 26.7°N at Bahia Asunción.

Timeline of Population Declines

Since the population declines due to Sea Star Wasting Syndrome (SSWS) occurred at different times in different regions, we first analyzed the data to determine which surveys could be classified as “pre” or “post” decline for each region separately. Because these regions are large, the intent is parsing data as pre- and post-decline using a general timeline for the region overall, not necessarily to pinpoint the precise timing of the crash. Notably, these timelines do not capture the considerable variability in outbreak and crash timing at smaller spatial scales. For more detail on within- and among-region outbreak timelines see published works (Bonaviri *et al.* 2017, Burt *et al.* 2018, Eisaguirre *et al.* 2020, Harvell *et al.* 2019, Konar *et al.* 2019, Menge *et al.* 2016, Miner *et al.* 2018, Montecino-Latorre *et al.* 2016, Rogers-Bennett and Catton 2019, Schultz *et al.* 2016). Further, since *Pycnopodia* can succumb to SSWS in a matter of days to weeks (Hewson *et al.* 2014) the onset of the outbreak itself was often missed by surveys. Thus, instead of focusing on the start of the outbreak, we focused on the region-wide timing of the population “crash”. Based on the density of *Pycnopodia* in each region over time ([Fig. 2](#)), we categorized a “crash phase” for each survey as pre- or post-crash depending on the region. We erred toward calendar year breaks when monthly crash timing was unclear, and erred toward later rather than earlier crash dates to ensure that only survivors were counted in post-crash populations.

Our data show clear population crashes in the three California regions and Baja California, Mexico by January 1, 2014 ([Fig. 2](#), red, orange, and yellow lines & orange dashed line). The crashes in southeast Alaska, north, central and coastal British Columbia, Salish Sea, Washington outer coast, and Oregon were less clear and often more gradual than in California ([Fig. 2](#), blue and green lines). We assigned an August 1, 2015 crash to these regions ([Fig. 2](#), green dashed line) based on data from the Hakai Institute and Simon Fraser University ([Table 1](#)), published papers (Burt *et al.* 2018,

Menge *et al.* 2016, Schultz *et al.* 2016) and conversations with scientists (K. Kroeker, P. Raimondi, A. Gehman, J. Burt pers. comm 2020). In the west and east Gulf of Alaska, the outbreak timing varied both within and among regions (Konar *et al.* 2019) but our data indicates that the population crashes all occurred by January 1, 2017 (Fig. 2, purple and pink lines & purple dashed line). We have sparse data for the Aleutian Islands (Fig. 2, gray line, n = 11 surveys), and it is unclear whether a crash occurred in that region (B. Konar pers. comm. 2020). We assigned a Jan 1, 2017 cutoff (Fig. 2, purple dashed line) for these data to match the timing in the Gulf of Alaska.

Depth and Habitat Patterns

To determine if depth and habitat were important considerations when estimating *Pycnopodia* population size, we analyzed whether each were important drivers of *Pycnopodia* density. Since most datasets did not have substrate and/or habitat type recorded, we used a dataset from ROV surveys taken along the entire California coast that spanned 17–93m depth and contained substrate-specific density data (Table 1; CDFW-MARE). Overall, we determined that *Pycnopodia* inhabit a very wide variety of benthic substrates and that densities did not vary more than approximately ten-fold between substrates in a given year. Since the magnitude of variation in *Pycnopodia* density was much higher among depths and regions (see below), we did not consider substrate nor habitat type when estimating population size.

On the other hand, *Pycnopodia* density was strongly influenced by depth. Using our global dataset of pre-crash populations, we found that *Pycnopodia* was most abundant in shallow nearshore waters less than 25 m (82 ft), less abundant at depths from 25 to 50 m (164 ft), and present but not abundant at depths between 50–300 m (Mean \pm SD: $39,077 \pm 226,556 \text{ km}^{-2}$, $1,996 \pm 5,573 \text{ km}^{-2}$, and $204 \pm 740 \text{ km}^{-2}$, respectively). The large standard deviations in these averages are because *Pycnopodia* tend to be patchily distributed. For the purposes of population estimates and density models (below), we grouped all surveys above 25 m as shallow and all data below 25 m as deep. We assumed all SCUBA dive surveys with no depth value were shallow (typical dive depth is <25 m) and that all trawl data with no depth value were deep (trawls typically in waters >25 m).

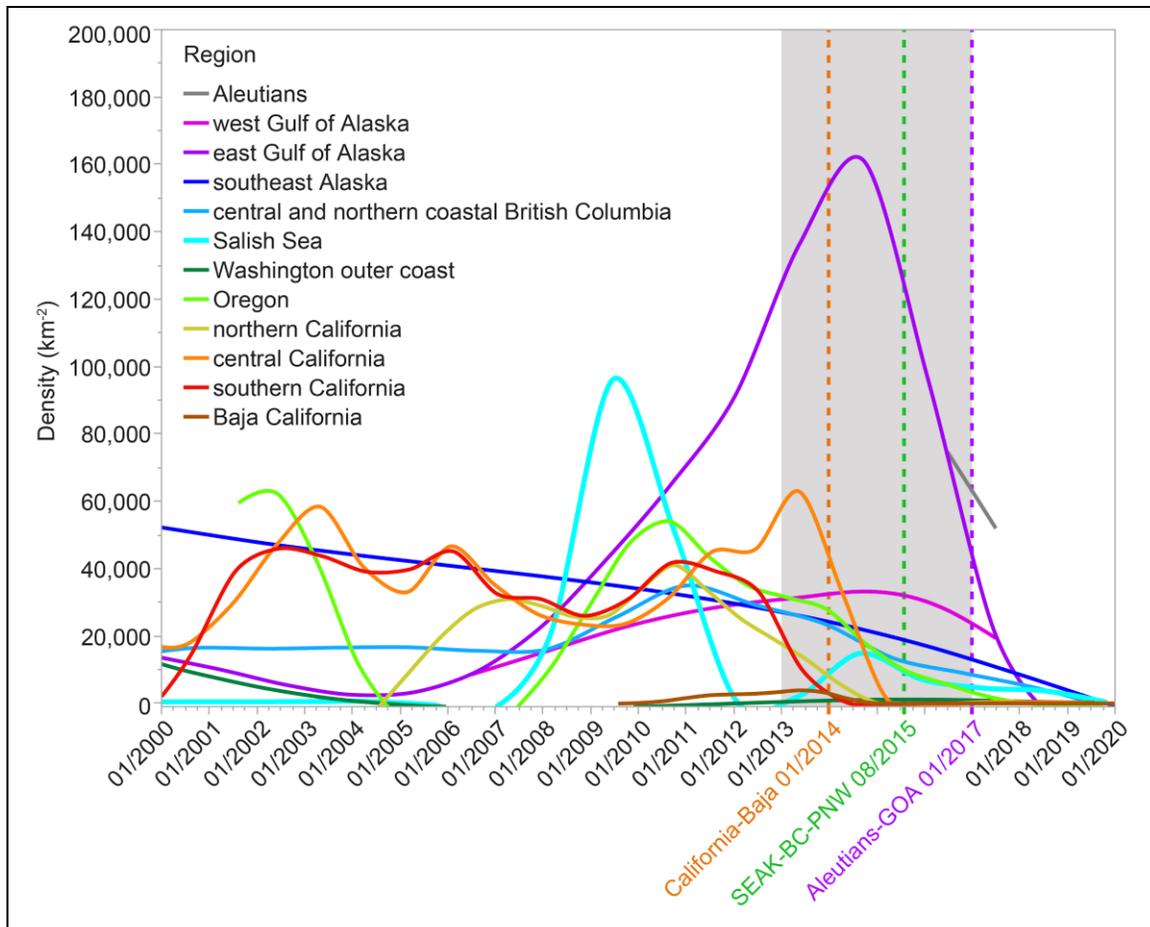


Figure 2. Smoothed fits of the average densities of *Pycnopodia helianthoides* over time (2000-2019) and among regions. The gray box indicates the years in which the sea star wasting syndrome outbreak occurred (2013-2017). Dotted lines indicate the dates used in each region to designate populations as pre or post SSWS-induced declines. Jan 1, 2014: California (northern, central, southern) and Baja California. Aug 1, 2015: southeast Alaska, coastal, northern and central British Columbia, Salish Sea, Washington outer coast, and Oregon. Jan 1, 2017: Aleutians, west and east Gulf of Alaska.

Estimated Population Size Before and After SSWS

To calculate estimated population size before and after the SSWS-induced population decline ([Table 2](#)), we first determined the mean density of *Pycnopodia* over space and time. For shallow depths (< 25 m), we were able to estimate density before and after the crash in most regions separately ([Table 2a](#)). However, for four regions we had very little post-crash data, so we grouped them as follows to increase sample size and presumably the accuracy of density estimates. We grouped the Aleutian Islands and the western Gulf of Alaska into “west Alaska” (n = 2 and 5 post-crash surveys, respectively) and grouped Washington and Oregon into “coastal Pacific Northwest” (n = 9 and 19 post-crash surveys, respectively). Deep depths had few *Pycnopodia* and limited data in many regions, so we did not consider regional variation and instead estimated density in deep depths globally ([Table 2b](#)). To calculate the surface area of the seafloor habitat available to *Pycnopodia* in each region and depth bin ([Table 2](#)), we used bathymetry maps, most of which were in contour map or raster formats ([Table 3](#)). From these bathymetry maps,

surface area in each region and depth bin was calculated in R using the raster, rgDal, sp, and rgeos packages. To estimate population sizes ([Table 2](#)), we multiplied the average density by the surface area of the seafloor in a given depth bin and either globally (deep depths) or regionally (shallow depths). We summed the population size in each region and depth to estimate global population size before and after the crash. We calculated percent declines as $100 * ((\text{pre pop size} - \text{post pop size}) / \text{pre pop size})$. **Overall, we estimated that global *Pycnopodia* population size declined by 90.6% due to sea star wasting disease ([Table 2c](#)).**

In shallow waters (where the majority of animals are found), the estimated population declines were higher than 91.9% in 10 of 12 regions globally, with a >97.2% decline recorded along the outer coastline of the contiguous United States and Mexico ([Table 2a](#)). Indeed, *Pycnopodia* is now very rare along this >2,500km stretch of coastline, with only 172 surveys detecting one or more animals over the last ~5 years out of 3,695 total surveys ([Table 4](#)). This corresponds to a 4.6% detection rate in 2015–2019 compared to a 47.1% detection rate in 2012. Further, most of these were sightings that occurred just after SSWS began, and sightings seem to be increasingly rare with time. For example, though two surveys sighted a *Pycnopodia* in Baja California Mexico in 2014 and 2015, no animals have been recorded since then ([Table 4](#)). Similarly, in all of the United States contiguous outer coast, only 22 of 3,976 total surveys recorded an animal between 2018–2019, with only seven in California ([Table 4](#)). Of these sightings, many have been juveniles (S. Lonhart, S. Marion, N. Treneman, pers. comms. 2020).

The only region with a moderate percent decline was western Alaska at 61.1% ([Table 2a](#); Aleutians and west Gulf of Alaska). This is promising, and anecdotal reports suggest that the disease did not cause severe declines in the Aleutian Islands (B. Konar pers. comm. 2020). However, our limited survey data in this region make this estimate uncertain, and more data is needed to determine the decline in this area.

Using the method of categorizing post-crash data as after Aug 1, 2015 in north, central and coastal British Columbia, we calculated a modest decline of 67.4% ([Table 2a](#)). However, we believe this is a substantial underestimate of the true population decline. In 2015, just after the SSWS crash, sites near Calvert Island, British Columbia experienced a recruitment event of young *Pycnopodia* (A. Gehman pers. obs. 2020). The juvenile recruits were abundant from 2015–2017 but largely disappeared by 2018 and 2019, presumably from a resurgence of SSWS (A. Gehman pers. obs. 2020). Therefore, we narrowed our post-decline population estimate using data from 2018-2019 only, and estimated that the decline in this region as 89.9% ([Table 2a](#)). This closely matches the 92% decline in biomass reported by Burt *et al.* (2018) in Central British Columbia. For calculating global population size, we elected to use the 2018-2019 post-crash population estimates from northern, central and southern British Columbia instead of the Aug 1, 2019–2019 population estimates because these data likely represent a more accurate, current population.

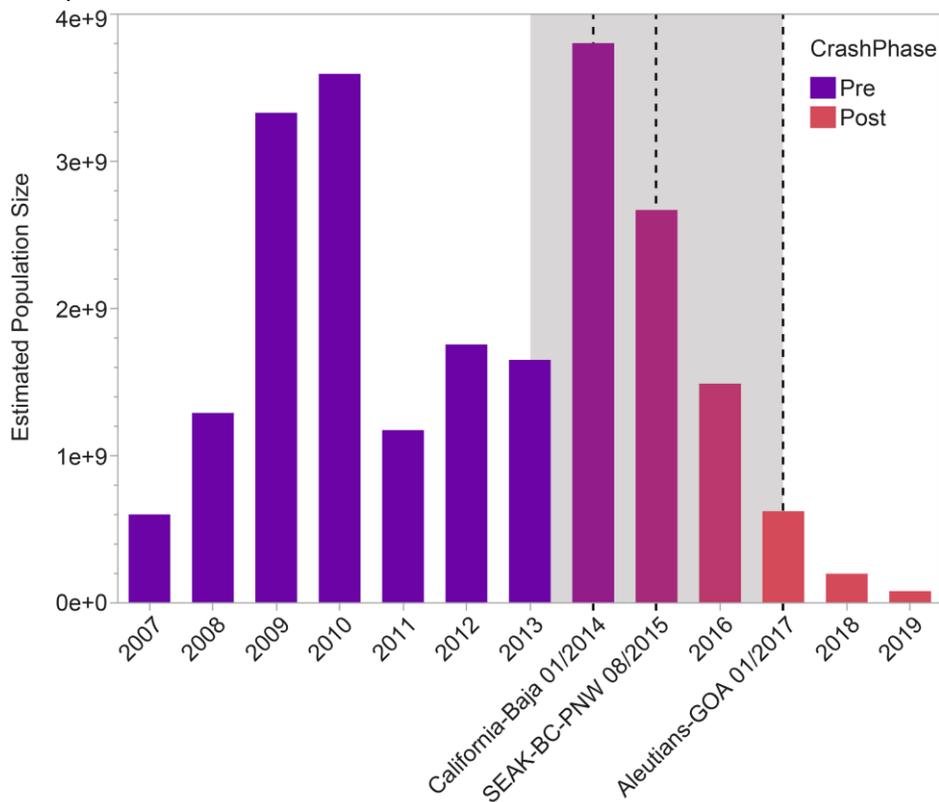
Estimated Population Size Over Time

To estimate yearly changes in population size, we calculated the mean densities among regions, depth bins, and years. We then multiplied this mean density (units: individuals¹ km⁻² depth bin⁻¹ region⁻¹ year⁻¹) by the area of the seafloor (units: km²) to get population size in each depth bin and region over time (units: individuals depth bin⁻¹ region⁻¹ year⁻¹).

We then summed the depth bins to get individuals¹ region⁻¹ year⁻¹. This was only possible for the years 1987–2019 and only those data from 2007 to 2019 had enough regional coverage that population estimates were reliable. We found that estimated population sizes varied greatly over time (Fig. 3a) and among regions (Fig. 3b). The global population decline occurred between 2014 and 2017, as different regions were affected by the disease in sequence (see Timeline of Population Declines section above).

Using yearly population size estimates (Fig. 3a), we attempted to estimate the percent decline over the past three generations of *Pycnopodia* (81-111 years, see Detailed Assessment Information: Generation Time below). However, the decline was non-linear, so no linear model accurately represented the data. Further, we had sparse data before 2007, so population sizes three generations in the past were difficult to determine. Since we have no reason to expect that populations systematically declined before the onset of SSWS in 2013, we elected to use the estimated population size before and after SSWS (see Estimated Population Size Before and After SSWS above) to calculate percent decline.

a) Global Population Size Estimates



b) Regional Population Size Estimates

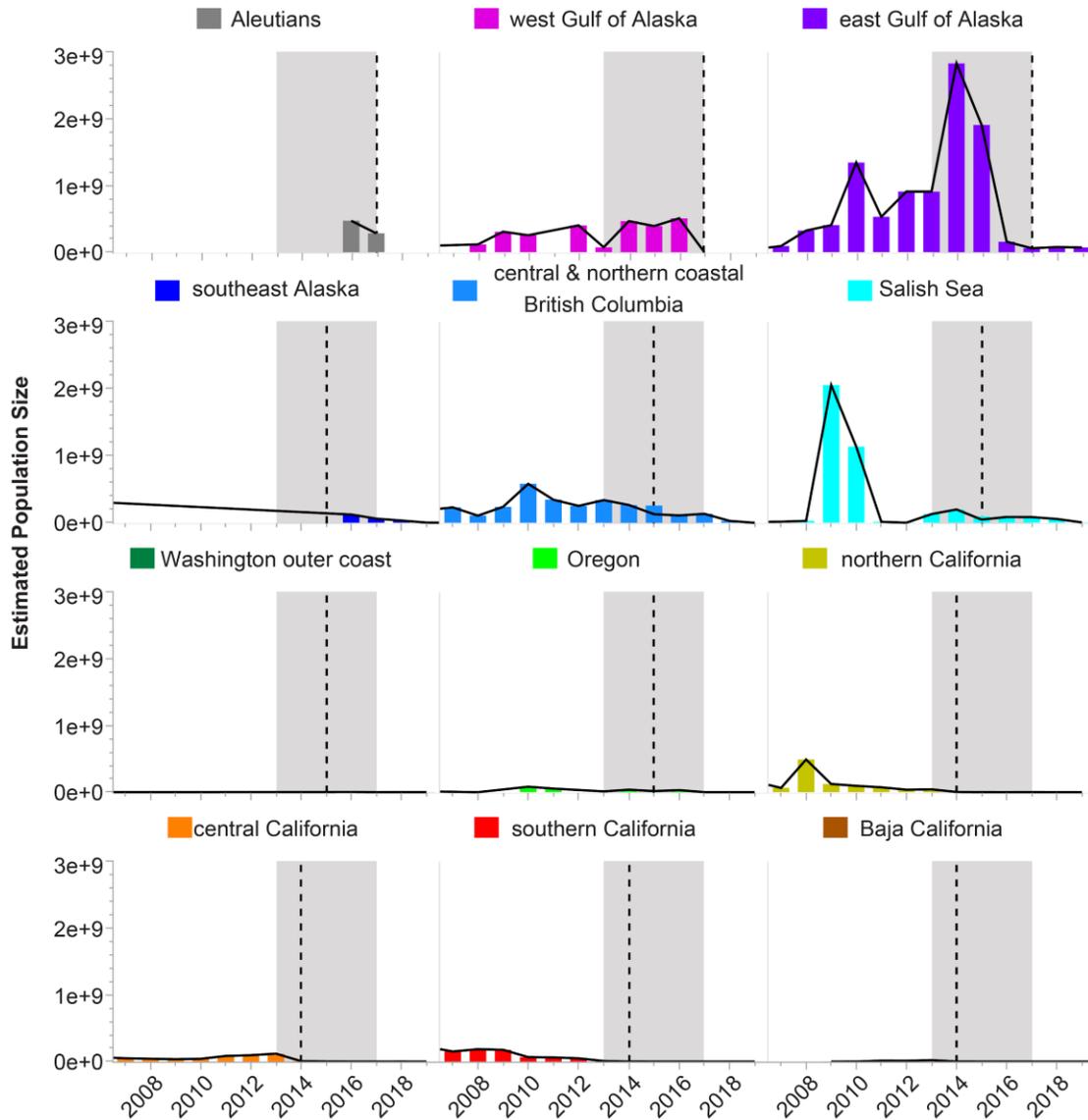


Figure 3. Yearly population size estimates a) globally and b) regionally for *Pycnopodia helianthoides* between 2007 and 2019. The gray box indicates the years in which the sea star wasting syndrome outbreak occurred (2013–2017). The dashed lines indicate the years of population crashes among geographic regions. Jan 1, 2014: California (northern, central, southern) and Baja California. Aug 1, 2015: southeast Alaska, coastal, northern and central British Columbia, Salish Sea, Washington outer coast, and Oregon. Jan 1, 2017: Aleutians, west and east Gulf of Alaska. Solid black lines in (b) are the population estimates and are shown for clarity when population sizes are small.

Table 2. Data descriptors, sample size, density metrics, estimated population sizes, and percent declines of *Pycnopodia helianthoides* populations before and after population crashes caused by the sea star wasting syndrome outbreak in 2013-2017. a) populations in shallow depths (< 25m) split by region. b) populations in deep depths (>25m) globally. c) populations at all depths globally. Western Alaska includes the Aleutian Islands and the western Gulf of Alaska. Pacific Northwest includes Washington and Oregon outer coasts. * indicates where low sample size made estimates uncertain. ^ indicates data that are likely underestimates because post-crash data included cohorts of juvenile animals that generally did not survive. # indicates data that are more accurate post-crash estimates of adult population size, population declines, and were used to calculate global population sizes.

Meta data			Density data				Population estimates	
Region	Crash phase	Seafloor area (km ²)	N surveys	Mean density (km ⁻²)	SD density	SE density	Population size	Decline
a) Regionally at shallow depths (< 25m)								
west Alaska	Pre	16,229	54	36,759	63,628	8,659	596,566,019	*61.1%
west Alaska	Post	16,229	7	*14,286	*37,796	*14,286	*231,842,857	
east Gulf of Alaska	Pre	11,569	204	108,018	288,041	20,167	1,249,662,640	94.9%
east Gulf of Alaska	Post	11,569	52	5,527	16,958	2,352	63,936,736	
southeast Alaska	Pre	5,912	47	118,715	98,711	14,399	701,843,426	94.7%
southeast Alaska	Post	5,912	37	6,239	13,238	2,176	36,883,423	
north, central & coastal BC	Pre	11,999	1146	17,444	28,082	830	209,310,484	^67.4% 2015-2019 #89.9% 2018-2019
north, central & coastal BC	Post 2015-2019	11,999	352	^5,689	^14,024	^747	^68,267,444	
north, central & coastal BC	Post 2018-2019	11,999	133	#1,755	#5,341	#463	#21,054,457	
Salish Sea	Pre	4,712	320	85,335	765,984	42,820	402,098,568	91.9%
Salish Sea	Post	4,712	160	6,954	16,633	1,315	32,764,937	
coastal PNW	Pre	3,235	91	45,176	51,041	5,351	146,144,616	97.9%
coastal PNW	Post	3,235	49	936	3,682	526	3,029,424	

Meta data			Density data				Population estimates	
Region	Crash phase	Seafloor area (km ²)	N surveys	Mean density (km ⁻²)	SD density	SE density	Population size	Decline
northern California	Pre	1,988	184	34,474	33,028	2,435	68,534,061	99.4%
northern California	Post	1,988	137	218	1,150	98	433,740	
central California	Pre	1,488	1048	38,786	47,665	1,472	57,712,841	97.2%
central California	Post	1,488	353	1,070	6,089	324	1,592,442	
southern California	Pre	1,566	1079	35,241	82,210	2,503	55,188,143	99.8%
southern California	Post	1,566	584	62	1,096	45	96,831	
Baja California	Pre	4,794	81	2,586	6,049	672	12,397,667	98.5%
Baja California	Post	4,794	216	39	448	30	184,953	
b) Globally at deep depths (> 25m)								
All	Pre	5,313,880	2037	537	2,673	59	2,851,376,995	92.9%
All	Post	5,313,880	368	38	212	11	202,431,727	
c) Globally at all depths								
All	Pre	5,377,374	6291	26,598	187,171	2,360	6,350,835,461	90.6%
All	Post	5,377,374	2096	1,882	8,964	186	594,251,528	

Table 3. List of the regional bathymetry maps used to calculate the surface area of the sea floor in each depth bin. These surface areas were used to calculate the estimated population size over time of *Pycnopodia helianthoides* globally.

Region	Bathymetry source	Source	Resolution
Aleutian, west and east Gulf of Alaska, southeast Alaska	Alaska Regional Digital Elevation Model v2.0 - Continental Shelf Stretch	Alaska Ocean Observing System	1 km
north, central and coastal British Columbia	British Columbia Marine Conservation Analysis EEZ Bathymetry Dataset	British Columbia Marine Conservation Analysis	0.1 km
Salish Sea	Puget Sound Depth Intervals Contour Map; British Columbia Marine Conservation Analysis EEZ Bathymetry Dataset	John Ashcoff; British Columbia Marine Conservation Analysis	0.1 km
Washington outer coast and Oregon	Alaska Regional Digital Elevation Model v2.0 - Continental Shelf Stretch; 25 Meter Oregon Depth Contour Map	Alaska Ocean Observing System; Active Tectonics and Seafloor Mapping Lab at Oregon State University	1 km
Northern, Central, and Southern California	200 m EEZ Bathymetric Grids	California Department of Fish and Wildlife Marine GIS	200 m
Baja California	GEBCO Bathymetry Maps	Dr. Rodrigo Beas-Luna	440 m

Table 4. The total number of surveys that observed one or more *Pycnopodia helianthoides* in each region and year since the outbreak of sea star wasting syndrome began in 2013. Subscripts indicate the total number of surveys performed. Data in grey were taken before populations declined due to SSWS in a given region. The total post column sums the years post-crash in that region (i.e. sums cells in black).

Region	2013	2014	2015	2016	2017	2018	2019	Total Post
Aleutians	16 ₁₅₆	ND	39 ₂₂₁	4 ₁₀	19 ₁₅₀	1 ₁	ND	20 ₁₅₁
west Gulf of Alaska	20 ₁₇₂	4 ₅	30 ₂₃₈	6 ₇	4 ₁₅₆	ND	ND	4 ₁₅₆
east Gulf of Alaska	45 ₂₀₂	26 ₂₉	58 ₂₈₅	16 ₃₃	19 ₂₃₁	8 ₁₅	8 ₁₄	35 ₂₆₀
southeast Alaska	25 ₆₄	32 ₄₂	6 ₈₄	21 ₂₂	24 ₈₂	21 ₃₅	9 ₁₅	75 ₁₅₄
north and central coastal BC	177 ₂₆₅	150 ₂₁₄	63 ₂₁₂	77 ₂₃₅	57 ₁₇₂	41 ₂₂₅	15 ₁₂₁	190 ₇₅₃
Salish Sea	1624 ₁₉₃₂	1085 ₂₀₃₂	677 ₁₇₆₄	682 ₁₆₅₉	577 ₁₅₄₂	525 ₁₄₈₂	408 ₁₄₈₃	2192 ₆₁₆₆
Washington outer coast	78 ₈₁	71 ₇₇	12 ₉₀	33 ₇₃	6 ₈₅	4 ₁₅	6 ₁₀	49 ₁₈₃
Oregon	107 ₁₅₉	33 ₈₇	25 ₅₃	15 ₄₂	2 ₆₈	1 ₄₁	4 ₂₄	22 ₁₇₅
northern California	21 ₂₅	11 ₅₀	8 ₄₁	6 ₂₇	4 ₄₈	0 ₃₃	0 ₁₀	29 ₂₀₉
central California	216 ₂₇₄	78 ₂₁₃	23 ₁₄₄	4 ₁₄₀	5 ₁₅₃	7 ₁₀₉	0 ₁₀₄	117 ₈₆₃
southern California	32 ₄₄₆	17 ₆₇₀	3 ₅₇₅	1 ₄₂₁	2 ₄₄₈	0 ₄₀₀	0 ₃₅₃	23 ₂₈₆₇
Baja California	11 ₃₅	1 ₂₈	1 ₂₉	0 ₃₂	0 ₄₀	0 ₄₅	0 ₄₂	2 ₂₁₆

Densities Among Regions and Depths

Methods. We used models to detect patterns in population density before and after SSWS among the regions and depths. Due to sparse data coverage in the deep depths but ample coverage in shallow depths (Fig. 4), we elected to perform separate models for these two depth bins. Similar to our analyses for population size, data for deep depths were unavailable for many regions (Fig. 4) so we did not consider regional variation in the model. For shallow depths (< 25m), we had enough data to analyze population densities of most of the regions separately, but we grouped the Aleutian Islands and the western Gulf of Alaska into “west Alaska” and coastal Washington and Oregon into “coastal Pacific Northwest” to increase our accuracy in estimating post-crash density. We performed models in JMP Pro 14 (SAS) using generalized linear models (GLMs) with *Pycnopodia* count as the response variable, log(area) as the offset variable, Poisson distributions, and log link functions. Crash phase (pre/post) was a response in both models. For the shallow model we also included region (grouped as above) and its interaction with the crash phase.

Results. Though not directly tested by our models, densities in deeper depths were generally much lower than for shallow depths (Fig. 4). We detected regional differences in the decline in density in shallow depths (Fig. 4 and Table 5a: region * phase: $P \leq 0.0001$). Follow-up tests showed that the density decline was significant in all regions except western Alaska, northern central and coastal British Columbia, the Salish Sea, and Baja California ($P > 0.05$ for these pre/post pairwise comparisons). The lack of significant declines in these regions were likely due to low sample size in western Alaska, to less drastic declines in north, central and coastal British Columbia, to high variability in pre-crash densities in the Salish Sea, and to low densities in both crash phases in Baja California (Fig. 4 and Table 2a). As expected based on our pre/post designations, we found that *Pycnopodia* density was much lower overall after the SSWS outbreak in both shallow and deep depths (Fig. 4 and Table 5: $P_{1,45924} < 0.0001$ and $P_{1,2486} < 0.0001$ for shallow and deep depths, respectively).

Continuing Decline in Density

To determine whether populations have continued to decline since SSWS and whether this varied among regions, we analysed densities between 2017–2019 when the outbreak had abated globally (though SSWS remains present). No data were available for the Aleutians or the west Gulf of Alaska for this time frame. We used a zero-inflated GLM and specified a Poisson distribution and log link function. We used *Pycnopodia* density as the response variable and date and region as the explanatory variables. Globally, we detected a decline in density over time since 2017, though the fit was very low (Fig. 5, top panel; Date: $P < 0.0001$, $R^2 = 0.016$). However, among regions there was significant variation (Fig. 5, bottom panel; Date * Region: $P < 0.001$). Densities have declined since 2017 in the east Gulf of Alaska, southeast Alaska, northern, central and coastal British Columbia, the Salish Sea, coastal Washington, and Northern California (Fig. 5, bottom panel). In Oregon, Central California, Southern California, and Baja California populations appear to have “flat-lined” at near-zero densities over the 2017–2019 time frame (Fig. 5, bottom panel). However, fits by region were quite low (Fig. 5, bottom panel; $R < 0.09$ in all regions), because remaining densities in these regions were variable. Overall, these data suggest a continued decline globally and a near-extirpation in some regions.

Table 5. Generalised linear model results analyzing the trends in *Pycnopodia helianthoides* densities among a) crash phases and regions at shallow depths (<25 m) and b) crash phases in all regions at deep depths (>25 m).

Term	df	Chi Sq.	P
a) Shallow Density Model			
Crash Phase	1	22.03	<0.0001
Region	9	34.79	<0.0001
Crash Phase * Region	9	34.50	<0.0001
b) Deep Density Model			
Crash Phase	1	26.27	<0.0001

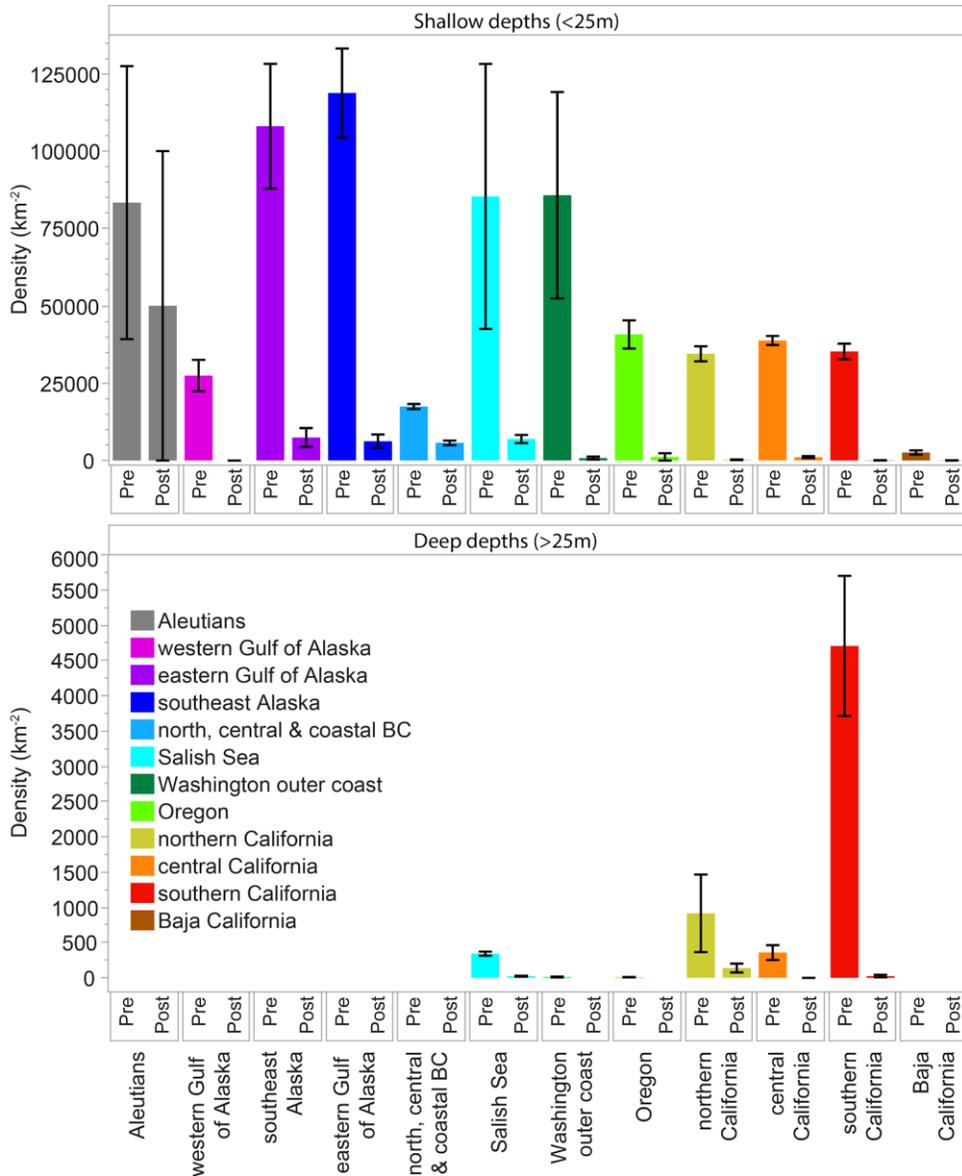


Figure 4. Mean (\pm SE) *Pycnopodia helianthoides* density in shallow (<25 m, top panel) and deep depths (>25 m, bottom panel) among regions (colors). Paired bars indicate before (pre) and after (post) population declines due to sea star wasting syndrome. No density data were available for deep depths in the four Alaskan regions, northern central and coastal British Columbia, or Baja California, nor after the crash in Oregon.

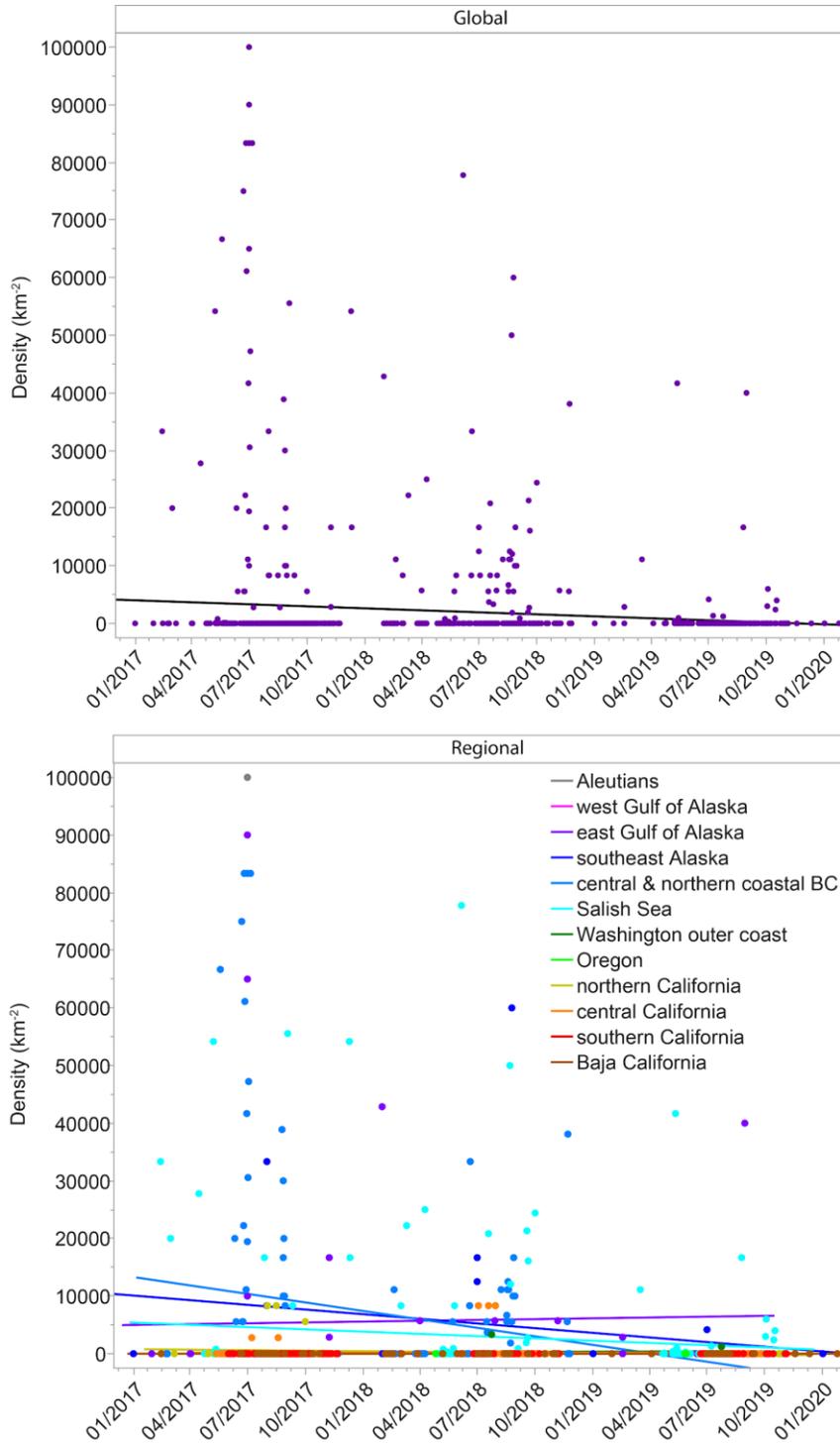


Figure 5. Global (top panel) and regional (bottom panel) densities of *Pycnopodia helianthoides* populations from 2017-2019, after populations had crashed due to sea star wasting syndrome.

Habitats and Ecology

Diet

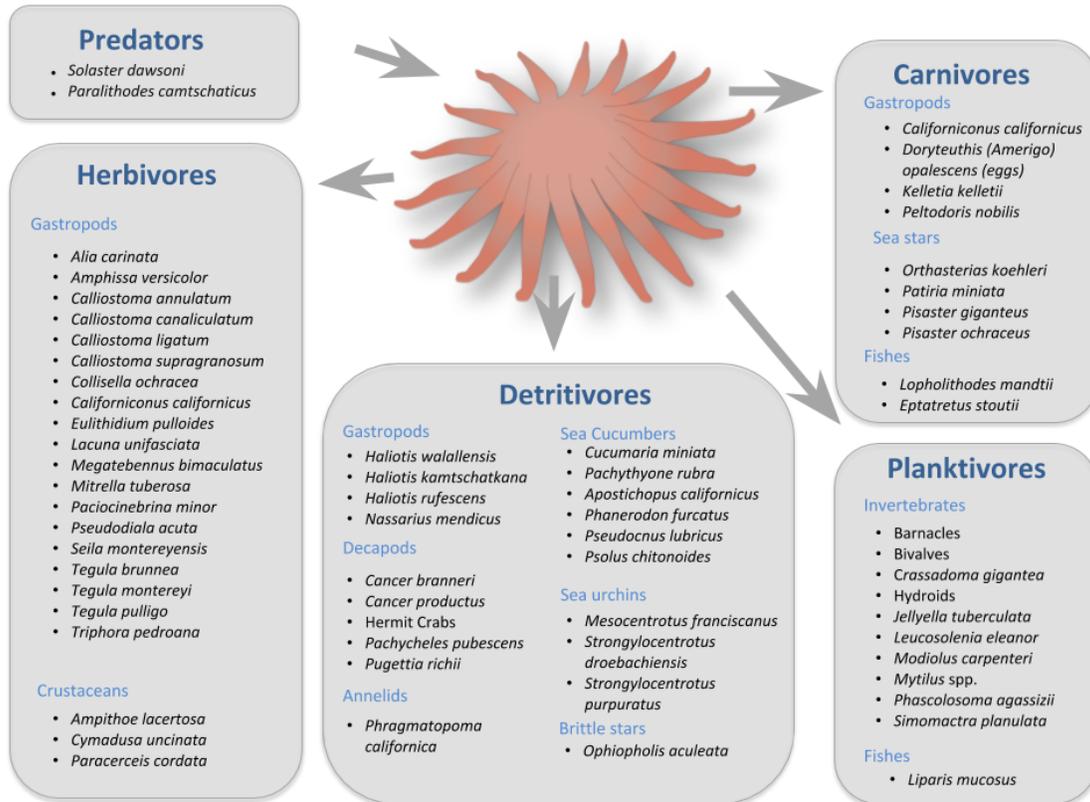


Figure 6. The few predators and a subset of the diverse prey consumed by the generalist predator *Pycnopodia helianthoides*. Arrows point from predator to prey. Figure by Rodrigo Beas-Luna.

Reproduction

Pycnopodia has separate sexes that broadcast spawn gametes (eggs and sperm) into the water column where eggs are fertilised and develop into pelagic larvae (Morris et al. 1980). Because of this spawning strategy, it is likely that adults must be close to one another (i.e. less than a few meters) for successful fertilization to take place (Lundquist and Botsford 2004). It is unknown if they aggregate to spawn, but they are mobile (speeds of up to 160 cm/minute) and often found in groups, so it is likely that they aggregate (Mauzey et al. 1968). There is substantial uncertainty around reproduction seasonality, but regional variation in timing is likely. Recent observations by J. Hodin (pers. comm. 2020) suggest that spawning occurs in winter in the Salish Sea because he observed no reproductive stars from spring to late summer (May to October), some marginally reproductive individuals in November, and ripe individuals in February. Other literature states that fertilizable eggs can be obtained from December to June (Morris et

al. 1980) or that the breeding season is May through June surrounding Vancouver, Island, British Columbia (Feder and Christensen 1966).

After fertilization, the embryos quickly develop into swimming, bilateral larvae that progress through the typical echinoderm larval phases of prism, bipinnaria, and pluteus larvae (Morris *et al.* 1980). The larvae feed on single-celled phytoplankton (Greer 1962). The length of the larval period is at least 50 days (J. Hodin pers. comm. 2020) but up to 146 days (Strathmann 1978). Most larvae metamorphose after 60-70 days into a juvenile sea star with five arms, and they grow more arms over time (Greer 1962).

While no studies have been conducted specifically on the age of maturity of *Pycnopodia*, we estimate it to be at least 5 years based on the age of first reproduction for *Pisaster ochraceus* (Menge 1975), a well-studied predatory sea star that lives in similar habitats, has some overlap in diet, and has a similar reproductive strategy (Giese *et al.* 1991, Menge 1975, Sewell and Watson 1993). It also is quite likely that *Pycnopodia*, like *Pisaster ochraceus*, increases in fecundity as it increases in size (S. Gravem and B. Menge, unpublished data).

Life History and Longevity

Sea stars are known to have indeterminate growth, meaning that individual growth rates and maximum size are strongly dependent on environmental factors like water temperature and food availability (Gooding *et al.* 2009, Sebens 1987). Because of this, it is difficult to age sea stars in the wild because their size does not provide a reliable indication of age. Usually, laboratory studies or cohort analyses are needed to understand sea star growth rates. However, *Pycnopodia* is notoriously difficult to maintain in captivity, resulting in limited controlled studies of its growth. Subsequently, although this species is frequently recorded on dive surveys, very limited data are available on growth, survival, and reproduction of *Pycnopodia* in captivity and in the wild. We were unable to find scientific literature that documented *Pycnopodia* growth rates, likely because they are extremely hard to tag individually. However, we did identify:

- Anecdotal evidence that juvenile *Pycnopodia* grow at a rate of roughly 5cm/year in diameter during the first several years of life in captivity (C. Long. pers. comm. 2020)
- A post-outbreak analysis of growth in juvenile wild *Pycnopodia* in central British Columbia that estimated early growth rates of 3-8 cm/year in diameter (A. Gehman. pers. obs. 2020)
- Anecdotal evidence that 30 captive mid-sized *Pycnopodia* (sizes 30–60 cm) at Friday Harbor Labs in Washington grew at a median rate of roughly 2 cm/year (J. Hodin, pers. comm. 2020).
- A report of a *Pycnopodia* at the Rotterdam Zoo, Netherlands that grew from 30 cm to 60 cm in 15 years, a rate about 2 cm/year

Unfortunately, the literature on sea star growth curves is sparse. What evidence does exist suggests that sea stars with adequate food grow exponentially within their first year (Lucas 1984, Wilmes *et al.* 2017, Yamaguchi 1974). However, after the first year growth rates begin to slow and eventually asymptote (Bos *et al.* 2008, Keesing 2017). That sea

stars have growth rates that decline over their lifetime is corroborated by literature on sea urchins, who are fellow echinoderms. There is a substantial body of literature that examines how the growth rates for sea urchins decrease over their lifetime with various experts preferring to model their growth curves using Von Bertalanffy, Richards, Tanaka, and logistic-dose models (Ebert and Russell 1992, Rogers-Bennett *et al.* 2003). Since the sea star literature also regularly uses the Von Bertalanffy model to estimate growth curves (Bos *et al.* 2008, Keesing 2017), we used this growth equation to estimate *Pycnopodia* life span.

Von Bertalanffy growth equation:

$$L=L_{\infty} (1-e^{-(Ka)})$$

with L = diameter in centimeters at age a , L_{∞} = maximum length in centimeters, K = the Von Bertalanffy growth parameter in cm yr^{-1} , and a = age in years. We set $L_{\infty} = 100$ cm as *Pycnopodia* is rarely found larger than this (Mauzey *et al.* 1968).

Alternatively, we can also use a Richards growth curve to represent theoretical *Pycnopodia* growth over lifetime. The Richards model is commonly used to describe sea urchin growth curves. It also allows for higher initial growth and slower growth later in life than the Von Bertalanffy model, a feature that several sea star experts suggested may be more realistic for *Pycnopodia*.

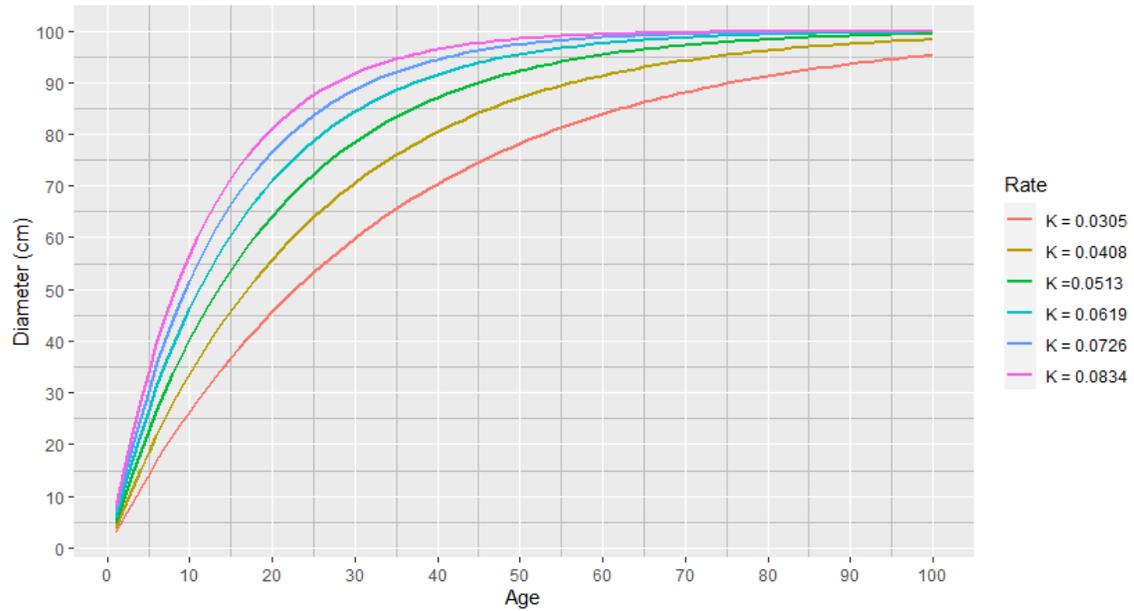
Richard's growth equation:

$$L= L_{\infty} (1-b*e^{-(Ka)})^{-n}$$

This equation is very similar to Von Bertalanffy model but includes two additional unitless shape parameters, b and n , which interact to control the zero time value and the shape of the curve, respectively. In our models we set $b = 1$ and $n = 0.88$. Anecdotal evidence suggests that under ideal conditions (i.e. limited competition for food) juvenile *Pycnopodia* grow to be 3–8 cm in the first several years of life (C. Long pers. comm. 2020, A. Gehman, pers. obs. 2020). If we estimate the range of first year of growth for *Pycnopodia* to be anywhere from 3 cm under low food conditions and 8 cm under ideal conditions, we can estimate K in the Von Bertalanffy equation to be $0.0305 \text{ cm yr}^{-1}$ - $0.0834 \text{ cm yr}^{-1}$ and K in the Richard's equation to range from 0.23 – 0.82 cm yr^{-1} . Using these data, we represented a range of theoretical *Pycnopodia* growth curves ([Fig. 7](#)).

These curves present a wide variety of growth trajectories, but anecdotal evidence of mid-life *Pycnopodia* growth rates suggest that these growth curves are realistic. Both the Rotterdam Zoo and J. Hodin informed us that the mid-sized *Pycnopodia* (i.e. 30–60cm) in their care were growing at an estimated rate of 2 cm yr^{-1} . The two middlemost growth trajectories for the Von Bertalanffy models ($K = 0.0513$ and $K = 0.0619$) predict that *Pycnopodia* may grow from 30 cm to 60 cm in diameter in 9–11 years, which equates to 3.3 and 2.7 cm yr^{-1} , respectively. Similarly, the two middlemost Richard's trajectories ($K = 0.42$ and 0.45) estimated this 30 cm increase over 9.5–13 years, which equates to 3.2 and 2.3 cm yr^{-1} , respectively. While these are both somewhat higher than numbers confirmed in captivity, they are similar enough to suggest that our curves are realistic.

a) Von Bertalanffy Growth Curves



b) Richards Growth Curves

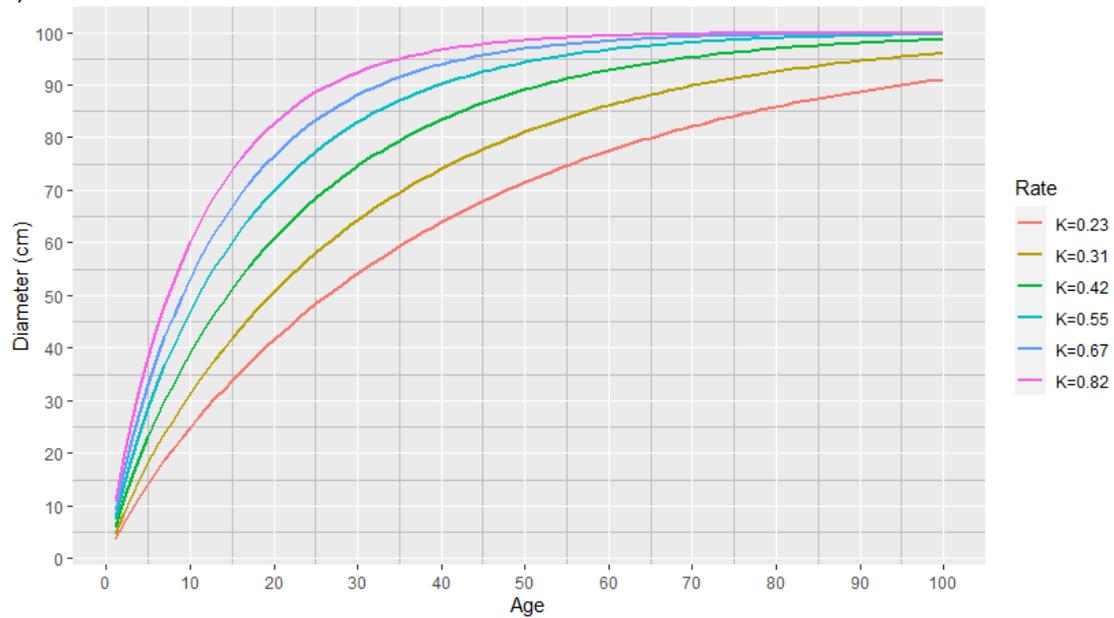


Figure 7. Estimated range of *Pycnopodia helianthoides* growth rates using a) a Von Bertalanffy model and b) a Richards model. The range of K parameters corresponds to a growth rate of 3-8 cm yr⁻¹ in the first year of life, and the estimate was informed by cohort growth analyses and anecdotal evidence. Colours represent the range of K used in each equation.

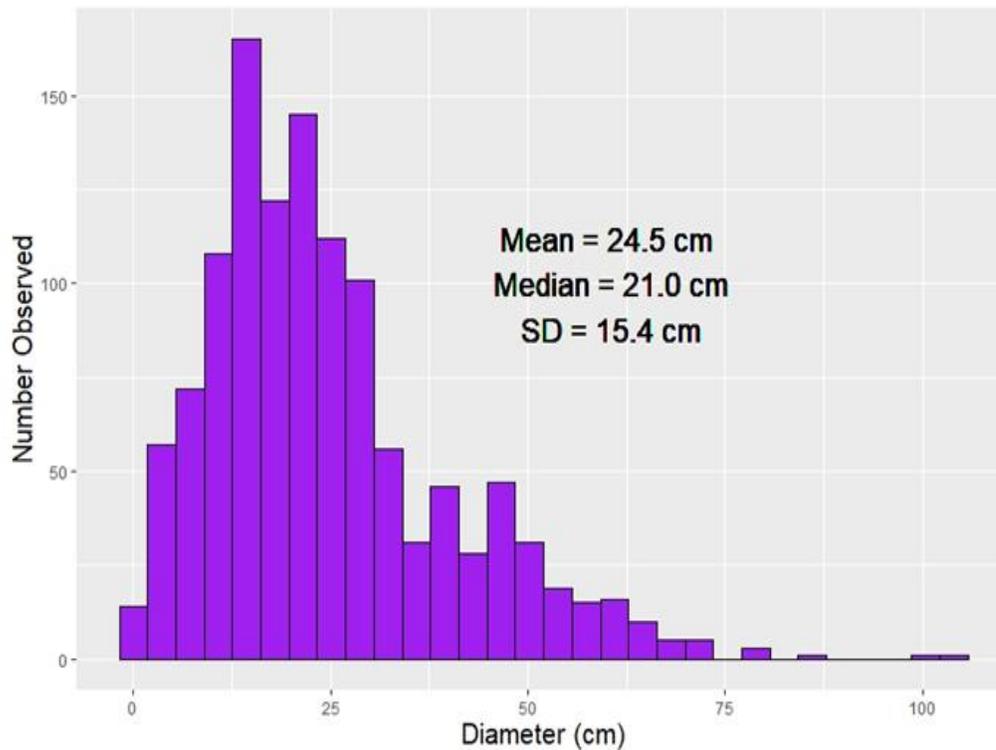


Figure 8. A histogram of the size structure of *Pycnopodia helianthoides* on Haida Gwaii and the Central British Columbia Coast in 2009–2012, before the sea star wasting syndrome outbreak began in 2013. Data were provided by Anne Salomon and collected with the informed consent of the Council for the Haida First Nation, the Heiltsuk Nation, Kitasoo/Xai'xias Nation, Nuxalk Nation, and the Wuikinuxv Nation.

Determination of Generation Time

While we still lack the age-specific survival and reproduction rates that would be needed to accurately assess generation time, previous IUCN Red List assessments of echinoderms have used the following equation to estimate a range for generation times:

$$\text{Generation Time} = \text{Age of First Reproduction} + (Z * \text{length of reproductive period})$$

We can estimate the age of first reproduction to be around 5 years old based on studies of the closely related *Pisaster ochraceus* (Menge 1975), studies of multiple sea star species by Sewell and Watson (1993) and J. Hodin (pers. comm. 2020). Z is a metric bounded by 0–1 that represents whether the bulk of reproduction happens early or later in life. Because we have limited information on age-specific fecundity and mortality to inform a particular estimate of Z , we set $Z = 0.5$ so that it does not skew generation time towards either early or late life reproduction. Although no studies have directly assessed

Pycnopodia longevity, we used anecdotal growth estimates and two growth models (Von Bertalanffy and Richards models) to estimate longevity (Table 6). Generation time is usually calculated based on maximum longevity (time to 95–100 cm) but we have also included estimates based on a more ‘normal’ longevity (time to 50 cm) for reference based on size structure data that shows few stars grow to sizes ≥ 100 cm (Fig. 8). **Based on the available models, our range of estimates for generation time for *Pycnopodia* is 20.5–65 years, with the middle-most estimates providing a narrower range of 27–37 years (Table 6). Using this middlemost estimate, we estimate three generations for *Pycnopodia* to be 81–111 years with upper and lower bounds of 61.5–195 years (Table 6).**

Table 6. Models and parameters used to estimate generation time in *Pycnopodia helianthoides*. In the “Time” columns, the top range of years were calculated with our middlemost estimates of longevity (see Fig. 7) and the bottom range in parentheses were calculated using the maximum and minimum estimates of our longevity models.

Model	Age of first reproduction	Time to 50 cm	Time to 100 cm	‘Normal’ generation time	Maximum generation time
Von Bertalanffy	5 years	11–13.5 (8.5–23)	48–59 (36–97)	8.5–9.75 (7.25–14.5)	27–32.5 (21–51.5)
Richards	5 years	11–14.5 (7.5–28)	48–68 (35–124)	8.5–10.25 (6.75–17)	27–37 (20.5–65)

Use and Trade

Commercial and Recreational Take

There are no targeted fisheries for *Pycnopodia*. In Canada, *Pycnopodia* is classified as ‘starfish sea star’, for which there is a daily limit of six. In the US, regulations vary by state. In Washington, *Pycnopodia* is categorised within ‘unclassified marine invertebrates’, which are closed to harvest in all areas. In California, *Pycnopodia* is not specifically protected, but is instead part of a group of invertebrates where take of 35 individuals with a sport fishing license is allowed between mean higher high tide line and 1,000 ft. Take of sea stars with a commercial fishing license is allowed to 1,000 ft with no specified limit. Take of sea stars with a Tidal Invertebrate Permit is allowed to 1,000 ft, with an unknown take limit. In Oregon and Alaska, *Pycnopodia* is not specifically protected, but is instead grouped in with a variety of miscellaneous invertebrates that can be taken and for which there is no limit. In Mexico, Baja California and Baja California Sur only allow harvest of finfish and squid with a fishing license. Their regulations do not specify any restrictions to sea stars, but collection of shells, corals, sea anemones and snails is prohibited, as is disturbance of the environment.

Extensive commercial fishery data libraries such as the Pacific Fisheries Information Network (PacFIN) and Alaska Fisheries Information Network (AKFIN) do not utilize codes for any sea star species. Rather, any sea star is categorised as an ‘unspecified

echinoderm'. Although most regions along the Pacific Coast technically permit some allowable personal-use and commercial harvest of *Pycnopodia*, all indications suggest that the harvest rate is extremely low, relatively undetectable, and perhaps absent.

Scientific Collection

Scientific collection permits in Alaska, Canada, Washington, Oregon, and California all require an application process that is reviewed by a panel of biologists, in their respective regions, to approve/deny lethal or non-lethal take of each species listed. Since the SSWS outbreak, applications in Washington, Oregon, and California have restricted or limited any lethal take of *Pycnopodia* to only research applications directly related to the assessment or recovery of *Pycnopodia*. At this time, Alaska does not restrict take of *Pycnopodia* for scientific collection. We lack information on the scientific take process in Mexico.

Bycatch

Despite the absence of any targeted fishery for *Pycnopodia*, it can be commonly encountered as bycatch in bottom-contacted pot/trap and trawl/seine fisheries ([Fig. 9](#) and [Fig. 10](#), unpublished data from WDFW crustacean test fishery and trawl survey, respectively). The actual encounter rate and survival rate in each of these gear types is unclear, as there are few available bycatch datasets that distinguish sea stars to the species level. Additional uncertainties for *Pycnopodia* as bycatch are the handling and release practices by harvesters, which have the potential to be directly related to their survival. For example, the complex and delicate body structure of *Pycnopodia* has been reported to be difficult at times to disentangle from pot, trap, or net fishing gear without some injury or mutilation (T. Frierson pers. obs. 2020). Survival rates following these types of injuries and handling prior to release would be very challenging to measure, but a conservative assumption is that survival is not 100%.

Fishing history

There is no history of direct fishing of *Pycnopodia*. The issues of bycatch described above have probably occurred consistently through time and vary directly with the intensity of bottom-contact fishing. There have been very few modifications to these fishing gear types over time with respect to *Pycnopodia*, so the survival rate per capture has likely been consistent over time. However, harvester participation in these fisheries has changed substantially over time. Commercial fisheries for crab, lobster, and shrimp have shown increased harvester participation over time in Washington, Oregon and California but not Alaska ([Fig. 10a](#)). On the other hand, commercial trawl/seine activities targeting fish have generally decreased in recent years with limited entry licensing, restricted areas, and regional closures ([Fig. 10b](#)).

Aquarium/Collector Trade

There is no evidence that this species is widely traded as a live animal in the aquarium trade. Its large size and predatory behaviour probably deter nearly all aquarists. Although not pervasive, dried “sunflower sea stars” are commercially sold individually online as decor. These are typically between 5–20 cm in diameter. We found multiple online retailers that sell animals specifically identified as *Pycnopodia* (Atlantic Coral Enterprise Inc., World Wildlife products, Wholesale Insects, and North Florida Shells, among others). The companies Buy the Sea Online and Loving Coastal Living sell dried

“Sunflower Sea Stars”, but the actual species is unknown. Many private users on Ebay and Esty also sell individual dried “Sunflower Sea Stars”, with some listed as *Pycnopodia*. Upon investigation, we found that some Etsy and Ebay sellers selling “sunflower sea stars” are actually selling *Heliaster kubiniji*, a sea star from the Pacific coast of Mexico and Central America. For those that trade *Pycnopodia*, it is unknown where the collections occur. Overall, this practice was not likely a threat to *Pycnopodia* populations before SSWS, but if it is still occurring in areas of low *Pycnopodia* density, then collections made for trade may hinder recovery.

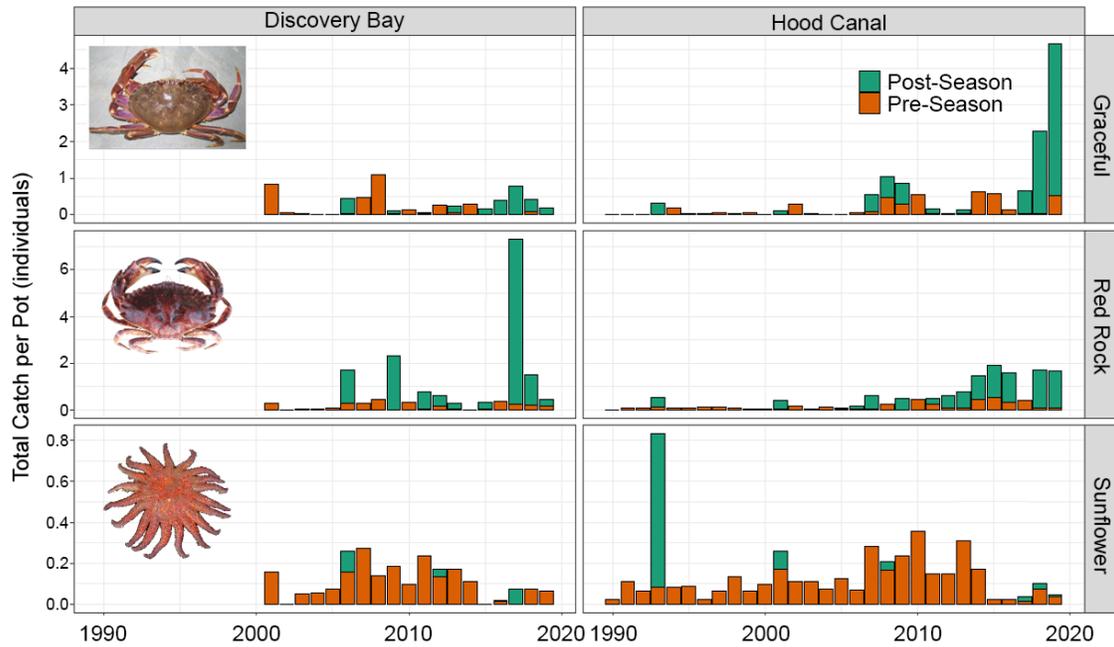
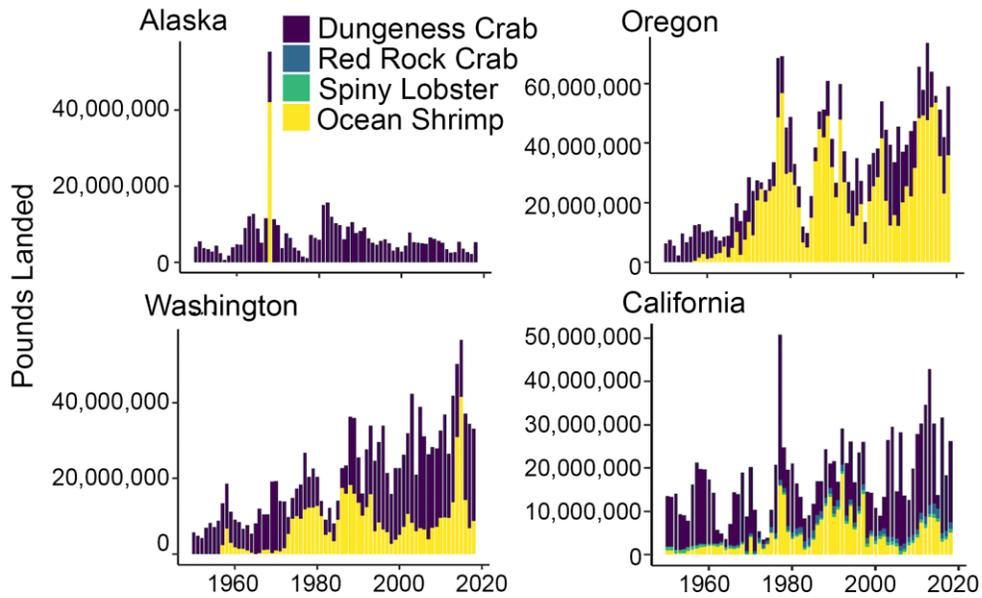


Figure 9. Washington Department of Fish and Wildlife crustacean test fishery results for graceful and red rock crab catch (top 2 panels) and *Pycnopodia helianthoides* sunflower sea star bycatch in crab pots (bottom panel in the Hood Canal region of Puget Sound, WA). Figure by Taylor Frierson.

a) Commercial Landings of Crustaceans



b) Commercial Landings of Fishes

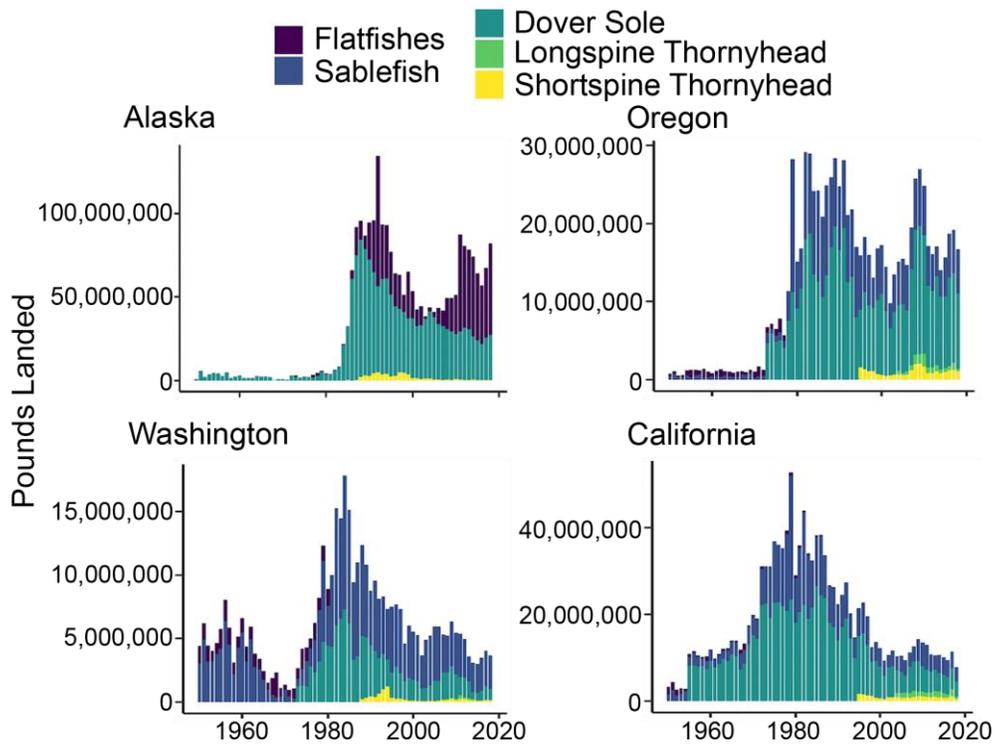


Figure 10. Landings for a) commercial trap (crabs and lobsters) and commercial trawl (shrimp) fisheries and b) commercial trawl and seine fisheries in California (CA), Oregon (OR), Washington (WA) and Alaska (AK) since the 1960s. Figure by Vienna Saccomanno.

Threats

Disease

The SSWS epizootic affected over 20 species of sea stars (Hewson *et al.* 2014). First observed on the outer coast of Washington in June 2013, the epizootic was observed along the entire North American Pacific Coastline from Mexico to the Aleutian Islands by 2016 (see Miner *et al.* 2018 for details on the progression). *Pycnopodia* appears to be the species most negatively affected by the disease (Montecino-Latorre *et al.* 2016, Schultz *et al.* 2016, Harvell *et al.* 2019). While the pathogenesis of SSWS in *Pycnopodia* has not been well characterized, disease progresses from subtle dermal lesions often characterized by discoloration, then increasing lesion diameter and depth, followed by loss of turgor pressure and body wall ruptures, limb autotomisation and ultimately death, leaving behind piles of calcified ossicles (Schultz *et al.* 2016). Microscopically, lesions seen include epidermal necrosis and ulceration, and dermal inflammation and edema in the body wall (Hewson *et al.* 2014). Experimentally, inoculated *Pycnopodia* showed symptoms 8–17 days post-exposure (Hewson *et al.* 2014) and field observations suggested that local populations could be extirpated within 21 days (Montecino-Latorre *et al.* 2016).

Signs of wasting in the 2013 outbreak were likely caused by disease agents, as aquariums that utilize UV sterilised sea water inflow did not see signs of disease, while disease did spread in non-treated aquariums (Hewson *et al.* 2014). However, the etiology or underlying cause for most asteroid wasting epizootics have been difficult to discern (Hewson *et al.* 2019) and there is still debate among scientists about the causative agent for the 2013 event (Hewson *et al.* 2018). Currently, wasting asteroid associated densovirus (WAADs, a group that contains sea star-associated densovirus; SSaDV; family Parvoviridae) are implicated as possible agents of SSWS in *Pycnopodia* based on (1) metagenomic analysis of bacteria and viruses in field samples, (2) experimental replication of disease in *Pycnopodia* challenged with non-heated viral-sized material, and (3) the correlation between SSWS progression and SSaDV loads (Hewson *et al.* 2014, 2018).

Climate Change

While it is unclear whether warming climate triggered the SSWS outbreak, it is clear that the disease is exacerbated by warmer conditions. Warming trends driven by climate change are widely associated with changed relationships between hosts and their parasites or pathogens (Harvell *et al.* 2002). Individual performance of both the host and pathogen are altered by changes in temperature, and the combination of these responses can lead to temperature-driven transmission of disease through populations. Although the exact mechanism of the relationship between temperature and SSWS is yet to be determined, there is some evidence for a link. Laboratory experiments showed increases in disease progression and mortality in warmer temperatures (Eisenlord *et al.*, 2016; Kohl *et al.* 2016). Anomalously warm water temperature is associated with region-specific timing of SSWS outbreaks in *Pycnopodia* (Eisenlord *et al.* 2016, Harvell *et al.* 2019), but not necessarily *Pisaster ochraceus* (Menge *et al.* 2016, Miner *et al.* 2018). Further, models that include temperature anomaly provide better fits to disease spread than those without temperature included (Aalto *et al.* 2020). Finally, previous localized outbreaks of putative “wasting syndrome” were often preceded by increases in water

temperature (Dungan *et al.* 1982, Eckert *et al.* 1998, Bates *et al.* 2009, Staehli *et al.* 2009). Understanding the mechanistic relationship between temperature and disease in this disease system will help to understand the continued risks for *Pycnopodia* recovery (Altizer *et al.* 2013, Gehman *et al.* 2018, Kirk *et al.* 2019, Mordecai *et al.* 2019, Aalto *et al.*, 2020).

Conservation Actions

Marine Protected Areas

We summarize MPAs within the global range and suitable habitat for *Pycnopodia* here: <https://docs.google.com/spreadsheets/d/10UM662HazRfvtnCrXdUJAszUn6jv0Ok-Yj5XiHETU30/edit?usp=sharing/>. The coastal waters of the western United States include four states within the range of *Pycnopodia* (Alaska, Washington, Oregon, and California), each with myriad local, state and federal marine protected areas (MPAs). Level of protection in these MPAs varies, from full no-take marine reserves to limitations placed on a few targeted species. Generally, these MPAs afford protection through extraction prohibitions, habitat protections, and reduced anthropogenic impacts (e.g., disturbance, pollution). These MPAs are classified under the following IUCN conservation categories: I (strict nature reserve), IV (habitat/species management area), and V (protected landscape/seascape).

The NOAA MPA Center (2020) collated information on all United States MPAs, and we used this database to identify current MPAs that contain suitable habitat and historically supported populations of *Pycnopodia*. With this filter, California has 145 MPAs (36,190 sq km), Oregon has 28 MPAs (306 sq km), Washington has 56 MPAs (14,146 sq km), and Alaska has 11 MPAs (25,757 sq km).

Canada has established numerous marine and coastal protected areas that total 184,254 sq km in British Columbia, and most of these areas overlap with known *Pycnopodia* habitat (DFO 2019). Relevant protected areas designations in Canada include marine protected areas (created under the Oceans Act), National Marine Conservation Areas (e.g., marine parks, national marine conservation area reserves), and marine portions of National Wildlife Areas, Migratory Bird Sanctuaries, National Parks, and provincial protected areas. Protected areas and other effective area-based conservation measures (OEABCM) both contribute to marine conservation targets. To date, all areas that qualify as OEABCM have been fisheries area closures. Fisheries area closures that meet OEABCM criteria are known as “marine refuges.”

In northern Baja California, Mexico there are five small marine reserves that are community-based and overlap with known *Pycnopodia* habitat. The government does not necessarily enforce their protection, rather it is the local fishermen who have the concession to protect and monitor the reserves (R. Beas-Luna pers. obs. 2020).

Detailed Assessment Information

Criterion A: Critically Endangered

The circumstances of the decline in *Pycnopodia* are best described by IUCN criterion A2: Population reduction estimated in the past where the causes of reduction may not have ceased and may not be reversible. Using 31 datasets including more than 61,043 surveys ([Fig. 1](#) and [Table 1](#)), we calculated that *Pycnopodia* has experienced a 90.6% global reduction in population size ([Fig. 3](#) and [Table 2](#)) since the outbreak of SSWS in 2013-2017 and very likely over the last three generations (81–111 years). This qualifies *Pycnopodia* as Critically Endangered under criterion A2a. While we were unable to attain observational data that spanned three generations, we expect that the pre-2014 population were likely representative of long-term population size throughout the 1900s because *Pycnopodia* is not exploited commercially, has a large range, and has not likely experienced extensive habitat destruction. Populations are not recovering, are still declining in many regions, and in others they have been driven to near local extinction ([Fig. 5](#)). We have reason to believe that the major threats to this species (disease and changing climate) have not abated and are preventing recovery in regions that still have appreciable adult populations (see Threats). Further, the threats of disease and climate change are not reversible.

Criterion A2a: estimated decline in population size from direct observations

The long generation time of *Pycnopodia* (27–37 years) combined with the non-linear, sudden decline in population size between 2013 and 2017 creates some uncertainty in the exact measure of percent decline in population size. Since the decline followed this abrupt non-linear pattern, we elected to compare the population decline before versus after the population decline caused by SSWS. In this approach, we used the IUCN guidelines for addressing complex patterns of decline (pp. 35-36 and Figure 4.3 in the *Guidelines for Using the IUCN Red List Criteria*). We assumed decline was negligible before the onset of the SSWS outbreak in 2013, and that our estimate of average pre-outbreak population size between 1987 and 2013 ([Table 2](#); 6,350,835,461 individuals) was an accurate estimate of population size at both 81 and 111 years in the past (in 1938 and 1908, respectively). We also assumed that the average post-outbreak population size between the region-specific crash year (see Timelines of Population Declines) and 2019 ([Table 2](#); 594,251,528 individuals) represents the current population size. For more detail on how we calculated estimated population size, please see Data Analysis above. Using this approach, we estimate that the global population has declined by 90.6% over the last three generations, and that *Pycnopodia helianthoides* meets the threshold for Critically Endangered under criterion A2a.

The benefits of using this approach are that we are able to overcome the challenges and complexity of a modeling decline that was caused by an abrupt, brief and widespread global collapse. We have simplified this to just two phases that are reflected in the data: namely before and after the SSWS-induced population decline. A caveat with this approach is that we are assuming populations did not vary substantially before SSWS. This may not be true, as is reflected by the modest fluctuations in population size we detected in our analysis ([Fig. 3](#)).

Criterion A2c: decline in extent of occurrence and area of occupancy

We conducted a pre-outbreak analysis of extent of occurrence (EOO) and area of occupancy (AOO) and compared it with post-outbreak estimates of these numbers. Because data collection across the species range was not taken in a coordinated manner, but was spatially and temporally patchy, we binned data into four-year categories that allowed for inclusion of many regions and resulted in a more standardized sampling effort. We took the post-outbreak period to be 2017–2020, excluded 2013–2016 data as this was the height of the outbreak, and took the pre-outbreak period to be 2009–2012. We used the 2009–2012 pre-outbreak period to create a ‘baseline’ estimate of these metrics that represents our best estimate of EOO and AOO three generations ago (Fig. 11 and Table 7). Like the analysis of population decline above, we believe this pre/post comparison in AOO and EOO is justified because there is no reason to believe that populations faced region-wide threats nor systematic declines before the SSWS outbreak in 2013. The only exception is that some areas, particularly southern California, have had reports of localized *Pycnopodia* disease events prior to 2013, which may have reduced population sizes cyclically on decadal time scales (Eckert *et al.* 2000). EOO was based on the minimum convex polygon around all known observations of *Pycnopodia* that was then constrained to the realistic bathymetric range (0–500 m below sea level) in order to exclude thousands of kilometers of unsuitable habitat in the form of 1) land and 2) deep sea below 500 m.

We estimated EOO to be 6,571,920 km² in the 2009–2012 pre-outbreak period and 5,430,060 km² in the 2017–2020 post-outbreak period (Fig. 11 and Table 7). EOO declined only marginally after the outbreak, despite dramatic declines in the abundance and density of *Pycnopodia*. We conclude that this is because occasional identifications of single individuals across the southern half of the species’ range kept the EOO from declining to the same degree.

Our estimates of AOO tell a different story. Pre-outbreak we estimated AOO to be 4,052 km², and post-outbreak we estimated AOO to be 1,716 km² (Fig. 11 and Table 7). This represents a decline of 57.6% compared to pre-outbreak. While some of this post-outbreak decline may be related to decreased trawl sampling in Alaska, it is primarily driven by the near extirpation of *Pycnopodia* in the southern half of its range (the outer coast of Washington to Baja California). This estimate of current AOO qualifies for “Vulnerable” status under criterion A2c.

Table 7. Changes in the extent of occurrence (EOO) and area of occupancy (AOO) for *Pycnopodia helianthoides* in 2009–2012, before the 2013–2016 outbreak of sea star wasting syndrome, and in 2017–2020, after the outbreak of sea star wasting syndrome.

Years averaged	Crash phase	Area (km ²)	% decline
Extent of occurrence			
2009-2012	Pre	6,571,920	17.4
2017-2020	Post	5,430,060	
Area of occupancy			
2009-2012	Pre	4,052	57.6
2017-2020	Post	1,716	

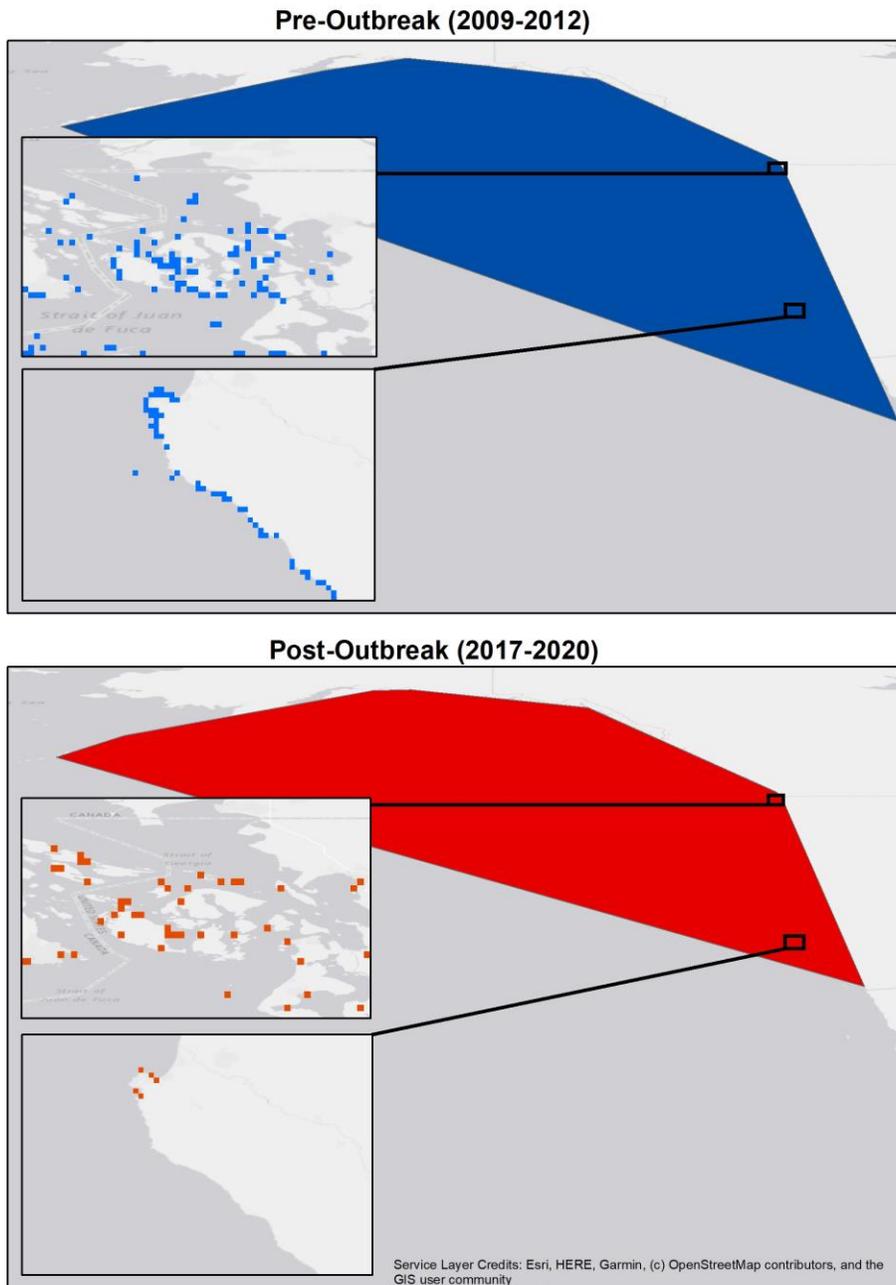


Figure 11. Maps of the extent of occurrence of *Pycnopodia helianthoides* with inset examples of the area of occurrence for a) the four years immediately before (2009–2012) and b) the four years after (2017–2020) the sea star wasting syndrome outbreak.

Criterion A2e: decline due to disease

Pycnopodia meets this criterion because disease was the primary driver of all population declines detailed in criteria A2a and A2c.

Criterion B: Vulnerable

Overall, *Pycnopodia* meets the definition of “Vulnerable” under criterion B2. The area of occupancy (1,717 km²) meets the 2,000 km² “Vulnerable” threshold for B2. Additionally, it meets subcriteria B2a and B2b, as the number of locations is estimated to be as low as one and no higher than 10, and because the species meets the definition for continuing decline (see justification below). Overall, *Pycnopodia* qualify as Vulnerable under criterion B2ab

Subcriterion B2

Subcriterion B2a: severe fragmentation and number of locations.

Pycnopodia does not meet the definition of severely fragmented. While in the southern half of its range, small remnant populations are likely fragmented, most of the remaining individuals exist in more continuously distributed populations across the northern half of the range. Additionally, its biology does not lend itself to severe fragmentation; *Pycnopodia* is a habitat generalist, its method of reproduction (broadcast spawning with a pelagic larval duration) has the potential for broad larval dispersal, and it has few barriers to dispersal.

Despite its large geographic extent, *Pycnopodia* does appear to have a limited number of locations (defined by IUCN as a geographically or ecologically distinct area in which a single threatening process can rapidly affect all occurrences of an ecosystem type). The primary threat to the species is SSWS, and it appears that all global *Pycnopodia* populations were affected by the disease. Thus, the minimum number of locations could be considered one, since the 2013–2017 outbreak demonstrated that all populations of this species can be rapidly affected by SSWS in a short period of time. However, considering the species’ broad geographic range, the true number of locations could be higher. For example, it appears that the western Gulf of Alaska and the Aleutian islands may have been less affected by the disease. If some locales were unaffected, the number of locations could be >1. While our current lack of understanding of this species’ biology, ecology, and threats limits our ability to put an upper limit on the number of locations, the fact that all populations of this species appear to have been affected within a three-year period by SSWS suggests that the number of locations is likely less than 10. Overall, we believe that the number of locations could be as low as one, which meets the threshold of “Critically Endangered” under subcriterion B2a.

Subcriterion B2b: continuing decline

Similar to our calculations of population decline under criterion A2a, the long generation time of *Pycnopodia* (27–37 years) combined with the non-linear, sudden decline in population size between 2013 and 2017 creates some uncertainty in the exact measure of continuing decline. Further, the causative agent for SSWS is unknown so we have no way to test the health of surviving individuals. Importantly, however, we continue to see evidence of SSWS in *Pycnopodia* and other species (see Threats) and it is quite possible that expression of the disease will return, especially if it is driven by warm

temperature anomalies associated with climate change. We believe this alone justifies a prediction of continued decline in the regions that still have remnant populations.

In addition, we analysed trends in population density since SSWS abated ([Fig. 5](#); from 2017-2019) and found that the global population exhibits a weak negative trend. Further, upon investigating this trend among regions, we found that densities in regions on the outer coast of the contiguous United States and Mexico, have “flat lined” at extremely low densities ([Fig. 5](#); Washington outer coast, Oregon, North, Central, Southern and Baja California). The regions with remaining populations, including much of Alaska and British Columbia (including the Salish Sea), have exhibited continuing declines since 2017. These findings suggest that *Pycnopodia* populations are experiencing a continued decline, which qualifies them for criterion B2b.

Subcriterion B2c: extreme fluctuations

While we detected some fluctuations in population size (and presumably mature individuals) over the 32-year time frame, we believe that this species does not generally undergo extreme fluctuations. First, the peak population size we detected in 2014-2015 was likely due to increased sampling effort, and was not a true increase in population size (see Declines for more information). Second, this species is long-lived (up to 65 years by our estimates), and reaches maturity within a few years, so this indicates that there are no extreme fluctuations in mature individuals. We also did not detect extreme fluctuations in EOO or AOO and we do not think there are true subpopulations in this widespread species. Overall, *Pycnopodia* does not meet the threatened threshold of extreme fluctuations for criterion B2c.

Criterion C: not threatened

With a post-outbreak population size estimate of 594,251,528 individuals ([Table 2](#)) and a 2019 population size estimate of 80,627,721 ([Fig. 3a](#)), most of which are mature, *Pycnopodia* does not qualify for threatened (<1,000 mature individuals) under criterion C.

Criterion D: not threatened

Although the population size and area of extent of *Pycnopodia* have greatly decreased since the outbreak of SSWS in 2013, our best estimate of AOO and population size as of 2019 was 1,716 km² and 80,627,721 individuals, respectively ([Table 7](#) and [Fig. 5a](#), respectively). These metrics are far above the thresholds of 20 km² and 1,000 individuals, respectively, required by criterion D and thus this species does not qualify for listing under criterion D.

Criterion E: Data Deficient

Burgman and Possingham (2010) note that some of the characteristics of a high quality population viability analysis (PVA) include deep knowledge of the species' biology, habitat preferences, dispersal capability, threats, individual and population-wide responses to those threats, and the risk posed by these threats in the future. Unfortunately, we have very limited information on most of these categories for *Pycnopodia*. The broad lack of understanding of *Pycnopodia* biology and ecology and of

the disease that severely impacted the species prevent any kind of mechanistic understanding of how this species may or may not rebound in coming decades.

Furthermore, we do not have the data available to do many traditional kinds of PVAs. For instance, in their overview of PVA Akçakaya and Sjögren-Gulve (2000) note that three of the most common kinds of PVA are meta-population occupancy models, structured population models, and individual-based models. While we have the presence/absence data needed for an occupancy model, occupancy models typically are only used for highly spatially structured metapopulations and thus are not applicable to *Pycnopodia*. Structured population models and individual-based models require at a minimum age-specific or stage-specific information on mortality and reproduction, which is not available for *Pycnopodia*. The only kind of PVA we are aware of that we might be able to use are time-series analysis, such as the kind used in Dennis *et al.* (1991) and Holmes and Fagan (2002). However, these analyses usually require regular censuses of species' population size, whereas the available population data on *Pycnopodia* are spatially limited and temporally patchy. Without a robust population time series or more detailed physiological, ecological, and epidemiological understanding of *Pycnopodia*, we do not think it is useful to conduct a PVA for this species' assessment.

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