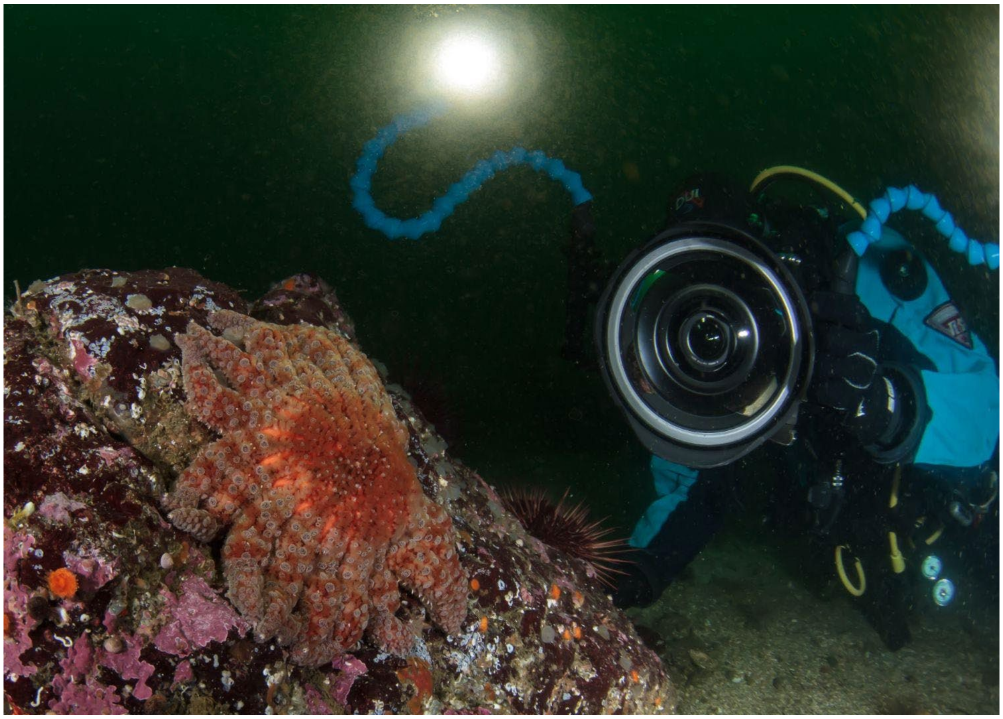
Endangered Species Act Status Review Report: Sunflower Sea Star (*Pycnopodia helianthoides*)



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COVER IMAGE: A large sunflower sea star being photographed off McNeil Island, WA. Photo: Amanda Bird, Paua Marine Research Group.

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REVIEW DRAFT

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Executive Summary

On August 18, 2021, the National Marine Fisheries Service (NMFS) received a petition from the Center for Biological Diversity to list the sunflower sea star (*Pycnopodia helianthoides*) as a threatened or endangered species throughout its range under the Endangered Species Act (ESA). After an initial evaluation using information provided in the petition and readily available in NMFS' records, we determined that the proposed action may be warranted (86 FR 73230) and a Status Review Team (SRT) was convened to initiate a full status review and evaluate overall extinction risk for the species. This team consisted of representatives from the NMFS West Coast and Alaska Regional Offices; NMFS Southwest, Northwest, and Alaska Fisheries Science Centers; United States Geological Survey; and Monterey Bay National Marine Sanctuary. This document is the status review and extinction risk assessment generated by the SRT and will be used to inform the listing decision for *P. helianthoides*, but does not in itself constitute a determination regarding protected status.

Pycnopodia helianthoides is a large, fast-moving, many-armed sea star native to the west coast of the continent of North America. The species occupies waters from the intertidal to at least 435 m deep and occurs over a broad array of soft-, mixed-, and hard-bottom habitats from the Aleutian Islands, AK, to Baja California, MX. The species is most abundant, however, in the waters off eastern Alaska and British Columbia. The species has separate sexes and is a broadcast spawner with a planktonic larval stage, facilitating current-driven distribution of offspring. Reproduction also occurs via larval cloning, enhancing potential reproductive output beyond female fecundity. *Pycnopodia helianthoides* hunts a range of bivalves, gastropods, crustaceans, and other invertebrates using chemosensory stimuli and is well known to dig for preferred prey in soft sediment. Through top-down predatory control of sea urchins and other kelp predators, *P. helianthoides* fills the role of a keystone mesopredator. The species also scavenges fish, birds, and octopus as available. While generally solitary, and highly competitive with conspecifics, *P. helianthoides* is known to seasonally aggregate, perhaps for spawning purposes.

Prior to 2013, the global abundance of *P. helianthoides* was estimated at several billion animals, but from 2013-17 sea star wasting syndrome (SSWS) reached pandemic levels, killing an estimated 90%+ of the population. Impacts varied by region across the range of the species and generally progressed from south to north, though a notable delay occurred off Oregon for unknown reasons. By 2017, *P. helianthoides* was rare south of Cape Flattery, WA, in areas where it had long been a conspicuous and ecologically important component of benthic marine ecosystems. Declines in coastal British Columbia and the Aleutian Islands were less pronounced, but still exceeded at least 60%, and more likely 80%. While the root cause of SSWS has not yet been identified, dozens of independent monitoring efforts using SCUBA, benthic trawls, and shellfish pots have documented similar declines in abundance, and sometimes spatial distribution, without subsequent recovery. Environmental factors such as temperature and dissolved oxygen likely contributed to the pandemic, and continue to interact with the disease agent to suppress recovery, but studies have failed to document conclusive linkages that apply on broad scales. Complex interactions among stressors, some of which have become more intense as a consequence of anthropogenic climate change, affect both the persistence of individuals and local populations.

Little is known about several fundamental biological aspects of the life history and demography of *P. helianthoides*. Parameters such as age/size at first maturity, fecundity, longevity, reproductive life span, and individual growth rate have not been validated. Furthermore, variation in these parameters over time and space, including any systematic differences among regions or habitats, have not been described. While regional asynchrony in SSWS impacts was observed during the pandemic, the degree to which this pattern aligns with population-level differences in genetics, population growth rate, disease susceptibility, and other factors is unknown. Any such relationship is also confounded by the fact that occurrence and abundance data have been collected independently using an array of methods over different timespans and seasons, resulting in a patchwork of information that is incomplete and not intended to provide information on these parameters.

Pycnopodia helianthoides is captured as bycatch in various fisheries that employ bottom contact gear, though species-specific reporting of interactions is limited. Recreational harvest of *P. helianthoides* is not allowed in Alaska, Washington, or Oregon, but is allowed in British Columbia, California, and Mexico. Estimates of harvest are unavailable, but total take is likely small as human consumption of the species is not known to occur and collection of individuals for preservation as curios is limited to small specimens. Other threats that face *P. helianthoides* include: habitat degradation and destruction, especially in nearshore, urbanized areas of the species' range; inadequate regulatory mechanisms in some jurisdictions that allow for harvest of the species, even under limited circumstances; and both direct and indirect (i.e., ecological) consequences of anthropogenic climate change. In recent years, however, impacts from these threats have all paled in comparison to population declines resulting from SSWS.

The SRT considered the best available science and information compiled from a multitude of sources about the biology of *P. helianthoides*, and threats potentially limiting population viability, to conduct an expert review and evaluation of overall extinction risk following the FEMAT method. Threats were broadly grouped into the five ESA Section 4(a)(1) categories of: 1) present or threatened destruction, modification, or curtailment of habitat or range; 2) overutilization for commercial, recreational, scientific, or educational purposes; 3) competition, disease, or predation; 4) adequacy of existing regulatory mechanisms; and 5) other natural or manmade factors affecting continued existence. When warranted, specific threats within a category were assessed independently to provide greater resolution. The time horizon for this extinction risk assessment was set at 30 years into the foreseeable future, a period over which the SRT determined that impacts from various threats could be reasonably projected.

Species-level impacts from SSWS, both during the 2013-17 pandemic and on an ongoing basis, was identified as the major threat affecting the long-term persistence of *P. helianthoides* on a global basis. SSWS directly affects abundance, distribution, productivity, and spatial connectivity at a scale that places *P. helianthoides* at a moderate risk of extinction throughout its range. Productivity, population growth rate, and phenotypic and genetic diversity may also be affected, but data were not available to directly assess these impacts. Impacts from anthropogenic climate change were also identified as a substantial threat to species persistence, but all other threats were determined to likely have minimal effects on species viability over the next 30 years on a range-wide basis.

To determine whether overall extinction risk might be higher for *P. helianthoides* within some significant portion of its range (79 FR 37578), the SRT considered several scenarios for dividing up the known range using biologically relevant geographic landmarks. The portions defined by these landmarks were evaluated with regard to two questions: 1) is the population here at a higher risk of extinction relative to population segments elsewhere in the range?; and 2) is the population segment biologically significant to the viability of the species overall? The only portion of the range where the SRT had sufficient data and information to determine that the regional population was both at a potentially higher risk of extinction, largely from impacts from SSWS, and likely to be biologically significant to the species, largely as an abundance stronghold and potential source population for regions both north and south of its location, was the British Columbia coast and Salish Sea region. After conducting a second extinction risk analysis considering only this portion of the range the SRT concluded that risk also fell into the moderate category for the foreseeable future.

After a comprehensive evaluation of the biology of *P. helianthoides*, threats facing the species, and consideration of how parameters describing both these realms are likely to change in the next 30 years, the SRT concluded that the species is facing a *moderate risk of extinction over the foreseeable future*.

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1. INTRODUCTION

1.1 Scope and Intent of the Present Document

On August 18, 2021 the National Marine Fisheries Service (NMFS) received a petition to list the sunflower sea star (*Pycnopodia helianthoides*) as either threatened or endangered under the U.S. Endangered Species Act (ESA). Under the ESA, if a petition is found to present substantial scientific or commercial information that the petitioned action may be warranted, a status review shall be promptly commenced (16 U.S.C. 1533(b)(3)(A)). NMFS determined that the petition presented substantial information for consideration and that a status review was warranted for the species. This finding was announced in the Federal Register on December 27, 2021 (86 FR 73230). This document is the status review for the sunflower sea star.

The ESA stipulates that listing determinations should be based on the best available scientific and commercial information. NMFS determined that staff within the West Coast Region (WCR), with support from the Alaska Region (AKR), were best suited to undertake a scientific review of the biology, population status and trends, threats, and future outlook for the sunflower sea star. The WCR designated a biologist to serve as chair and formed a Status Review Team (SRT) composed of biologists, ecologists, statisticians, and natural resource management specialists to complete the review and conduct an extinction risk analysis for the sunflower sea star. The charge of the SRT was to make conclusions regarding the biological status of the species now and for the foreseeable future, as defined by available data.

This document reports the scientific review as well as the SRT's conclusions regarding the extinction risk of the sunflower sea star. The conclusions in this status review are subject to revision should important new information arise in the future. Where available, we provide literature citations to review articles that provide more extensive citations for each topic. Data and information were reviewed through June of 2022.

1.2 Key Questions in ESA Status Reviews

In evaluating a biological entity to determine whether listing under the ESA is warranted, two key questions must be addressed: 1) is the entity in question a species as defined by the ESA?; and, if so, 2) is the species currently in danger of extinction, or likely to be in danger of extinction in the foreseeable future, throughout all, or a significant portion, of its range?

For purposes of the ESA, a species is defined as "any species or subspecies of wildlife or plants, or any distinct population segment [DPS] of any species of vertebrate fish or wildlife, which interbreeds when mature" (50 CFR § 424.02). Evidence for such interbreeding can include direct observation, but often incorporates a broad array of physiological, anatomical, and genetic data, as available. Aspects of distribution, behavior, and natural isolation are also taken into account. In all cases, interbreeding is broadly assessed by the level of similarity among putative populations such that a species or DPS is distinct in a number of biologically meaningful aspects and largely, or completely, reproductively isolated from other species.

Once a biological entity is determined to meet the definition of a species, NMFS considers a variety of information to evaluate the level of extinction risk faced by the species. Important considerations include: 1) absolute population abundance, or an index thereof, and spatiotemporal distribution; 2) current abundance relative to historical abundance and carrying capacity of the habitat, when known; 3) documented spatiotemporal trends in abundance; 4) natural and human-influenced factors that generate variability in abundance and survival; 5) possible threats to genetic integrity from artificial rearing, when present; and 6) recent events (e.g., changes in management) that have predictable short- or long-term consequences for species abundance or distribution. Addressing this latter consideration involves a review of existing and planned conservation efforts at all jurisdictional levels that have the capacity to affect the extinction risk of the species, whether their impacts have yet been realized, according to the Policy for Evaluation of Conservation Efforts When Making Listing Decisions (68 FR 15100). Additional risk factors, such as disease prevalence or changes in life history traits, are also considered, when pertinent, to assess overall extinction risk. The determination of whether a species is "in danger of extinction" or "likely to become an endangered species within the foreseeable future" is ultimately made on the basis of the best scientific and commercial information available.

2. LIFE HISTORY AND ECOLOGY

2.1 Taxonomy and Distinctive Characteristics

The sunflower sea star (*Pycnopodia helianthoides*) was originally described as *Asterias helianthoides* by Brandt (1835), a species of sea star unique in having 16–20 rays (arms) (Figure 1) and found in coastal marine waters near Sitka, Alaska. Stimpson (1861) later designated it as the type species of the new genus *Pycnopodia*, and listed as the only known species of the family Pycnopodiidae. Fisher (1906) described a new genus and species, *Rathbunaster californicus*, and included it in Pycnopodiidae due to its many rays and overall morphological similarities with *Pycnopodia*. Verrill (1914) recognized this group of two monotypic genera as a subfamily (Pycnopodiinae) of the diverse sea star family Asteriidae, and stated that *P. helianthoides* was characterized by having 20-24 rays, contrary to Brandt's original description. Just a few years later, Fisher (1922) described the new species *Lysastrosoma anthosticta*, subsequently asserting that this species "is remarkable for being the only genus known which is very closely related to *Pycnopodia* Stimpson" (Fisher 1924). Thus, the genus *Rathbunaster* was no longer considered a close relative of *Pycnopodia*, and subsequent authors (e.g., Fisher 1928) have included only *Pycnopodia* and *Lysastrosoma* in the subfamily Pycnopodiinae. Fisher (1928) also states that *P. helianthoides* is characterized by having 15-24 rays, merging the meristic counts of Brandt (1835) and Verrill (1914). *Pycnopodia helianthoides* has no known synonyms, and the validity of the species has not been questioned in the taxonomic literature.

Figure 1. A large sunflower sea star (*Pycnopodia helianthoides*) on rocky habitat. Photo: Ed Gullekson.

Pycnopodia helianthoides is among the largest sea stars in the world, reaching over 1 m in total diameter from ray tip to ray tip across the central disk (Figure 1). Its closest relative, *Lysastrosoma anthosticta*, has only five rays and reaches a much smaller maximum size. The two species, which collectively constitute the subfamily Pycnopodiinae, are distinguished from other sea stars of the family Asteriidae by their greatly reduced abactinal (dorsal) skeleton with no actinal plates, and by their prominently crossed pedicellariae (Fisher, 1928). Very young *P. helianthoides* generally have less than a dozen rays (Figure 2), and additional rays are added by budding in symmetrical pairs as the individual grows. Other sea stars in the northern Pacific Ocean with many rays include several sun stars of the genera *Solaster*, *Crossaster*, and *Rathbunaster*, but these species generally have 8–17 rays, as opposed to the 20 or more rays commonly found in *P. helianthoides*, and all of the sun stars are considerably smaller and less massive than *Pycnopodia* (Fisher 1906). In describing *P. helianthoides*, Fisher (1928) said:

> “When under "full sail," with its thousands of tube-feet lashing back and forth, it is an impressive animal, and its numerous cushions of tenacious pedicellariae and the wide expanse of its flexible body make it a formidable engine of destruction.”

Based on long-standing taxonomic analysis, and lacking any evidence to the contrary, we find that *Pycnopodia helianthoides* represents a unique species as defined by Section 3 of the ESA.

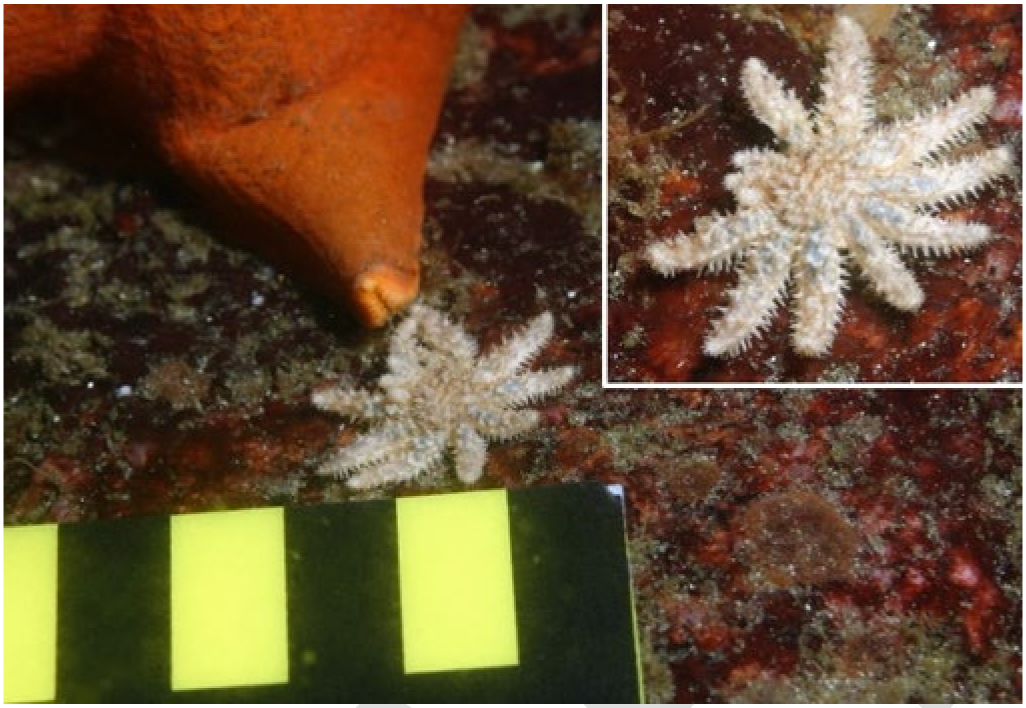

Figure 2. Juvenile sunflower sea star (*Pycnopodia helianthoides*) near the tip of an adult bat star (*Patiria miniata*, orange). This juvenile has a disc diameter of roughly 1 cm but already has 12 rays visible (see inset; 9 intact rays and 3 newly regenerating). Photos: Steve Lonhart.

2.2 Range and Habitat Use

The described maximum geographic range of *P. helianthoides* spans the Northeastern Pacific Ocean from the Aleutian Islands to Baja California (Sakashita 2020). This range includes 33 degrees of latitude (3,663 km) across western coasts of the continental United States, Canada, and northern Mexico. The farthest reaches of *P. helianthoides* observations include: northernmost - Bettles Bay, Anchorage Alaska (Gravem et al., 2021); westernmost – central and eastern Aleutian Islands (Kuluk Bay, Adak Island east to Unalaska Island, Samalga Pass, and Nikolski) (Feder 1980; O'Clair and O'Clair 1998; Jewett et al. 2015; Gravem et al. 2021); and southernmost - Bahia Asunción, Baja California Sur, Mexico (Gravem et al. 2021). *Pycnopodia helianthoides* is generally more common from the Alaska Peninsula to Monterey, California.

This species has no clear associations with specific habitats and is considered a habitat generalist (Gravem et al. 2021 and citations therein). The large geographic and depth range of *P. helianthoides* indicates this species is well adapted for a wide variety of environmental conditions and habitat types. They are found along the outer coasts and inside waters, which have complex geophysical features including glacial fjords, sounds, embayments, and tidewater glaciers. Preferring temperate waters, they inhabit kelp forests and rocky intertidal shoals (Hodin et al. 2021), but are regularly found in eelgrass meadows as well (Dean and Jewett 2001; Gravem et al. 2021). *Pycnopodia helianthoides* occupies a wide range of benthic substrates including mud, sand, shell, gravel, and rocky bottoms while roaming in search of prey (Konar et al. 2019; Lambert et al. 2000). They dwell in the low intertidal and subtidal zones to a depth of 435 m

(1,427 ft) but are most common at depths less than 25 m (82 ft) and rare in waters deeper than 120 m (394 ft) (Fisher 1928; Lambert 2000; Hemery et al. 2016; Gravem et al. 2021). This characterization of their prevalence across depth ranges, however, may be biased by: 1) differential sampling methods and effort, with SCUBA-based observations dominating records; and 2) the propensity to record all sea stars as "sea star unidentified" when they occur incidentally in various survey and fishery records.

2.3 Reproduction, Growth, and Longevity

2.3.1 Sexual Reproduction

Most asteroid species have separate sexes (i.e., dioecious), and sexes are externally indistinguishable from one another (Chia and Walker 1991). Sex ratios are commonly equal in sexually reproducing sea stars (Pastor-de-Ward et al. 2007; Mariante et al. 2010; Baeta et al. 2016). With few exceptions, each arm of an adult asteroid contains a pair of gonads, so that a five-armed star would possess 10 gonads (Chia and Walker 1991). In forcipulate sea stars, such as *P. helianthoides*, "the gonads are elongated, branched sacs, which enlarge during gametogenesis to fill the length of each ray" (Chia and Walker 1991, p. 306). Each gonad has a gonopore located between the bases of the arms. Gametes of most asteroids are broadcast into the surrounding seawater through these gonopores and fertilization occurs externally. Some asteroid species brood embryos and bypass a planktonic larval phase or produce a pelagic larva that does not feed in the plankton (i.e., lecithotrophic) (Strathmann 1987; Chia and Walker 1991; Byrne 2013). However, many broadcast spawning sea stars, including *P. helianthoides*, develop through the pelagic planktotrophic larval stages of bipinnaria and brachiolaria, which possess ciliary bands for capturing planktonic food and have well-developed digestive tracts (Strathmann 1971; 1978; Byrne 2013). Broadcast spawning sea stars with planktotrophic development typically release millions of eggs (Strathmann 1987; Chia and Walker 1991; Byrne 2013). Several researchers have attempted to rear *P. helianthoides* in captivity and describe early embryonic and larval development through metamorphosis (Mortensen 1921; Greer 1962; Strathmann 1970; 1978; Hodin et al. 2021). These efforts are thoroughly reviewed below.

2.3.1.1 Reproductive Seasonality

A number of environmental factors, such as food availability, seawater temperature, photoperiod, salinity, and the lunar cycle, may control seasonality of asteroid reproductive cycles (Chia and Walker 1991; Pearse et al. 1986). Typically, the reproductive cycle of sea stars is ascertained by following:

> … periodic changes throughout a year (or longer) using gonad index (ratio of gonad wet weight to body wet weight multiplied by 100). When samples of a given population are large, the gonad index grossly reflects reproductive status (Chia and Walker 1991, p. 317).

Seasonal changes in oocyte-diameter frequency distributions have also been used to estimate spawning season in sea stars (Fraser et al. 1981). Although the reproductive season of several Northeast Pacific sea stars have been estimated using these, ultimately lethal, methods (Farmanfarmaian et al. 1958; Mauzey 1966; Fraser et al. 1981; Pearse and Eernisse 1982; Sanford and Menge 2007), to the best of our knowledge no one has examined temporal changes in gonad index (aka, gonadosomatic index) or seasonal changes in oocyte diameter in field-collected *P. helianthoides*. However, a number of researchers have estimated reproductive seasonality of the species based on observations of either field or laboratory spawning.

Mortenson (1921, p. 194) reported that *P. helianthoides* "was found to have its breeding season in May–June" at Nanaimo, British Columbia. Greer (1962, p. 280) collected adult broodstock from the intertidal zone at San Juan Island, Washington and stated:

> On the morning of Apr 8, 1960, the animals in captivity spawned; the male spawned first in each tank. One large female had been observed to spawn earlier during the latter part of Mar.

Feder (1980, p. 128) stated that: "Fertilizable eggs have been obtained from December to June." It is unclear, however, if this statement refers to reproductive timing over the whole geographic range of the species or applies only to California, as this reference is focused on intertidal asteroids of California (Feder 1980). Strathmann (1987, p. 551) stated:

> Spawning occurs late March-July, mostly May-June (Greer 1962; Mortensen 1921; R. Shimek pers. comm.) with some subtidal spawnings by large males December-January (S. McEuen & B. Rivest pers. comm. to Fernald unpubl.).

Gravem et al. (2021, Supplementary Information) cited Feder and Christensen (1966) as saying that the breeding season is May-June around Vancouver Island, British Columbia. However, we were unable to locate any information on the breeding season of the sunflower sea star in Feder and Christensen (1966).

More recently, Hodin et al. (2021) suggested that the reproductive season for females begins in November-January and ends in April-May in Washington. In addition, Hodin et al. (2021, p. 248) stated:

> Mature and fertilizable oocytes from *P. helianthoides* in SE Alaska were isolated by a colleague in July 2019. It is likely that the reproductive season for females is later in this northern part of the species range.

Hodin et al. (2021) acknowledged that their estimates for spawn timing of sunflower sea stars in the San Juan Archipelago of Washington State (November-May) were different from those proposed in previous literature. Furthermore, Hodin et al. (2021, p. 256) stated:

> … we have seen mature oocytes as early as November and little evidence for mature oocytes after April–May. We observed four spontaneous spawning events in captivity, all between March and May, which is a bit earlier than the peak spawning timing noted in Strathmann (1987).

Typically, sea stars with planktotrophic larval development from the temperate nearshore Northwest Pacific Ocean spawn in late winter or early spring, which serves to provide the best growing conditions for their offspring by synchronizing the presence of their obligate plankton-feeding larvae with the peak of the spring phytoplankton bloom (Menge 1975; Strathmann 1987). The spawning seasons of several other asteriid sea stars with planktotrophic larval development in the Pacific Northwest and on the U.S. West Coast, including *Pisaster ochraceus* (Brandt), *Pisaster brevispinus* (Stimpson), *Pisaster giganteus* (Stimpson), *Evasterias troschelii* (Stimpson), and *Orthasterias koehleri* (deLoriol), occurs between March and August (Mortensen 1921; Farmanfarmaian et al. 1958; Mauzey 1966; Feder 1980; Fraser et al. 1981; Pearse and Eernisse 1982; Strathmann 1987; Pearse et al. 1988; Sanford and Menge 2007). Planktotrophic larvae of *P. helianthoides* developing during winter (November to February) in the Northeast Pacific Ocean would be at a distinct disadvantage due to the scarcity of planktonic algae at that time of year.

Each of the *P. helianthoides* reproductive events documented in Hodin et al. (2021, their tables 1 and S1) occurred after broodstock had been held in captivity for many months before spontaneous spawning occurred, or before artificial propagation was attempted by arm amputation. In some cases, captive adult stars completed a reproductive cycle and became reproductive again while in captivity (Hodin et al. 2021). In addition, Hodin et al. (2021, p. 244) stated:

> … we maintained adults in 1-m-deep, partially covered outdoor opaque flow-through natural seawater aquaria under high flow. We fed adults a diet consisting mainly of mussels (*Mytilus trossulus*) every other day. A standard feeding consisted of 1 large mussel (~70–120 g wet weight) or 2 medium mussels (~30–60 g wet weight).

It is possible that a slightly altered photoperiod and constant availability of food may have caused captive *P. helianthoides* broodstock to exhibit altered reproductive seasonality, and this may explain the discrepancy between spawn timing observed by Hodin et al. (2021) and previous researchers. It is known that reproductive seasonality and gametogenic output in captive sea stars can be altered by increased food availability (Chia and Walker 1991), as well as by changes in natural photoperiod (Pearse and Eernisse 1982; Pearse et al. 1986). Pearse and Eernisse (1982) stated:

> A photoperiod regime 6 mo out of phase between December 1978 and August 1980 resulted in gametogenesis, gonadal growth, and spawning in laboratory-

> maintained sea stars [*Pisaster ochraceus* (Brandt)] 6 mo out of phase with individuals in the field or laboratory on normal celestial photoperiods at Santa Cruz, California (USA).

In addition, many temperate sea stars, such as the ochre star (*Pisaster ochraceus*), have seasonal, cyclical feeding patterns, such that feeding activity is reduced during the late fall and winter (Feder 1980; Mauzey 1966; Sanford and Menge 2007). This may also be the case for *P. helianthoides* but direct documentation of this phenomenon is lacking.

2.3.1.2 Gametes

2.3.1.2.1 Sperm

Chia et al. (1975, their figure 4) provides a photomicrograph of the spherical sperm of *P. helianthoides*, which is approximately 3.0 µm in diameter including the middlepiece, but not the elongated sperm tail. This is typical of asteroid sperm, in which "the head is essentially spherical with the acrosome positioned at the anterior end of the nucleus in a depression, while the mitochondrial middle piece takes the form of an annular band at the posterior end of the nucleus" (Chia et al. 1975, p. 554). Spermatogenesis in *P. helianthoides* has not been described in detail, but Hodin et al. (2021) were able to detect motile sperm all year long in captive males. Mauzey (1966) was also able to detect motile sperm in testes smears from *Pisaster ochraceus* at all times of the year.

2.3.1.2.2 Egg Size and Fecundity

Mortensen (1921) reared embryos of *P. helianthoides* collected at Nanaimo, British Columbia, a short period into the gastrula stage, but did not comment upon egg size or fecundity of captive specimens. Greer (1962) reported that *P. helianthoides* from San Juan Island, Washington, had a small egg 120 µm in diameter. Strathmann (1987) later confirmed this observation. Chia and Walker (1991) described and illustrated the early development of *P. helianthoides* from just after fertilization to the four-cell stage. They did not comment on initial egg size; however, they illustrate a fertilized egg after the fertilization membrane has lifted away from the egg surface. The fertilized egg cytoplasm in this photograph measures ~210 µm in diameter in shortest dimension, based on the scale bar on their micrograph (Chia and Walker 1991, p. 326, their figure 9). It is likely that unfertilized oocytes would be somewhat smaller than the illustrated example in Chia and Walker (1991), but it is unlikely they would be as small as 120 µm in diameter.

Hodin et al. (2021) presented *P. helianthoides* oocyte diameters both graphically (their figure 2) and in tabular form (their table S1), although all measurements were derived from eggs extracted from gonads after arm amputation. Hodin et al. (2021, p. 245) state:

> Oocytes are often oblong in shape; our reported diameters are averages of the longest diameter and the diameter perpendicular to that, both passing approximately through the centroid (n = 10–20 oocytes measured per individual).

According to Hodin et al. (2021, their caption figure 2):

> There appears to be an annual cycle, with peak oocyte sizes in the late autumn to mid-late spring. All mature oocytes were >155 µm on average.

Furthermore, Hodin et al. (2021, p. 248) state:

> Individuals in which the largest oocytes were ~150 µm in diameter or less did not undergo GVBD [germinal vesicle breakdown] and did not fertilize (n = 8). … [Fertilizable] egg sizes across all individuals that we examined ranged from 155 to 170 µm.

As noted above, Greer (1962) provided the only previous direct documentation of egg size in *P. helianthoides*, at 120 µm in diameter. Hodin et al. (2021, p. 256) contested this finding and stated:

> Prior studies stated that mature eggs of *P. helianthoides* were ~120 µm in diameter (Greer, 1962; Strathmann, 1987), but we could not find primary data to support this assertion. Our data for *P. helianthoides* from both AK and WA populations show that the egg size in *P. helianthoides* is 155–170 µm in diameter, which is consistent with the one measurement of a fertilized *P. helianthoides* egg of which we are aware (G. von Dassow, University of Oregon, pers. comm.) prior to the recent SSW [sea star wasting syndrome] event. Therefore, it does not seem that egg sizes have changed in *P. helianthoides* populations in response to the recent SSW event. We have observed the rare egg within a batch that was smaller than 155 µm and successfully matured and fertilized. Nevertheless, when the maximum oocyte size for a given female was less than 150 µm, the oocytes failed to mature and, thus, remained unfertilizable.

We were unable to find direct estimates of fecundity for female *P. helianthoides*. However, Strathmann (1987, p. 551) stated: “Ripe ovaries of specimens about 60 cm across may weigh 400–800 gms (R. Miller pers. comm.).” Comparison of this estimate with fecundity estimates for the ochre star, a related Northeast Pacific asteriid sea star that has similar egg size (150–160 µm) and reproductive strategy, may give some insight to potential fecundity of the sunflower sea star.

Menge (1974, p. 87) estimated that a female ochre star weighing 100 g wet weight (the estimated size at maturity) would produce about 2.4 million eggs, and stated:

> A typical-sized female (400 g wet weight) would spawn about 40 x 10^6 eggs. Since many individuals are considerably larger than that …, fecundity of this starfish can obviously be even greater.

As the wet weight of ochre stars ranges up to 650 g (Menge 1975), a female of this size may spawn many more than 40 million eggs in a season. However, Fraser et al. (198l) believed that Menge's (1974) estimate of 40 million eggs for a 400 g adult female ochre star was somewhat high. Fraser et al. (198l, p. 1705) estimated – based on their calculation of 2.1 (±0.4) x 10^5 eggs in one milliliter of settled eggs – that 40 million eggs would be equivalent to "about 200 ml of settled eggs per female," and the maximum volume of eggs they had found "from a single female was 100 ml." Fraser et al. (198l) estimated that the average female ochre star in their study weighed 315 g and contained about 40 ml of settled eggs, or about 8 million total eggs. Gravem et al. (2021, Supplementary Information) stated: "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)."

Although there are few equivalent studies with published wet weight values for *P. helianthoides*, Lambert (2000, p. 139) stated: "It is also probably the heaviest known sea star, weighing in at about 5 kg." In addition, Fisher (1928, p. 160) stated:

> *Pycnopodia* when fully grown is probably the heaviest known sea star. … In the Monterey region specimens seldom exceed a diameter of 18 inches or 450 mm., but in the region of Puget Sound they grow much larger. Dr. C. McLean Fraser has reported measuring a specimen 800 mm. in diameter (32 inches). Dr. John C. Brown, who made color notes at Port Renfrew, Vancouver Island, reported several as weighing 10 pounds when taken from the water.

A ten-pound sunflower sea star is equivalent to approximately 4.5 kg (wet weight). Ochre stars in the San Juan Islands apportion "an average of 9%-10% of their weight to reproductive activities" (Menge 1974, p. 88). Assuming *P. helianthoides* and ochre star invest similar resources into reproductive efforts, and a 315 g ochre star produces an average of 8 million eggs (Fraser et al. 198l), then it is conceivable that a 4.5 kg female sunflower sea star could produce upwards of 114 million eggs in a gonadal cycle. This level of potential egg production is comparable to estimates for the crown-of-thorns sea star *Acanthaster* spp., for which Babcock et al. (2016, p. 1 of 7) stated:

> The highest oocyte production was estimated to be >100 million oocytes, which is the highest ever recorded for an individual female starfish. These relationships imply that the largest *Acanthaster* reported may have fecundities greater than 200 million eggs per season.

Furthermore, Babcock et al. (2016, p. 6 of 7) stated:

> The only other multi-armed asteroid of equivalent size is *Pycnopodia helianthoides* which can reach diameters similar to *Acanthaster* (average diameters of 50 cm and up to 1 m …), but there are no published data on the gonad indices for this species. If *Pycnopodia* develops GI [gonad index] values as high as other temperate multi-armed species (e.g. *Coscinasterias, Stichaster*), it may well rival *Acanthaster* as the world's most fecund starfish.

However, this high potential fecundity of *P. helianthoides* is debatable given recent observations of gonad size in captive broodstock individuals. Hodin et al. (2021, p. 256) stated:

> … we have noted that recently collected stars, even when reproductively mature, tended to have small gonads (a few centimeters in length), relative to what is seen in other sympatric asteroids (JH, pers. obs.).

In regard to size at sexual maturity in *P. helianthoides* near Bremerton, Washington, Kjerskog-Agersborg (1918, p. 252) stated:

> Maturity is not entirely dependent on the size of the animal; i.e., the diameter varies: In immature up to 12 inches; in males from 10-16.5 inches; in females from 10.5-20 inches. The females are on the average larger than are the males.

Gravem et al. (2021, Supplementary Information) stated:

> 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 …

Similarly, Chia and Walker (1991, p. 312) stated that "sexual maturity [of the ochre star] is apparently not reached until 4 or 5 years of age."

Without additional information on the size at first maturity, fecundity, reproductive seasonality, and reproductive senescence of the sunflower sea star, and how these demographic parameters vary throughout the range of the species, it is impossible to accurately predict annual reproductive output of populations or to adequately evaluate resiliency and rebound potential in response to environmental perturbations. Indications from other asteriids, however, suggest that reproductively viable females can produce at least tens of millions of eggs annually, possibly for several decades. Under appropriate environmental conditions, this represents considerable reproductive and recruitment potential.

2.3.1.3 Spawning and Egg Fertilization

2.3.1.3.1 Aggregation and Spawning Behavior

Sea stars may modify their behavior during spawning in ways that improve the chances of egg fertilization, including aggregating, modifying their positions and postures, and spawning synchronously (Strathmann 1987; Chia and Walker 1991; Dams et al. 2018).

Although many asteroids appear to aggregate during spawning (Strathmann 1987; Minchin 1987; Chia and Walker 1991; Babcock and Mundy 1992; Raymond et al. 2007; Himmelman et al. 2008; Dams et al. 2018), it is uncertain whether *P. helianthoides* does so. This uncertainty is highlighted by two conflicting statements in the Supplementary Information section of Gravem et al. (2021):

> 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.

And:

> 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).

Kjerskog-Agersborg (1918) studied *P. helianthoides* in Puget Sound at Bremerton, Washington, and suggested that individuals migrated to shallower waters during the spawning season and were present in large aggregations at this time of year. Kjerskog-Agersborg (1918, p. 246–247) stated:

> Temperature together with the impulse to breed are still other causes for migration…. That *Pycnopodia* should move up to shallow water during the spawning season seems reasonable, for the temperature in deeper waters is undoubtedly lower than at the surface even during the spring. … *Pycnopodia* was found in large numbers on a certain side of a bay, during spring, while it was totally absent from these grounds later on, during the summer. As a matter of fact, during the spring of 1915, on the … [east side of Port Washington Narrows near Bremerton] more than one hundred specimens were counted, while in July of the same year not a single specimen was seen in the same area.

A number of other sea stars move into shallow water during the spawning season, supporting that movement into shallow water may be an adaptive behavior that promotes fertilization in some way (Babcock et al. 2000). Some fertilization rate modeling results for the crown-of-thorns sea star *Acanthaster* spp. (Babcock et al. 1994) indicate that shallower water increases fertilization rates relative to deeper water because of reduced dilution of gametes in waters shallower than 5 m (Babcock et al. 2000).

Aggregation at the time of spawning is commonly observed in other asteriid sea stars, such as *Marthasterias glacialis* (Minchin 1987) and *Asterias rubens* (Raymond et al. 2007; Himmelman et al. 2008; Dams et al. 2018), as well as in *Acanthaster* spp. (Babcock and Mundy 1992). Both Miller (1989) and Chia and Walker (1991) note that pheromones are likely involved in the coordinated aggregation and synchronous release of gametes during such events, allowing both sexes to ensure mates are available at suitable densities to allow for effective mating.

Many sea stars arch their bodies upward, remaining in contact with the substratum by the tips of their arms during spawning. This posture elevates the gonopores through which the gametes are shed into the flow field (Galtsoff and Loosanoff 1939; Strathmann 1987; Minchin 1987; Chia and Walker 1991; Dams et al. 2018). This behavior is commonly observed in other asteriid sea stars, such as *Marthasterias glacialis* (Minchin 1987) and *Asterias rubens* (Himmelman et al. 2008; Dams et al. 2018), as well as in *Acanthaster* spp. (Babcock and Mundy 1992). Dams et al. (2018) used laboratory experimentation and theoretical modeling to show that an arched posture promoted downstream dispersion of gametes and was more effective than stars lying in the flat position.

It is common knowledge that *P. helianthoides* also arch their bodies upward in this characteristic spawning posture. Although we were unable to locate specific reference in the scientific literature, there are numerous photographs and depictions of sunflower sea stars assuming this spawning posture on the internet (e.g., Echinoblog, KUOW - Scientists race to rescue world's fastest sea star from oblivion, and Port Townsend Marine Science Center Blog).

In addition to aggregation and body arching, many large sea stars, such as *Marthasterias glacialis* (Minchin 1987), *Asterias rubens* (Himmelman et al. 2008), and *Acanthaster* spp. (Babcock and Mundy 1992), are known to climb onto rocks, boulders, or coral outcrops to gain elevation during spawning. To the best of our knowledge, this behavior of climbing to a high point to assist in gamete dispersal during spawning has not been recorded for *P. helianthoides*.

Since released gametes (especially sperm) may remain viable for as little as 2 h (Strathmann 1987; Benzie and Dixon 1994), many sea stars increase the chances of egg fertilization by spawning synchronously (Feder and Christensen 1966; Babcock and Mundy 1992; Babcock et al. 1994; Mercier and Hamel 2013). These include the asteriid sea stars *Asterias rubens* (Hancock 1958; Raymond et al. 2007; Himmelman et al. 2008) and *Asterias forbesi* (Galtsoff and Loosanoff 1939). In many published observations of spawning, males consistently spawned before females (Mercier and Hamel 2013). Even though synchronous spawning is necessary for successful fertilization to occur, synchronization must be accompanied by relatively close proximity for successful fertilization (Mercier and Hamel 2013). As noted above, there is conflicting information regarding whether synchronous aggregative spawning is exhibited by *P. helianthoides*, but evidence from ecologically similar sea star species and anecdotal observations for *P. helianthoides* strongly suggest this is the case.

2.3.1.3.2 Spawning Density

As noted above, broadcast-spawning marine invertebrates with separate sexes, such as *P. helianthoides* must spawn in temporal and spatial synchrony in order to maximize the probability of successful production of progeny. When populations decline below sufficient densities to ensure contact of distributed eggs and sperm with one another, Allee effects may hinder population persistence and/or recovery (Lundquist and Botsford 2004; 2011). Standard population models predict that a reduction in adult density should be associated with a decrease in intraspecific competition leading to an increase in growth rate, survival, and gamete production. However, these advantages may be countered by decreases in the rate of successful fertilization among sparsely distributed individuals (Levitan 1995; Levitan and Sewell 1998; Gascoigne and Lipcius 2004). Fertilization success may be a limiting factor in reproduction, and hence recruitment.

Since Pennington's (1985) field and laboratory experiments on fertilization success in the green sea urchin *Strongylocentrotus droebachiensis* (Müller), numerous empirical (for reviews, see Levitan 1995; Levitan and Sewell 1998) and modeling (see references in Lundquist and Botsford 2004; Lauzon-Guay and Scheibling 2007) studies have investigated the effects of spawner number and density, flow rate, and gamete age on fertilization success in broadcast spawning echinoderms. Babcock et al. (1994) cite several experimental studies of *in situ* fertilization rates for free-spawning sea urchin species with very low, even near-zero, success unless animals spawn with in synchrony and in extremely close proximity (<1 m) (Pennington 1985; Levitan 1991; Levitan et al. 1992). Nevertheless, successful fertilization rates of the crown-of-thorns sea star *Acanthaster* spp. during a natural mass spawning event were estimated at 83% (Babcock and Mundy 1992).

Laboratory and field studies on sea star fertilization rates have centered on gamete age and distance between spawners in the crown-of-thorns seas star *Acanthaster* spp. (Babcock and Mundy 1992; Babcock et al. 1994; Benzie and Dixon 1994), but also have included studies on *Coscinasterias muricata* (Babcock et al. 2000), *Oreaster reticulatus* (Metaxas et al. 2002), and *Asterias rubens* (Williams and Bentley 2002). We did not find published data from directed studies of *in situ* fertilization success in *P. helianthoides*.

Williams and Bentley (2002) showed that under experimental conditions oocytes of the asteriid *Asterias rubens* were fertilizable at 100% for only four hours after release and that fertilization rate fell to zero after 24 h. Similarly, Benzie and Dixon (1994) detected a decline in fertilization success rate of *Acanthaster* spp. oocytes after three hours, which dropped to only 20% at seven hours. An effect of aging on fertilization rate of sperm was also apparent, with fertilization rate falling to zero within 24 h for *Asterias rubens* (Williams and Bentley 2002), and declining within one hour, and dropping to zero after three to four hours, for *Acanthaster* spp. (Benzie and Dixon 1994).

Although results demonstrate there is a relatively short period during which asteroid gametes are viable, fertilization rates are affected both by viability and contact, and the latter is affected by both small- and large-scale water flow patterns. Gametes may be spread quickly by swift currents, expanding the range over which fertilization may occur, or entrained by eddies, resulting in minimal dispersion. Several researchers have used experimentation and modeling to examine the potential for long-distance fertilization in *Acanthaster* spp. (Babcock and Mundy 1992; Babcock et al. 1994; Benzie and Dixon 1994), *Coscinasterias muricata* (Babcock et al. 2000), and *Oreaster reticulatus* (Metaxas et al. 2002). Babcock and Mundy (1992), working with *Acanthaster* spp., found experimental fertilization rates up to 60% at 10 m downstream of a spawning male. Furthermore, Babcock and Mundy (1992, p. 529) stated:

> Fertilization trials with starfish induced to spawn artificially showed that rates of fertilization decreased little for females up to 8 m downstream from spawning males… Fertilization rates dropped rapidly at distances greater than this, but the rate was still surprisingly high (22.6% ± 10.3) at 64 m downstream, the greatest distance tested.

As Benzie and Dixon (1994, p. 150) stated: "These values are much greater than those of sea urchins, which show 5% fertilization at 5 m, dropping to zero at distances greater than 10 m (Pennington, 1985)." Surprisingly high experimental egg fertilization rates at distances greater than 10 m downstream of sperm release were also shown for the sea stars *Coscinasterias muricata* (Babcock et al. 2000) and *Oreaster reticulatus* (Metaxas et al. 2002). Fertilization rates in *C. muricata* ranged from 11–43% at 16 m and averaged 14% at 32 m downstream of a spawning male (Babcock et al. 2000). Similarly, Metaxas et al. (2002, p. 92) stated:

> Rate of fertilization in *Oreaster reticulatus* decreased exponentially with increasing distance downstream from a spawning male for all experimental runs at all sites … mean rate averaged across all sites ranged from 74% at x = 1 m through 34% at x = 16 m to 31% at x = 32 m.

These rates of successful fertilization suggested that low population density of *O. reticulatus* may not be prohibitive to successful fertilization and zygote production (Metaxas et al. 2002). While *in situ* gamete viability and fertilization effectiveness studies do not exist for *P. helianthoides*, provided temporal synchrony in gamete release it is likely individuals must be within several tens of meters of one another for fertilization to occur at any meaningful rate.

2.3.1.4 Larval Development and Settlement

2.3.1.4.1 Larval Development

As described earlier, several researchers have, with varying degrees of success, attempted to rear *P. helianthoides* and describe early embryonic and larval development through to metamorphosis (Mortensen 1921; Greer 1962; Strathmann 1970; 1978; Chia and Walker 1991; Hodin et al. 2021). Mortensen (1921) reared embryos collected at Nanaimo, British Columbia, to just beyond the gastrula stage. Chia and Walker (1991) illustrate early development from just after fertilization to the four-cell stage, but do not discuss subsequent development.

Greer (1962), Strathmann (1970; 1971; 1978), and Hodin et al. (2021) reared *P. helianthoides* larvae to metamorphosis. Greer (1962) reported that time from fertilization to metamorphosis for larvae from San Juan Islands, Washington, ranged from 60-70 days when reared at 10-12°C. Strathmann (1970; 1971; 1978) reared *P. helianthoides* larvae as part of his seminal studies on the feeding behavior of planktotrophic echinoderm larvae. Strathmann (1978) reported that time from fertilization through to settling ranged from 90-146 days at natural local water temperatures (7-13°C) encountered in the San Juan Islands, Washington, in the late 1960s. Hodin et al. (2021) reared *P. helianthoides* larvae from Washington at 11°C and 14°C and observed first spontaneous settlement of larvae at seven weeks, in larvae held at 10-11°C. Peak metamorphosis occurred at eight weeks in larvae derived from Alaskan broodstock, compared to 11 weeks for larvae from Washington broodstock. Hodin et al. (2021) reported that larvae first became competent to metamorphose at seven weeks post-fertilization at 10-11°C, compared to the nine weeks reported by Greer (1962) when reared at 10-12°C. Together, these studies indicate that larval duration may be as short as seven weeks or as long as 21, and that temperature is a key parameter determining the extent of this period.

The Supplementary Information in Gravem et al. (2021) stated:

> 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).

However, prism and pluteus larval stages are restricted to sea urchins (Phylum Echinodermata, Class Echinodea). Larvae of *P. helianthoides* progress through the typical asteroid planktotrophic larval phases of bipinnaria and brachiolaria, prior to metamorphosis (Greer 1962; Strathmann 1978; Hodin et al. 2021). The bipinnaria and brachiolaria are sequential developmental stages, the bipinnaria always developing first (Chia and Walker 1991; McEdward et al. 2002).

Unlike the pentaradial symmetry of adult asteroids, bipinnaria and brachiolaria larvae are bilaterally symmetrical (Chia and Walker 1991). The feeding bipinnaria larva is characterized by two bilaterally symmetrical ciliary bands and an open, functional gut (McEdward et al. 2002).

The planktotrophic bipinnaria, and the later brachiolaria, ingest diatoms and other single-celled algae, and may also utilize dissolved organic matter nutritionally (Chia and Walker 1991). Bipinnaria larvae of *P. helianthoides* were estimated to form on the 5th (Greer 1962) or 6th day (Hodin et al. 2021) after fertilization. In planktotrophic forcipulates like *P. helianthoides*, the bipinnaria transforms into a planktotrophic brachiolaria larva, which:

> …develops three anterior brachiolar arms with glandular tips surrounding a central adhesive disc … The larva attaches to the substratum by the tips of the brachiolar arms and the central adhesive disc. The larval body is gradually reduced to a stem anchoring a developing juvenile with five primary rays. … In multi-rayed forms the additional rays appear later [Strathmann 1987, p. 538].

At metamorphosis, the brachiolar arms, central adhesive disk, and other larval structures are resorbed into the juvenile body (Chia and Walker 1991; McEdward et al. 2002). At this stage, juveniles are typically about 0.5-1.0 mm in diameter (Strathmann 1987).

2.3.1.4.2 Larval Dispersal Distance

To understand the population dynamics of *P. helianthoides* on a range-wide basis it is crucial to develop an understanding of larval longevity and capacity for dispersal. Time from egg fertilization to metamorphosis for *P. helianthoides* under various conditions has been described as 49-77 days (Hodin et al. 2021), 60-70 days (Greer 1962), and 90-146 days (Strathmann 1978). As noted by Gravem et al. (2021), broadcast spawning with a long pelagic larval duration has the potential for broad larval dispersal, especially in open coastal areas with few geographic barriers. Along more heterogeneous, complex shorelines like those found inside the Salish Sea or Southeast Alaska, however, complex flow patterns may result in localized entrainment of larval and reduce dispersal capacity.

Minimum and maximum dispersal periods based on laboratory studies of planktotrophic larvae reveal how varying environmental and nutritional conditions influence the extent of the planktonic period (Pechenik 1990). Basch and Pearse (1996) showed, in studies with planktotrophic larvae of the sea star *Patiria* (as *Asterina*) *miniata*, that larvae grown in phytoplankton-rich conditions had greater survival, were in better condition, settled and metamorphosed sooner, and produced larger juveniles compared to larvae grown in low food concentrations. Planktotrophic larvae of many species of asteroids can delay metamorphosis in the absence of suitable settlement cues (Metaxas 2013), and are capable of long-range dispersal (Scheltema 1986; Metaxas 2013). Strathmann (1978) found the maximum time to settlement in culture for the sand star, ochre star, and sunflower sea star to be 20, 32, and 21 weeks, respectively. Strathmann (1978) emphasized that the duration of pelagic larval life is important in recruitment dynamics and, ultimately, to the distribution of a species.

Although, mortality of asteroid larvae during the planktonic larval stage has not been measured, it is expected to be high (Metaxas 2013), and it is likely that delaying metamorphosis would expose larvae to an additional period of predatory pressure (Basch and Pearse 1996) and stress associated with food availability.

2.3.1.4.3 Settlement and Recruitment

Keough and Downes (1982) define settlement of the larvae of marine benthic invertebrates, including sea stars, as contact with the post-larval substratum, resulting in metamorphosis from the larval to the post-larval form. Metamorphosis in planktotrophic asteroids results in the transformation of the bilaterally symmetrical larva into a pentaradially symmetrical juvenile (Chia and Walker 1991; Byrne 2013). Anatomical details of this process are described in Chia and Walker (1991) and Hodin et al. (2021). Asteroid larvae may respond to a suite of biological, chemical, and/or physical cues that induce metamorphosis and settlement, including the presence of coralline algae, microbial films, and kelp (Metaxas 2013).

Hodin et al. (2021, p. 256) stated that for *P. helianthoides*:

> Competent larvae will settle spontaneously and in response to a variety of natural biofilms, but settlement proportions and rates are greatly enhanced in response to a biofilm collected in the presence of adult sunflower stars or if larvae are exposed to fronds of the articulated coralline alga, *Calliarthron tuberculosum*. The combination of these two cues seems to enhance settlement even further. We also found that turbulence exposure induces a more rapid and synchronous settlement response to the aforementioned cues…

It is generally accepted that planktotrophic larvae are typically dispersed considerable distances away from adult populations and have little impact on recruitment to the natal habitat (Sewall and Watson 1993; Robles 2013). However, Sewall and Watson (1993) described a situation at the semi-enclosed bay of Boca del Infierno (Nootka Island, British Columbia) where larvae were entrained and settled within the adult habitat, contributing to the source population. During three years between 1987 and 1991, *P. helianthoides* recruits were observed on *Sargassum muticum* on the floor of the channel leading into the bay (Sewell and Watson 1993). In general, sea stars "are thought to have relatively low annual recruitment of larvae, punctuated by unusually strong settlement events in some years" (Sanford and Menge 2007, p. 9), the so-called boom and bust cycle characteristic of a broad diversity of marine fishes and invertebrates with planktonic larval dispersal (e.g., McLatchie et al. 2017; Schnedler-Meyer et al. 2018).

2.3.2 Asexual Reproduction

2.3.2.1 Adult Autotomy and Fission

Sea stars have the ability to regenerate lost rays/arms and parts of the central disc, although the regenerative process may take up to a year to complete. Rays may detach (autotomize) when a sea star is injured, as a defense reaction when attacked by a predator, or when handled excessively (Emson and Wilkie 1980; Chia and Walker 1991). Hodin et al. (2021) predicted that

P. helianthoides would take from 2.7-4.2 y (95% confidence interval) to fully regenerate lost or amputated arms based on observed regeneration rates in captive specimens. Mladenov et al. (1989) isolated an autotomy-promoting factor (APF) from *P. helianthoides* that were induced to autotomize arms following scalding. Mladenov et al. (1989, p. 169) stated:

> When injected into the coelom, APF elicits a complex behavioral response that culminates within minutes in multiple arm autotomy and a generalized softening of the body wall. Injection of fluid from intact, untreated sea stars does not promote the autotomy response

In addition to regenerating rays, some sea star species can reproduce asexually through clonal fission (where the animal divides in half, generally through the central disc) and subsequently each half regenerates into a complete sea star (fissiparity). Although an estimated 1,800 species of sea stars have been described, only 21 (Mladenov 1996) to 26 (Chia and Walker 1991) species are known to reproduce asexually by whole body fission. Some members of the genera *Linckia* and *Ophidiaster* are able to regenerate an entire new individual from a single autotomized arm (Pandian 2018). According to Emson and Wilkie (1980, p. 170):

> … mature sperm or oocytes … [are] found in almost all fissiparous species of all three classes. It is also clear that regeneration and sexual development occur simultaneously in most, if not all, fissiparous species.

Larvae of asteroids are also capable of regenerating lost body parts (Vickery and McClintock 1998; Vickery et al. 2002; Allen et al. 2018). When surgically bisected, cultured larvae of the ochre stars and sand stars were capable of completely regenerating lost body parts (Vickery and McClintock 1998; Vickery et al. 2002).

2.3.2.2 Larval Cloning

Asexual reproduction through the process of larval cloning – budding off of tissue fragments that regenerate into complete larvae – of asteroid bipinnaria and brachiolaria larvae was first detected in plankton samples in the late 1980s from the Gulf Stream and the western Sargasso Sea (Bosch et al. 1989) and in the Bay of Bengal off the east coast of India (Rao et al. 1993). Asteroid larvae undergoing cloning were later detected in additional field-collected plankton samples in tropical waters (Jaeckle 1994; Knott et al. 2003) and in laboratory cultures of numerous sea stars (Vickery and McClintock 2000; Kitazawa and Komatsu 2001; Blackburn and Allen 2013; Allen et al. 2019).

Recently, Hodin et al. (2021) reported that bipinnaria and brachiolaria larvae of *P. helianthoides* also have the capability to clone in a laboratory setting, describing cloning as “commonplace” in all larval cultures. The degree to which larval *P. helianthoides* clone in nature may have profound implications for life history (e.g., fecundity, dispersal distance), population dynamics, and population genetic structure (Knott et al. 2003; Balser 2004; Rogers-Bennett and Rogers

2008; Allen et al. 2018; 2019). Therefore, the phenomenon of larval cloning in asteroids is more thoroughly reviewed below.

From 10–90% of *Luidia* spp. planktotrophic bipinnaria larvae from plankton samples taken in the tropical and subtropical western Atlantic Ocean cloned a secondary larva from the primary larva (Bosch et al. 1989; Jaeckle 1994; Knott et al. 2003). Within 12-15 hours of separation from the primary larva, the secondary larva developed into a feeding bipinnaria. Bosch et al. (1989) found that after the clone was released, the primary larva either entered another clonal phase or resumed growth, differentiation, and eventual metamorphosis. In culture, Vickery and McClintock (2000) found that up to 24% of ochre star larvae fed a mixed algal diet developed secondary clonal larvae. Secondary clonal larvae were functionally and morphologically identical to primary larvae in the cultures (Vickery and McClintock 2000). Allen et al. (2019) reported the frequency of larval cloning in crown-of-thorns sea star cultures to be ~3-10%.

Three different modes of cloning in bipinnaria and brachiolaria larvae of asteroids have been documented: 1) autotomization (or self-amputation) of the preoral lobe; 2) paratomy of the posterolateral larval arms; and 3) budding of blastula or gastrula-like embryos from the larval body and apical tips of the arms (Jaeckle 1994; Mladenov 1996; Knott et al. 2003; Allen et al. 2018). According to Balser (2004, p. 5):

> Detachment of the clone from the parent larva occurs after the secondary individual develops to the gastrula or early bipinnaria stage. Clones that remain attached to the parent larva as early bipinnaria begin to independently feed prior to separation. After separation, the clone continues to develop and grow and has the potential, itself, to produce another generation of larvae by asexual reproduction. Larvae that clone are capable of metamorphosis and settlement to become the benthic juveniles.

Besides *P. helianthoides*, larval cloning has been observed in cultures of other sea stars in the Order Forcipulatida, including the ochre star (Vickery and McClintock 2000), *Distolasterias nipon* (Doderlein) (Kitazawa and Komatsu 2001), and *Asterias forbesi* (Desor) (Blackburn and Allen 2013). Since the initial descriptions of larval cloning in asteroids (Bosch et al. 1989; Rao et al. 1993), larval cloning has been reported in all echinoderm classes except the crinoids (Eaves and Palmer 2003; Balser 2004; McDonald and Vaughn 2010).

In a recent review of asexual reproduction in larval invertebrates, Allen et al. (2018, p. 75) tabulated the potential benefits of larval cloning as:

> 1. increases female fecundity without an apparent increase in resource allocation to reproduction;
> 2. may increase … the likelihood that a member of a genet survives;

3. may increase the probability that a member of a genet will locate a suitable settlement site by sampling a greater geographic area;
4. may reduce the genet's susceptibility to loss (i.e., predation) by increasing propagule number; and
5. may reduce the genet's susceptibility to loss (i.e., predation) by decreasing propagule size

On the other hand, Allen et al. (2018, p. 75) listed likely costs associated with larval cloning as:

1. a decrease in larval feeding rate;
2. a decrease in larval growth rate;
3. an increase in the time to metamorphosis (with potentially increased exposure to planktonic predators); and
4. a decrease in juvenile size.

Cloning in laboratory cultures of echinoderm larvae can be induced by providing an abundance of phytoplankton food (Vickery and McClintock 2000; MacDonald and Vaughn 2010; Allen et al. 2019) or exposure to fish mucus meant to simulate apparent predation pressure (Vaughn and Strathmann 2008; Vaughn 2010). Abiotic factors, such as temperature, may also increase the frequency of larval cloning (Vickery and McClintock 2000; Allen et al. 2018). Up to 24% of ochre star larvae reared at their optimal temperature of 12-15°C and given the highest concentrations of a mixed diet of phytoplankton grew to a larger size, produced clones, and produced significantly more clones than when subjected to lower temperature and food availability (Vickery and McClintock 2000). Larvae grown at 7-10°C produced no clones. Those fed on a monospecific phytoplankton diet produced far fewer clones than larvae fed a mixed diet (Vickery and McClintock 2000). These results led Vickery and McClintock (2000) to conclude that cloning was an adaptive mechanism to increase larval populations and leverage environmental conditions when they are most conducive to larval growth and survival.

Some researchers have postulated that echinoderm larvae clone in response to predation and have experimentally induced cloning in cultured larvae in the presence of fish mucus (Vaughan and Strathmann 2008; Vaughan 2010). Vaughn (2010, p. 1302) stated:

> Cloning under favorable conditions might be expected. The exploitation of an advantageous but ephemeral resource (food) through intensified reproduction makes good adaptive sense. The adaptive significance of larval cloning in response to predators is less obvious although possible advantages include (1) a rapid increase in the number of larval prey (safety in numbers hypothesis) and (2) a rapid reduction in larval size (prey-size selectivity hypothesis).

Larval cloning has the potential to alter several aspects of asteroid life history by increasing fecundity, larval dispersal distance, and chances of successful settlement of a larva or at least its genetically identical clone (Bosch et al. 1989; Balser 2004; Rogers-Bennett and Rogers 2008; Allen et al. 2019). Balser (2004) noted that cloning serves to increase female fecundity to >1 juvenile per egg, altering recruitment intensity. This lack of a one-to-one relationship between female productivity and realized recruitment potential complicates estimation of stock-recruit relationships without additional information about environmental impacts on cloning rate. Allen et al. (2019) emphasized that ignoring the impacts of planktonic cloning meant that both realized reproductive output and larval dispersal period had been underestimated in prior population modeling efforts for asteriids (Rogers-Bennett and Rogers 2008).

Asexual reproduction by larval cloning amplifies the number of individuals and increases the likelihood that at least one or more genetically identical representatives of the primary larva will survive to the next generation (Jaeckle 1994). The term teleplanic (meaning far-wandering: Scheltema 1971), has been applied to long-lived planktotrophic larvae that have the ability to disperse over great distances, even over ocean basins. Rogers-Bennett and Rogers (2008) suggested that larvae that have the ability to clone, perhaps multiple times, clearly fit this teleplanic dispersal model. Consequences of serial larval cloning and dispersion include the potential for population-level genetics to be homogenized, facilitating invasion (Rogers-Bennett and Rogers 2008), as well as accumulation of deleterious genetic traits, including those that could increase disease susceptibility. However, how ecologically significant cloned larvae are to overall population demography requires evidence that clones can successfully recruit to the population and, themselves, sexually reproduce (Allen et al. 2019). To date, evidence of the existence of sexually mature sea star individuals in wild populations that originated from cloned larvae is lacking for any species (Knott et al. 2003), including *P. helianthoides*. Thus, despite a demonstrated capacity to clone as larvae, estimates of female *P. helianthoides* fecundity considered in this report are limited to gross estimates of egg production on a seasonal basis.

2.3.3 Growth, Longevity, and Generation Time

No studies have been conducted to establish natural growth rates throughout the lifetime of *P. helianthoides*, due in part to the difficulty of tagging and effectively tracking individuals. The IUCN *P. helianthoides* assessment lists several observations of juvenile growth rates from anecdotal observations and laboratory studies as being between 3 and 8 cm/y, and 2 cm/y for mid-sized individuals (Gravem et al. 2021). Laboratory estimates may not be entirely representative of growth rates in the field because sea star growth is affected by water temperature and food availability (e.g., ochre stars [Gooding et al. 2009], *Acanthaster* spp. [Deaker et al. 2020; Dealer and Byrne 2022]). Sea star growth rate also generally decreases with increasing size of individuals (e.g., *Crossaster papposus* Carlson and Pfister 1999; *Archaster angulatus* Keesing 2017). Some sea stars can persist for long periods with little or no food (Nauen 1978; Deaker et al. 2020; Byrne et al. 2021), potentially complicating estimates of age based on size and resulting in episodic growth only when resources are adequate to exceed base metabolic needs.

Hodin et al. (2021) reared post-metamorphic, laboratory-cultured *P. helianthoides*. The fastest growing individuals were able to reach a diameter of three cm in 288 days (about 9.5 months) post-settlement (Hodin et al. 2021, their figure 10). Juvenile *P. helianthoides* reared by Hodin et al. (2021, their figure S4) grew slowly for several months after settlement, but grew faster after they reached about 10 cm in diameter, at which time they could feed on live juvenile bivalves.

In one of the few published reports of *P. helianthoides* growth under pseudonatural conditions, Miller (1995) described growth of juveniles found on settlement collectors on the Oregon coast. Miller (1995, p. 92–93) stated:

> Eleven red-orange juveniles survived during the first two weeks after sampling… These juveniles were observed to feed on partially crushed juvenile snails *(Lacuna* sp.,) and mussels (< 1 mm prey size) placed in the containers. By the third week after sampling, these juveniles captured and preyed upon juvenile snails and mussels. By 46 days after the sample date (age 47-61 days post settlement), all eleven juveniles had developed a sixth arm bud, indicating this species was *Pycnopodia helianthoides.* Juveniles were 2.10 mm mean AL [arm length] (range=1.53-2.55 mm) when the sixth arm formed. In all 11 juveniles the sixth arm formed on the interradius of the madreporite. At 63 days after sampling, juveniles were 3.65 mm mean AL (n=6). The three largest (3.85-4.62 mm AL) had buds for arms 7 and 8 on the interradii adjacent to the sixth arm. By 99 days after sampling (5-6 mm AL), arms 9 and 10 were forming adjacent to arms 7 and 8, on the interradii between arms 7 and 8 and the primary juvenile arms (not adjacent to arm 6). At three months (5-6 mm AL), *Pycnopodia helianthoides* also fed on lab-reared juvenile sea urchins *(Strongylocentrotus purpuratus* and *S. franciscanus)* at 1-3 mm test diameter.

These juvenile *P. helianthoides* grew from a mean arm length (AL) of 0.41 mm at sampling, to a mean AL of 3.65 mm at 63 days, and 5–6 mm AL at 99 days. Thus, juveniles increased in size by a factor of nearly nine times after two months and up to 14 times after three months from sampling (Miller 1995).

In response to the call for public comments on our 90-day finding for the petition to list sunflower sea stars under the ESA (86 FR 73230), a dataset demonstrating growth of putative cohorts of juvenile sunflower sea stars was submitted for Holmes Harbor on the east side of Whidbey Island, in the Southern Salish Sea, Washington (K. Collins, pers comm.). During repeated SCUBA-based sampling of the size distribution of populations of *P. helianthoides* at several index sites between March of 2020 and 2022, recruitment pulses of individuals could be identified from frequency of occurrence data. Between March of 2020 and March of 2021, the average diameter of one such group of juvenile sunflower sea stars increased 7.99 cm, from ~9-17 cm. This annual growth rate aligns with the rapid growth period identified by Hodin et al.

(2021), concomitant with the ability to consume small bivalves. While this estimate is for one small population in the Salish Sea and is cohort-based rather than tracking target individuals, it provides insight into the growth of juvenile *P. helianthoides* that is not available elsewhere.

The longevity of *P. helianthoides* in the wild is unknown, as is the age at first reproduction and the period over which a mature individual is capable of reproducing, but these parameters are needed to calculate generation time. It is also unknown if, or how much, any of these crucial life history parameters vary across the range of the species. The 2020 International Union for Conservation of Nature (IUCN) assessment for the sunflower sea star used a generic echinoderm equation to estimate generation times as 20.5-65 years or 27-37 years, depending on maximum longevity (reaching maximum size observed of 95-100 cm diameter) or more typical longevity (time to reach 50 cm diameter) estimated from two different growth models (Gravem et al. 2021). These generation time figures utilized an estimated age at first reproduction of 5 years, based on the ochre star and other species, as this information is not available for *P. helianthoides* (Gravem et al. 2021). In the absence of adequate species-specific data, we find that an estimated generation time of at least 30 years is tenable and employ it in our assessment of extinction risk below.

2.4 Diet and Foraging Behavior

Larval and pre-metamorphic *P. helianthoides* are planktonic feeders and no data exist to suggest a prey preference at this stage. The diet of adult *P. helianthoides* generally consists of benthic and mobile epibenthic invertebrates, including sea urchins, snails, crab, sea cucumbers, and other sea stars (Mauzey et al. 1968; Shivji et al. 1983), and appears to be driven largely by prey availability. Sea urchins were the major dietary component in the intertidal along the outer coast of Washington in a study by Mauzey et al. (1968). Sea urchins are ingested whole and egested after digestion (Mauzey et al. 1968). For *P. helianthoides* inhabiting kelp forests in central California, however, 79% of the diet was gastropods, and only four sea urchins were found in the gut contents of 41 adults (Herrlinger 1983). *Pycnopodia helianthoides* also feeds on sessile invertebrates, such as barnacles and various bivalves (Mauzey et al. 1968). Mussels are a common prey of *P. helianthoides* feeding in intertidal regions in Alaska (Paul and Feder 1975). Clams can also constitute a major proportion of their diet, with up to 72% coming from clams at subtidal sites within Puget Sound (Mauzey et al. 1968). Adult *P. helianthoides* excavate clams from soft or mixed-substrate bottoms by digging with one or more arms (Smith 1961; Mauzey et al. 1968) (Figure 3). Foraging pits are left behind, which can be difficult to distinguish from those made by sea otters (Traiger et al. 2016). *Pycnopodia helianthoides* also scavenge fish, seabirds, and octopus (Shivji et al. 1983). *Pycnopodia helianthoides* locate their prey by chemosensing and may show preference for dead or damaged prey (Brewer and Konar 2005), likely due to reduced energy expenditure associated with catching and subduing active prey.

Figure 3. A sunflower sea star (*Pycnopodia helianthoides*) digging for clams in a mixed substrate habitat in Alaska. Photo: Sarah Traiger.

2.5 Social Behaviors

Pycnopodia helianthoides are broadcast spawners that require close proximity to mates for successful fertilization (Morris et al. 1980; Lambert 2000; Lundquist and Botsford 2004; Hodin et al. 2021). While individuals are generally considered solitary, documentation of seasonal, patchy distribution suggests that individuals aggregate to spawn (Mauzey et al. 1968; Gravem et al. 2021). Though reproductive seasonality is largely undocumented, localized studies have observed breeding or reported females with ripe ovaries from December through July (Morris et al. 1980; O'Clair and O'Clair 1998; Gravem et al. 2021), and broad geographic variation linked with water temperature and other environmental factors is likely. When spawning, individuals have been documented to adopt a domed posture, standing on the tips of their rays, presumably to enhance gamete dispersal (see section 2.3.1.3.1 Aggregation and Spawning Behavior).

Sunflower sea stars are voracious predators and will compete with both conspecifics and other sea star species directly for prey, including direct theft (O'Clair and O'Clair 1998). O'Clair and O'Clair (1998) report adult sunflower stars flailing at one another with their tube feet agonistically upon meeting, before eventually moving apart.

3. DISTRIBUTION AND ABUNDANCE

3.1 Historical Population Size and Population Trends

Prior to the onset of a coast-wide sea star wasting syndrome (SSWS) pandemic in 2013 (see below and section 5.3 Competition, Disease, or Predation), directed population monitoring for *P. helianthoides* was haphazard and typically the result of short-term research projects rather than long-term monitoring programs. Such efforts were rarely focused on the sea star itself, but it was often included as one component of the local invertebrate assemblage, and generally secondary to the primary species of interest. While indigenous peoples of the West Coast of North America have known of *P. helianthoides* since time immemorial, we could find no oral histories or other traditional ecological knowledge that aided in our understanding of long-term population distribution or abundance. In response to our 90-day finding on the petition to list *P. helianthoides* (86 FR 73230) several First Nation and tribal entities reached out to provide recent monitoring data, some of which was integrated into our population viability analysis (section 3.4 Species Status Assessment). Several of the data sets lacked pre-pandemic occurrence records, however, and could not be used to evaluate declines in abundance or density relative to appropriate baseline values.

Recent descriptions of *P. helianthoides* distribution and population declines by Harvell et al. (2019), Gravem et al. (2021), and Hamilton et al. (2021) relied on datasets gathered either exclusively or predominantly during the 21st century and, in some cases, as a direct response to losses due to SSWS. The most intensive of these losses occurred over just a few years from 2013-17, generally commencing later in more northern portions of the range, and impacts varied by region. Hence, our understanding of the historical abundance of *P. helianthoides* is patchy in both time and space, with substantial gaps.

Summary data presented in Gravem et al. (2021) indicate that prior to the 2013-17 SSWS outbreak *P. helianthoides* was fairly common throughout its range, with localized variation linked to prey availability and various physiochemical variables. Starting in 2012, Konar et al. (2019) assessed rocky intertidal populations in the Gulf of Alaska and described *P. helianthoides* prior to the 2016 wasting outbreak as “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). Abundances varied geographically in Alaska: infrequent in Kachemak Bay (<0.005 m^2); fairly common in the Kenai Fjords National Park (~0.075/m^2); and quite common in western Prince William Sound (average 0.233/m^2) (Konar et al. 2019). In subtidal rocky reefs near Torch Bay, southeast Alaska, densities were high (0.09±0.055/m^2) in the 1980s (Duggins 1983). In Howe Sound, near Vancouver, British Columbia, densities were high at 0.43±0.76/m^2 in 2009-10 before the SSWS pandemic (Schultz et al. 2016). Montecino-LaTorre et al. (2016) found that *P. helianthoides* abundance averaged 6-14 individuals per roving diver survey throughout much of the Salish Sea from 2006-13. In deep water habitats off the coasts of Washington, Oregon, and California, 2004-14 pre-outbreak biomass averaged 3.11, 1.73, and 2.78 kg/10 ha, respectively (Harvell et al. 2019). In 2019, a remotely operated vehicle survey of the Juan de Fuca Canyon encountered a number of large *P. helianthoides* at depths ranging from 150-350 m (OCNMS 2019). While population connections between these sea stars and those in shallow water remain unknown, this suggests that deep waters may serve as a biomass reservoir for the species (J. Waddell, pers. comm.).

Along the north and central California coastline, average population densities were 0.01-0.12/m^2 prior to 2013 (Rogers-Bennett and Catton 2019). The oldest density records come from kelp forests near central California in Monterey Bay, where densities were 0.03/m^2 in 1980-81 (Herrlinger 1983). More recently in central California, densities of *P. helianthoides* were even lower and fluctuated from 0.01-0.02/m^2 between 1999 and 2011 (Smith et al. 2021). In southern California, sites in the Channel Islands have been studied extensively, and from 1982-2014 *P. helianthoides* densities ranged from 0-0.25/m^2 (Bonaviri et al. 2017), from 1996-98 they were 0-0.02 m^2 (Eckert 2007), from 2003-07 they were 0-0.07m^2 (Rassweiler et al. 2010), and from 2010-12 they were ~0.10-0.14/m^2 (Eisaguirre et al. 2020).

The pattern of decline by latitude is striking. Hamilton et al. (2021) noted a 94.3% decline throughout the range of *P. helianthoides* after the outbreak of SSWS. The 12 regions defined by Hamilton et al. (2021) encompass the known range of *P. helianthoides* and each region exhibited a decline in density and occurrence, with the six more northern regions declining less (40-96% declines) than the six regions south of the Washington outer coast, where *P. helianthoides* is locally exceptionally rare (99.6-100% declines). Further, while anecdotal observations indicate *P. helianthoides* recruitment continues in the U.S. portion of the Salish Sea, British Columbia, and Alaska, few of these juveniles appear to survive to adulthood (A. Gehman, personal communication). We are not aware of any observations of *P. helianthoides* recruits or adults in California or Mexico since 2017.

3.2 Population Structure

There are not, to date, any range-wide or regional assessments of systematic variation in life history parameters, morphological characteristics, genetic traits, or other attributes that can be used to delineate specific populations of *P. helianthoides*. As such, we have no direct biological data to establish that *P. helianthoides* is anything but a single, panmictic population throughout its range. As habitat generalists that use a wide variety of substrates over a broad depth range, and dietary generalists that consume diverse prey based largely on their availability and encounter rate, differentiation of subpopulations is not expected to be driven by strong selection for particular environmental needs. In the 2020 IUCN status assessment report (Gravem et al. 2021), putative population segments were identified largely based on a combination of legal boundaries and data availability across a wide variety of voluntarily shared monitoring efforts.

As relatively sessile, benthic organisms in the settled juvenile through adult life stages, the overwhelming majority of population structuring events would be determined during the pelagic larval phase. This is a common feature of broadcast spawning, benthic, marine organisms and these groups typically exhibit partitioning based upon strong biogeographic features (i.e., Queen Charlotte Sound, Point Conception). Within these biogeographic regions such organisms typically exhibit either genetic homogeneity for species with prolonged pelagic larval phases or, for species with shorter pelagic larval duration, a stepping-stone dispersal resulting in isolation-by-distance. Within the historical range of *P. helianthoides*, there are two major biogeographic regions (Longhurst 2007), the "Alaska Coastal Downwelling Province" and the "California Current Province." These regions are essentially formed by the bifurcation of the North Pacific Current into the northward-flowing Alaska Current and the southward-flowing California Current. This bifurcation occurs in the vicinity of Vancouver Island, though the exact location varies with shifting climatic conditions and bulk water transport processes, with a transition zone between Queen Charlotte Sound and Cape Flattery (Cummins and Freeland 2007).

For some echinoderm species that have been more thoroughly examined, regional variation in phenotypic and genetic traits along the west coast of North America have been documented. Bat stars (*Patiria miniat*a) largely overlap with *P. helianthoides* in geographic range and depth distribution, and share similar planktonic larval duration, so can potentially be used as a proxy to make demographic inferences. Keever et al. (2009) used a combination of mitochondrial and nuclear markers to study bat stars range-wide and provided support for two genetically distinct populations, essentially split across Longhurst's (2007) biogeographic provinces. Within the California Current Province there was little detectable genetic structure, but within the Alaska Coastal Downwelling Province there was a high degree of structure, potentially as a consequence of marked differences in geographic complexity between the two regions. Gene flow simulations showed that larvae of the bat star don't disperse far despite a relatively long pelagic larval duration (Sunday et al. 2014). The red sea urchin (*Strongylocentrotus franciscanus*) also overlaps in range, depth, and planktonic dispersal with *P. helianthoides* but shows no clear signal of genetic partitioning (Debenham et al. 2000) throughout its range. Similarly, the ochre star shares these same life history parameters and exhibits no genetic partitioning (Harley et al. 2006). Overall, the lack of demonstrated genetic structure in these echinoderm proxy populations suggests that *P. helianthoides* are likely genetically homogeneous throughout their range, though there remains a possibility that some structure could exist between populations across the two biogeographic provinces.

3.3 Description of Fisheries Interactions

There are no commercial, and few directed personal use, fisheries for *P. helianthoides*, and small individuals may occasionally be collected, dried, and sold as decorative curios (Gravem et al. 2021). In Alaska (https://www.adfg.alaska.gov/index.cfm?adfg=viewing.tidepooling), Washington (https://www.eregulations.com/washington/fishing/shellfish-seaweed-species-rules), and Oregon (https://www.eregulations.com/oregon/fishing/marine-zone) harvest of *P. helianthoides* is not allowed under current recreation or personal use fishing regulations. Collection for *bona fide* scientific purposes or educational display requires an Aquatic Resources, Scientific Collection, or Scientific Take Permit, depending on the jurisdiction (https://www.adfg.alaska.gov/index.cfm?adfg=otherlicense.aquatic_resource; https://wdfw.wa.gov/licenses/environmental/scientific-collection;

https://www.dfw.state.or.us/fish/license_permits_apps/scientific_taking_permit.asp). In British Columbia personal use harvest of sea stars is allowed, by hand collection only, from all marine waters where harvest is not otherwise restricted (e.g., marine protected areas) (https://www.pac.dfo-mpo.gc.ca/fm-gp/rec/tidal-maree/a-s17-eng.html), and scientific collection requires a Scientific License (https://www.pac.dfo-mpo.gc.ca/fm-gp/licence-permis/scientific-scientifique-eng.html). In California, collection of sea stars is not allowed from the high tide mark to 1000 ft. seaward of the low tide mark, and harvest outside the exclusion area must occur while freediving (https://wildlife.ca.gov/Fishing/Ocean/Regulations/Sport-Fishing/Invertebrate-Fishing-Regs). Scientific collection is regulated similar to other jurisdictions on the West Coast and requires a permit (https://wildlife.ca.gov/Licensing/Scientific-Collecting). Estimates are not available of how many sea stars are taken annually in British Columbia or California, in aggregate or by species.

Lethal and non-lethal bycatch both occur in a variety of recreational, artisanal, and commercial fisheries, however. These include fisheries for: finfishes (e.g., rockfish, flounder, sole, and codfish) using moderately selective pots/traps and poorly selective hook-and-line, trawl, and seine gear; crustaceans (e.g., shrimp, lobster, and crab) using moderately selective gear such as pots/traps, ring nets, and castable snares; and other marine invertebrates (e.g., scallop, sea cucumber, urchin) using poorly selective dredges and trawls. The broad use of diverse habitats by *P. helianthoides*, in addition to its high mobility and voracious appetite, means that any marine fishery operating in West Coast waters shallower than 500 m and employing relatively non-selective gear and/or bait will interact with the species to some degree. Much bycatch goes unreported, however, because animals are simply removed from the gear and discarded at sea without being logged in any way. When data are recorded, often by at-sea observers or dockside samplers rather than the fishers themselves, information for all sea stars is often aggregated to reporting categories such as “sea star, general” or “sea star, unidentified,” making species-specific evaluations of spatiotemporal bycatch patterns impossible. Furthermore, we could find no field studies where the post-release condition of *P. helianthoides* was assessed across a variety of gear types, or even a single gear type, used in West Coast fisheries.

The sunflower sea star is, generally speaking, capable of tolerating handling during regular fishing operations, such as removal from a crab pot or shrimp trap, or even capture in a benthic trawl net. While the soft body structure and numerous rays may make disentanglement from some gear types challenging (Gravem et al. 2021), individuals are well documented to regenerate rays after autotomy and/or injury in nature (see section 2.3.2.1 Adult Autotomy and Fission), strongly suggesting that recovery from handling stress is probable. Whether stress associated with such handling might increase short- or long-term susceptibility to SSWS and/or compromise reproductive potential is unknown and will require systematic evaluation to clarify proximate and ultimate causes.

3.4 Species Status Assessment

3.4.1 Prior Work

There are two prior status assessments of *P. helianthoides*, both of them very recent, that investigate its response to SSWS and evaluate current condition range-wide from the Aleutian Islands to Baja California: Gravem et al. (2021, the IUCN Red List Report) and Hamilton et al. (2021).

In 2020, the IUCN conducted the first ever status assessment for *P. helianthoides* throughout its range (Gravem et al. 2021). Estimates of population size were based on mean density in various regions and the availability of habitat. Data sources included a variety of stand-alone ecosystem monitoring efforts that regularly encounter *P. helianthoides*, many of them SCUBA-based, with several geographic regions having sparse spatiotemporal coverage. The IUCN assessment concluded that the status of the sunflower sea star on a range-wide basis was Critically Endangered, citing a >90% loss in overall abundance since 2013, largely as a direct consequence of the SSWS pandemic (Gravem et al. 2021). Additionally, Hamilton et al. (2021) used logistic models (general linear model with binomial errors and logit links) and presence-absence data to estimate the timing and extent of the decline in occurrence among the 12 regions used in the IUSC assessment. Range-wide occurrence declined by 52.3%, with more severe declines of 92.2% in occurrence from Oregon southward to Mexico. Where density data were available, Hamilton et al. (2021) also used zero-inflated generalized linear models (with Poisson errors and log-link) to estimate the change in density among regions and between phases (pre- and post-SSWS). Density declined by 99.2% from Baja California to the Washington coast, while declines were slightly lower (but greater than 87.8%) in regions from British Columbia through the Aleutian Islands.

3.4.2 Population Viability Analysis (PVA): Multivariate Autoregressive State Space Models (MARSS)

The population viability analysis (PVA) presented here used multivariate autoregressive state space (MARSS) models (Holmes et al. 2020; Tolimieri et al. 2017) to build upon and temporally expand the assessments of Gravem et al. (2021) and Hamilton et al. (2021) by analyzing population trends of *P. helianthoides* prior to and following the onset of SSWS. That is, in the MARSS analyses, separate estimates of population growth rate were obtained for the period prior to and after the onset of SSWS in 2013 for three major regions: Alaska; British Columbia and the Salish Sea; and the West Coast (from Washington to Baja California). These three regions were chosen based on the results of model comparisons of multiple models evaluating different regional scenarios (see Appendix A for complete details of all models).

MARSS models are a common form of count-based (or density-based) PVA and have a number of benefits. In MARSS, one can incorporate multiple time series to estimate a state process (i.e., population trend or population trajectory). There can be one state process or multiple; for example, all time series might follow the same trajectory from Alaska to Baja California, or different regions (and different data sources) may follow different trajectories and represent alternative states. Additionally, these state processes can have the same or different rates of population growth. Importantly, one can also separate process variance (i.e., biological variation in population size around the longer-term abundance trend) from observation variance (i.e., that due to sampling error), which may also be the same or differ among states. The estimates of population growth rate and process variance can then be used to calculate extinction risk, typically defined as the probability that population size will drop below some predetermined threshold (Dennis et al. 1991; Holmes et al. 2020). MARSS models are adept at handling multiple data sources with different characteristics (e.g., methodologies), time series with missing data and of different length, and incorporating space (here, region). More detail on the utility and construction of MARSS models is given in Appendix A.

As part of the IUCN status assessment process, Gravem et al. (2021) contacted a broad array of government, non-government, academic, and private data holders engaged in both direct and indirect monitoring of *P. helianthoides* occurrence, abundance, density, and habitat use throughout the range of the species. After careful evaluation of the temporal span, accuracy, taxonomic resolution, and verifiability of this suite of data sources, they identified 31 data sets that met minimum criteria for use in describing abundance trends over time (their Figure 1 and Table 1).

The majority of data used in the MARSS analyses here were originally compiled by Hamilton et al. (2021) and Gravem et al. (2021). However, many of the time series in the IUCN data set contain only presence/absence data. These presence/absence data sets were not used in the present analyses because they can only inform estimates of population trend, rather than providing an objective metric of abundance. The remaining data sets that contained density information were assessed for use in the MARSS analyses. The data sets were of varying length and sampling frequency. Data sets with fewer than five (5) years of observations were eliminated from that analysis, as were two data sets that contained only pre-SSWS information from well before the recent time period. One data set was removed and replaced with updated information. For the remaining data sets, we reached out to data providers to obtain any new data collected since submittal to the IUCN assessors. As a result of the global COVID-19 pandemic, few updates were available. Because MARSS can incorporate time series with different methodological approaches, several new data sets obtained in response to the international data call in the 90-day petition finding (86 R 73230), or through NMFS staff, were added. These data sets are explored and evaluated more thoroughly in Appendix A.

While MARSS can use “gappy” data with missing observations and time series of different lengths, the data do need to be in a time-series format. For some data sets, the data were summarized to produce time series. For example, data from the West Coast Groundfish Bottom

Trawl Survey (WCGBTS), which come from a depth-stratified random sampling design, were averaged within latitude and depth bins for each year to create a times series for that bin.

See Appendix A: Population viability analysis of *Pycnopodia helianthoides* for a more complete examination of the data, MARSS model structures, and detailed results of the PVA analysis.

3.4.2.1 Model Comparison and Selection

Numerous models were compared to evaluate data support for multiple different hypotheses about the spatial structure of *P. helianthoides* population trends (states) and population growth rates (Appendix A). All models included a time-varying component, with a pre-2013 and post-2013 estimate to account for the rapid decline resulting from the SSWS pandemic. The focus of model comparisons was to identify the appropriate regional scale of *P. helianthoides* population dynamics and several regional configurations were tested:

- A single range-wide region
- Three regions: Alaska, British Columbia & the Salish Sea, and the West Coast
- Four regions: Alaska, British Columbia, the Salish Sea, and the West Coast
- Eleven regions: west Gulf of Alaska, east Gulf of Alaska, southeast Alaska, British Columbia, Salish Sea, Washington, Oregon, Northern California, Central California, Southern California, and Baja California (to coincide with regions used in the IUCN assessment [Gravem et al. 2021])

Model comparisons also evaluated evidence for a single population growth rate across all regions or separate growth rates for each region. In addition, comparisons also evaluated shared or separate state processes for different data sources within regions and for shared or different process variance among data sources within regions.

Model selection was based on Akiake's Information Criterion for small sample sizes (AICc) (Burnham and Anderson 2002) and the total number of parameters. Models with AICc were considered candidate models, and the model with the fewest parameters and an AICc was considered the best-fit model. See Appendix A for a more complete description of the models run and results.

For the primary model selection exercise, zeros in the time series were replaced with NAs, which is not uncommon for MARSS (Tolimieri et al. 2017; Holmes et al. 2020). Retaining the zero (0) observation asserts that there were no *P. helianthoides* present, while they may just have been at such a low density that the survey method failed to observe them given sampling effort. Setting the zeros to NA allows the model to estimate those values through the use of a Kalman filter. However, using the NAs may underestimate the rate of decline, especially in cases where there are large numbers of zeros in the latter portion of the time series. Therefore, replacing zeros with some other small value was also investigated for the best-fit model (hereafter, best-fit w/NA or best-fit w/min) and region-specific models, which included only data for one of the three major regions. Zeros were replaced with a small number (0.1% of the pre-2013 mean of the time series) to allow data to be log transformed.

3.4.2.2 MARSS Results

The best-fit model from the primary MARSS model comparisons had the most data support for different population growth rates for three major regions: Alaska; British Columbia and the Salish Sea; and the West Coast from coastal Washington to Baja California. This was the only model with a $\Delta AICc \leq 2.0$. Below, this is referred to as the "best-fit w/NA" model. The second-best model had an AICc value 8.39 points higher and provided some weak data support for splitting British Columbia and the Salish Sea; this model also included separate rates of population growth for each of the four regions in the model.

For the West Coast and combined British Columbia and the Salish Sea region, *P. helianthoides* population growth rate was positive during the period prior to the onset of SSWS (pre-2013) at 1.7% (u=0.017) and 9.4% (u=0.09) (Table 1). Post 2013, West Coast populations declined rapidly at 25.8% (-0.299) per year. The rate of decline in British Columbia and the Salish Sea was somewhat less, but still substantial at 14.1% (-0.151) per year.

The results for Alaska from this best-fit model should be interpreted cautiously, at least for the pre-2013 period. The model estimated a decline in *P. helianthoides* abundance in the pre-SSWS period of 19% per year (-0.21) and an incredibly steep decline in the post-SSWS period from 2013-21 of 91.6% per year (-2.475). However, there are scant time-series data in the pre-2013 period, and the Konar_Intertidal_AK data set was the only one with both pre-2013 information (back to 2005) and post-2013 information (Figure 4, and Appendix A Figure A3.10). Observation error balloons in the pre-2013 period for CACS_Intertidal_AK data set (Appendix A Figure A4.3), and the process variance for the CACS_Intertidal_AK data set is large (Appendix A Table A4.3), which suggests that the model is struggling to fit this time series. Moreover, it is this time series in that state that is driving the negative trend during the pre-2013 period, without any data supporting that negative trend (Appendix A Figure A4.3). Estimates for this period in Alaska in the best-fit model are likely being driven by low data availability, as well as low process and observation variance coming in from data sharing from the rest of the data.

Table 1. Summarized estimates of population growth rate, annual rate of change, percent decline since 2013 for the West Coast region from four models. The best-fit modes included data for the entire range with zeros replaced either by NAs or by minimum values (see Appendix A). Regional-only models contain only data for that region. Best-fit w/NA is the top model from the primary model comparison. U1 = pre-2013 growth rate, U2 = post-2013 growth rate.

Region	Model	U1	Pre-2013 annual %	U2	Post-2013 annual %	% decline since 2013
Alaska	Best-fit w/NA	-0.210	-19.0	-2.475	-91.6	100.0
	Best-fit w/min	-0.069	-6.6	-1.447	-76.5	100.0
	AK only w/NA	0.207	23.0	-0.182	-16.7	80.6
	AK only w/min	0.374	45.3	-1.017	-63.8	100.0
BC & SS	Best-fit w/NA	0.090	9.4	-0.151	-14.1	74.4
	Best-fit w/min	0.129	13.8	-0.384	-31.9	96.8
	BC only w/NA	0.005	0.5	-0.142	-13.2	72.0
	BC only w/min	-0.017	-1.7	-0.271	-23.7	91.3
West Coast	Best-fit w/NA	0.017	1.7	-0.299	-25.8	93.2
	Best-fit w/min	-0.021	-2.1	-0.246	-21.8	89.1
	WC w/NA	0.056	5.8	-0.465	-37.2	98.5
	WC w/min	0.013	1.3	-0.260	-22.9	90.3

Running a similar MARSS model but including only data for Alaska produces more reasonable results (Table 1) with positive rates of change prior to 2013 being driven by the Konar data set (Figure 4a). Replacing zeros with a small value resulted in a steeper decline after 2013 but this model was unable to estimate process variance (Appendix A Table A4.6, Figure 4b).

For completeness, similar models were run for the other two regions and for all regions with the zeros replaced by NAs or by minimum values (Table 1, Figures 4b, 5, 6).

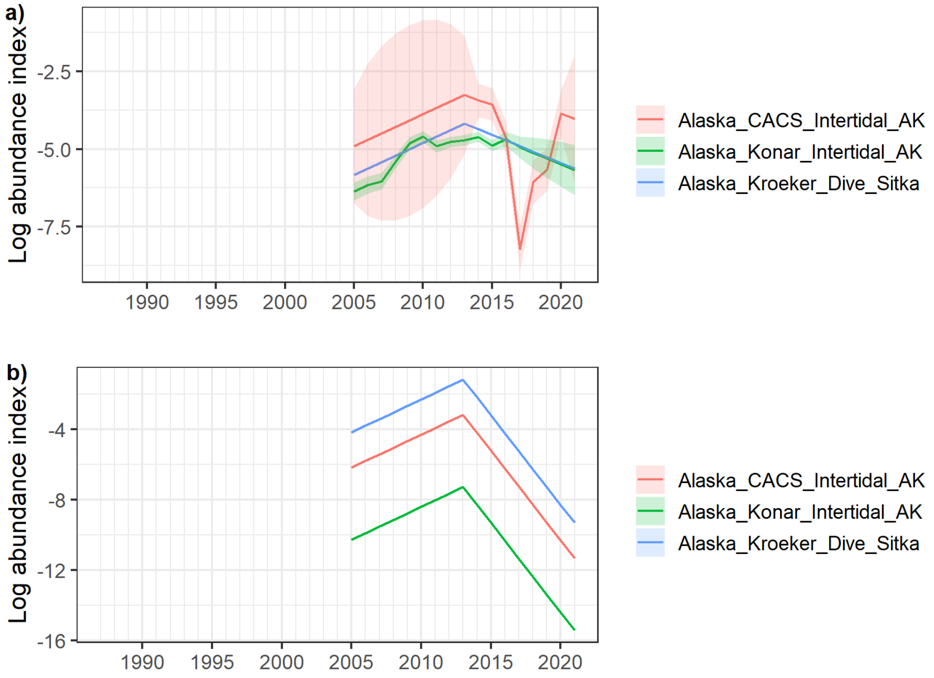

Figure 4. Log abundance index of *P. helianthoides* abundance in Alaska from 2005-21 based on MARSS analysis using only Alaska data. Error envelopes indicate one standard error. a) results from the model with zeros replaced by NAs; b) results from the model with zeros replaced by a minimum value. Note, the inflated errors in some time series (pre-1999) occur because there are no data for that time series in that time period.

Results for British Columbia and the Salish Sea were similar to those for the best-fit models (Table 1, Figures 5 and 6). The models with zeros replaced by NAs estimated a 72-74% decline since 2013, while the alternate models estimated over a 92% decline (Table 1). However, for the BC-only w/NA model, process variance exploded (Appendix A Table A4.5). This increase in process variance comes from the model trying to fit large fluctuations in abundance (caused by the replacement of zeros with low values instead of NA) that would otherwise have been ‘interpolated’ by the Kalman filter.

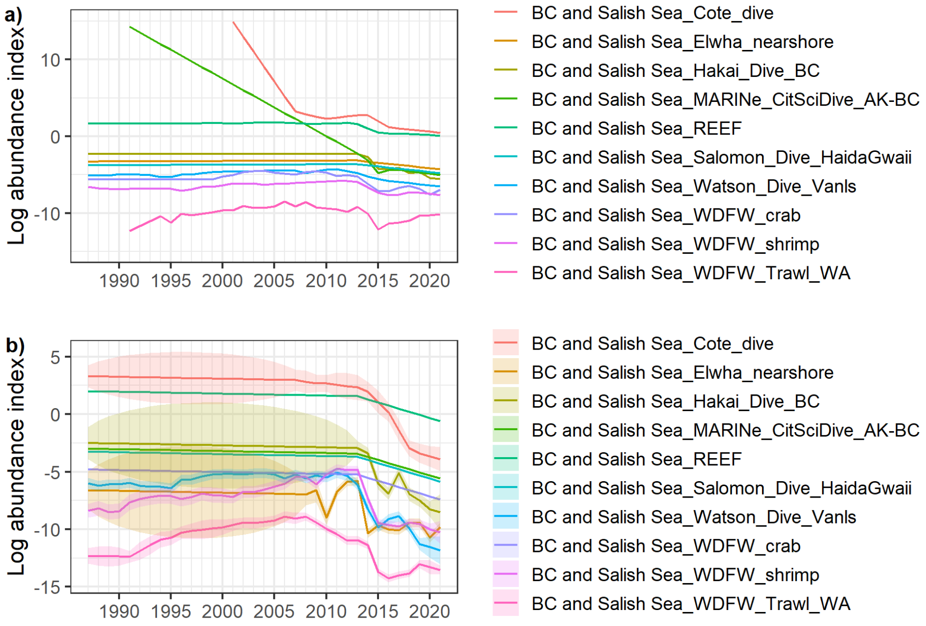

Figure 5. Log abundance index of *P. helianthoides* abundance in British Columbia and the Salish Sea from 1987-2021 based on MARSS analysis using only British Columbia and the Salish Sea data. Error envelopes indicate one standard error. a) results from the model with zeros replaced by NAs, b) results from the model with zeros replaced by a minimum value. Note, the inflated errors in some time series (pre-1999) occur because there are no data for that time series in that time period. Error envelopes are not plotted in a) because they are extremely large.

West Coast region only models were similar to their best-fit versions (Table 1), although the rate of post-2013 population decline was higher in the WC-only w/NA model than in the best-fit w/NA, a 99% versus 93% decline since 2013. Process variance exploded in the WC-only w/min model.

Interestingly, for the West Coast replacing zeros with minimum values instead of NAs lead to lower rates of population decline after 2013 for both the full models and the region-specific ones (less negative, Table 1). The same was true for Alaska in the full models; however, in other cases replacing the zeros with small values resulted in higher rates of decline. Additionally, replacing NAs with minimum values lead to substantial increases in observational variance in many cases (Appendix A. Population viability analysis of *Pycnopodia helianthoides*), again caused by forcing the model to fit a more variable time series.

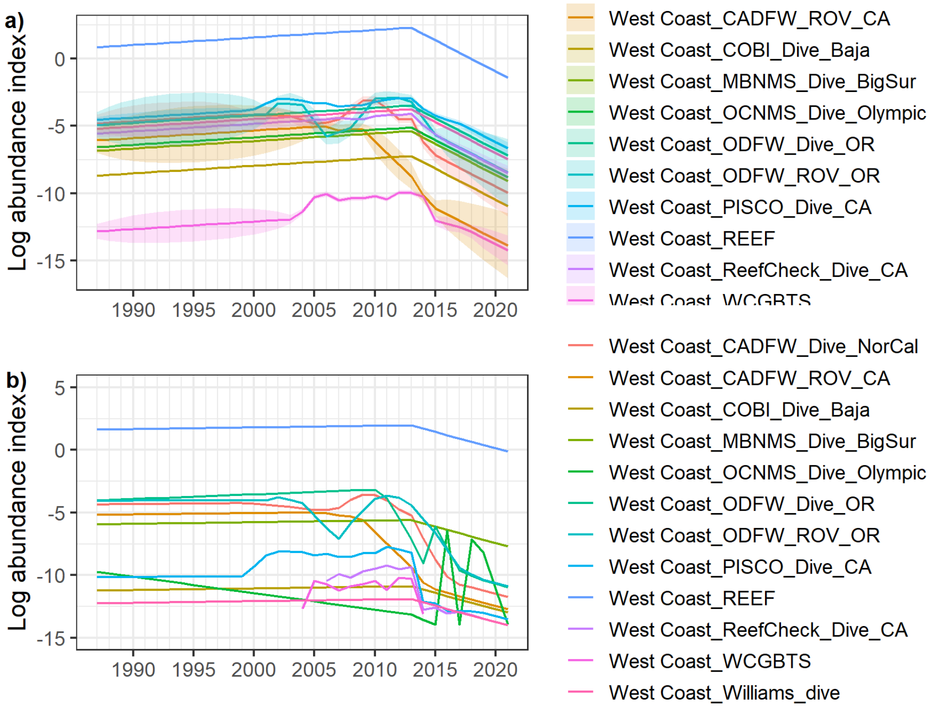

Figure 6. Log abundance index of *P. helianthoides* abundance on the West Coast from 1987-2021 based on MARSS analysis using only West Coast data. Error envelopes indicate one standard error. a) results from the model with zeros replaced by NAs, b) results from the model with zeros replaced by a minimum value. Note, the inflated errors in some time series (pre-1999) occur because there are no data for that time series in that time period. Error envelopes are not plotted in b) because they are extremely large.

3.4.2.3 Extinction Risk

Estimating both the population growth rate and process variance allows one to calculate extinction risk (Dennis et al., 1991), which is usually defined as the probability that a population will drop below some predetermined threshold (other than zero). Here, the threshold was set to 1% of the population size in 2013 (see Appendix A. Population viability analysis of *Pycnopodia helianthoides*). Models with identified problems, with inflated process variance, or that failed to estimate process variance were not included.

Using post-2013 growth rates, which are all negative, assumes that population growth remains negative into the future because of continuing SSWS impacts and, potentially, Allee effects resulting from extremely low local population size (Lundquist and Botsford 2004; 2011. Under these conditions, the risk of declining below 1% of the 2013 population size is essentially 100% and the only question is how quickly that threshold is reached. An alternative scenario is that the effects of SSWS abate, Allee effects are negligible, and *P. helianthoides* populations begin to grow at annual rates seen prior to 2013. Both scenarios are presented here for each region for all four model results for that region by estimating extinction risk based on both the pre-2013 and post-2013 estimates of population growth for each region.

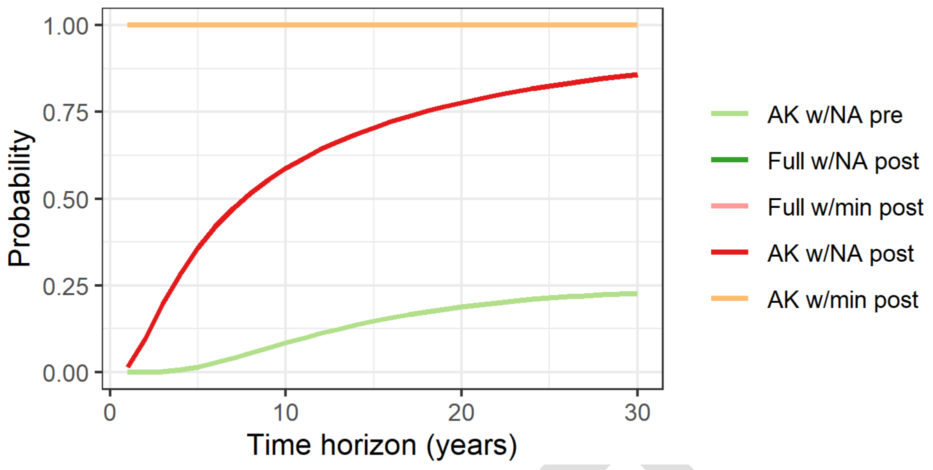

Figure 7. Extinction risk for *P. helianthoides* in the Alaska region from four models. The Full models the best-fit model with zeros replaced by NAs or minimum values. The AK only models include only the AK data. Estimates are presented using either the pre-2013 or post-2013 population growth rate. This risk is the probability that the population size will drop below a threshold 1% of its value in 2013. Results are not shown for two models due to a lack of spatiotemporal coverage that prevented the models from resolving.

The question of whether SSWS ceases to have strong impacts on *P. helianthoides* population growth rates is central to evaluating the realized risk of extinction. All of the models here suggest there is a high risk that *P. helianthoides* populations will drop below 1% of their 2013 sizes if SSWS does not abate and population growth continues to be negative (Figures 7-9); this result is hardly surprising given the projected continued population decline from assuming post-2013 rates of change.

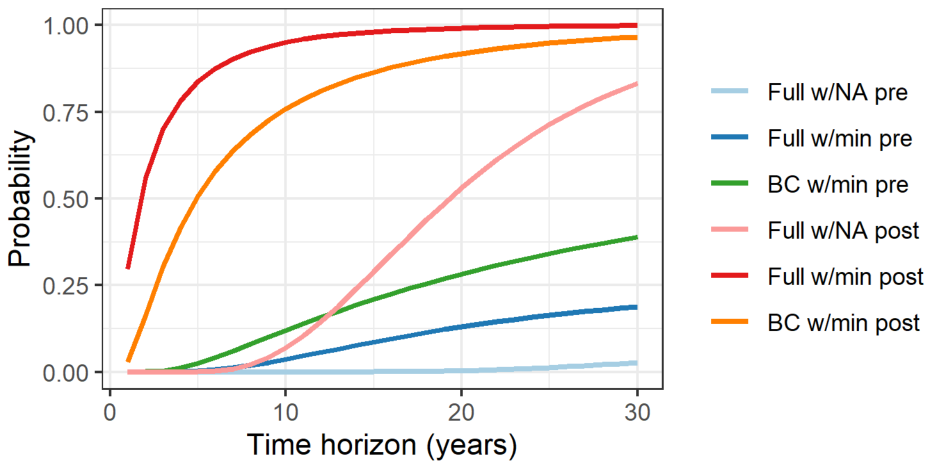

Figure 8. Extinction risk for *P. helianthoides* in the combined British Columbia and Salish Sea region from four models. The Full models the best-fit model with zeros replaced by NAs or minimum values. The BC-only models include only the time series from British Columbia and the Salish Sea. Estimates are presented using either the pre-2013 or post-2013 population growth rate. The risk is the probability that the population size will drop below a threshold 1% of its value in 2013.

Should SSWS abate, and in the absence of strong Allee effects, populations appear likely to recover if growth rates return to pre-2013 levels. As discussed above (section 2.3 Reproduction, Growth, and Longevity), information on *P. helianthoides* reproductive biology is limited, but the species is likely similar to other echinoderms that exhibit boom-bust population dynamics and recovery could occur quickly under favorable conditions. However, the time series show little to any signs of recovery in recent years, suggesting that post-2013 population declines may continue into the future. The exception is the REEF data for the Salish Sea, which show a small, persistent increase for Canadian waters and observations above zero in US waters (Appendix A Figure A3.23). Most other time series remained at zero individuals post-crash with no sign of recovery.

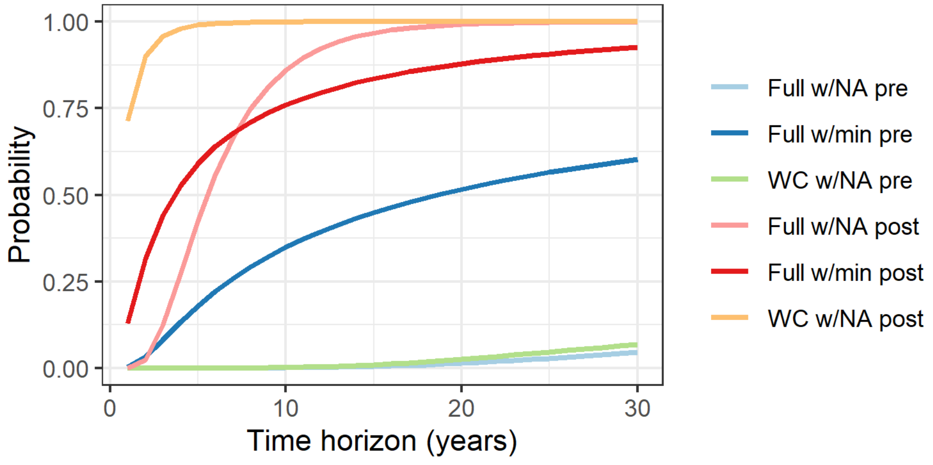

Figure 9. Extinction risk for *P. helianthoides* in the West Coast region from four models. The Full models the best-fit model with zeros replaced by NAs or minimum values. The WC-only models include only the time series from the West Coast. Estimates are presented using either the pre-2013 or post-2013 population growth rate. The risk is the probability that the population size will drop below a threshold 1% of its value in 2013.

Anecdotal reports of cohorts of small *P. helianthoides* from areas both within the Salish Sea (e.g., K. Collins, pers. comm.) and northward portions of the range are promising, but limited in both scope and duration. Hamilton et al. (2021) report some recruitment in the Gulf of Alaska and British Columbia, but note that these individuals fail to persist to adults, likely because of ongoing impacts of SSWS. Several of the time series here did show minor, but ephemeral, increases in abundance after the ~2013 die-off. For example, the Watson dive data for Vancouver Island and the WDFW shrimp test-fishery both show short-lived increases. Clearly understanding whether SSWS will persist and continue to kill off recruitment pulses is key to understanding future population dynamics.

The three major analyses of *P. helianthoides* population status, Hamilton et al. (2021), Gravem et al. (2021), and the MARSS analysis conducted here, all generally agree on substantial declines in abundance across the species' range (Table 2). One should expect this result given that all three analyses use similar data sets provided by a limited number of data providers. Declines were strongest in the southern portion of the species' range (here, West Coast region). However, the results are somewhat more variable for Alaska, ranging from 40-100% for Hamilton et al. (2021) and 61%-95% for Gravem et al. (2021) across various Alaskan regions. MARSS estimates of decline in Alaska since 2013 ranged from 81-100%, depending on whether zeros were replaced with NAs or minimum values, with w/NA models estimating smaller declines.

Table 2. Change in density and occurrence after the onset of SSWS through 2020 from Hamilton et al. (2021) and Gravem et al. (2021) and through 2021 for the MARSS analyses here. Summarized results from the MARSS analysis are shown in the two right columns. The MARSS % decline is the mean across all models for that region. The range shows the range of estimated decline.

Hamilton regions	% decline in density	Gravem regions	% decline in density	MARSS Region	Mean MARSS % decline	MARSS % range
Aleutians	40.0	Aleutians				
West Gulf of Alaska	100.0	West Alaska	61.1	Alaska	95.2	80.6-100
East Gulf of Alaska	93.8	East Gulf of Alaska	94.9			
Southeast Alaska	96.0	Southeast Alaska	94.7			
British Columbia	87.9	British Columbia	87.9	BC & SS	83.6	72-96.8
Salish Sea	92.4	Salish Sea	91.9			
Washington coast	99.6	Coastal PNW	99.6	West Coast	92.8	89.1-98.5
Oregon	100.0					
Northern California	99.2	Northern California	97.9			
Central California	99.5	Central California	97.2			
Southern California	100.0	Southern California	99.8			
Baja California	100.0	Baja California	98.5			

4. DISCUSSION OF VIABLE POPULATION DESCRIPTORS AND EVALUATION OF HOW THEY MAY CONTRIBUTE TO EXTINCTION RISK

The health of a biological population can be assessed using a wide variety of descriptors of its current size, historic size, distribution across diverse habitats, rate of growth or decline, phenotypic variability, genetic distinctiveness, and other attributes (e.g., Adams and Ham 2011; Smith et al. 2018; Bednaršek et al. 2021; Yan et al. 2021). Effective conservation and restoration of plant and animal species requires adequate knowledge of these fundamental parameters (e.g., Smallwood 2001; Mills 2013), or that managers take a precautionary approach that is risk averse in the face of incomplete data (e.g., Lauck et al. 1998; Darcy and Matlock 1999; Fenichel et al. 2008).

In 2000, McElhany et al. developed a framework to evaluate the viability of salmonid populations using four key demographic parameters: abundance, spatial distribution, productivity, and diversity. This Viable Population (VP) framework has since been adapted and applied to the assessment of a broad variety of other species in response to ESA listing petitions (e.g., McElhaney et al. 2004; Gustafson et al. 2006; 2011; Cooney et al. 2007; Hand et al. 2007; BRT 2009; Cameron et al. 2010; Drake et al. 2010a; 2010b; McCandless et al. 2014; Miller et al. 2014a; b; Young et al. 2017). Here, we briefly discuss how these parameters are measured, estimated, and evaluated to reach conclusions about population robustness and to support assessment of extinction risk.

4.1 Abundance

The number of individuals making up a population is a fundamental metric correlated with resilience to stressors, adaptability, and role in the ecosystem. When conspecifics are plentiful, finding mates, selecting mates based on desirable traits, maintaining social structures, weathering disease outbreaks, swamping/mobbing predators to reduce predation risk, and other behavioral and physiological mechanisms to facilitate population persistence are feasible, depending on the species (e.g., Kocan et al. 2001; Ostro et al. 2001; Moreau and Vincent 2004; Krams et al. 2009; Schwenke et al. 2018; Bried et al. 2021). Population size may be affected by top-down controls, like predation, disease, and harvest, as well as bottom-up controls, like prey availability and habitat suitability. Often it is a combination of control types that dictate abundance, with the relative importance of any given factor changing as a consequence of abundance itself, and being tightly correlated with spatial scale (Sibly et al. 2002; Munch et al. 2005; Hunt and McKinnell 2006).

With regard to extinction risk, small populations can be imperiled by a suite of factors inherent to being few in number. Loss of even a few mature, reproductively active individuals from a small population as a consequence of predation, disease, starvation, environmental variation, or catastrophic events carries with it an increased risk that the population may permanently lose the capacity to rebuild itself without an influx of recruits from an external source (Shaffer and Samson 1985; Lande 1993; Gerber and Hilborn 2001; Schoener et al. 2001). When a population represents the whole of a species, such loss can result in extinction. When population size is small, the probability of finding mates can decrease while the probability of accumulating maladaptive genetic and phenotypic traits can increase, further increasing the probability of population crash from relatively more common, low intensity threats (Allee et al. 1949; Fowler and Baker 1991; Lande 1998; Lundquist and Botsford 2004; 2011). More abundant populations are typically buffered against threats of this nature, though events that result in isolation of unique subsets of the population, such as habitat fragmentation, may still impact the long-term genetic legacy of the species (Young et al. 1996; Honnay and Jacquemyn 2007; Keyghobadi 2007). However, abundance alone, or an abundance trend, is often a poor predictor of extinction risk when not considered alongside dynamic parameters like population growth rate (Keith et al. 2015).

In the case of *P. helianthoides*, a range-wide decrease in abundance of >90% was estimated by the IUCN, with regional abundance in waters south of Neah Bay, WA, near zero (Gravem et al. 2021). After communicating with data providers to extend the data series used in this assessment from 2019 to 2021 or 2022, as available, and performing MARSS analyses with this updated information, we were able to largely confirm these findings (Section 3.4 Species Status Assessment). However, the range of region-specific population decline we estimated was sensitive to how missing data were treated and ranged from 72-100%. We were also able to statistically estimate extinction risks assuming either that SSWS impacts are ongoing or that pre-2013 population growth rates will manifest in the near future (3.4 Species Status Assessment) and show low levels of risk under certain conditions. From Cape Flattery south to Mexico, however, mature sunflower sea stars are now rare or nonexistent in all of the monitoring data sets considered (<1 observation annually in most cases). In these southern portions of the range, population density may now be so low that individuals are not capable of finding sufficient mates for breeding. Anecdotal reports of juveniles 3-10 cm in diameter, from northern California and the Channel Islands, however, negate the assumption of local extirpation following the SSWS pandemic, meaning these southern reaches still represent occupied habitat.

4.2 Spatial Distribution/Connectivity

How individuals are distributed across the landscape, and the degree to which they are capable of interacting with one another, is a crucial element affecting population viability and extinction risk. This parameter is closely linked with abundance, with regard to mating and other social interactions as noted above, but a suite of density dependent physiological and behavioral effects can also arise at extremely high or low densities. Longevity, fecundity, individual growth rate, home range size, degree of conspecific agonism, predation risk, and the proportion of an animal's time budget spent engaging in specific tasks can all be directly affected by population distribution and dispersion (e.g., Walker 1967; Kritzer and Davies 2005; Hixon et al. 2012; Niemela et al. 2012; Duckworth and Anguillon 2015; Wright et al. 2019). If population abundance is high on a landscape scale but individuals occur at densities low enough to reduce social interaction and mating opportunities, such isolation can increase the likelihood of recruitment failure and local extirpation as adults senesce and die, potentially leading to global extinction as local populations slowly decline and disappear (Gascoigne et al. 2009; Guizien et al. 2014). Open populations of marine organisms with broadly distributed larvae have the capacity to overcome low adult density, but are dependent on prevailing currents and local hydrodynamics to maintain connectivity among populations (Karlson and Levitan 1990; Cowen and Sponaugle 2009).

For species with specialized habitat requirements, spatial distribution and connectivity are tightly linked with occurrence of suitable habitat, be it on the micro or macro scale (Munday et al. 1997; O'Hara and Barmby 2002; Wilson et al. 2008). If such habitat is rare, either naturally or as a consequence of anthropogenic influences, local extirpation or global extinction may result as a consequence of disease outbreaks, increased predation risk, or other stressors acting on a local or regional basis (Arthington et al. 2016; Cartwright 2019). Habitat generalists, however, as well as specialists who associate with a broadly available habitat type or that are common within a unique habitat type, are typically more resilient given the scale required for a single stressor, or suite of stressors, to act on a biologically meaningful portion of the species (Reynolds 2003; Munday 2004; Williams et al. 2009; Polidoro et al. 2012; Carscadden et al. 2020). Broad-scale stressors can certainly impact extinction risk, but the wider niche a species occupies with regard to an array of habitat variables the less likely it is that a stressor can affect enough individuals to result in long-term, deleterious impacts to the species (Wilson et al. 2008; Slatyer et al. 2013).

In the case of *P. helianthoides*, disparate monitoring efforts using SCUBA, trawls, pots, and hand sampling in the nearshore have documented marked, sometimes orders of magnitude, density declines across broad swaths of the species' range from Alaska to northern Mexico between 2013 and 2017 as a direct result of SSWS (Gravem et al. 2021; Section 3.4 Species Status Assessment). Several of the data sets used for these analyses were long-term ecological indicator series that had firmly established *P. helianthoides* as a regular component of the regional biota on a diversity of habitats. While the size of individuals was not reported for most surveys, the sampling tools used were in all cases insufficient to detect larvae or newly settled individuals smaller than several centimeters in diameter. Therefore, a substantial gap remains in our understanding of the spatial distribution of early life stages.

Concurrence among disparate sources across the range of the species provides compelling evidence that abundance of larger individuals has fallen to levels that *P. helianthoides* are now rare in locations where they have long been common, demonstrating substantial changes in spatial distribution of these life history stages. However, there are considerable geographic gaps both within and among regions covered by these surveys, and coverage is often seasonally sparse. Anecdotal reports provided as public comment on the 90-day finding (86 FR 73230) and through direct contact with researchers document occurrence of *P. helianthoides* in places they have not previously been prevalent, such as in protected fjords in northern British Columbia (A. Gehman, pers. comm.). The degree to which redistribution of individuals across the landscape, and/or concentration of mature individuals within such "bastion" habitats, affects long-term habitat usage and connectivity on a range-wide basis remains unknown. The environmental factors that affect spawning adults and dispersing larvae of echinoderms vary considerably, resulting in a decoupling of population dynamics and complicating estimates of realized habitat use (Uthicke et al. 2009). Recent settlement events and reported occurrence of juvenile *P. helianthoides* in many regions indicate that reproductive capacity remains within the population, though the degree to which larval cloning is contributing to current recruitment strength is unknown.

4.3 Productivity/Growth Rate

Long-term persistence of a species under natural conditions requires that individuals be added to the population, on average, at a rate equal to or greater than they are lost (Quinn and Deriso 1999; Schoen 2007; Allen and Hightower 2010). The mechanism by which any given species achieves this balance varies on a continuum from those that produce few, well-developed, competent offspring with low natural mortality to those that produce millions or billions of low-investment offspring of which only a scant few survive to reproduce. Natural variability in the annual effectiveness of reproduction can be relatively high as a result of numerous environmental and biological factors, however, such that populations display regular boom and bust cycles, like those characteristic of many marine invertebrates and small fishes (e.g., Botsford and Wickham 1979; Pepin 1991; Uthicke et al. 2009; Pikitch et al. 2012). Additionally, not only reproduction but immigration must be considered as a source of new individuals, and the full suite of spatially variable natural and anthropogenic mortality sources must be accounted for, complicating estimates of regional population growth rate for species that have highly mobile life history stages, such as planktonic larvae or broadly dispersing adults.

Understanding and accurately predicting the growth rate for a species or population is most easily accomplished when data are readily available for a number of life history parameters. Individual growth rate, maturation schedule, mating behavior, reproductive output/fecundity, reproductive longevity, dispersion capacity, and life span all contribute to the ability of an individual to effectively mate and produce offspring and, thus, to population growth rate. In populations for which such detailed biological knowledge is not available, consistently collected abundance data for the same life history stage over a series of successive cycles can be used. When consistently collected time-series information is lacking, as is often the case for imperiled species, shared trends in population growth rate within and among diverse taxa can be used to make informed estimates for the species of interest (e.g., Drake 2010; Dulvy et al. 2014; Anderson et al. 2017).

In the case of *P. helianthoides*, growth rate, fecundity, reproductive life span, spawning frequency, longevity, and other key metrics critical to directly estimating spatially explicit population productivity and growth rate are largely lacking. Region-specific estimates can be derived from data series presented in prior assessments (Gravem et al. 2021), and updated here

(Section 3.4.2.2 MARSS Results, Table 3.1). As *P. helianthoides* is the sole member of a genus whose closest relative is also a monotypic genus, with the two organized into the subfamily Pycnopodiinae (Section 2.1 Taxonomy and Distinctive Characteristics), use of proxy species to refine empirically estimated growth rate is of minimal utility.

4.4 Diversity

In synergy with the other VP parameters, morphological and physiological diversity are key elements of population resiliency and thus, closely linked with extinction risk. Environments are inherently variable with regard to physical, chemical, and biological aspects ranging from erosion rate, to pH, to prey abundance. For populations to adequately respond to this variability, persist, and survive to pass on their genes, individuals within the population must also vary in their fitness relative to a host of stressors. Genes affecting growth rate, reproductive capacity, energy storage, disease resistance, and innumerable other traits are the foundation upon which selection works, as reflected in shifts in the relative frequency of such genes in populations over time (Wright 1948; Slatkin 1987). Organisms have no way of accurately predicting long-term changes in the complex array of natural conditions they, or their offspring, might face, and sexual reproduction involves an element of random assignment of genetic material to gametes. In species with parental care, social systems may mediate direct impacts of environmental variability on adaptive or maladaptive traits and allow transmission of diversity over several generations. For broadcast spawners, however, localized fluxes in microhabitat conditions are critically important during early development, and maintenance of genetic diversity is driven largely by stochastic processes. For populations in which diversity is reduced substantially as a consequence of catastrophic events or other broad stressors, supplementation of natural populations based on genetic screening and carefully designed outplanting may be a valid recovery approach (e.g., Small et al. 2009; Gruenthal et al. 2014; Glasscock et al. 2021).

In the case of *P. helianthoides*, very little is known about morphological, physiological, or genetic diversity on any spatial scale. The species occupies a broad array of habitats in which physiochemical traits vary over wide ranges, suggesting resilience and adaptability that may stem from regionally distinct diversity. Considerable additional research is needed, however, to confirm this broad assumption.

5. DISCUSSION OF ESA SECTION 4(a)(1) FACTORS AND CONTRIBUTION TO EXTINCTION RISK

Pursuant to the ESA and implementing regulations, NMFS determines whether species are threatened or endangered based on any one or a combination of the following Section 4(a)(1) factors: (1) the present or threatened destruction, modification, or curtailment of habitat or range; (2) overutilization for commercial, recreational, scientific, or educational purposes; (3) disease or predation; (4) inadequacy of existing regulatory mechanisms; and (5) other natural or man-made factors affecting the species' existence. Below, we provide information on threats from each of the five factors specific to *P. helianthoides*.

5.1 Present or Threatened Destruction, Modification, or Curtailment of Habitat or Range

The SRT did not consider the destruction, modification or curtailment of habitat as posing a substantial risk to *P. helianthoides* because its broad geographic and depth distributions buffer the species against activities and catastrophic events that are limited in spatial and temporal scale. For example, coastal development and construction projects typically have a narrow geographic scope, uncertain or indirect effects on *P. helianthoides*, or occur infrequently. Sedimentation, erosion, and sea level rise have the potential to produce more widespread impacts, especially in coastal environments near urban development. Log booms could create localized habitat destruction as water-soaked bark rains down a river into coastal waters, creating anoxic areas. This linkage to the lumber trade was noted in Gravem et al. (2021). Still, because *P. helianthoides* is distributed in areas and at depths that provide refuge from these threats throughout their range, the team agreed that these factors, by themselves, would not currently put the species at danger of extinction.

The SRT expressed uncertainty regarding how habitat shifts (e.g., kelp forest to urchin barren) caused by larger scale processes such as climate change or long-term removal (via hunting or disease) of keystone predators or prey items may contribute to the species' risk of extinction over coming years and decades. Loss of kelp forest habitat throughout the range at varying scales is a concern given the apparent high level of use by *P. helianthoides*, but the importance of kelp habitats relative to the full distribution of the species is assumed based largely on SCUBA-based sampling in discrete areas. Risk associated with loss of kelp forests is mitigated by the abundance of suitable habitat for this generalist throughout its range, much of which is protected by restricted use designations (e.g., marine protected areas, rockfish conservation areas, NOAA marine sanctuaries) and/or ecosystem protections implemented by various mechanisms for other species (e.g., kelp forests, eelgrass meadows, rocky reefs). These habitat protections offer potentially direct and indirect benefits to *P. helianthoides* and its prey. Generally, the SRT concluded that habitat degradation is not anticipated to have dramatic, population-level impacts on this species in the immediate future.

Some members of the SRT stated that curtailment of *P. helianthoides* range is likely in the south, especially from Oregon, USA, to Baja California, MX, following the SSWS pandemic. Other team members stated that some signs of recovery (i.e., recent recruitment events) indicate that the southern range is still occupied, albeit at substantially reduced densities. All team members agreed that fragmentation of populations could lead to local extirpation and, thus, loss of range in the future, but there was disagreement over whether this broader threat is imminent.

5.2 Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

Pycnopodia helianthoides is not the object of targeted commercial fisheries historically or currently. Bycatch mortality from trawl and bottom-contact trap/pot fisheries pose a low-level risk now and potentially a higher level of future risk, especially in areas where populations are declining or already at very low levels. *Pycnopodia helianthoides* exhibits aggregative behavior (Kjerskog-Agersborg 1918; Mauzey et al. 1968), which may occur during spawning season, making breeding individuals more vulnerable to localized fisheries impacts. Handling from bycatch could generate stress, increasing an individual's susceptibility to disease or other stressors. However, these potential risks are offset by the following observations: 1) the majority of commercial trawl fisheries occur in waters outside of preferred *P. helianthoides* depth zones (< 25 m or 82 ft) based on the information regarding highest documented densities (Gravem et al. 2021); and 2) sunflower sea stars are reported as being resilient to handling stress during regular fishing operations, though post-release monitoring is not reported in the literature. The scope and severity of bycatch is muddled by uncertainty over the exact species composition in bycatch categories that lump all sea stars together (e.g., "sea star, general" and "sea star, unidentified'), incomplete documentation of injury/mortality following handling, and uncertainty regarding how localized fisheries impacts, especially in areas where populations are declining, may increase risk to the species throughout its range over longer time scales.

Recreational harvest of *P. helianthoides* is permitted in both British Columbia and California, and is unrestricted in Mexico, but estimates of recreational harvest are not available. Evidence does not exist for regular human consumption of the species, so all collection is assumed to be for private exhibition or curiosity. Whether these individuals are held for a short period before being released or permanently removed from the population is unknown. The Commercial trade to support a curio market is thought to affect primarily small individuals, and at low levels of impact, and collection of scientific purposes (including live display) requires a permit in all U.S. and Canadian jurisdictions within the species' range. Recreational harvest and trade may become a greater concern in areas where abundance levels are extremely low or declining. Additional regulations prohibiting retention except under very limited conditions could offset this threat in the future. At this time, recreational harvest and commercial trade are believed to impact a very small number of individuals and, therefore, the SRT agreed that they pose a very low level of risk to *P. helianthoides*.

5.3 Competition, Disease, or Predation

Beginning in 2013, SSWS caused ~72-100% declines in locally monitored populations of *P. helianthoides* across its range. The global *P. helianthoides* population declined by an estimated 90.6% due to SSWS (Gravem et al. 2021). Some local populations were functionally extirpated within a matter of weeks, such as those in the northern Channel Islands. Recent laboratory studies suggest that *P. helianthoides* die as quickly as 2-4 days after exposure to SSWS (A.

Gehman, pers. comm.). Throughout the range some populations have undergone significant declines and there are concerns that remaining *P. helianthoides* are too widely dispersed for successful reproduction. There is considerable variation in the degree of impact, however, associated with depth, latitude, and recent temperature regime, in some cases. Small increases in temperature have been shown to increase susceptibility of *Pisaster ochraceus* to SSWS (Bates et al. 2009), and decreased temperature has been demonstrated to slow progression of the disease, though the end results is still death (Kohl et al. 2016).

The causative agent of SSWS is currently unknown and various hypotheses regarding transmission dynamics and the lethality of SSWS under diverse physiochemical circumstances exist. Initially, SSWS was thought to be caused by a densovirus or suite of densoviruses (Parvoviridae; Hewson et al. 2014, 2018). Subsequent studies, however, have determined that the disease is more complex. A number of factors ranging from environmental stressors to the microbiome in the sea stars may play a role (Lloyd and Pespeni 2018; Konar et al. 2019; Aquino et al. 2021). Ocean warming has also been linked to outbreaks, hastening disease progression and severity (Harvell et al. 2019; Aalto et al. 2020). For more detail see section 5.5 Other Natural or Manmade Factors Affecting the Species' Continued Existence. Regardless of the pathogen's unknown etiology to date, stress and rapid degeneration ultimately result with symptomatic sea stars suffering from abnormally twisted arms, white lesions, loss of body tissue, arm loss, melting, and death.

The SRT concluded that SSWS has been, and continues to be, the primary stressor threatening the continued existence of *P. helianthoides*. The disease has caused mass mortality and local extirpation of some populations, especially in the southern portion of its range. The SRT expressed major concern about the potential for SSWS outbreaks to recur on the West Coast, resulting in rapid loss of the remaining fraction of the population that survived the 2013-17 pandemic. This is the single greatest concern flagged by the majority of team members as contributing to extinction risk. As modeled above in section 3.4 Species Status Assessment, if recent SSWS-associated population declines continue extinction is all but certain throughout the range. If population growth rates are able to return to pre-pandemic levels in coming years, however, likelihood of population persistence is moderate in the Alaska Region and the British Columbia and Salish Sea Region, but lower in the West Coast Region.

Pycnopodia helianthoides has very few predators and while predation could further reduce abundance levels, the SRT agreed that predation does not constitute a major threat to the species. Geographic scope and intensity of predation pressure is likely limited and, therefore, not expected to have population-level impacts across the range. Predatory risk is likely highest during the planktonic larval phase, but this stressor is tempered by the fact that *Pycnopodia helianthoides* is a broadcast spawner, creating millions of offspring per female during a spawning cycle.

5.4 Adequacy of Existing Regulatory Mechanisms

Current regulations to control anthropogenic climate change are likely insufficient to have a measurable impact on reversing ocean warming trends and slowing ocean acidification by the end of the century. Given that elevated ocean temperatures likely contributed to the decline of *P. helianthoides* because warmer water temperatures are correlated with accelerated rates of SSWS transmission and disease-induced mortality, the lack of adequate regulations to stall the impacts of climate change is an important concern for the species' long-term viability. The team expressed uncertainty regarding ways in which additional climate change regulations could reduce the extinction risk of *P. helianthoides* without a better understanding of the relationships between climate change impacts (especially temperature stress), SSWS dynamics, and species-specific disease vulnerability.

Place-based regulations that accompany areas such as MPAs and sanctuaries should have net positive effects on *P. helianthoides* and its ecosystems at large. Additional support for enforcing the protections provided in these areas would help to achieve the overarching goal of ecosystem resiliency. Current regulations prohibit retention of *P. helianthoides* along much of the West Coast and directly protect the species, but could be extended to all waters of the range. Bycatch, as detailed above (section 5.2 Overutilization for Commercial, Recreational, Scientific, or Educational Purposes), likely presents a low level of risk to the species, but may be considerably unreported and/or underestimated. The SRT agreed that place-based and fisheries regulations are currently working to protect *P. helianthoides*, but some felt that more could be done by expanding protections to places where potentially viable populations remain.

5.5 Other Natural or Manmade Factors Affecting Continued Existence

Warming ocean temperatures, extreme fluctuations in ocean temperature, harmful algal blooms, ocean acidification, and low dissolved oxygen events, all byproducts of anthropogenic climate change, could impose direct and indirect stress on *P. helianthoides* and increase their vulnerability over the coming decades. There is uncertainty regarding causal links between climate change and impacts to *P. helianthoides*, and the scale over which these potential impacts are taking place. For example, local temperature-related stress, low dissolved oxygen events, and harmful algal blooms may be buffered by the refuge that a broad geographic and depth range provides to this species. Overall, the team expressed a wide range of opinions, reflecting a high degree of uncertainty, regarding the likelihood that climate change will accelerate extinction risk for *P. helianthoides*. Most team members were concerned that increasing sea surface temperatures associated with climate change would trigger another disease outbreak rendering the species at risk of extinction in the foreseeable future.

Evidence for direct impacts of pollutants and environmental contaminants on *P. helianthoides* are lacking. The team was concerned about the impacts that pollutants and contaminants might have on the ecosystems upon which *P. helianthoides* depend, in particular the food that they eat. The team concurred that impacts due to pollutants and environmental contaminants are either unknown or are low enough such that they are unlikely to contribute to the species' risk of extinction now or in the foreseeable future.

6. EXTINCTION RISK ANALYSIS

The Endangered Species Act (ESA) (Section 3) defines endangered species as "any species which is in danger of extinction throughout all or a significant portion of its range." Threatened species is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." Neither NMFS nor the U.S. Fish and Wildlife Service (USFWS) have developed any formal policy guidance about how to interpret the definitions of threatened or endangered species in the ESA. In numerous prior NMFS status reviews, a team has been convened to compile the best available information on a species and conduct a risk assessment by evaluating demographic risks and threats facing the species. They then provide an evaluation of overall extinction risk, accompanied by a detailed narrative justifying their conclusion. This information is used by the NMFS Office of Protected Resources, after consideration of the legal and policy dimensions of the ESA, and standards and benefits of ongoing conservation efforts, to make a listing determination. For purposes of this risk assessment, the SRT composed of biologists, resource managers, ecologists, statisticians, and listing process experts convened to complete the evaluation process and arrive at a conclusion regarding overall extinction risk for *P. helianthoides*.

The ability to measure or document risk factors and quantify their explicit impacts to marine species is often limited, and quantitative estimates of abundance and life history information are sometimes lacking altogether. Therefore, in assessing extinction risk of a data limited species, it is important to include both qualitative and quantitative information. In previous NMFS status reviews, assessment teams have used a risk matrix method to organize and summarize the professional judgment of members. This approach is described in detail by Wainwright and Kope (1999) and has been used in Pacific salmonid status reviews, as well as in reviews of various marine mammals, bony fishes, elasmobranchs, and invertebrates (see http://www.nmfs.noaa.gov/pr/species/ for links to these reviews). In the risk matrix approach, the condition of a species is summarized according to four demographic risk criteria: abundance, growth rate/productivity, spatial structure/connectivity, and diversity (see section 4. Discussion of Viable Population Descriptors and Evaluation of How They May Contribute to Extinction Risk). These viability criteria, outlined in McElhany et al. (2000) reflect concepts that are well-founded in conservation biology and that, individually and collectively, serve as strong indicators of extinction risk. Employing these concepts here, the SRT conducted a demographic risk analysis for *P. helianthoides* to determine population viability. Likewise, the SRT performed a threats assessment for the species by scoring the severity of current threats to the species and their likely impact on population status into the foreseeable future (see section 6.1 Foreseeable Future). The summary of demographic risks and threats obtained by this approach was then considered by the SRT to determine the species' overall level of extinction risk, both currently and in the foreseeable future. Specifics on each analysis are provided below.

6.1 Foreseeable Future

Consistent with Wainwright and Cope (1999) and NMFS ESA guidance, the term "foreseeable future" was defined here as the timeframe over which threats can be reliably predicted to impact the biological status of the species. To determine an appropriate foreseeable future time frame, the SRT first considered available information pertinent to the life history of *P. helianthoides*.

Pycnopodia helianthoides is characterized by indeterminate growth, as are most echinoderms, but limited data are available regarding its longevity, age at maturity, size at maturity, fecundity, reproductive life span, spawning frequency, and other fundamental biological attributes. Further, the degree to which these parameters vary over the range of the species is unknown. Gravem et al. (2021) estimated the generation time of *P. helianthoides* to vary between 20.5 and 65 years, but used an estimate of 27-37 years for the IUCN assessment.

Monitoring data for *P. helianthoides* at locations spread throughout its range documented dramatic declines from 2013-17 as a consequence of SSWS. Despite considerable research in the last several years (e.g., Hewson et al. 2014; 2018; 2019; Aquino et al. 2021; Jackson et al. 2021), the causative agent of SSWS remains elusive, as does the environmental trigger or triggers that led to the pandemic. Extending and augmenting the analysis of Gravem et al. (2021), we demonstrated that if post-pandemic negative trends in population abundance continue extinction risk is very high (see section 3.4.2.2 MARSS Results, Table 3.1). However, if populations are able to return to pre-pandemic population growth rates long-term persistence is moderate to high. Which of these two scenarios is more likely depends on disease resistance, current local population dynamics, and a myriad of environmental factors affecting both *P. helianthoides* and the SSWS agent(s). If individuals who survived the pandemic are able to successfully reproduce even a few times over the next several years, and ocean conditions are adequate to support larval survival and settlement, a substantive recruitment pulse could result. There is evidence of such a pulse in the Salish Sea, Coastal B.C., and elsewhere, indicating that reproductive potential still exists on the local and regional scale. The degree to which larval cloning contributes to abundance, distribution, and population-level impact of this recruitment pulse is unknown. Whether the causative agent of SSWS exists in an environmental or biological reserve, however, is also unknown. If it does, this recruitment pulse could be short lived and individuals may not survive to reach reproductive age. There is a high level of uncertainty regarding potential outcomes, and predictive capacity is limited as a consequence of the unique combination of ocean conditions and disease prevalence in recent years.

Directed fisheries for *P. helianthoides* are currently limited throughout the species' range, largely because of a lack of marketability or identified human usage. While recreational harvest may occur in British Columbia, California, and Mexico under current regulations there is no evidence that harvest levels are substantial enough to affect population viability. Bycatch is common only in select bottom-contact fisheries. When bycatch occurs, individuals can be handled in a manner that minimizes stress and promotes survival. There is no reasonable expectation that fisheries for *P. helianthoides* will further develop in the next several decades, at a minimum.

Pycnopodia helianthoides has been documented on a broad diversity of habitats and across an extensive depth range throughout the whole of their known range (see section 2.2 Range and Habitat Use). Nearshore development in urban centers along the northwest coast of North America will continue, and likely intensify, but recent fluctuations in ocean temperature, pH, and carbon dioxide levels are more uncertain. While climate models make projections of changes in these parameters with relatively high confidence over several decades, the consequences of these changes on biological systems are far less certain. Additionally, there is conflicting evidence to support whether sea surface temperature and other environmental variables exacerbate SSWS prevalence and transmissibility (Bates et al. 2009; Kohl et al. 2016; Harvell et al. 2019; Konar et al. 2019; Aquino et al. 2021; Hamilton et al. 2021).

After considering the best available information on *P. helianthoides* life history, projected abundance trends, likelihood of a resurgence of SSWS to pandemic levels, and current and future management measures, the SRT concluded that after 30 years uncertainty in these factors became too great to reliably predict the biological status of the species. We, therefore, agreed that a biologically reasonable foreseeable future timeframe would be 30 years. Though potential impacts from threats like nearshore habitat degradation and anthropogenic climate change can be projected further into the future, the SRT concluded that the impacts of these threats to *P. helianthoides* could not be adequately predicted given the behavioral patterns of the species with regard to habitat use and diet. The SRT felt that the intensity and high regional variability of potential disease impacts limited our ability to assess the effects of additional threats on species viability beyond the temporal range of 30 years.

6.2 Methods

6.2.1 Demographic Risk Analysis

The SRT reviewed all relevant biological and commercial information for *P. helianthoides*, including: current abundance relative to historical abundance estimates, and trends in survey data; what little is known about individual growth rate and productivity in relation to other species, and its effect on population growth rate; spatial and temporal distribution throughout its range; possible threats to morphological, physiological, and genetic integrity and diversity; and natural and human-influenced factors that likely cause variability in survival and abundance. Each SRT member then assigned a risk score to each of the four VP factors (abundance, productivity, spatial distribution, and diversity) throughout the whole of the species' range. Risks for each VP factor were ranked on a scale of 0 (unknown risk) to 3 (high risk) using the following definitions:

> 0 = Unknown: Information/data for this demographic factor is unavailable or highly uncertain, such that the contribution of this factor to the extinction risk of the species cannot be determined.
>
> 1 = Low risk: It is unlikely that the particular factor directly contributes significantly to the species' current risk of extinction, or will contribute significantly in the foreseeable future (30 yrs).
>
> 2 = Moderate risk: It is likely that the particular factor directly contributes significantly to the species' current risk of extinction, or will contribute significantly in the foreseeable future (30 yrs), but does not in itself currently constitute a danger of extinction.
>
> 3 = High risk: It is highly likely that the particular factor directly contributes significantly to the species' current risk of extinction, or will contribute significantly in the foreseeable future (30 yrs).

Team members were given a template to fill out and asked to rank each factor's contribution to extinction risk (Table 3). After scores were provided to the team lead (Lowry), they were anonymized and shared with the entire team, who then discussed the range of perspectives for each of the demographic risks, and the supporting data/information upon which they were based. Team members were then given the opportunity to revise scores after the discussion, if they felt their initial analysis had missed any pertinent data discussed in the group setting. Final scores were reviewed and considered, then synthesized, to arrive at the overall demographic risk determination from the team (see section 6.3 Demographic Analysis Results). Although this process helps to integrate and summarize a large amount of information, there is no simple way to translate the risk matrix scores directly into a determination of overall extinction risk. Thus, it should be emphasized that this exercise was simply used as a tool to help the SRT organize information and guide thought processes for determining overall risk of extinction for the species. Other descriptive statistics, such as mean, variance, and standard deviation, were not calculated as the SRT felt these metrics would add the appearance of artificial precision or accuracy to the results.

Table 3. Template for the demographic risk analysis scoring used in Status Review Team deliberations. The matrix is divided into four sections that correspond to the parameters for assessing population viability (McElhany et al. 2000).

Viable Population Factor	Contribution to Species' Risk of Extinction	Justification
ABUNDANCE		
PRODUCTIVITY		
SPATIAL DISTRIBUTION		
DIVERSITY		

6.2.2 Threats Assessment

Section 4(a)(1) of the ESA requires the agency to determine whether the species is endangered or threatened because of any of the following factors:

1) destruction or modification of habitat;
2) overutilization for commercial, recreational, scientific, or educational purposes;
3) disease or predation;
4) inadequacy of existing regulatory mechanisms; or
5) other natural or human factors

Similar to the demographic risk analysis, SRT members were given a template to fill out and asked to rank each threat in terms of its contribution to the extinction risk of the species throughout the whole of the species' range. Specific threats falling within the five categories provided in Section 4(a)(1) were identified from sources included in this Status Review Report, and included as line items in the scoring template (Table 4). Below are the definitions that the Team used for ranking:

0 = Unknown: The current level of information is insufficient for this threat, such that its contribution to the extinction risk of the species cannot be determined.

1 = Low: It is unlikely that the threat is currently significantly contributing to the species' risk of extinction, or will significantly contribute in the foreseeable future (30 yrs).

2 = Moderate: It is likely that this threat will contribute significantly to the species' risk of extinction in the foreseeable future (30 yrs), but does not in itself constitute a danger of extinction currently.

3 = High: It is highly likely that this threat contributes significantly to the species' risk of extinction currently.

The template also included a column in which team members could identify interactions between the threat being evaluated and specific demographic parameters from the prior analysis (Section 6.2.1 Demographic Risk Analysis), as well as other threats included in this analysis (Table 4). After scores were provided to the team lead (Lowry) and anonymized, the Team discussed the range of perspectives for each of the threats and the supporting data/information upon which they were based. They also delved into the interactions among threats and specific demographic parameters, or other threats, to ensure that scoring adequately accounted for these relationships. Team members were then given the opportunity to revise scores after the discussion, if they felt their initial analysis had missed any pertinent data discussed in the group setting. The scores were then reviewed and considered, then synthesized, to arrive at an overall threats risk determination (Section 6.4 Threats Analysis Results). Again, it should be emphasized that this exercise was used simply as a tool to help the SRT members organize the information and assist in their thought processes for determining the overall risk of extinction for the sunflower sea star. Other descriptive statistics, such as mean, variance, and standard deviation, were not calculated as the SRT felt these metrics would add the appearance of artificial precision or accuracy to the results.

Table 4. Template for the threats analysis scoring used in Status Review Team deliberations for the Extinction risk Analysis.

4(a)(1) Factor	Threat	Contribution to Species' Risk of Extinction	Interaction with other threats or demographic factors (list)?	Justification
Habitat destruction, modification, or curtailment				
Overutilization	*Commercial, recreational, and artisanal fisheries including bycatch*			
	Trade (e.g., curio market)			
Disease or Predation	*Disease, esp. SSWS*			
	Predation			
Inadequacy of existing regulatory mechanisms				
Other natural or manmade factors affecting the species' continued existence	*Pollutants and environmental contaminants*			
	Climate change			

6.2.3 Overall Extinction Risk

Guided by the summarized results of the demographics risk analysis and threats assessments, the SRT members used their informed professional judgment to make an overall extinction risk determination for the species. For this analysis, SRT members used three levels of extinction risk as defined in the NMFS Guidance on Responding to Petitions and Conducting Status Reviews under the Endangered Species Act (updated February 1, 2021):

> 1 = Low risk: A species, subspecies, or DPS is at low risk of extinction if it is not at moderate or high level of extinction risk (see "Moderate risk" and "High risk" below). A species, subspecies, or DPS may be at low risk of extinction if it is not facing threats that result in declining trends in abundance, productivity, spatial structure, or diversity. A species, subspecies, or DPS at low risk of extinction is likely to show stable or increasing trends in abundance and productivity with connected, diverse populations.
>
> 2 = Moderate risk: A species, subspecies, or DPS is at moderate risk of extinction if it is on a trajectory that puts it at a high level of extinction risk in the foreseeable future (see description of "High risk" below). A species, subspecies, or DPS may be at moderate risk of extinction due to current and/or projected threats or declining trends in abundance, productivity, spatial structure, or diversity. (This Team has agreed that the foreseeable future for sunflower sea stars is 30 yrs).
>
> 3 = High risk: A species, subspecies, or DPS with a high risk of extinction is at or near a level of abundance, productivity, spatial structure, and/or diversity that places its continued persistence in question. The demographics of a species, subspecies, or DPS at such a high level of risk may be highly uncertain and strongly influenced by stochastic or depensatory processes. Similarly, a species, subspecies, or DPS may be at high risk of extinction if it faces clear and present threats (e.g., confinement to a small geographic area; imminent destruction, modification, or curtailment of its habitat; or disease epidemic) that are likely to create imminent and substantial demographic risks.

It should be noted that while these definitions include the option of assessing a Distinct Population Segment (DPS) for listing, this concept only applies to vertebrate species and is, thus, not relevant here (16 U.S. Code § 1532[16]).

To allow individuals to express uncertainty in determining the overall level of extinction risk facing *P. helianthoides*, the SRT adopted the "likelihood point" (FEMAT) method (FEMAT 1993; Table 5). This approach has been used in previous status reviews (e.g., oceanic whitetip shark, various species of Pacific salmon, southern resident killer whale, Pacific herring, and black abalone) to structure the Team's thinking and express levels of uncertainty in assigning threat risk categories. For this approach, each Team member distributes 10 ‘likelihood points’ among the three extinction risk levels and then justifies the distribution of points in narrative form. After scores were provided to the team lead (Lowry) and anonymized, the Team discussed the range of perspectives for the species and the supporting data on which scores were based. SRT members were then given the opportunity to revise scores, if desired, after the discussion to incorporate updates to their thought process.

At the conclusion of this assessment process the SRT did not make recommendations as to whether *P. helianthoides* should be listed as threatened or endangered. Rather, the Team drew scientific conclusions about the overall risk of extinction faced by the species under present conditions, and in the foreseeable future, based on an evaluation of the species’ demographic risks and assessment of threats.

Table 5. Template for overall extinction risk scoring used in Status Review Team deliberations for the Extinction risk Analysis. Points allocated to the low, moderate, and high categories summer to ten for each team member.

Species is at low risk	Species is at moderate risk	Species is at high risk	Total
			10
Justification:			

6.3 Demographic Analysis Results

6.3.1 Abundance

SRT members universally recognized stark declines in nearly all available data sets, range-wide from 2013-17, with little evidence of recent recruitment or rebound. While variability in abundance estimates was high prior to the SSWS pandemic and boom/bust cycling was apparent in many areas, detection rates have been very low since ~2015 in the majority of time series. Data sets from the Oregon and California coasts are notable because they report several years of regular observation of *P. helianthoides* leading up to 2013, followed by several years of absence at the same index sites. In cases where *P. helianthoides* continued to be detected, density decreased by an order of magnitude or more. Data providers for these time series categorize this trend as local or functional extirpation, but dedicated efforts have reported juveniles in several of these areas (e.g., the Channel Islands) demonstrating that some reproduction and settlement is occurring. In areas where adults have not been detected for several years, SRT members noted that the potential for deleterious stochastic events, such as marine heat waves, to destroy what remains of the population is likely to be considerably increased. Abundance prior to the SSWS pandemic was substantially greater in northern portions of the range from Alaska to the Salish Sea, and declines in these areas were less pronounced.

The current range-wide (i.e., global) population estimate for *P. helianthoides* is nearly 600 million individuals, based on a compilation of the best available science and information (Gravem et al. 2021). While substantial, this represents less than 10% of the estimated abundance prior to 2013 and likely reflects an even greater decrease in biomass due to the loss of adults from SSWS. There is considerable uncertainty in this global abundance estimate, however, and in regional estimates that contribute to it. Low sampling effort prior to the SSWS pandemic, depth-biased disparities in data richness, inadequate species-specific documentation of occurrence, and missing information about several crucial life history parameters all contribute to this uncertainty. While confidence is relatively high in estimates from more southerly, nearshore areas that are well-sampled via SCUBA, the majority of the species' range consists of deep, cold, and/or northern waters that are less well sampled. How segments of the population in these poorly sampled areas contribute to and are connected with the overall health and stability of the species remains largely unknown. *Pycnopodia helianthoides* in these areas are less susceptible to impacts from nearshore stressors and could serve as source populations to support population rebound, but evidence to support this role is lacking. Based on the broad geographic range over which the remaining population is spread, the generalist nature of *P. helianthoides* with regard to both habitat use and diet, and the possibility that deep-water individuals may serve as source populations to bolster recovery, SRT members concluded that the current state of the abundance VP parameter was a moderate factor in affecting extinction risk in the foreseeable future.

Ecological consequences of declines in *P. helianthoides* abundance have been noted in several portions of the range. The most prominent of these is rapid increases in sea urchin abundance due to a relaxation of predation pressure, leading to degradation and loss of kelp forests as grazing pressure intensifies. Due to missing information and uncertainty with regard to *P. helianthoides* recruitment potential, growth rate, and longevity, the timeframe for recovery of these iconic and ecologically important habitats is unknown. Additionally, both kelp survival and SSWS have been linked with sea surface temperature and pH such that persistent low abundance of both kelps and *P. helianthoides* could result in an irreversible shift from kelp forests to urchin barrens.

6.3.2 Productivity

Little is known about the natural productivity of *P. helianthoides* on both an individual and population basis. Lack of information about growth rate, longevity, age at maturity, fecundity, natural mortality, the influence of larval cloning, and other fundamental biological attributes require that broad assumptions be applied and proxy species used to inform estimates on both regional and range-wide bases. Regardless of the values of nearly all of these parameters, however, the loss of ~90% of the global population of *P. helianthoides* from 2013-17 is likely to have had profound impacts on population-level productivity. The standing crop of individuals capable of generating new recruits has been decreased, possibly to levels where productivity will be compromised on a regional or global basis. The combined factors of spatial distribution of individuals across the seascape and ocean conditions are crucial to dictating whether productivity is sufficient to allow population rebound. Broadly dispersed individuals may lack the ability to find mates, further reducing realized productivity despite abundance being high enough to theoretically result in population persistence.

SRT members noted that as a broadcast spawner with indeterminate growth, traits shared with many other echinoderms, the capacity for allometric increases in fecundity and high reproductive output certainly exists in *P. helianthoides*. Hodin et al. (2021) noted that gonads are small in *P. helianthoides* compared to other asteriids but also documented prolonged periods over which spawning apparently occurs (i.e., gonads are ripe). If the SSWS pandemic resulted in the loss of the large, most reproductively valuable individuals across both nearshore and deep-water habitats it could take a decade or more for sub-adults to mature, settlement to occur at detectable levels, and population rebounds to be documented. There is evidence in some areas (e.g., the Salish Sea) that recruitment has occurred, demonstrating that local productivity is still occurring, but it may be years before these individuals reach maturity and themselves spawn. The ongoing threat of a second SSWS pandemic caused SRT members to be cautious when predicting population growth rate into the foreseeable future.

Provided mating continues to occur, even on a local basis, the prolonged planktonic period of larval *P. helianthoides* affords the opportunity for substantial dispersal prior to settlement. During this period, however, larvae are at the mercy of prevailing currents, temperature variation, and a suite of biophysical variables that affect survival. Even if populations maintain relatively high levels of productivity, the SRT noted that recent conditions in the northeast Pacific Ocean have not been favorable to larval survival for many species due to repeated marine heat waves, falling pH, and localized oxygen minimum zones. Additionally, given the predominant flow regime along the West Coast of North America, propagules are expected to be carried both northward and southward from British Columbia following the North Pacific Current as it bifurcates into the Alaska and California Currents, respectively. Given the distance larvae must travel with the currents, populations in British Columbia are not expected to contribute markedly to repopulation in the southern portion of the range off Oregon, California, and Mexico. While the Davidson Countercurrent and California undercurrent may seasonally carry propagules northward from Mexico and California (Thomas and Krassovski 2010), abundance of *P. helianthoides* in this portion of the range is not currently likely to be high enough to serve as a source population to areas off Washington, Oregon, or northern California. SRT members noted that studies of connectivity across the range of *P. helianthoides* will be crucial to evaluating how large-scale population patterns are affected by local and regional productivity in the future.

Taking into account the many unknowns about life history, population level reproductive capacity, and functional implications of environmental conditions on population connectivity in the foreseeable future, SRT members scored the productivity VP parameter anywhere from a low to high contributor to extinction risk over the next 30 years, but the slight majority agreed it was a moderate contributor. Depensatory impacts from abundance declines have likely decreased productivity on a local and regional scale, but the adults that remain are assumed to live long enough that opportunities to mate will manifest in time, provided they are able to find one another and mate. Until more is known about the underlying biology of the species, this parameter, and its effects on long-term viability, will remain poorly defined.

6.3.3 Spatial Distribution and Connectivity

Despite substantial population declines from 2013-17, *P. helianthoides* still occupies the whole of its historic range from Alaska to northern Mexico, though in nearshore areas from the outer coast of Washington to Mexico the species is now rare where it was once common. Natural resource managers and researchers in the contiguous United States consider several local populations off Oregon and California to be functionally extirpated, but reports of newly settled juveniles and occasional adults in these regions demonstrates continued occupancy. With so few individuals, a new wave of SSWS or other catastrophic event could wipe the species out in these areas, but SRT members felt that the lack of adequate sampling of deep waters and patchy encounter reporting in bottom-contact fisheries with a high likelihood of interaction (e.g., crustacean pot/trap fisheries) introduced sufficient uncertainty to preclude stating that *P. helianthoides* had been eliminated throughout this southern portion of its range.

Spatial distribution and connectivity are integrally related with the abundance and productivity VP parameters. Species occurrence, density, habitat use, and intraspecific interaction rate, alongside environmental parameters, ultimately determine population productivity and abundance. As a habitat generalist with broad resilience to physiochemical environmental variables, *P. helianthoides* utilizes most available benthic habitats from the nearshore down to several hundred meters deep throughout its range. Loss of over 90% of the population in southern portions of the range almost certainly resulted in population fragmentation, but the only areas where data exist to confirm this are shallow, SCUBA-accessible habitats. Kelp forests and rocky reefs, in particular, are well sampled and may represent key habitats for *P. helianthoides*, but regular occurrence on mud, sand, and other soft-bottom habitats is also well documented. Undersampled, deep-water habitats represent the majority of suitable habitat for *P. helianthoides* by area, however, additional effort is needed to characterize both how individuals in these waters are distributed and how they connect demographically with populations in shallow waters. Less accessible nearshore areas, largely those associated with sparsely populated areas, also suffer from undersampling.

Direct evidence to assess the connectivity of *P. helianthoides* populations at various geographic scales is lacking. Without meristic, morphological, physiological, and/or genetic studies to demonstrate similarities or differences among population segments linkages cannot be adequately evaluated. As noted above (section 6.3.2 Productivity) assumptions can broadly be made about larval distribution as a consequence of prevailing flow patterns, but the SRT found evidence both for and against connections over large geographic scales for echinoderm populations on the West Coast. Several members also noted that population declines associated with the SSWS pandemic were severe enough that historic patterns of spatial distribution and connectivity could have been obliterated in the last decade, and may continue to change into the foreseeable future.

After taking into account the best available information on both the historic and present spatial distribution of *P. helianthoides*, the majority of SRT members felt this VP parameter contributed to a moderate risk of extinction. This was largely due to evidence of population fragmentation in nearshore areas and several data series demonstrating very low abundance across broad portions of the range. The team was unable to adequately assess connectivity due to a lack of data.

6.3.4 Diversity

Systematic comparisons of morphology, life history, behavior, physiology, genetic traits, and other aspects of diversity do not exist for *P. helianthoides*. While some authors note that animals in the northern portion of the range grow to a large diameter and mass, this general statement is not backed up by data. As a result of this lack of information, the SRT struggled to adequately evaluate the impact of this parameter on extinction risk. Data from proxy species, such as *Pisaster ochraceus*, demonstrate that variation in physical characteristics such as color can be both genetically and ecologically controlled in asteriids (Harley et al. 2006; Raimondi et al. 2007). While examples exist of echinoderm species with both substantial population structuring and a complete lack of population structure on the West Coast, where *P. helianthoides* falls along this spectrum could not be determined due to the lack of fundamental biological knowledge pertinent to population dynamics. As a result, the team scored this factor as having an unknown contribution on overall extinction risk.

Several SRT members noted that variation in habitat across the range of *P. helianthoides* could speak to assumed variation in physiological traits like temperature tolerance. Near extirpation at a local level, then, in southern portions of the range could have resulted in a loss of diversity prior to requisite data being collected. Loss of genetic adaptation to warmer water, if present, is a potentially large concern as global warming continues to threaten West Coast waters in the foreseeable future. Schiebelhut et al. (2018) document shifts in allele frequencies at the population level for *Pisaster ochraceus* before and after the SSWS pandemic. Juveniles now reflect the surviving population, which differs significantly from the pre-wasting population. Whether a similar shift in evolutionarily relevant genetic traits occurred for *P. helianthoides* is unknown, but did give several SRT members cause for concern.

6.4 Threats Analysis Results

6.4.1 Habitat Destruction, Modification, or Curtailment

Pycnopodia helianthoides is a habitat generalist known to occur in association with a broad diversity of substrate types, grades of structural complexity, and biogenic habitat components. Habitat degradation and modification in nearshore areas of the West Coast as a consequence of direct human influence is largely focused in urbanized centers around estuaries and embayments, with considerable tracts of sparsely populated, natural shoreline in between. This is especially true of the northern portion of the range. In urbanized areas, nearshore modification to accommodate infrastructure has dramatically changed the available habitat over the last two hundred years. Shoreline armoring, dredging, diking of estuaries for agriculture, and a plethora of other land use practices have fragmented the landscape, resulting in the loss of sensitive habitats, such as kelp forests and rocky reefs. The relative importance of such habitats to the range-wide health and persistence of *P. helianthoides* is difficult to quantify, however, because suitable habitat occurs well beyond the depth range where most sampling occurs. Members of the SRT also noted that human impacts on nearshore habitats and species of the West Coast have long been recognized, and that marine protected areas, sanctuaries, and other place-based conservation measures have been created in a variety of jurisdictions in recent decades. While these measures have not explicitly targeted *P. helianthoides*, many of them are centered on sensitive habitats and provide protections to the ecosystem at large, including both *P. helianthoides* and their prey base. Under current nearshore management practices, *P. helianthoides* has persisted in urban seascapes at apparently healthy population levels until very recently, when SSWS resulted in the death of 90% or more of the population. As a result, SRT members evaluated nearshore habitat destruction or modification as a low-level contributor to overall extinction risk, but noted that systematic sampling is needed to establish whether certain habitat types are critical to specific life stages or behaviors, and limiting. If, for instance, kelp forests are demonstrated to represent an important and irreplaceable role in the life history of *P. helianthoides*, their loss could represent a critical threat.

Pycnopodia helianthoides also occurs on benthic habitats to depths of several hundred meters, and anthropogenic stressors affecting these offshore waters are markedly different from those affecting the nearshore. Quantifying impacts to *P. helianthoides* habitat in deeper waters is more complicated, however, and less information is available to support a rigorous evaluation. Fishing with bottom contact gear, laying communications cables, mineral and oil exploration, and various other human activities have direct influence on benthic habitats in offshore waters of the North Pacific Ocean. The activities are highly likely to interact with *P. helianthoides* at some level, but data are lacking regarding both the distribution of individuals in these deeper waters and impacts from particular stressors. As a result, the SRT was unable to effectively assess the contribution of deep-water habitat modification or destruction on overall extinction risk. Some members, however, noted that the geographic input of all potential stressors was likely to be small relative to the documented range of *P. helianthoides* and that the species' adaptability and resilience were unlikely to make habitat impacts in these areas a substantial threat.

Curtailment of the range of *P. helianthoides* has not yet been demonstrated, despite the fact that the species has become rare from the Washington coast south to California since the SSWS pandemic, in areas where it once was common. The total population estimate for this region still stands at over five million individuals (Gravem et al. 2021). Population fragmentation as a consequence of dramatic losses in abundance could result in range curtailment in the foreseeable future, but occasional reports of juvenile *P. helianthoides* at locations along the West Coast as far south as the Channel Islands demonstrate that local extirpation has not yet occurred. If juveniles do not mature and successfully reproduce because of a resurgence of SSWS, or some other factor, a substantial reduction in distribution could occur at the southern extent of the currently documented range.

6.4.2 Overutilization

6.4.2.1 Commercial, Artisanal, and Recreational Fisheries, Including Bycatch

There are currently no substantial directed fisheries for *P. helianthoides*, but recreational harvest is allowed in British Columbia, California, and Mexico and occurs at unquantified levels. Impacts from these fisheries cannot be evaluated because data are not available on either an aggregate or species-specific basis, however, market drivers for this species are minimal and human consumption is not known to occur.

The majority of the SRT agreed that bycatch impacts are a low-level concern for a variety of fisheries that use bottom contact gear. This includes fisheries for benthic fishes and invertebrates that employ trawls, pots, traps, nets, and, to a limited degree, hook-and-line. Information to quantify the encounter rate in specific fisheries is largely lacking, as are data demonstrating direct impacts of these encounters, and frequent aggregation of all sea star catch into a single reporting category precludes a species-specific assessment. That said, *P. helianthoides* is relatively resilient to handling and mortality rates as a direct effect of gear contact, removal from gear, and placement back in the water are likely to be low in most cases.

Several SRT members noted that post-release, handling-related stress could exacerbate symptoms of SSWS or increase susceptibility to other sources of mortality. This could make handling during fisheries a greater threat in regions where population abundance is especially low, such as from coastal Washington to the southern extent of the species' range. The importance of any particular fishery to the overall health of the species depends on the geographic footprint, seasonal duration, and participation level, and how these variables change year to year. Unfortunately, as a non-target species, systematic reporting of *P. helianthoides* encounters does not occur at this time. The tradeoff between decreased encounter rate and residual impacts on remaining individuals will vary by fishery and is likely to be linked with environmental conditions such as sea surface temperature.

6.4.2.2 Trade

The collection, drying, and trade of small "sunflower stars" is noted in Gravem et al. (2021) and in the ESA-listing petition received from the Center for Biological Diversity. This practice predominantly affects small stars under 6 in. in diameter and the retailers that offer these curios often do not list the species, site of collection, or other details necessary to determine whether populations of *P. helianthoides* are being directly impacted. Given that sea stars can be collected in British Columbia and Mexico, and in California seaward of a tidal exclusion zone, a more thorough evaluation of retail offerings is needed. Without additional information, the SRT applied the weight of evidence approach to unanimously score this threat as having an unknown, but likely negligible, impact on extinction risk in the foreseeable future due to a lack of demand and evidence of a substantial market.

6.4.3 Disease or Predation

6.4.3.1 Disease

The SRT unanimously recognized disease, specifically SSWS, as the single greatest threat affecting the persistence of *P. helianthoides* now and into the foreseeable future. While the etiology of the disease remains unknown, as well as what trigger(s) resulted in its rapid spread to pandemic levels (Hewson et al. 2018), the widespread occurrence of, and impacts from, the disease from 2013-17 are broadly documented. Populations were diminished range-wide, and in southern portions of the range estimated losses are on the order of 95% or more. There was considerable variation in the degree of impact, however, associated with depth, latitude, and (sometimes) recent temperature regime, but projected losses in all regions where data were sufficient amounted to ~90% or more (Gravem et al. 2021). Here, we demonstrated that these declines have continued at least through 2021 in most regions (section 3.4.2.2 MARSS Results), though recent settlement events have been recorded in the Salish Sea and Alaska. Whether new cohorts survive long enough to reproduce, or succumb to SSWS, is highly uncertain. Whether reproductive adults who survived the SSWS pandemic demonstrate resistance or immunity to future outbreaks is also crucial to species survival. Until more is known about this highly lethal disease and its impacts on the remaining population of *P. helianthoides*, predictions about species persistence cannot be accurately made. While environmental variables like sea surface temperature and pH have been provisionally linked with SSWS the relationships are complex and inconsistent (Hewson et al. 2018; Harvell et al. 2019), hinting that interactions among variables may be important.

The SRT found no evidence that other known diseases constitute substantial threats to the continued persistence of *P. helianthoides* now or in the foreseeable future. One complicating factor is that the physiological response of sea stars to numerous stressors is to develop lesions, autotomize arms, and/or disintegrate. These symptoms, and ultimate disposition, are shared with SSWS, making it possible that a suite of disease pathogens or stressors jointly contribute to the observed syndrome. As the end result of any such disease is loss of life within just a few days, the threat from disease still remains high whether SSWS is caused by a single pathogen or many.

6.4.3.2 Predation

Very few predators are known to consume adult *P. helianthoides* and this is not expected to change even under generous projections of ecosystem changes as a consequence of global climate change or other factors. Predation risk is likely highest during the planktonic larval phase when indiscriminate filter feeders consume small larvae and selective pickers target larger, more developed individuals. The prolonged duration of the larval period could enhance this risk, but there is no evidence to suggest that current risks of predation are any higher than they were prior to the pandemic when populations were healthy. Additionally, while the fecundity of *P. helianthoides* is not well known, even conservative estimates suggest that an individual female likely produces millions of eggs in a single spawning event. Based on the information available, the SRT concluded that predation is not likely to be a substantial contributor to extinction risk, now or in the foreseeable future.

6.4.4 Inadequacy of Existing Regulatory Mechanisms

In Alaska, Washington, and Oregon harvest/collection of *P. helianthoides* is not allowed, but in British Columbia, California, and Mexico recreational harvest is. Though data are not available to determine how intensive this harvest is, human consumption of *P. helianthoides* is not known to occur and large markets for dried or otherwise processed specimens do not exist. Considering this information, the SRT determined that current harvest/collection regulations do not contribute substantially to the extinction risk of *P. helianthoides*, nor are they likely to in the foreseeable future. Inconsistency of regulations across jurisdictions could complicate enforcement, however, unless coordinated efforts to standardize or reconcile rules occur. It may also become necessary in the foreseeable future to propose and publicize handling recommendations for bycaught *P. helianthoides* to reduce handling stress and mortality, should data support that this is a more significant threat than initially recognized.

A patchwork of place-based conservation measures exists across the known range of *P. helianthoides* that are designed to protect ecologically sensitive and/or important habitats and species. While none of these are specifically directed at conservation of *P. helianthoides* or its habitat, many of them provide indirect protection to the species, its habitat, and its prey. If new data identify specific habitat features that are crucial to the survival of remnant populations of *P. helianthoides*, especially in the southern portion of the species' range, it may be prudent in the foreseeable future to extend place-based management to such areas in the form of marine protected areas, conservation zones, etc. At this time, however, the SRT determined that insufficient information is available to effectively implement such measures.

The effectiveness of regulations controlling anthropogenic climate change are a considerable concern because they affect stressors like elevated sea surface temperature and lowered pH, which have sweeping effects on marine prey base and living conditions. Projections show that even draconian cuts now will have little impact on continued warming and ocean acidification for several decades. If or how SSWS prevalence, transmissibility, and lethality are linked to these stressors is unknown but warrants investigation. If regulations are unable to reduce the impact of these stressors in both the short- and long-term it is unlikely that *P. helianthoides* populations will have the capacity to adapt rapidly enough to ecosystem changes to persist.

It is unclear what regulatory mechanisms might effectively reduce extinction risk as a consequence of SSWS. While a given disease can sometimes be isolated to a geographic region or eliminated by a combination of quarantine, transport embargos of specimens carrying the pathogen, or the administration of vaccines, these actions all require considerable knowledge of the disease itself. In the case of SSWS, the pathogen has not yet been identified, the cause may be several pathogens with similar etiologies, and the disease has been observed across the full range of the species. For these reasons, the SRT found that while existing regulatory mechanisms are insufficient to address the threat of SSWS it is unlikely that any effective regulatory approaches will arise in the foreseeable future without considerable research.

6.4.5 Other Natural or Manmade Factors

6.4.5.1 Pollutants and Environmental Contaminants

Direct impacts of environmental pollutants to *P. helianthoides* are unknown, but they likely have similar effects to those seen in other marine species, given physiologically similar processes. Reductions in individual health and disruption of nutrient cycling through food webs are hallmarks of industrial chemicals, heavy metals, and other anthropogenic contaminants. With *P. helianthoides* representing a monotypic genus there is substantial uncertainty involved with projecting potential impacts into the foreseeable future, and SRT members were not comfortable extrapolating whether any specific chemical or suite of chemicals represented a direct, tangible threat to range-wide population viability of *P. helianthoides*. Any impacts that do exist are likely to be more intensive near their source, such as urban bays and estuaries, though many persistent contaminants are known to propagate long distances over the course of several decades or more.

6.4.5.2 Climate Change

The addition of anthropogenically released greenhouse gasses into the atmosphere since the industrial revolution has resulted in climate change that is affecting organisms and environments on a global basis. While direct linkages between climate change and *P. helianthoides* population status have not been made in the literature, impacts to prey base, habitat, and SSWS can all be inferred from available data.

Larval life stages of numerous shell-forming marine organisms are highly sensitive to chemical composition of pelagic waters, including aragonite saturation level, such that ocean acidification can increase physiological stress and decrease survival in a broad array of organisms (e.g., Barton et al. 2012; Gazeau et al. 2013; Waldbusser et al. 2015). Additionally, life stages of various planktonic organisms are sensitive to temperature, with elevated temperature increasing metabolic rate and, thus, nutritional requirements. Furthermore, some marine organisms rely on seasonal shifts in temperature and other environmental cues to identify suitable spawning times, aligning planktonic feeding periods of larvae with phytoplankton blooms. Changes in the spatiotemporal availability and quality of prey affect planktotrophic larvae and may result in reduced growth, delayed settlement, starvation, and various other negative outcomes. Though the planktonic diet of *P. helianthoides* larvae has not been adequately described, it is likely that they consume shell-forming organisms to various degrees depending on spatiotemporal variability in abundance, quality, and encounter rate. Members of the SRT arrived at a variety of conclusions with regard to the potential impact of perturbations in prey base integrity on the extinction risk of the species, with broad uncertainty making a consensus elusive.

Nearshore benthic communities can also be affected in myriad ways by elevated carbon dioxide levels, reduced pH, increased temperature, and other physiochemical changes resulting from anthropogenic climate change. Interspecific variation in tolerance to such changes can result in some algal species outcompeting others, simplifying community composition and reducing habitat complexity (Harvey et al. 2021). Mobile species may respond to such stressors by seasonally, or permanently, shifting their range to exploit deeper, less affected waters or shorezone areas where local hydrodynamics ameliorate the threat to some degree (e.g., through wave action, longshore currents, or upwelling). Impacts from climate change have also been linked to the frequency and intensity of harmful algal blooms in marine waters (Griffith and Gobler 2020), which can toxify the food web and deoxygenate otherwise productive waters to levels where mass fish and invertebrate kills occur. While these effects of climate change are unlikely to affect *P. helianthoides* across its full range simultaneously, the SRT determined that decreases in habitat suitability were likely on a localized basis and that such stressors could exacerbate consequences of low abundance noted above, especially in southern portions of the range. Again, high levels of uncertainty regarding interactions among climate-related stressors and their impacts specifically on *P. helianthoides* population viability make it impossible to adequately project effects on extinction risk into the foreseeable future.

Temperature change, and specifically temperature differential, are known stressors of asteroids, thus even without considering SSWS, elevated temperature is likely to result in population-level impacts on *P. helianthoides*. These effects are likely to be highly variable across time and space, though marine heat waves that affect the whole of the northern Pacific Ocean are capable of producing range-wide stress. While temperature change has been linked with SSWS in some cases (Hewson et al. 2018; Harvell et al. 2019) it might be temperature differential rather than absolute temperature that induces a stress response and increases disease susceptibility. Taking into account all likely impacts of climate change on *P. helianthoides*, and accounting for knowledge gaps and uncertainty, the SRT determined that it is likely to moderately affect extinction risk both now and into the foreseeable future.

6.5 Overall Extinction Risk Conclusions

6.5.1 Throughout the Range of the Species

Little is known about several fundamental biological aspects of *P. helianthoides*, such as age at maturity, longevity, reproductive output, population resiliency, etc. However, *P. helianthoides* is a broadcast spawner, utilizes a broad range of habitats and prey, and has a broad geographic distribution, all of which buffer the species against catastrophic events and reduce overall extinction risk. The abundance and density of the species have clearly declined recently throughout the vast majority of its range, though data are highly uncertain in deep waters and less accessible/well surveyed regions. In some areas functional extirpation is likely in the foreseeable future of 30 years, though surveys may not capture the youngest age classes, and rebounds in these areas may be impossible due to a lack of mate availability and sufficient reproductive capacity in remaining individuals. Best estimates available indicate that the remaining range-wide abundance of *P. helianthoides* is approximately 600 million individuals, with the highest abundances off Alaska and British Columbia, primarily in deeper water (at lower densities).

Given the widespread impacts of SSWS from 2013-17, it is likely that surviving individuals of *P. helianthoides* were exposed, giving hope (but no direct evidence) that they bear some resistance to the causative agent of the disease, though this agent remains unknown. SSWS is the single greatest threat to *P. helianthoides* on a range-wide basis, and may be exacerbated by global warming, ocean acidification, toxic contaminants, etc. A conclusive link has not been demonstrated but is likely given physiology and known stressors of this, and other sea star, species. Regions most likely to be impacted by climate change factors are in the south, where the population was most heavily impacted by the SSWS pandemic. Fishing pressure (including bycatch), the curio trade, and habitat degradation are threats, but are not anticipated to have dramatic, population-level impacts in the next 30 years on par with likely impacts from SSWS. Regional variability in threat severity could result in total loss of the species in the southern portion of its geographic range, but whether the loss of this portion of the population compromises the long-term viability of the species is unknown. Overall, threats to population persistence exist, with high uncertainty about potential impacts, and trajectories in many areas continue downward. **As a result of this synthetic analysis of aspects of species viability and threats facing the species, the SRT concluded that *P. helianthoides* is at moderate risk of extinction now and in the foreseeable future throughout its range.** SRT members were unanimous in individually assigning their highest number of points to this extinction risk tier, though two team members also assigned the same number of points to the low risk tier. On average, team members individually assigned less than two points to the high risk tier, and only 18% of total points across all members were allocated there.

6.5.2 Significant Portion of its Range Analysis

In order to be listed, Section 3 of the ESA requires a species to be either endangered or threated "throughout all or a significant portion of its range." Having concluded that the sunflower sea star is at moderate risk of extinction now and in the foreseeable future throughout its range (section 6.5.1 Throughout the Range of the Species), an assessment of population status and overall extinction risk within any and all significant portions of its range (SPR) was undertaken to determine whether it may currently be in danger of extinction in any identified SPR. If found to be in danger of extinction in any SPR, NMFS may then consider elevating the proposed listing from "threatened" to "endangered."

In 2014, the USFWS and NMFS issued a joint policy on interpretation of the phrase "significant portion of its range" (79 FR 37578). Subsequent challenges to the Services' interpretation lead to several court rulings invalidating certain aspects of the policy. However, consistent with elements of the policy that remain intact, to help facilitate the SPR determination NMFS asks: 1) what is the status of the population segment and is it at a higher risk of extinction relative to population segments elsewhere in the range?; and 2) is the population segment biologically significant to the overall viability of the species? Biological significance is evaluated using the same viable population criteria applied to the range-wide evaluation (i.e., abundance, productivity, spatial distribution/connectivity, and diversity). Ultimately, the goal of asking these questions is to identify specific areas – SPRs – in which threats are acting on a critical population segment to produce a heightened extinction risk, thus resulting in the possible elevation of the proposed listing for the species at large.

To conduct the SPR analysis, SRT members were provided a base map of the northeast Pacific Ocean labeled with several geophysical features either referenced in the IUCN status assessment of *P. helianthoides* or known to be associated with demographic breaks in a variety of other marine organisms (Figure 10). Team members were given ten days to independently consider all available data and information known about the VP parameters and threats to *P. helianthoides* on a regional basis and generate proposals for areas that could represent an SPR. These portions were to be highlighted on the map, and detailed justifications provided regarding the intensity of specific threats to, and biological significance of, the population segment in the identified portion(s).

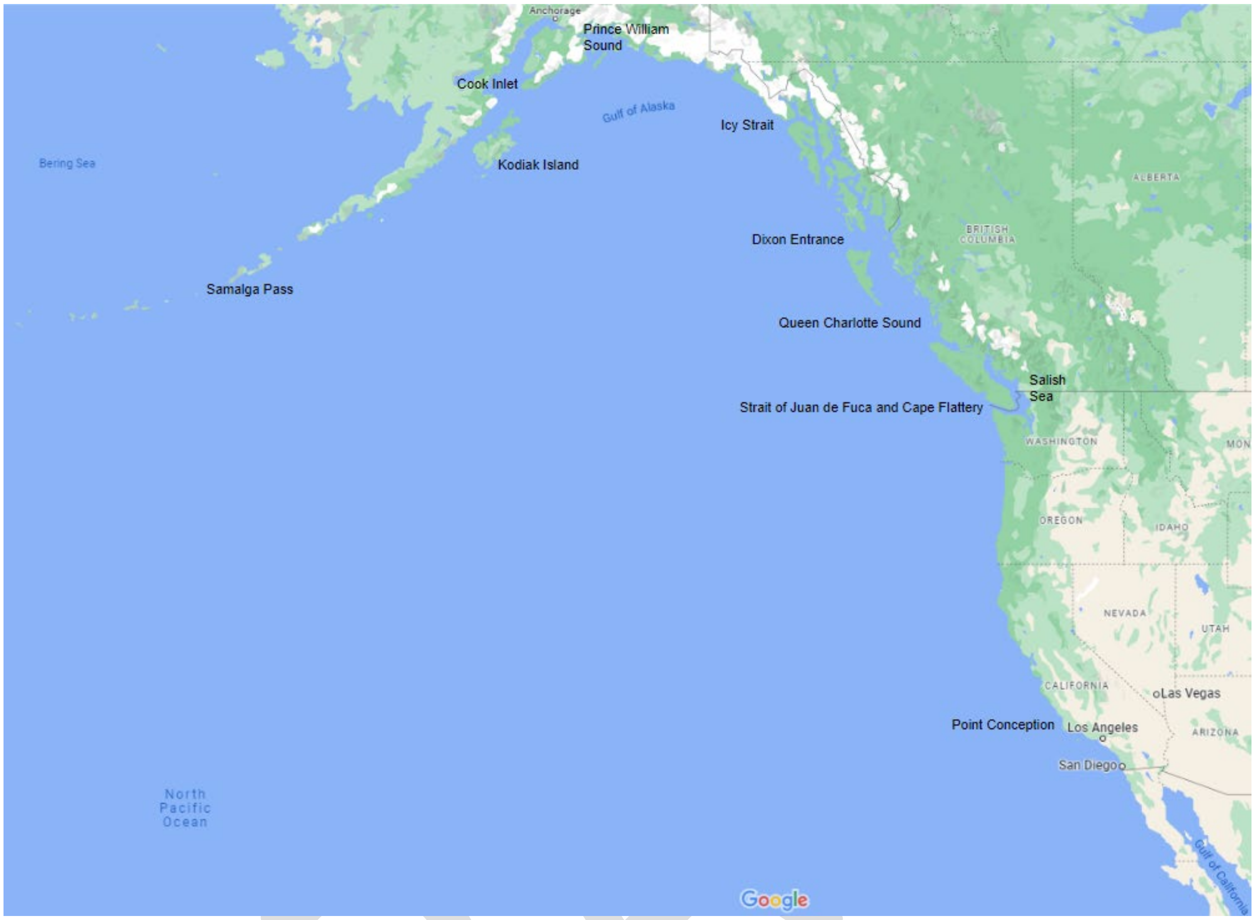

Figure 10. Map provided to members of the Status Review Team to annotate in order to identify potential significant portions of the range of *Pycnopodia helianthoides*. Annotations were accompanied by written justifications of variation in viable population parameters and intensity of identified threats. Place names represent major geophysical features of the West Coast that were either used in the IUCN assessment for this species (Gravem et al. 2021) or that have been previously associated with demographic breaks in other marine species.

After the allotted time, four scenarios to approach the significant portion of the range analysis were proposed. The first, and most granular, divided the range of *P. helianthoides* into twelve portions based largely on population abundance data series availability, and often coinciding with political boundaries (e.g., the Oregon Coast portion). The portions proposed matched those used in the IUCN assessment (Gravem et al. 2021, their Figure 1a), facilitating direct comparison, and allowing for a high-resolution evaluation of biology and threats. Team members noted, however, that a lack of information about variation in VP parameters among these proposed portions prohibited evaluation of biological significance at this scale. Additionally, major threats affecting the extinction risk of *P. helianthoides*, such as SSWS and climate change, operated across multiple proposed portions at apparently similar intensity. This resulted in the team merging several portions to produce a second scenario consisting of six potential portions: 1) the Aleutian Islands and western Gulf of Alaska (including Kodiak Island and Cook Inlet); 2) the eastern Gulf of Alaska and Southeast Alaska to Dixon Entrance; 3) coastal British Columbia and the entirety of the Salish Sea; 4) the outer coast of Washington and Oregon; 5) the California coast to Point Conception; and 6) the Southern California Bight and Baja California to the southernmost end of the range (Figure 11).

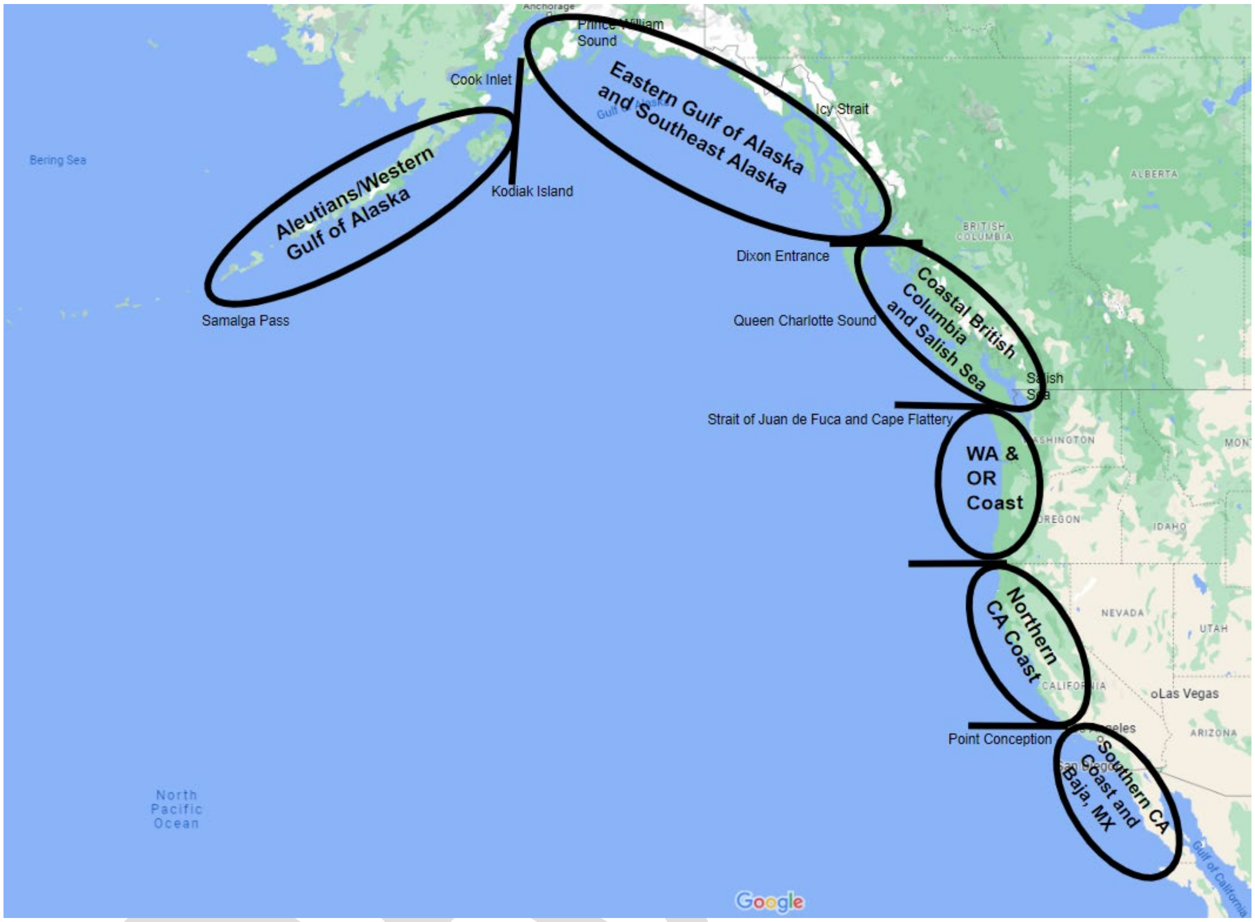

Figure 11. Map identifying six potentially significant portions of the range of Pycnopodia helianthoides identified as Scenario Two by the Status Review Team.

In this second scenario, Portion 1 is distinct in having the lowest apparent impact from SSWS (61%) (Gravem et al. 2021; section 3.4 Species Status Assessment) and being, perhaps, the least impacted by climate change and other anthropogenic influences as a consequence of its remoteness and low human population. These conclusions about threats are largely inferential, however, as distribution and population trend data are comparatively sparse here. This population segment is also likely to receive larval input from Portion 2, and possibly Portion 3, by way of the Alaska Current, but to maintain viability largely by intraregional recruitment facilitated by complex local flow patterns. Without additional VP parameter data to differentiate the population in Portion 1 from Portion 2, the SRT determined that their shared environmental and climatic conditions, dominant ocean circulation regime, and large-scale ecological similarity argued for their merger (see third scenario below). Portion 3 is distinct for having an intermediate estimated population loss due to SSWS (90-92%) and being located where the North Pacific Current impacts the North American continent and bifurcates into the Alaska

Current and the California Current. Seasonal and decadal variation in current intensity and bifurcation location drives distinct climatic and ecological patterns in this region, which are amplified by the convoluted, complex nature of the shoreline. Populations of *P. helianthoides* in this portion could serve as larval source populations for portions both to the north and south based on patterns seen in other broadcast spawners, though direct biological data to confirm this connection are lacking. Additionally, the Salish Sea region is dominated by several large cities and ports (e.g., Vancouver, Bellingham, Seattle, Tacoma) where human population density contributes to increased intensity of contamination, fishing pressure, and other threats. Portions 4, 5, and 6 vary with regard to relatively minor population viability threats and have distinct ecological profiles, but the impact of the SSWS pandemic was a >95% estimated loss of abundance in all three areas. Additionally, little information is available to distinguish among these areas with regard to aspects of the VP parameters, but all are likely to receive larval input from Portion 3 (with the connection diminishing with distance) while being unlikely to reciprocate given the southward flow of the California Current. Seasonally, the California undercurrent and Davidson Current could provide limited transport of larvae northward (Thomas and Krassovski 2010), but it is unknown how spawn timing and larval distribution match up temporally with these complex flow patterns. Given the shared pattern of impacts from key threats, dominant flow patterns, and the lack of data available to demographically separate population segments within these portions, the SRT felt that merger was, again, appropriate.

Merging portions as described above, the SRT then considered a third scenario with three portions: 1) all waters of the range north of Dixon Entrance; 2) coastal British Columbia and the Salish Sea; and 3) all waters of the range south of Cape Flattery, to Baja California. These align with the shared population trends assessed above (section 3.4 Species Stock Assessment) and shared attributes of these portions are also noted in discussion of the second scenario. Pre-pandemic abundance and density estimates further support these separations. In waters shallower than 25 m, where assessment data are most readily available and comprehensive (Gravem et al. 2021; section 3.4 Species Status Assessment), over 72% of the pre-pandemic abundance of *P. helianthoides* occupied Portion 1 (i.e., waters off Alaska). In the Gulf of Alaska and Southeast Alaska density estimates are in excess of 100,000 individuals/km^2. Portion 2 (i.e., coastal British Columbia and the Salish Sea) is estimated to have held ~17.5% of the population, with densities over 85,000 individuals/km^2 in waters of the Salish Sea and over 17,000 individuals/km^2 along the outer coast. Despite being geographically extensive, Portion 3 (i.e., coastal Washington, Oregon, California, and Mexico) was estimated to be occupied by the remainder of the species, just under 10% of the total shallow-water population. Densities throughout this portion ranged from 34-45,000 individual/km^2 with the exception of Baja Mexico, where the density was estimated at just 2,586 individuals/km^2. It should be noted that nearly 45% of the pre-pandemic population was estimated to occupy waters deeper than 25 m, which are disproportionately located off of Alaska and coastal British Columbia, further amplifying these patterns. Taken together, the SRT determined that these estimates indicate a population center in the North

Pacific, a transition zone along coastal British Columbia and into the Salish Sea, and a southward extension of the species through temperate waters at limited abundance/density until thinning out in the subtropics around the Southern California Bight. As the fourth potential scenario the SRT considered merging Portion 2 with Portion 3, but this reduced inference power by incorporating an ecologically and biologically distinct transition zone into the trends observed in southern waters.

Having established three geographic regions to include in the significant portion of the range analysis, the SRT turned explicitly to the questions of status, threats, and biological significance at this scale. The population center of *P. helianthoides* is in Alaskan waters, and the population segment here was less impacted by SSWS with considerably more individuals surviving (over 275 million in shallow waters and as many as 400 million in deep waters [Gravem et al. 2021]). Given these facts, the SRT determined that the population segment occupying Alaskan waters is not at higher risk of extinction than the species overall and does not, therefore, constitute a significant portion of the range for ESA status assessment purposes. Conversely, waters off of coastal Washington, Oregon, and California are estimated to have held less than ten percent of the pre-pandemic population of *P. helianthoides* and saw losses >95% from 2013-17, with few signs of recovery. While it is possible that individuals in this portion who survived the pandemic are disease resistant, or contain genes for thermal tolerance or adaptability to other environmental parameters, data do not exist at this time to support this assertion. Furthermore, being at the southern end of a current system that flows predominantly southward it is unlikely that these traits could be naturally transmitted into northern populations via planktonic drift. Taken together, this caused the SRT to conclude that while risk of extinction may be higher in the southern portion of the range due to dramatically decreased abundance and density post-pandemic, loss of this population segment would not be biologically significant relative to the overall evolutionary trajectory of *P. helianthoides*. As such, the portion from Cape Flattery south does not constitute a significant portion of the range for ESA status assessment purposes.

The final portion under consideration (coastal British Columbia and the Salish Sea) is situated where currents flow both north and south into other portions, uniquely positioning it to serve as a biologically significant source population shaped by a distinctive ecological system. Populations of *P. helianthoides* in this portion experienced substantial declines from SSWS, but not as substantial as those noted farther south. In addition, while there is some recruitment to offshore sites, and relatively healthy populations in some glacial fjords, there is evidence of source/sink dynamics within this area with lack of older/reproductive animals in the offshore area and a lack of juveniles that mature past a few years in the nearshore. Higher abundance within the Salish Sea may, in fact, allow the population here to serve as a source to Coastal British Columbia, and beyond. The possibility of disease resistance in these remaining individuals cannot be discounted, but has not yet been directly demonstrated. Persistent low encounter rates in the region, however, suggest a degree of resiliency despite ongoing occurrence of the causative agent of the disease (whatever it may be) in the environment. The Salish Sea region is influenced by a number of other threats, such as toxic contamination, pressure from a diversity of fisheries, and extensive habitat degradation/destruction associated with creation and maintenance of human infrastructure. To assess whether these threats elevated overall extinction risk in the coastal British Columbia and Salish Sea region, a second overall extinction risk scoring sheet (Table 8) was distributed and team members were directed to independently assess this portion of the range. Though there is a high degree of uncertainty with regard to the potential impact of SSWS and other threats on the population segment in this portion, the SRT determined that overall extinction risk is moderate, matching that of the range-wide assessment.

The SRT evaluated the likelihood that a significant portion of the range of *P. helianthoides* exists in which threat intensity is higher than that experienced by the species at large, the population segment occupying the area is of biological significance to the persistence of the species, and the overall extinction risk is higher than that observed for the species at large. This evaluation occurred at four scales, as detailed above, and in no case did the SRT conclude that more than a moderate risk of extinction existed for any particular portion of the range.

7. SUMMARY AND CONCLUSIONS

This status assessment was initiated in response to a petition from the Center for Biological Diversity to list the sunflower sea star *Pycnopodia helianthoides* as a threatened or endangered species under the Endangered Species Act (ESA). A Status Review Team consisting of federal biologists, ecologists, resource managers, statisticians, and ESA process experts was convened, and expert testimony was provided by numerous knowledge holders. After reviewing and summarizing all available information on the life history, ecology, abundance, and distribution of the species, the team performed an extinction risk assessment by evaluating the contribution of viable population parameters and specific threats to the overall extinction risk of the species now and 30 years into the foreseeable future. The threats considered were the ESA Section 4(a)(1) factors: (1) the present or threatened destruction, modification, or curtailment of habitat or range; (2) overutilization for commercial, recreational, scientific, or educational purposes; (3) disease or predation; (4) inadequacy of existing regulatory mechanisms; and (5) other natural or man-made factors affecting the species' existence. The team concluded that disease, specifically sea star wasting syndrome, and climate change represented the two major threats to *P. helianthoides*, but that several other factors also increased overall extinction risk. In the end, the team unanimously determined that *P. helianthoides* is at moderate risk of extinction throughout its range in the foreseeable future. The team then conducted an analysis to determine if there was any portion of the range in which status was demonstrably lower, threat intensity was demonstrably higher, the population segment residing there was biologically significant, and extinction risk was likely to also be higher. After evaluating four scenarios in which the range was parsed up at varying scales the SRT determined that there were no significant portions of the range in which extinction risk was elevated. As such, the team concludes that overall extinction risk for *P. helianthoides* is moderate under the criteria and guidelines set forth for evaluation of ESA listing petitions.

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