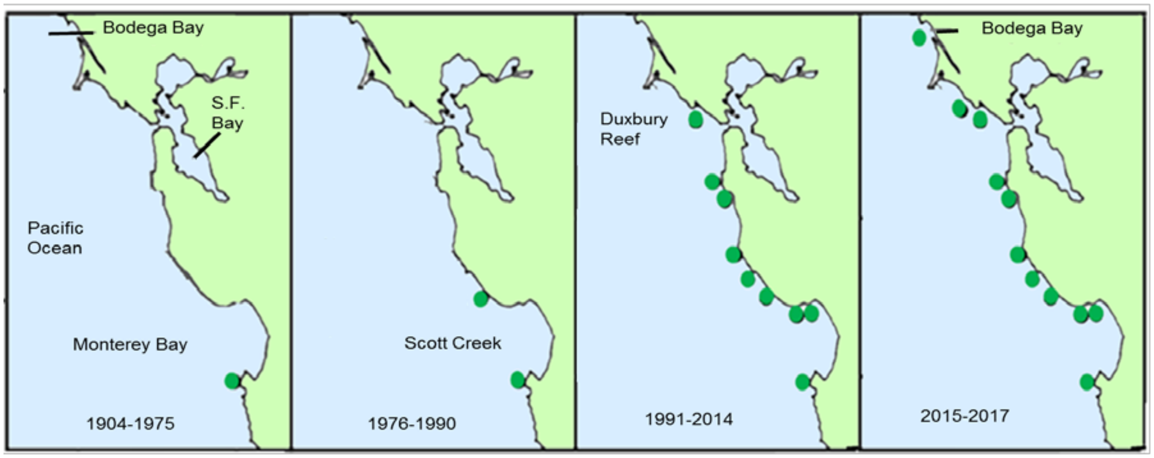
NUDIBRANCH RANGE SHIFTS

A species of nudibranch sea slug is expanding its range northward along the California coast in response to warming ocean conditions.

Figure 1. Northernmost locations of *Phidiana hiltoni* along the California coast (1904-2017)



Source: Adapted from Goddard et al., 2011, updated 2017

What does the indicator show?

Historical surveys of nudibranch populations along the California coast show a 210 kilometer (km) northward shift in the range for *Phidiana hiltoni* (*P. hiltoni*) since the mid-1970s (Goddard et al., 2011; 2016). Figure 1 shows locations where *P. hiltoni* had been observed (green dots) during four different periods, starting in 1904. Until 1975, *P. hiltoni's* most northern location was on the Monterey Peninsula. Beginning in the late 1970s, its range expanded north across Monterey Bay to Santa Cruz County. By 1992, it had spread another 110 km up the coast into the San Francisco Bay area as far north as Duxbury Reef. By 2015, it had reached Bodega Bay. Following its initial spread, *P. hiltoni* has persisted at each of these sites to the present day.

Warm water conditions occur periodically in California's coastal waters, usually as part of the El Niño-Southern Oscillation. From late 2013 to 2016, the West Coast experienced unusually warm sea surface temperatures (Bond et al., 2015; Di Lorenzo and Mantua, 2016). Fish and other marine organisms, including many nudibranchs, shifted their distributions farther north during this unprecedented marine heat wave (Cavole et al., 2016). All told, 26 sea slug species were found at new northernmost locations (Goddard et al., 2016; Goddard, 2017). Among these was *P. hiltoni*, which after inhabiting Duxbury Reef for 13 years, was found for the first time in Bodega Bay in 2015. Warm ocean conditions ended in 2016, yet as of late 2017, *P. hiltoni* has persisted at this new northernmost location.

Why is this indicator important?

The habitats of nudibranchs overlap with commercially important organisms, including abalone, crab, and lingcod. Although changes in the ranges of small, short-lived marine organisms such as nudibranchs may seem inconsequential, the nudibranch's response to ocean warming may foretell larger ecological changes that may already have been set in motion by climate change.

Photo Credit: Jeffrey Goddard

The nudibranch sea slug *Phidiana hiltoni* is a soft-bodied marine organism found on the California coast. Nudibranchs are recognized for their intricate shapes and striking colors. They are bottom-dwelling, specialized predators of aquatic invertebrates such as sponges, jellyfish, and in a few cases, other nudibranchs. Lifespans vary from weeks to about a year depending on species. Nudibranchs are not harvested by humans, and many are conspicuous and easy to count in the marine environment (Schultz et al., 2011).

Species live in habitats defined by certain physical conditions, such as temperature and salinity. These conditions often show gradual change through space, creating an environmental gradient across latitudes, elevations, or depths. As conditions change, such as with warming ocean temperatures, species' distributions along an environmental gradient can provide important insights into how they will respond to climate change. For example, many species that can only survive within defined temperature ranges moved to higher elevations with long-term climate warming (IPCC, 2014). *P. hiltoni* has remained in its expanded range even after cooler temperatures have temporarily returned to coastal waters. With climate change driving a longer-term increase in global ocean temperature, scientists expect some of the other northward range shifts observed during the past few years in California to become permanent. Northern populations of these nudibranchs are being closely monitored.

The expansion of marine organisms into new territories can have negative biological impacts on resident organisms, similar to those of invasive species. Population declines in other nudibranch species have occurred at Duxbury Reef, where particularly high densities of *P. hiltoni* have been observed (Goddard et al., 2011). These declines appear to have resulted from *P. hiltoni* preying on other nudibranchs and competing for common prey species. Scientists suggest the range shift of this predatory species may therefore be disrupting food webs and altering community composition at sites along the California coast where its populations are dense.

What factors influence this indicator?

Nudibranchs inhabit the California Current System (CCS), which includes the span of coastline from Oregon to Baja California Sur. In this system, the El Niño-Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO) influence sea surface temperatures (SSTs), coastal upwelling and strength of southerly currents. During certain phases of these oscillations, including El Niño events in which coastal waters shift from relatively cool to warm temperatures and poleward movement of ocean currents increases, researchers have found episodic northward range expansions of nudibranch species.

Local and basin-scale fluctuations in ocean climate can affect larval development, mortality, and transport, and these in turn can affect adult population dynamics. The transport of larval-stage nudibranchs, called *larval advection*, is hypothesized to explain the relationship between ocean climate conditions and changes in adult population abundance. For example, El Niño conditions appear to increase larval advection of nudibranchs from southern source populations, extending their ranges northward and increasing population sizes in shallow water (Schultz et al., 2011; Goddard et al., 2016).

The strong El Niños of 1982-83 and 1997-98 drove transient shifts of many nudibranchs from southern and central California to their northernmost sites (Engle and Richards, 2001; Goddard et al., 2016). In 1976-77 a shift from a cool to warm phase of the PDO and increased sea surface temperatures also corresponded with northward expansion of nudibranchs. When this warm phase ended in 2007 and cooler sea surface temperatures returned in 2008, *P. hiltoni* was the only nudibranch to remain in its expanded range. Interestingly, additional evidence presented by Goddard et al. (2011) suggests that *P. hiltoni* did not occur north of Monterey during the previous warm phase of the PDO, which lasted from 1925 to 1946 (Mantua and Hare, 2002).

Phidiana hiltoni and other nudibranchs are responding in a manner similar to other marine fishes and invertebrates, which have shifted their distributions to higher latitudes and/or into deeper depths in response to warmer conditions (Lluch-Belda et al., 2005; Cavole et al., 2016). A very strong El Niño contributed to an unprecedented multiyear marine heat wave along the Pacific Coast from late 2013 to 2016 and caused extensive biological impacts, including range shifts, at all trophic levels. Investigators documented range shifts for 48 species of sea slugs from 2014 through late 2017 along the California and Oregon coastline associated with the unusually warm ocean conditions (Goddard et al., 2016; Goddard, personal communication). Twenty-six species were found at new northernmost localities, while the remainder were located at or near northern range limits established during previous El Niños. It remains to be seen how many of these species will persist in their northern locations — as *P. hiltoni* has — when ocean conditions shift back to cooler temperatures.

Technical Considerations

Data Characteristics

Historical data (before 1969):
Qualitative searches for sea slugs, especially nudibranchs, were conducted from Monterey to Sonoma Counties by taxonomic specialists. Results are scattered in published papers and monographs, as well as the online database of the Invertebrate Collection at the California Academy of Sciences (http://researcharchive.calacademy.org/research/izg/iz_coll_db/index.asp). The counts of sea slugs in San Mateo County reported by Bertsch, et al. (1972) were conducted intermittently from 1966 to 1970 and were semi-quantitative in nature. The taxonomic results in Marcus (1961) were based largely on collections made in Marin and Sonoma Counties in 1958–9, and those in Steinberg (1963) on collections from Monterey to Sonoma Counties from 1948 to 1963.

Duxbury reef data:
Nudibranch population abundances prior to the arrival of *P. hiltoni* at Duxbury Reef were

estimated based on five timed counts conducted in June and July 1969, January and June 1970, and June 1972; and three more in December 1974 and May and December 1975. Since December 2007, 11 more timed counts of nudibranchs in the same area as the original counts were conducted. Data from all counts were standardized to number of individuals per hour per observer or number of species per hour per observer (Goddard, 2011).

Strengths and Limitations of the Data:

Historical data (before 1969):

Since the 1940s, coastal nudibranch counts by taxonomic specialists have had good geographic representation from Monterey to Sonoma County. Geographic coverage was more limited for the first half of the 20th century, when the only marine laboratory in the region was at Pacific Grove. However, collections of nudibranchs were made in the greater San Francisco Bay region in the early 20th century, and deposited in the Invertebrate Collection at the California Academy of Sciences (CAS), with the associated data now available via the CAS online database (Goddard et al., 2011).

Data since 1969:

The timed counts at Duxbury Reef in the 1960s-70s and again starting in 2007 were conducted by the same two taxonomic specialists in nudibranchs, assisted at times by experienced observers familiar with intertidal nudibranchs from California. This continuity ensures minimal effect of observer on those counts. Since 2011, additional timed counts, as well as qualitative surveys, have been conducted in Marin and Sonoma Counties, supplemented by observations of Bodega Marine Laboratory personnel and citizen scientists. Currently, three sites in Sonoma County, plus two in Mendocino County are being surveyed at least once a year for the presence of *P. hiltoni*.

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