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Cover Page Footnote
We thank Will and Ziggy Goddard for their expert assistance in the field, Jackie Sones and Eric Sanford of the Bodega Marine Laboratory for sharing their observations and knowledge of the intertidal fauna of Bodega Head and Sonoma County, and David Anderson of the National Park Service and Richard Emlet of the University of Oregon for sharing their respective observations of Okenia rosacea in northern California and southern Oregon. We also thank Kate Wayne, James Treneman and Dana Garves for assisting us at Cape Arago, Emily Anthony for her assistance in southern Oregon, Craig Cornu and Anne Donnelly for their hospitality in Coos Bay, and Karin Fletcher for her persistence in helping obtain the dates of observation of southern nudibranchs pictured in Lamb and Hanby (2005). BG thanks Allison Gong and Josh Hallas for support and assistance in the field. We also thank Liz Kools for her assistance at CAS, Gary McDonald for sharing his field data and for permission to use two of his images, and three anonymous reviewers for their helpful comments which improved the manuscript. Finally, we would like to acknowledge Robin and Marisa Agarwal, Spencer Dybdahl-Riffle, Cassidy Grattan, Matt Knoth, Donna Pomeroy, and Ken-ichi Ueda. Their dedicated, ongoing observations of nudibranchs in California have added significantly to our knowledge of the shifting distributions of nudibranchs in the region.

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Nudibranch Range Shifts Associated with the 2014 Warm Anomaly in the Northeast Pacific

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Abstract.—The Northeast Pacific Ocean was anomalously warm in 2014, despite ENSO-neutral conditions in the tropical Pacific. We document northern range shifts associated with this anomaly for 30 species of nudibranchs and other shallow-water, benthic heterobranch gastropods from southern California to southern Oregon. Nine of these (*Placida cremoniana*, *Trapania velox*, *Doriopsilla fulva*, *Janolus anulatus*, *J. barbarensis*, *Flabellina cooperi*, *Anteaeolidiella chromosoma*, *A. oliviae*, and *Noumeaella rubrofasciata*) were recorded from new northernmost localities, while the remainder were found at or near northern range limits which we show were established mainly during El Niño events. All 30 species have planktotrophic larval development, and six were observed spawning at northern localities, increasing the likelihood that their ranges will continue to shift poleward as the strong 2015-16 El Niño develops. Notable among these was *Okenia rosacea*, usually found south of San Francisco and last observed in Oregon as a single specimen found during the 1997-98 El Niño. In 2015 this bright pink nudibranch reached high densities and was observed spawning throughout northern California and into southern Oregon. *Okenia rosacea* is therefore poised to exploit abundant prey resources previously out of its reach in northern Oregon and Washington. Our results not only demonstrate a striking biological response to the 2014 warm anomaly in the North Pacific Ocean, but also support early physical indications of a larger regional climate shift, one reinforced by long-term global warming. Combined with historical data, these results highlight how shallow-water nudibranchs, with their planktotrophic larvae, short life cycles, conspicuous coloration, and accessibility are excellent biological indicators of ocean climate in the region.

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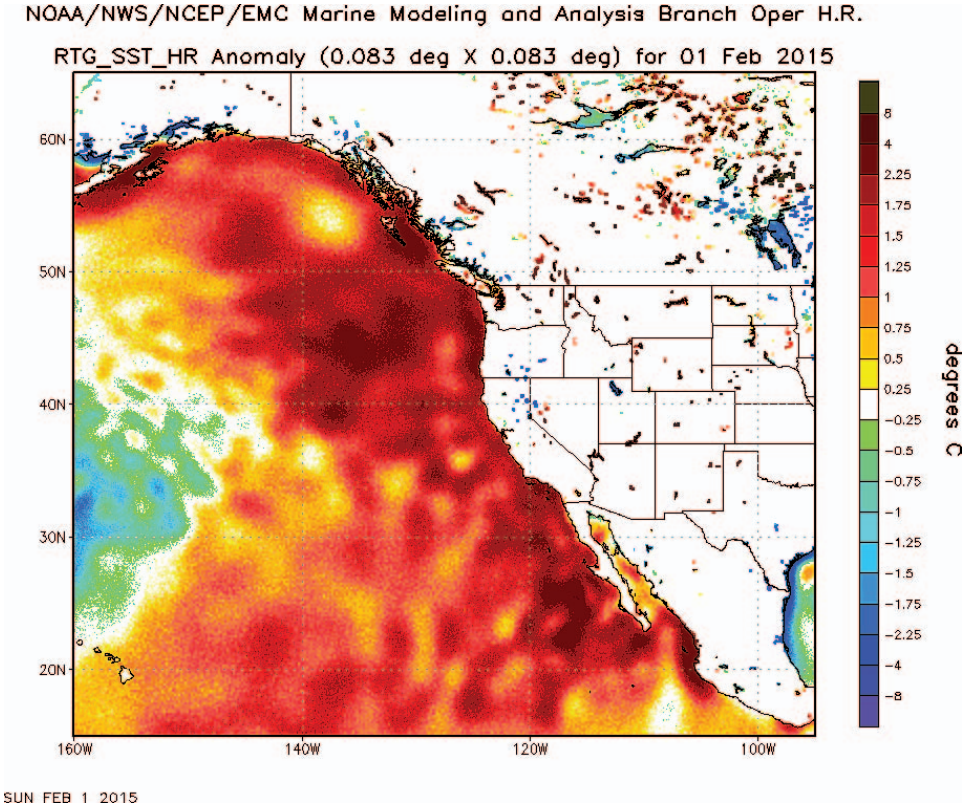

Fig. 1. SST anomalies in the NE Pacific Ocean, 1 February 2015. Source: NOAA

The winter of 2013-14 in the NE Pacific Ocean was unusually warm, with peak sea surface temperature (SST) anomalies greater than 2.5°C observed over a large part of the Gulf of Alaska in February (Bond et al. 2015). By May the warm SSTs had spread to the coastal zone and southward, where they merged with similarly warm anomalies resulting in part from reduced upwelling off southern California and northern Baja California (Leising et al. 2014). Despite the lack of even a moderate El Niño, the remainder of 2014 and early 2015 was marked by warmer than normal SSTs along the entire west coast of North America (Fig. 1) (Leising et al. 2014; CCIEA 2015). As indicated by the Pacific Decadal Oscillation (PDO) index, multivariate El Niño Southern Oscillation (ENSO) index (MEI), and the North Pacific Gyre Oscillation (NPGO), the entire region had undergone a major phase shift in ocean conditions (Leising et al. 2014), potentially similar to the 1976-77 climate shift in the North Pacific Ocean (Miller et al. 1994; Mantua and Hare 2002). Indeed, the value of the PDO index for December 2014 was the highest ever recorded for that month (Heberton 2015).

The California Current Ecosystem encompasses the coastline from Oregon to Baja California Sur. In this system positive values of the MEI and PDO are associated with warmer SSTs and reduced upwelling, and negative values of the NPGO are associated with weakened southerly flow and reduced nutrients and primary production (reviewed by CCIEA). As demonstrated by Schultz et al. (2011), these conditions (which include moderate to strong El Niño events) are correlated with increased intertidal abundance of nudibranch gastropods in California,

especially southern species, and can sometimes also force long-term shifts in their northern range limits (Goddard et al. 2011).

Our observations in 2014 and early 2015 of nudibranchs and other sea slugs in long-term intertidal study sites in southern and central California, combined with dive reports from southern California, and posts on various photo and observation-sharing websites, indicated that similar range shifts and increases in abundance of southern species of sea slugs were occurring again in California. Most conspicuous among these was the dramatic increase in intertidal density in northern California of the bright pink dorid nudibranch *Okenia rosacea* (Kraybill-Voth 2015; Stephens 2015). We therefore intensified sampling of sea slug populations in northern California and southern Oregon, and alerted colleagues from northern California to Washington about changes they might expect to see in the composition of the nudibranch fauna. Here, we summarize our findings, not just to document changes in distribution and abundance associated with the unusual, non-El Niño related warming of 2014, but also because we predict that many of the species observed in this study will likely be carried to unprecedented northerly latitudes by the strong 2015-16 El Niño in the Pacific Ocean (Climate Prediction Center/ NCEP 2015).

Materials and Methods

To quantify the abundance of nudibranchs and other sea slugs we conducted timed counts in the low intertidal zone at 28 sites from Los Angeles County, California to Coos County, Oregon (Fig. 2, Table 1). Additionally, CH used SCUBA to sample four subtidal sites in Santa Barbara, Ventura, and Los Angeles Counties, and BG used SCUBA to sample Point Cabrillo, Monterey and the Santa Cruz Wharf. We also qualitatively sampled the sides of floating docks in Charleston, Oregon and the Santa Cruz and Monterey Harbors in California. Intertidally we focused on pools, the under-rock microhabitats supporting the sessile prey of nudibranchs, and green macro-algae known to support sacoglossan sea slugs. Intertidal surveys usually started approximately 1 h before low tide and lasted 2-3 h depending on the size of the site and the numbers of observers, which varied from one to seven. Subtidal surveys lasted approximately 60 minutes each, with the number of trained observers varying between one and three. For analyses and presentation, data for each species from the timed counts were converted to number of individuals h^{-1} $observer^{-1}$. When possible we collected vouchers specimens and deposited them in the Invertebrate Zoology Collection at the California Academy of Science (CAS). These are referenced below by CASIZ followed by the collection number. For additional reports of unusual occurrence, we monitored posts on Flickr, iNaturalist, OCDiving, SoCal Underwater Photographers on Facebook, and Bodegahead.blogspot.com. From these internet-based sources we used only records accompanied by an image and the date and locality of observation.

With two exceptions, we chose a cut-off date of 31 August 2015 for inclusion of new observations from all sources. The exceptions were (1) large *Aplysia vaccaria* observed subtidally on the Monterey Peninsula in mid-September 2015 (see Results), and (2) a large specimen of the nudibranch *Janolus barbarensis* found on 12 September 2015 (see Results). These individuals would have recruited months earlier to the benthos, prior to the full impact in the region of the developing 2015-16 El Niño.

While examining our results it became apparent that many of the species we observed in this study have only been observed at some of our northerly study sites during previous warm water events, especially moderate to strong El Niños. Where appropriate we describe these patterns of occurrence, utilizing historical records and following Null's (2015) classification of El Niño events as weak, moderate or strong. Additionally, our study sites include those described by

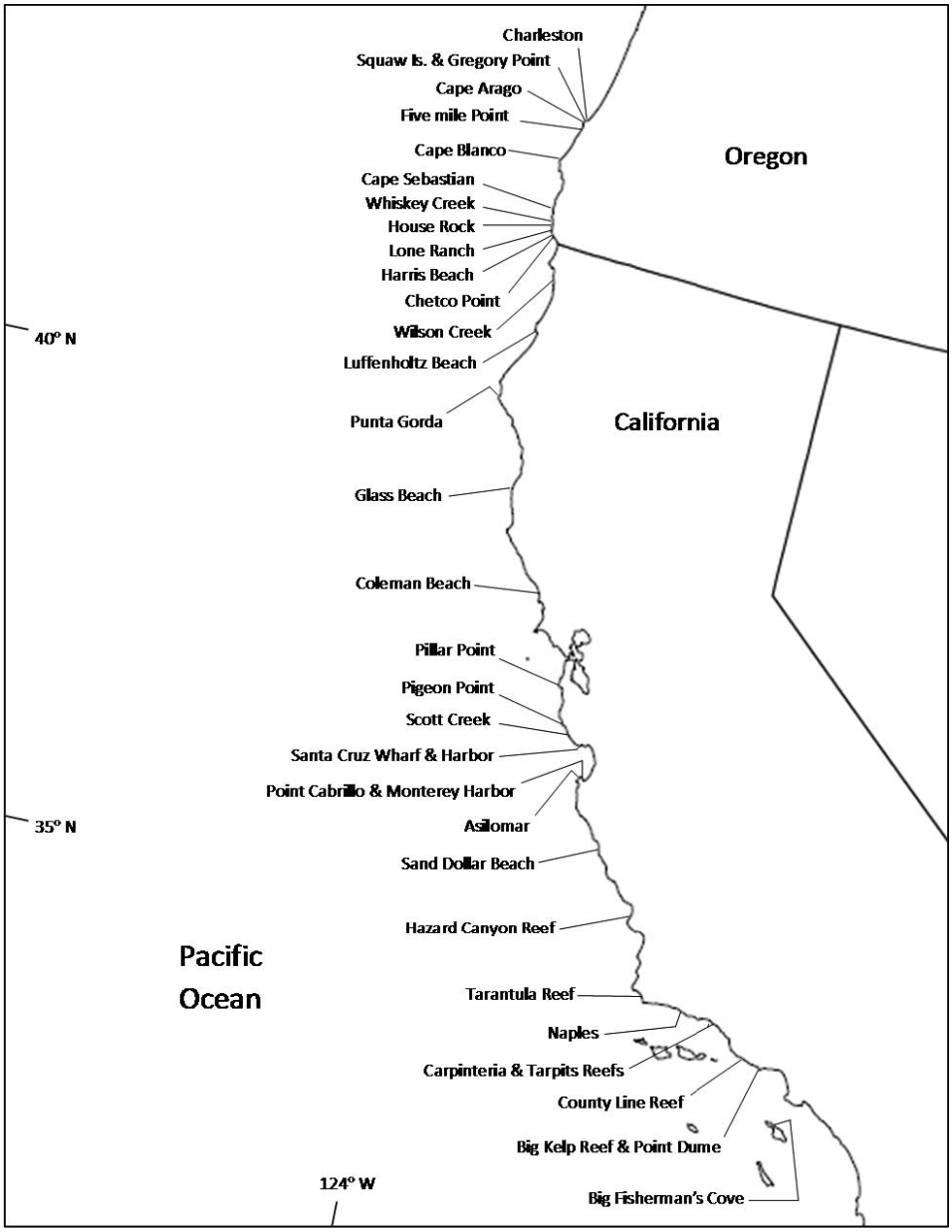

Fig. 2. Location of study sites on the coast of California and Oregon.

Schultz et al. (2011) and Goddard et al. (2011), and where appropriate we follow their geographic classification of nudibranch species in the region as southern, northern, or widespread.

We obtained historical records of occurrence from: (1) published literature, (2) the online database for the Invertebrate Zoology Collection at the California Academy of Science (CAS), (3) historical time series provided by Schultz et al. (2015) and Goddard et al. (2015), and (4) unpublished field accounts of California nudibranchs by James R. Lance, Richard A. Roller, and Gary R. McDonald. The field accounts of Lance and Roller are housed at CAS,

Table 1. Location of study sites shown in Figure 1. All sites intertidal unless indicated otherwise.

Site	Geographic coordinates
Charleston Boat Basin (docks)	43.3453, −124.3220
Gregory Point	43.3400, −124.3749
Squaw Island	43.3375, −124.3774
Cape Arago	
North Cove	43.3094, −124.3986
Middle Cove	43.3026, −124.4007
South Cove	43.3026, −124.3988
Five-mile Point	43.2199, −124.4003
Cape Blanco, north side	42.8401, −124.5634
Hunters Cove, Cape Sebastian	42.3205, −124.4261
Whiskey Creek (= Boardman SP of Goddard, 1990)	42.2227, −124.3830
House Rock	42.1130, −124.3550
Lone Ranch	42.0997, −124.3493
Harris Beach	42.0641, −124.3087
Chetco Point	42.0436, −124.2899
Wilson Creek	41.5947, −124.1051
Luffenholtz Beach	41.0407, −124.1209
Punta Gorda	40.2747, −124.3640
Glass Beach, Fort Bragg	39.4513, −123.8139
Coleman Beach	38.3632, −123.0708
Pillar Point	37.4938, −122.4994
Pigeon Point, north side	37.1847, −122.3969
Scott Creek	37.0455, −122.2380
Santa Cruz Wharf (subtidal)	36.9587, −122.0178
Santa Cruz Harbor (docks)	36.9642, −122.0018
Point Cabrillo (subtidal)	36.6214, −121.9016
Monterey Harbor (docks)	36.6043, −121.8912
Asilomar	36.6282, −121.9421
Sand Dollar Beach	35.9216, −121.4716
Hazard Canyon, Montana de Oro SP	35.2899, −120.8845
Tarantula Reef, Jalama	34.4954, −120.4968
Naples	34.4320, −119.9493
Carpinteria Reef (subtidal)	34.3930, −119.5400
Tarpits Reef, Carpinteria SP	34.3869, −119.5166
County Line Reef (subtidal)	34.0472, −118.9710
Big Kelp Reef (subtidal)	34.0046, −118.7925
Point Dume, south side	34.0031, −118.8037
Big Fisherman's Cove (subtidal)	33.4445, −118.4847

and the data from the Lance accounts for outer coast sites in San Diego County are publicly accessible online (California Academy of Sciences and Goddard 2013). The McDonald data, which cover the years 1967–2010, primarily in central California, are in an unpublished spreadsheet sent to the senior author (G. R. McDonald, personal communication to JG, March 9, 2010). We reference specimens from CAS using the collection number, prefaced by CASIZ, or entire groups of conspecific specimens simply as "CASIZ collection records". As indicated above, those records are publicly available online.

Results

Significant locality records of nudibranchs and other sea slugs in California and Oregon in 2014-15 are listed systematically by species and documented below. Nine of these represent

new or previously unpublished northernmost locality records and are marked with an asterisk (*). The remaining 21 species included below have previously been recorded from at least as far north as we found them in 2014-15, usually during strong El Niño events, but typically occur significantly farther south. For each of these we note their usual and extreme northerly range limits and describe the anomalous patterns of distribution and abundance we observed from late 2013 through August 2015. Locality records obtained from non-peer reviewed sources or websites (excluding museum databases) are referenced in footnotes, as are images we posted online of specimens we found during this study.

Sacoglossa
Limapontiidae

**Placida cremoniana* (Trinchese, 1892)

The single specimen of *Placida cremoniana* found on 10 Oct 2014 at 12 m at Stony Point, Santa Catalina Island[1] is the first record of this widespread tropical sacoglossan in the northeast Pacific north of La Paz, Baja California Sur (Angulo-Campillo 2002). Another specimen was found on 23 May 2015 at about 27 m depth at Casino Point, Santa Catalina Island.[2]

Cephalaspidea
Aglajidae

Navanax inermis (Cooper, 1863)

Navanax inermis is a Californian species rare north of Point Conception. It has been recorded as far north as the Bolinas Lagoon (Behrens 1998; Behrens and Hermosillo 2005) and Bodega Bay (Gosliner and Williams 2007), where it was reported by J. Standing and colleagues as rare to common.[3] The Bolinas record was linked by Behrens (1998) to the 1992-93 El Niño, and similarly the latter record from Bodega Bay can probably be linked to the strong El Niño of 1972-73, which coincided with sampling conducted by Standing et al. in the early 1970's in Bodega Bay.[3] On 4 June 2015 Grace Ha found one specimen of *Navanax inermis* in Bodega Bay.[4]

We found *N. inermis* crawling on the concrete wall below the Harbor Master's Office in the Monterey Harbor on 25 October 2014, 10 January 2015, and 21 May 2015, the first time we had seen this species in the Monterey Harbor since beginning observations there in 2008. On 14 May 2015 Robin Agarwal found a specimen in the Santa Cruz Harbor.[5]

Anaspidea
Aplysiidae

Aplysia californica (Cooper, 1863)

[1] Peterson, B. 2014. Warmer California waters bring new opportunities for photographers. Retrieved 12 July 2015 from: californiadiver.com/warmer-california-waters-bring-new-opportunities123/

[2] Halstead, A. 2015. Photos from Aaron Halstead's post in SoCal Underwater Photographers. Retrieved 11 September 2015 from: https://www.facebook.com/photo.php?fbid=10153463203903054&set=gm.463220240513533&type=1&theater

[3] Standing, J., B. Browning, and J. W. Speth. 1975. The natural resources of Bodega Harbor. State of California, Department of Fish and Game. 224 pp.

[4] Sones, J. 2015. Inhaling bubbles. The Natural History of Bodega Head, 4 June 2015. Retrieved 27 July 2015 from: http://bodegahead.blogspot.com/2015/06/inhaling-bubbles.html

[5] http://www.inaturalist.org/observations/1488901

Aplysia californica rarely occurs on the outer coast north of Point Conception, but has been recorded in bays as far north as Yaquina Bay, Oregon, the latter during the strong 1982-83 El Niño (Pearcy and Schoener, 1987).

On 1 December 2013, we found 20 individuals in the intertidal zone at Hazard Canyon Reef, the first we had seen in 14 years of approximately semi-annual sampling there. We did not find any at Hazard Canyon during two trips in May 2014, but observed two individuals on 18 May 2015. In temporally more limited sampling at Tarantula Reef beginning in 2009, we had not found *A. californica* until 2 February 2015, when the senior author counted 64 individuals. Similarly, two of us (WP and DM) have been sampling the Monterey Harbor since 2008 and found *A. californica* there for the first time on 23 September 2014, and through July 2015 had seen it there on five more visits. From August 2014 through April 2015 BG observed many *A. californica*, 8 to 15 m deep, off Monterey and Pacific Grove, and on 20 May 2015 found one specimen intertidally at San Dollar Beach, in southern Monterey County. By mid-2015 high densities had also been reported from two sites on the outer coast of Sonoma County[6,7], as well as from San Francisco and Tomales Bays (Anonymous 2015; Bay Nature Staff 2015).

On 14 August 2015, Dr. Troy Nash and his summer Invertebrate Zoology class from the Oregon Institute of Marine Biology (OIMB) found three specimens on a wave-protected rocky shore (43.3400° N, 124.3750° W) at Gregory Point, near Charleston, Oregon (T. Nash, personal communication to JG, 22 Oct 2015). Based on the image posted by OIMB[8], one of the slugs was about 17 cm long and found on the red alga *Neorhodomela larix* (Turner, 1819). These specimens are to our knowledge the first ever found on the outer coast of Oregon.

Examination of the dates of collection of the specimens at CAS of *A. californica* collected from Monterey Bay north since 1950 reveals that all but one were collected during El Niño events. CASIZ 57362, collected in San Francisco Bay in December 1984, may have been a 2nd generation holdover from the 1982-83 El Niño, one of the strongest on record.

Aplysia vaccaria Winckler, 1955

We have been sampling Naples semi-annually to monthly since fall 2006 and on 20 September 2013 found *Aplysia vaccaria* for the first time there. We recorded single specimens again in September, October, and November 2014. *Aplysia vaccaria* has been recorded as far north as Monterey Bay, California (Behrens 1991; Behrens and Hermosillo), and large specimens were observed subtidally by Cheryl Mitchell off the Monterey Breakwater on 18 September 2015[9].

Nudibranchia
Goniodorididae

Okenia angelensis Lance, 1966

This species has been recorded once from as far north as San Francisco Bay, in September 1964 (Lance 1966), and from Monterey Bay in September 1963 (Lance) and again in October 1971 (CASIZ 9168). 1963-64 was a moderate El Niño, but 1971 was a moderate La Niña. DM

[6] Sones, J. 2015. Munching at Miwok. The Natural History of Bodega Head, 23 May 2015. Retrieved 27 July 2015 from: http://bodegahead.blogspot.com/2015/05/munching-at-miwok.html
[7] http://www.inaturalist.org/observations/1183373
[8] http://oimb.uoregon.edu/sea-hares/
[9] https://www.facebook.com/cheryl.mitchell.750/videos/888884974530765/; [*Aplysia vaccaria* in video at 0:36 and 5:05]

Table 2. Comparison of abundance of *Okenia rosacea* at six sites in central California in early 2015 with historical highs recorded at same sites.

2015			Previous highs[1]		
Site	Date	No. inds.h^{-1} obs.$^{-1}$	No. inds.h^{-1} obs.$^{-1}$	Date	Sampling period
Duxbury Reef	01/01/15	≅12[a]	0.0	6/69-12/75	6/69-12/75
			0.7	Nov 2010	12/07-12/10
Pillar Point	02/17/15	122.7	13.0	Jul 1993	9/88-2/95
			0.2	Jan 2008	1/08-12/10
Scott Creek	01/20/15	65.0	11.4	Mar 1978	6/75-10/78
			0.3	Mar 2009	12/07-10/10
Asilomar	01/22/15	13.5	5.8	Oct 1969	10/69-7/73
			1.0	Nov 2007	11/07-10/11
Sand Dollar Beach	01/31/15	40.0	48.0	Dec 1997	Dec 1997
			1.3	Mar 2009	3/08-3/14
Hazard Canyon	01/19/15	≅150	≅4	Mar 1968	5/67-11/71
			4.4	Jul 2012	11/99-5/14

[a] Data from: R. Agarwall (http://www.inaturalist.org/observations/1156561)
[1] Data from: Goddard et al. (2015) (Duxbury Reef); Schultz et al. (2015) (Pillar Point, Scott Creek, Asilomar); R. Roller, unpublished California field accounts, CASIZ collection (Hazard Canyon 1967-71); Goddard, unpublished data (Sand Dollar Beach and Hazard Canyon 1997-2015).

found one individual[10] of *O. angelensis* on the H dock in the Monterey Harbor on 30 September 2014 and more at the same locality in April and June, 2015. On 17 July 2015 Donna Pomeroy and Robin Agarwal found *O. angelensis* on floating docks in the Pillar Point Harbor in Half Moon Bay, San Mateo County[11].

Okenia rosacea (MacFarland, 1905)

Okenia rosacea (Fig. 3A) was present in low abundance at two sites in central California in spring 2014 (Fig. 4). However, by fall, its abundance at both sites had increased an order of magnitude, and by winter 2014-15 had reached levels not seen before at our historical study sites in central California (Table 2). The density observed at Sand Dollar Beach, Monterey County during the strong El Niño of 1997-98 matched the densities we observed in 2015, and brief, qualitative observations by the senior author at Scott Creek on 28 December 1997 indicated similarly high abundance. On 3 January 2015 Jackie Sones of the Bodega Marine Laboratory (BML) reported finding 14 *O. rosacea* in a 2 m section of low intertidal shore at Bodega Head, the first specimens she had seen of this species in ten years of sampling at Bodega Head[12].

On 21 January 2015 we counted 7.7 *O. rosacea* h^{-1} observer^{-1} at Coleman Beach, followed by 19.7 *O. rosacea* h^{-1} observer^{-1} at Glass Beach, Fort Bragg on 16 Feb 2015, the same day that Spencer Dybdahl Riffle (personal communication to JG, 17 February 2015) counted 46 individuals at Patrick's Point SP near Trinidad in Humboldt County, and the day before David Anderson (personal communication to JG 21 April 2015) found 12 individuals at False Klamath Cove in Del Norte County. In March BG observed 13 *O. rosacea* at Luffenholtz Beach, near Trinidad (CASIZ 204572) and another seven at Wilson Creek, False Klamath Cove

[10] https://www.flickr.com/photos/39365853@N07/15406214295
[11] https://www.flickr.com/photos/dpom12/19647657349
[12] Sones, J. 2015. Finally! The Natural History of Bodega Head, 3 January 2015. Retrieved 28 August 2015 from: http://bodegahead.blogspot.com/2015/01/finally.html

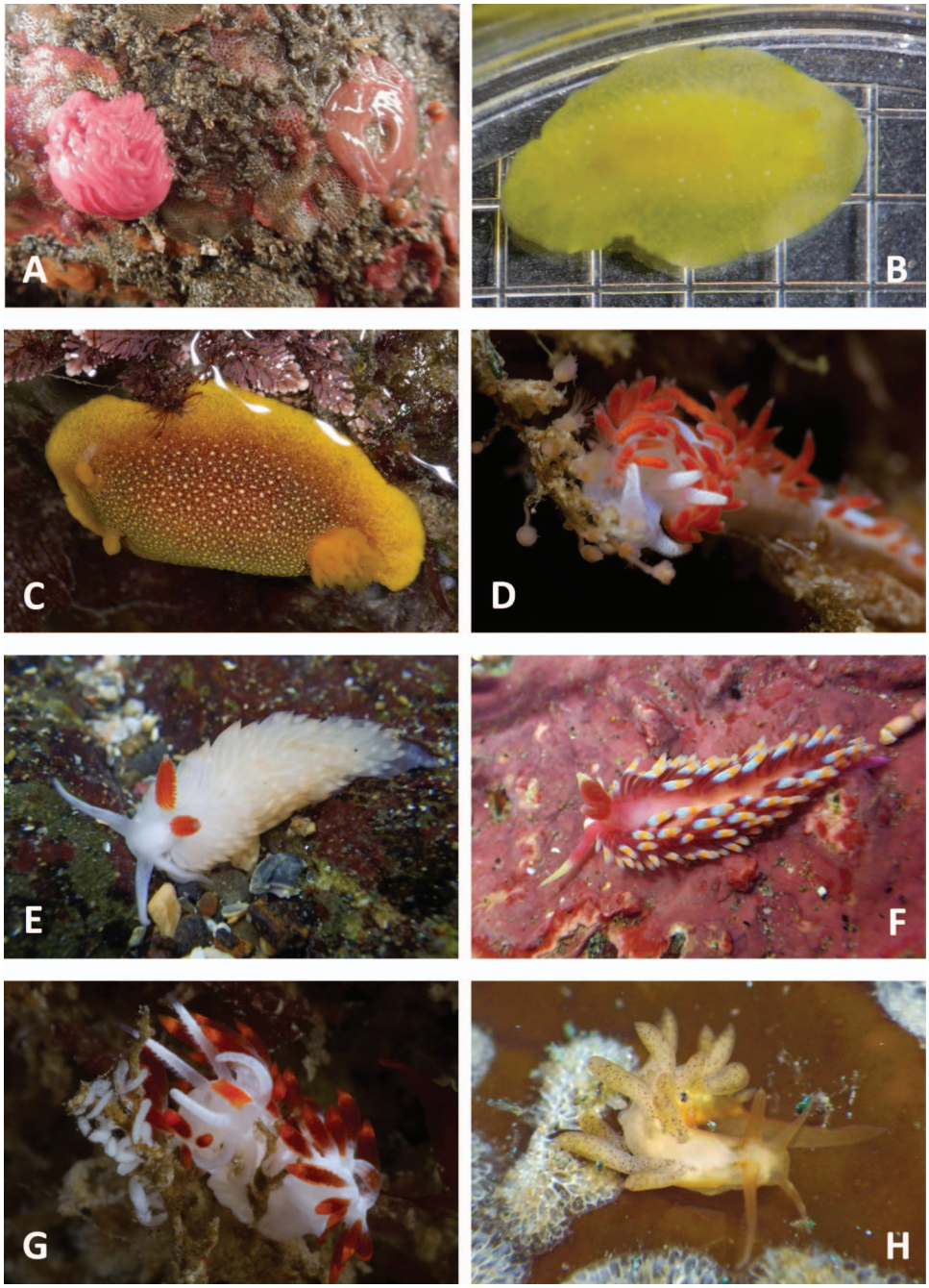

Fig. 3. Selected nudibranchs found in 2014-15 north of their usual geographic ranges. **A** *Okenia rosacea* and egg ribbons, Lone Ranch, Oregon, 18 July 2015. Image by NT. **B** *Doriopsilla fulva*, Whiskey Creek, Oregon, 16 June 2015. Image by NT. **C** *Doriopsilla gemela*, Tarpits Reef, Carpinteria, 19 May 2015. Image by CH. **D** *Flabellina bertschi*, Big Fishermans Cove, Santa Catalina Island, 2 January 2015. Image by CH. **E** *Anteaeolidiella oliviae*, Glass Beach, 16 February 2015. Image by DM. **F** *Babakina festiva*, Pigeon Point, 19 January 2015. Image by DM. **G** *Noumeaella rubrofasciata* laying eggs, County Line Reef, Malibu, 21 February 2015. Image by CH. **H** *Cuthona phoenix*, Monterey Harbor, 24 July 2014. Image by DM.

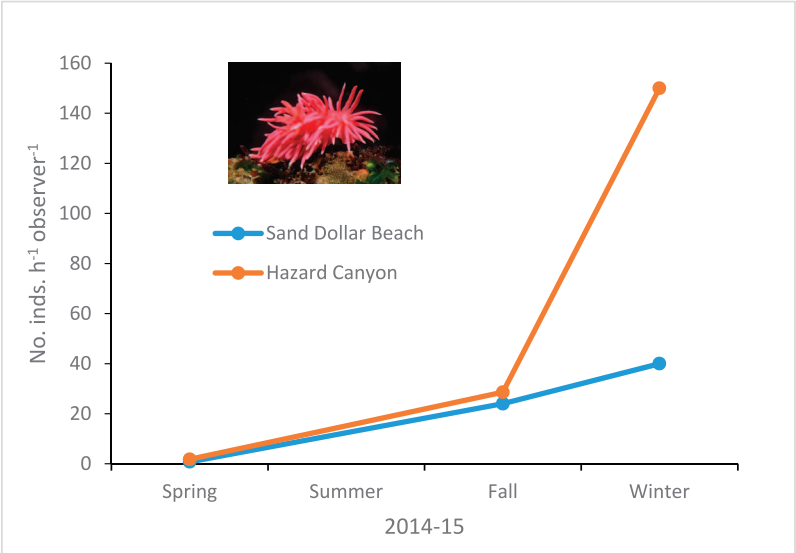

Fig. 4. Increase in abundance of *Okenia rosacea* at two sites in central California, spring 2014 to winter 2015. Sites were not sampled in summer. Image of *O. rosacea* by Gary McDonald.

(CASIZ 2014576). On May 7, two weeks after we asked him to be on the lookout for *O. rosacea* at Cape Arago, Oregon, Richard Emlet of OIMB and his Invertebrate Zoology class found a specimen just south of Sunset Bay, Cape Arago (R. Emlet, personal communication to JG, 8 May 2015).

In May, June and July 2015 in Oregon we found *O. rosacea* at Harris Beach, Lone Ranch, House Rock, Whiskey Creek, and Middle Cove, Cape Arago, and Gregory Point. The specimen from Lone Ranch on 18 July was spawning (Fig. 3A), and the highest number of *O. rosacea* we found at the Oregon sites was 21 (or 1.0 individuals h^{-1} $observer^{-1}$) on 16 June 2015 at Whiskey Creek. We deposited specimens of *O. rosacea* from Whiskey Creek and Middle Cove, Cape Arago at CAS (CASIZ 204855 and 204854, respectively). On 2 July 2015 Spencer Dybdahl Riffle found abundant *O. rosacea* and egg masses intertidally at Patrick's Point SP, Humboldt County[13]. On 28 August 2015 NT found one *O. rosacea* at North Cove Cape Arago, the first specimen ever recorded from that site.

The above specimens from Oregon are not only the most ever observed in the state, but the first recorded from Oregon since JG found one individual of *O. rosacea* at Middle Cove, Cape Arago on 24 July 1998, after 16 years of sampling for nudibranchs at Cape Arago, and during that year's exceptionally strong El Niño (JG, unpublished data and photograph). The only other record of *O. rosacea* in Oregon is from Steinberg (1963) who, based on observations by L. Andrews, recorded it (as *Hopkinsia rosacea*) from Coos Bay. However, *Integripelta bilabiata*, the sole prey of *O. rosacea*, does not occur inside Coos Bay, but rather on the open coast at nearby Cape Arago (JG, personal observations). Further, the specimen observed by L. Andrews was in an aquarium at OIMB and may actually have been collected in California (L. Andrews, personal communication to JG, 19 November 2009). Therefore, the northernmost verified locality for this species should be recorded as Gregory Point, Oregon.

**Trapania velox* (Cockerell, 1901)

[13] https://www.flickr.com/photos/riffle_nature_photos/19533897215

BG found one specimen at 5 m depth on sponges on a piling underneath the Santa Cruz Pier on 31 August 2015 (CASIZ 209038), extending the known range of this Californian species across Monterey Bay from Carmel, California (Behrens and Hermosillo). After one day in captivity in Santa Cruz, the specimen laid two egg masses. All records of *Trapania velox* from Carmel (in 2004, 2006 and 2009)[14,15] can be associated with weak to moderate El Niños, or in the case of 2006, a short, weak La Niña following the 2003-04 and 2004-05 El Niño events.

Onchidorididae

Acanthodoris rhodoceras Cockerell in Cockerell and Eliot, 1905

This species has been found as far north as central Oregon (Goddard 1997), during the moderate 1991-92 El Niño, and the only other published record of this species from Oregon (Goddard 1990) can be associated with the strong 1987-88 El Niño. In August 2015, NT found a total of eight specimens during five trips to Hunters Cove, on the south side of Cape Sebastian, Oregon. The specimens were the dull colored form as pictured in Figure 15 of McDonald and Nybakken (1980).

Polyceridae

Crimora coneja Marcus, 1961

Until recently *Crimora coneja* was known from only three mainland sites between Cape Arago, Oregon and San Diego County, California: Punta Gorda, Humboldt County (Goddard 1987), and Montana de Oro State Park and Morro Bay in San Luis Obispo County[16]. On 18 June 2015 we found two specimens at Middle Cove, Cape Arago, and on 15 July two more at Whiskey Creek, and on 15 August one specimen at Lone Ranch. All of the specimens from Oregon were found on *Hincksina minuscula*, the only known prey of *C. coneja*. Additionally, three other new locality records were added in 2015: (1) Trinidad, Humboldt County by Cassidy Grattan[17], (2) Pillar Point by Matt Knoth[18], and (3) Palmer's Point, Humboldt County by Cassidy Grattan, who on 2 August reported 10 specimens from Trinidad[19]. Since these reports additional specimens have been found at Pillar Point[20], and NT found a single specimen at North Cove, Cape Arago on 28 August.

During 14 years of observation at North and Middle Coves, Cape Arago from 1980 to 2008 *Crimora coneja* was found in seven years: three during the second year of strong El Niño events (1982-83, 1987-88, 1997-98), two during weak La Niñas (1984-85, 1985-86), and once during ENSO-neutral conditions (1981) (Goddard 1984, and unpublished data).

Polycera atra MacFarland, 1905

This southern species has been found in Oregon, mainly in bays, only during strong El Niño events (Goddard 1984, unpublished data) and has been recorded once from Westport, just inside Grays Harbor, Washington, during the 1997-98 El Niño (Lamb and Hanby 2005; A. Lamb, personal communication to K. Fletcher, forwarded to JG, 13 Sept 2012). On 17 June 2015 we found two specimens of *P. atra* on the sides of floating docks in the outer Charleston boat Basin.

[14] http://www.seaslugforum.net/showall/trapvelo
[15] http://www.baue.org/images/galleries/v/FieldGuide/Opisthobranchs/Trapania_velox/;
[16] Goddard, J. and C. Hoover. 2011. *Crimora coneja* Marcus, 1961. Retrieved 11 September 2015 from: http://slugsite.us/bow2007/nudwk758.htm
[17] https://www.flickr.com/photos/128077533@N05/17113424562
[18] http://www.inaturalist.org/observations/1728102
[19] http://www.inaturalist.org/observations/1834134
[20] http://www.inaturalist.org/observations?taxon_id=50057

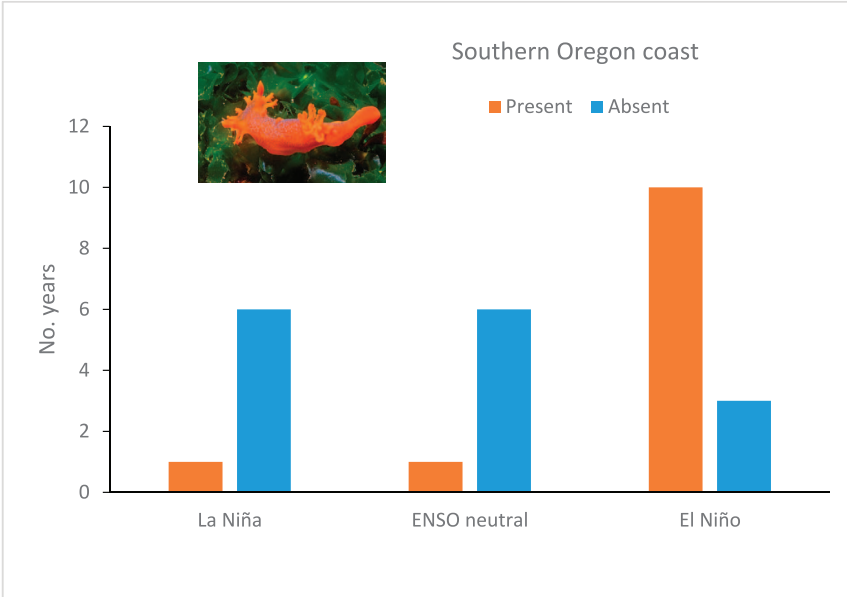

Fig. 5. Number of years *Triopha maculata* present or absent on the southern Oregon coast by phase of ENSO, 1980-98 and 2006-2014. Data for Whiskey Creek, Cape Blanco, and all three coves of Cape Arago combined, from Goddard (1984) and JG and NT (unpublished data). Image of *T. maculata* by Gary McDonald.

Triopha maculata MacFarland, 1905

Although recorded from Bamfield, British Columbia (Millen 1983) and Cape Arago, Oregon (Goddard 1984), *Triopha maculata* rarely occurs north of Cape Mendocino, California. From 18 May to 4 July 2015 in Oregon we found *T. maculata* at Chetco Point, Harris Beach, Lone Ranch, House Rock, Whiskey Creek, Cape Blanco, all three coves at Cape Arago, and Squaw Island. One of us (NT) has been sampling four of these sites for nudibranchs since 2008 and never observed this species before, and records of *T. maculata* from southern Oregon between 1980 and 2010 show that it occurred mainly during El Niño events (Fig. 5). Large specimens have also been observed in the Charleston boat basin during El Niño events (JG, personal observations), and on 28 August 2015 NT found one specimen there 6 cm long.

Dorididae

Thordisa bimaculata Lance, 1966

Thordisa bimaculata has been reported from Isla Natividad, Baja California to Carmel, California (Lance). Although it can be locally abundant on rocky shores in San Diego County (Sphon and Lance 1968; California Academy of Sciences and Goddard 2013), there are only a few records of this species from Santa Barbara County (Sphon and Lance 1968; CASIZ 98793), none from San Luis Obispo County, and besides the single specimen reported by Lance from off Carmel, there have been few sightings from Monterey County[21]. On 5 July 2015 Regina Roberts found a specimen laying an egg mass on a brown sponge at an unspecified depth off Point Joe, on the Monterey Peninsula[22].

[21] Bauder, C., 2001 *Thordisa bimaculata* from Carmel, California. Retrieved 7 September 2015 from: http://www.seaslugforum.net/find/3881.

[22] https://www.flickr.com/photos/reginadiver/19265753508

We found a total of eight *T. bimaculata* on 6 November 2014, 30 January 2015, and 17 March 2015 at Tarpits Reef, Carpinteria. These were the first specimens we had found at that site since beginning semi-annual to quarterly sampling there in May 2008. At Naples we recorded our first specimens on 3 May and 5 November 2010, during that year's moderate El Niño, and did not find any more there until finding one specimen on 19 February 2015 and another on 22 April 2015. On 3 July 2015 CH found one specimen at 7 m at Carpinteria Reef, and on 1 September 2015 CH found one specimen of *T. bimaculata* at 7 m depth at Punta Bocana, Bahia Magdalena, Baja California Sur, a new southernmost locality for this species.

Chromodorididae

Felimare californiensis (Bergh, 1879)

CH found three *Felimare californiensis* at 8 m on Carpinteria Reef on 3 July 2015, and five more at this same site on 18 July 2015. This species appears to have gone regionally extinct in southern California in 1984 (Goddard et al. 2013), and these specimens are the first to be reported on the mainland of the Santa Barbara Channel since its recovery in the Southern California Bight began in 2003, near the end of the moderate 2002-03 El Niño (Hoover 2015).

Felimida macfarlandi (Cockerell, 1901)

This brilliantly colored chromodorid nudibranch has been recorded from Bahia Magdalena, Baja California Sur (Bertsch 1978) to Monterey, California (MacFarland 1966) but is usually found south of Point Conception. On 6 March 2015, Jon McNeill found one individual subtidally at Point Lobos (J. McNeil, personal communication and image to JG, 9 October 2015). This was followed by Dave Baessler's subtidal observations at the Monterey Breakwater of one specimen[23] on 7 July 2015, and two more[24] on 29 July 2015. These are the first specimens documented from the Monterey Peninsula since the strong 1998 El Niño, when Gary McDonald found one subtidally at Del Monte Beach[25]. Gary McDonald also found one individual intertidally at Carmel Point in February 1986, during ENSO neutral conditions following a weak La Niña.

CAS has six lots of specimens of *F. macfarlandi* collected from the Monterey Peninsula in the following years: 1906, 1908, 1909, 1941, 1963 and 1978. Based on the values of the extended multivariate ENSO Index presented by Wolter and Timlin (2011), moderate El Niño events occurred in 1906, 1941, and 1963, and 1978 was a weak El Niño following the 1976-77 decadal climate shift. 1908-09 experienced weak to moderate La Niñas, indicating that either *F. macfarlandi* is not always dependent on El Niño conditions to reach the Monterey Peninsula, or that once arrived (in this case, in 1906) populations can persist locally for a few years through self-recruitment.

Dendrodorididae

**Doriopsilla fulva* (MacFarland, 1905)

Hoover et al. (2015) reinstated *Doriopsilla fulva* as distinct from *D. albopunctata*. The latter, which is more common intertidally in southern California, can be recognized externally

[23] https://www.flickr.com/photos/73739720@N00/19380471779
[24] https://www.flickr.com/photos/73739720@N00/19702924544
[25] http://www.inaturalist.org/observations/844135

by its white spots around and between the dorsal tubercles, compared to the single, apically-located white spot per tubercle on *D. fulva*. *Doriopsilla fulva* is also usually bright yellow in color and is more common intertidally than *D. albopunctata* north of Point Conception (Hoover et al. 2015).

We found one specimen of *D. fulva*, 8 mm long, at Whiskey Creek on 16 June 2015 (CASIZ 208751; Fig. 3B). This is the first record of this species in Oregon, and extends its known range from Abalone Beach in Humboldt County, California (Jaeckle 1984). NT found an additional specimen, 11 mm long, at Lone Ranch on 15 August 2015, and we found another specimen[26]. 14 mm long, at Punta Gorda, California on 15 June 2015. On 22 Jan 2015 at Asilomar we recorded 28.2 *D. fulva* obs^{-1} h^{-1}, the highest recorded since Nybakken and colleagues counted 24.7 obs^{-1} h^{-1} in April 1973, during that year's strong El Niño (see Schultz et al. 2015). Additionally, *D. fulva* was reported to be more abundant at Bodega Head in 2015 compared to previous years[27].

Doriopsilla gemela Gosliner, Schaefer and Millen, 1999

After seven years of approximately semi-annual sampling at Tarpits Reef, Carpinteria we found this species for the first time on 20 April 2015 and again on 19 May 2015. On both dates we found three large, mature adults (Fig. 3C), all with the combination of yellow gills and densely packed, opaque white spots concentrated in the middle of the dorsum characteristic of this species. At Naples we had observed single specimens on 5 February 2008, 29 November 2009, and 24 November 2012. However, on five of 11 sampling trips from April 2014 to May 2015 we found a total of nine specimens. BG found one specimen at 15 m off Point Cabrillo, Monterey on 13 October 2014. There is only one other verified record of this species in central California (also from 2014, off the Monterey Peninsula; see Hoover et al.), and the southern coast of Santa Barbara County, which includes Naples and Point Conception, appears to mark its usual northern range limit.

Hancockidae

Hancockia californica MacFarland, 1923

There are only two historical records of this species from north of Marin County: (1) Jaeckle's (1984) record from Trinidad, Humboldt County, which contrary to Behrens and Hermosillo is the northernmost record of *Hancockia californica*, and (2) Behrens (2004) record for Fort Bragg, Mendocino County. However, the record from Fort Bragg was based on a misidentified specimen[28] of *Dendronotus subramosus* MacFarland, 1966 (confirmed by D. Behrens, personal communication to JG, 4 April 2008). On 23 May 2015 Jackie Sones found a specimen of *Hancockia californica* at Coleman Beach, Sonoma County[29], and on 2 August 2015 Spencer Dybdahl-Riffle found a specimen, 5 mm long, at Trinidad[30].

[26] https://www.flickr.com/photos/34486353@N07/18524191074

[27] Sones, J. 2015. Sea salt. The Natural History of Bodega Head, 10 February 2015. Retrieved 8 August 2015 from: http://bodegahead.blogspot.com/2015/02/sea-salt.html

[28] Behrens, D. 2003. *Hancockia californica*. The Slug Site. Retrieved 5 January 2016 from: http://slugsite.us/bow/nudwk373.htm

[29] Sones, J. 2015. Be still my… The Natural History of Bodega Head, 25 May 2015. Retrieved 14 September 2015 from: http://bodegahead.blogspot.com/2015/05/be-still-my.html

[30] https://www.flickr.com/photos/riffle_nature_photos/20326335435

Dotoidae

Doto form A of Goddard (1996)

Doto form A is the most common *Doto* in the southern California bight and is commonly observed subtidally on campanularid hydroids growing on kelp and other macroalgae. It has been found as far north as Drake's Estero, Point Reyes National Seashore (Goddard 1996) but rarely occurs north of Point Conception. Goddard (1996) argued for the separation of this form from *D. amyra* Marcus, 1961 based on morphological and developmental evidence, and the genetic evidence presented by Shipman and Gosliner (2015) corroborate this. Compared to *Doto amyra*, *Doto* form A has cerata with brighter colored cores and longer, distinctly white papillae. It also has smaller eggs than *D. amyra* and planktotrophic development. Since mid-2014 Robin Agarwal and Donna Pomeroy have made numerous sightings of this species (cited as *Doto amyra*), frequently with its egg masses, in Morro and Monterey Bays, and at Pillar Point[31]. BG collected two specimens from the Santa Cruz Harbor on 28 August 2015 (CASIZ 207370)

Dironidae

Dirona picta MacFarland in Cockerell and Eliot, 1905

Dirona picta has been reported from as far north as Cape Meares, Oregon (Goddard 1997) but has rarely been observed on the outer coast of Oregon (Goddard 1984: 159, 1990), and the only specimen recorded from Cape Arago was during the strong 1997-98 El Niño (JG, personal observations). We found single specimens of it on 17 June 2015 at Cape Blanco and in the Charleston outer boat basin, and another specimen at 5-Mile Point on 1 August 2015.

**Janolus anulatus* Camacho-Garcia and Gosliner, 2006

On 13 August 2015 one of us (CH) found one specimen of *Janolus anulatus* at Tarpits Reef, the first seen there since the first specimens were recorded from this site on 9 May, 20 June, and 4 July 2012 (CASIZ 189420)[32], following a transition from a weak La Niña to moderately positive values of the MEI. Previously, this species was known from La Jolla, California to Costa Rica (Behrens and Hermosillo; Camacho-Garcia et al. 2005).

Based on data collected by James Lance and colleagues from 1964 to 2002, *J. anulatus* (distinguished from *J. barbarensis* and referred to by Lance first as *Antiopella* sp. and later as *Janolus* sp.) peaked in abundance in La Jolla, California during strong El Niño events (excluding the 1987-88 event), as well as following the 1976-77 climate shift (Fig. 6).

**Janolus barbarensis* (Cooper, 1863)

This Californian and Panamic species has been recorded from as far north as San Francisco Bay (Jaeckle 1983; Behrens and Hermosillo 2005) but is rare north of Morro Bay. On 28 July 2015 Benson Chow of the Tiburon Romberg Center collected one specimen in the Sausalito Marina, inside San Francisco Bay (CASIZ 207372). On 25 August 2015 Robin Agarwal found an additional specimen on the side of a floating dock in San Francisco Bay[33], a day after

[31]https://www.flickr.com/photos/30314434@N06/19114409924; https://www.flickr.com/photos/dpom12/18492397230

[32]Goddard, J. 2012. *Janolus anulatus* Camacho-Garcia and Gosliner, 2006. Retrieved 28 2015 from: http://slugsite.us/bow2007/nudwk785.htm

[33]http://www.inaturalist.org/observations/1892051

finding one in the Santa Cruz Harbor[34], where she had first sighted one on 15 October 2014[35]. On 11 September 2015 Shawn Brumbaugh and Chris Kwan found a *J. barbarensis* at the Spud Point Marina, Bodega Bay, California and informed Jackie Sones and Eric Sanford from BML, who the next day found one specimen 63 mm long on *Bugula neritina* on the side of a floating dock at the same locality[36].

Flabellinidae

Flabellina bertschi Gosliner and Kuzirian, 1990

This Panamic species ranges from the northern Gulf of California to Panama (Gosliner 1994), and has also been reported from the outer coast of Baja California (Goddard and Schickel 2000), as well as Catalina Island (Behrens, 2004; Behrens and Hermosillo 2005). Behrens (2004) represents the northernmost record of this species, but did not include an image or reference to voucher specimens. CH found one specimen (Fig. 3D) at 2 m depth at Big Fisherman's Cove, Santa Catalina Island on 2 January 2015, feeding on a species of *Eudendrium* similar to that shown with *F. bertschi* in Mexico in Fig. 4B of Millen and Hermosillo (2007).

**Flabellina cooperi* (Cockerell, 1901)

Known mainly from southern California, the northern range limit of *Flabellina cooperi* has been Elkhorn Slough, Monterey Bay since 1970 (McDonald 1983). Green and Gosliner (2016) presented molecular genetic evidence that specimens of a previously unidentified *Flabellina* with smooth to slightly wrinkled rhinophores and a notum irregularly covered with opaque white pigment collected by JG from Tarpits Reef, Santa Barbara County (CASIZ 195988) and Coleman Beach, Sonoma County (CASIZ 195990) are identical to *F. cooperi* from La Jolla, and (see below) Santa Cruz, California. Coleman Beach is therefore now the northernmost locality known for *F. cooperi*. The two specimens of *F. cooperi* from Coleman Beach (CASIZ 181322 and 195990) were collected on 29 April 2009 and 25 March 2010, respectively, at the beginning and end of the moderate 2009-10 El Niño.

On 28 August 2015 BG found one specimen of *F. cooperi* (CASIZ 207369)[37] in the Santa Cruz Harbor, and based on the morphology of the above specimens included by Green and Gosliner, two specimens of *Flabellina* found on 27 April 2015 by DM on the sides of floating docks in the Monterey Harbor[38] can now also be assigned to *F. cooperi*. Additionally, we have been sampling Naples regularly since 2006 and from 28 February to 3 May 2010 found a total of 30 *F. cooperi* (e.g., CASIZ 182720, 195986, as *Flabellina* sp.) [39], our first specimens of this species at that site. More recently, we found our first specimens of *F. cooperi* at Tarantula Reef on 3 January 2015, and additional specimens at Tarpits Reef on 30 January and 19 May 2015.

The original sightings of *Flabellina cooperi* at Elkhorn Slough consisted of a total of three specimens collected on 16 November and 7 December 1970, during a moderate La Niña (McDonald 1983). Two years later, during a strong El Niño, Gary McDonald (unpublished field data) found an estimated total of 30 individuals on 18 and 19 October 1972.

[34]http://www.inaturalist.org/observations/1888084
[35]https://www.flickr.com/photos/30314434@N06/14938263624
[36]Sones, J. 2015. Straight outta Santa Barbara. The Natural History of Bodega Head, 12 September 2015. Retrieved 12 September 2015 from: http://bodegahead.blogspot.com/2015/09/straight-outta-santa-barbara.html
[37]http://www.inaturalist.org/observations/1906734
[38]https://www.flickr.com/photos/39365853@N07/16697361803
[39]https://www.flickr.com/photos/34486353@N07/5424958579

Flabellina iodinea (Cooper, 1863)

Although long known from as far north as the west coast of Vancouver Island (Bernard 1970) and Puget Sound, Washington (Bergh, 1879), this highly conspicuous species rarely occurs on the outer coast north of Monterey Bay (Gosliner and Williams 1970; Bertsch et al. 1972; Goddard et al. 2015; Schultz et al. 2015). There are no published records from Oregon, and the only recent record from Washington is from subtidally near Cape Flattery during the strong 1997-98 El Niño (Lamb and Hanby 2005; A. Lamb personal commmunication to K Fletcher, forwarded to JG, 13 Sept 2012). On 15 May 2014 we found our first specimen at Hazard Canyon Reef since beginning our sampling there in 1999. We found another specimen at the same site on 18 May 2015. Further north, we found a specimen of *F. iodinea* on 20 January at Scott Creek, and by May 2015, specimens had been found in Bodega Bay[40], Coleman Beach (J. Sones personal communication to JG, 23 May 2015), and Trinidad, Humboldt County[41]. *Flabellina iodinea* was first reported from Trinidad by Jaeckle (1984). On 4 July 2015 Spencer Dybdahl Riffle counted 23 *F. iodinea* in the tidepools at Trinidad[42].

Aeolidiidae

**Anteaeolidiella chromosoma* (Cockerell and Eliot, 1905)

On 21 May and 7 June 2015 we found a total of four specimens on the H dock in the Monterey Harbor. This species was previously known from as far north as Morro Bay (Behrens 1980) and ranges south to the Galapagos Islands (Camacho-Garcia et al. 2005). On 15 July 2015 Robin Agarwal found a specimen in the Santa Cruz Harbor, on the north side of Monterey Bay[43], and on 25 August 2015 found two specimens and their egg masses in San Francisco Bay[44]. At Naples, *A. chromosoma* was more abundant in the first half of 2015 than at any time in the past ten years, with a lesser peak in abundance during the 2009-10 El Niño (JG, unpublished data).

**Anteaeolidiella oliviae* (MacFarland, 1966)

The northern range limit of this species has long been Duxbury Reef, Marin County, California (Gosliner and Williams 1970). On 21 January 2015 we found one specimen at Coleman Beach, Sonoma County, and on 16 February 2015 we found one specimen at Glass Beach in Fort Bragg, Mendocino County (Fig. 3E). The latter specimen had unusually pale cerata, probably reflecting an atypical complement of the anthozoans normally consumed by this species (Beeman and Williams 1980).

Facelinidae

Emarcusia morroensis Roller, 1972

This small (to 15 mm) cryptic species has been found only a few times since its original description and has been reported from Mission Bay, San Diego to San Francisco Bay (Roller 1972; Gosliner 1990). It is known mainly from bays (Roller 1972; McDonald 1983; CASIZ

[40]Sones, J. 2015. Fiery and flamboyant. The Natural History of Bodega Head, 19 May 2015. Retrieved 28 August 2015 from: http://bodegahead.blogspot.com/2015/05/fiery-and-flamboyant.html

[41]https://www.flickr.com/photos/riffle_nature_photos/16898166880; http://www.inaturalist.org/observations/1387158

[42]https://www.flickr.com/photos/riffle_nature_photos/19287584140

[43]https://www.inaturalist.org/observations/1767403

[44]https://www.flickr.com/photos/30314434@N06/20876669342

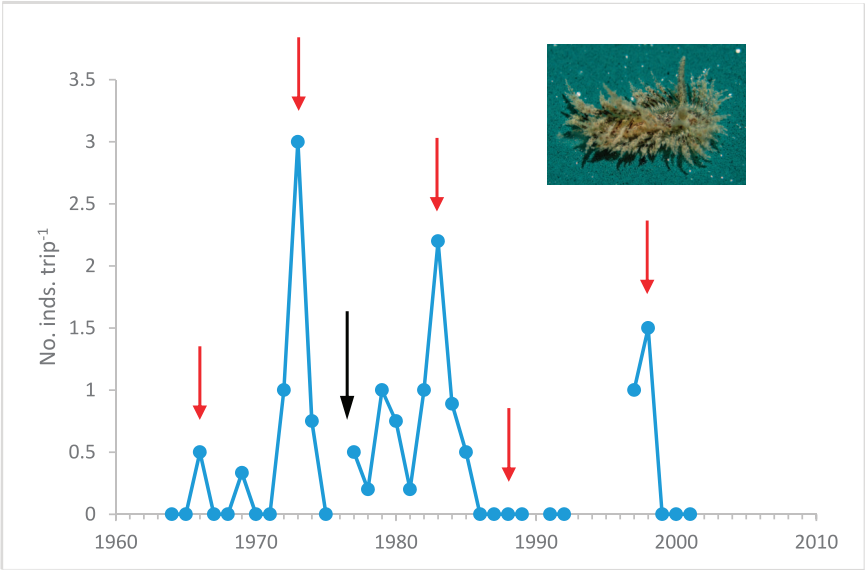

Fig. 6. Number of *Janolus anulatus* observed per sampling trip, La Jolla, California, 1964-2001. Red arrows indicate strong El Niños, and black arrow indicates 1976-77 climate shift. From data collected by James Lance and colleagues during 51 total sampling trips to intertidal sites at South Casa and Windansea Reefs (California Academy of Sciences and Goddard 2013). Image of *J. anulatus* by JG.

collection records) and has been previously observed on the outer coast only twice: in September 1972 from a buoy anchor chain in Monterey Bay (CASIZ 69806), and in December 2007 from 15 m depth off Redondo Beach[45].

On 20 May 2015 the senior author found six specimens intertidally on the south side of Point Dume, Malibu[46]. Robin Agarwal found a specimen in Morro Bay in September 2014, and another on 26 July 2015 in the Monterey Harbor[47]. Two specimens were found in the Santa Cruz Harbor in August 2015, one by BG on the 28th (CASIZ 207371)[48], and another on the 31st by Robin Agarwal[49].

Babakina festiva (Roller, 1972)

Babakina festiva is known from Nayarit, Mexico to Duxbury Reef (Behrens and Hermosillo 2005). However, it has been reported previously only twice from north of Point Conception (Gosliner 1990) and both sightings can be linked to the strong El Niño of 1987-88. In 2015 we found two specimens on the north side of Pigeon Point, one on 19 January 2015 (Fig. 3F), and the other on 3 July 2015. Three more specimens were observed between February and July 2015 in the Fitzgerald Marine Reserve in San Mateo County[50].

[45]Kopp, K. 2007. *Emarcusia morroensis* Roller, 1972. Retrieved 26 August 2015 from: http://slugsite.us/bow2007/nudwk581.htm
[46]https://www.flickr.com/photos/34486353@N07/17724610780
[47]http://www.inaturalist.org/observations/1806084
[48]https://www.flickr.com/photos/lemurdillo/21011780632
[49]https://www.flickr.com/photos/30314434@N06/20428988314
[50]http://www.inaturalist.org/observations?taxon_id=50489

**Noumeaella rubrofasciata* Gosliner, 1991

On 21 February 2015 CH found a single specimen laying an egg string (Fig. 3G) at 18 m depth at County Line Reef, extending the known range of this species north from Santa Catalina Island (Gosliner 1991). CH observed two more at County Line Reef on 19 April 2015, and five specimens at Big Kelp Reef, Malibu on 7 March 2015. These specimens are the first CH has observed at these sites in four and five years of observation, respectively.

Tergipedidae

Cuthona phoenix Gosliner, 1981

This slender, distinctive aeolid has reported once from Monterey Bay (Behrens 1991) and also been observed in Morro Bay and a few sites total in southern California, the Gulf of California, and Costa Rica (Behrens 1980 [as *Tergipes* sp.]; Gosliner 1981; Camacho-Garcia et al. 2005; CASIZ collection records). *Cuthona phoenix* has usually been found among hydroids growing on flotsam, floats, or giant kelp, *Macrocystis*. On 14 September 2014 Robin and Marisa Agarwal found two specimens on *Macrocystis* next to docks in Morro Bay[51], on 24 July 2014 one of us (DM) found four specimens on *Macrocystis* at the H dock in the Monterey Harbor (CASIZ 199397) (Fig. 3H), and on 24 August 2015 Donna Pomeroy found specimens on *Macrocystis* in the Santa Cruz Harbor[52].

Discussion

We documented northward range shifts related to the 2014 warm anomaly in the NE Pacific for 30 species of nudibranchs and other benthic sea slugs. Nine of these were recorded from new northernmost localities (Fig. 7), and the remainder, including *Okenia rosacea*, which reached unprecedented densities in northern California and Oregon, were found at or near their known northern range limits. Only the strong El Niños of 1982-83 and 1997-98, as well as the 1976-77 climate shift are known to have forced similar shifts in the nudibranch fauna of the region (Pearcy and Schoener 1987; Engle and Richards 2001; Goddard et al. 2011; Schultz et al. 2011; see Goddard 1984, p. 157; and specific results above). During the 1976-77 climate shift, when the PDO shifted from cold to warm phase, the total abundance of southern species of nudibranchs in central California increased as northern species declined (Fig. 2 in Schultz et al. 2011). We observed a similar transition in 2014-15 at sites we have been monitoring regularly since at least 2008 (Fig. 8).

Our results demonstrate a striking biological response to the 2014 warm anomaly in the North Pacific Ocean. They also (1) reinforce indications that the anomaly was part of a regional climate shift, and (2) further demonstrate, as originally proposed by Schultz et al. (2011), that intertidal populations of nudibranchs - with their short life cycles and planktotrophic larvae - closely track nearshore ocean conditions. Range shifts of these brilliantly colored species therefore constitute useful biological indicators of regional ocean climate. In fact, for much of the Oregonian Biogeographic Province, which stretches from Los Angeles to the northern end of Vancouver Island (Briggs and Bowen 2012), the population fluctuations of one species alone, *Okenia rosacea*, may serve as a valuable indicator. *Integripelta bilabiata*, its encrusting bryozoan prey, is locally abundant to British Columbia, and as we predicted for 2015 (see Kraybill-Voth 2015; Stephens 2015; and Appendix, reference 21), when populations of this

[51]http://www.inaturalist.org/observations/878045
[52]http://www.inaturalist.org/observations/1889538

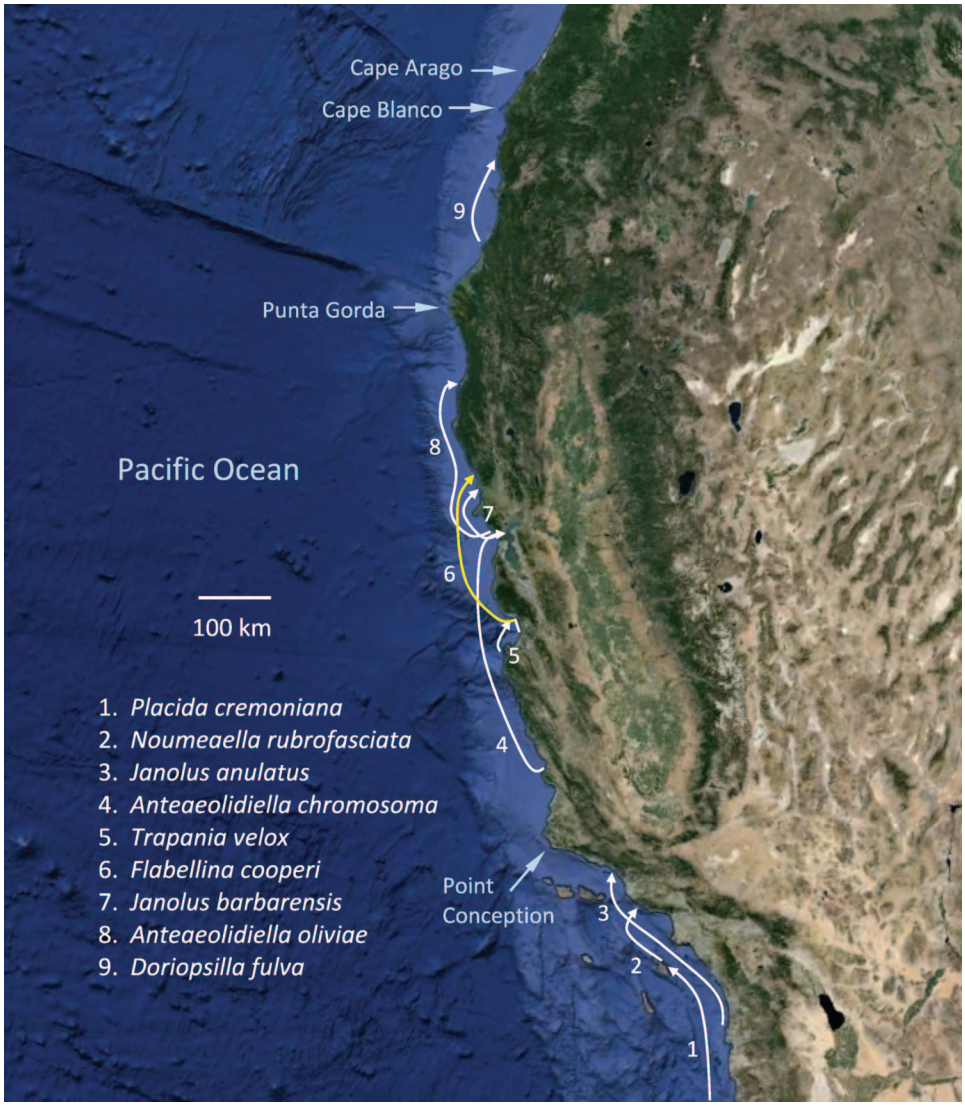

Fig. 7. Range extensions in 2014-15 from previous northernmost known localities of the sacoglossan *Placida cremoniana* and eight species of nudibranchs in the NE Pacific Ocean. The previous northernmost locality at La Paz, Mexico for *P. cremoniana* is not shown, and the yellow part of the line for *Flabellina cooperi* indicates a range extension in 2009-10 (see Results).

conspicuously pink dorid increase north of San Francisco, other southern species follow. *Triopha maculata*, which historically has occurred more frequently and at more sites than *O. rosacea* in Oregon, especially during El Niño events (Fig. 5), would also appear to be a good indicator of elevated SSTs and increased poleward transport of coastal waters. Similarly, in the Californian Province, the appearance of *Janolus anulatus* in the San Diego area has historically been highly correlated with strong El Niño events (Fig. 6).

The mechanisms by which southern species of nudibranchs expand their ranges northward include increased poleward and onshore transport of planktonic larvae from southern source

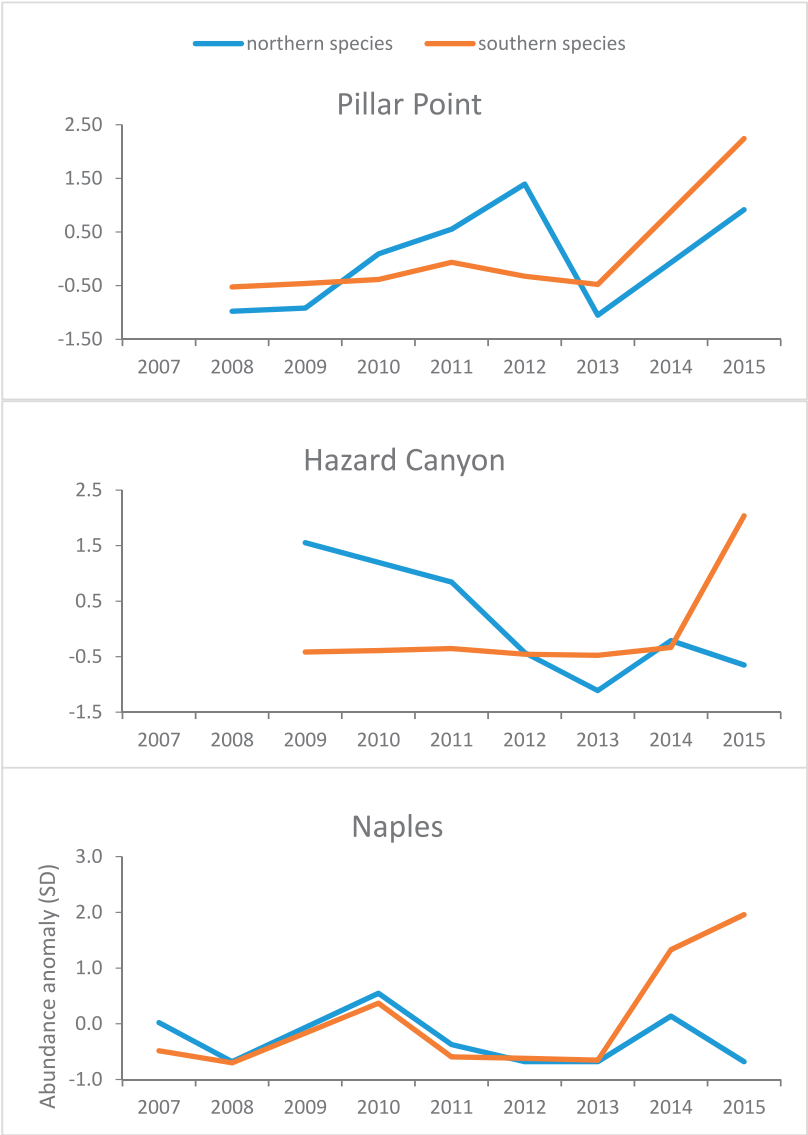

Fig. 8. Total abundance of southern and northern species of nudibranchs at three intertidal sites in California, winters only, 2007-15. Data plotted as anomalies (deviation from mean over years shown, in units of standard deviation). Missing values (2009 at Naples, 2010 at Hazard Canyon, and 2014 at Pillar Point) were filled in by interpolation.

populations, especially during periods of reduced upwelling and with the late summer development in the Southern California Bight of the poleward inshore countercurrent, which north of Point Conception in the autumn becomes the strong poleward Davidson Current (Strub and James 2002; Schultz et al. 2011). Upwelling in 2014 off northern Baja California and southern California was anomalously low (Leising et al. 2014), and episodes of strong poleward transport of surface waters were measured by High Frequency Radar (HFR) in Fall 2014 and Winter 2015 off California by the Central and Northern California Ocean Observing System (CeNCOOS).

For example, surface flows of at least 50 cm sec^{-1} were observed from Eureka to Cape Blanco from 4 to 9 Feb 2015 (Fig. 9), fast enough and over a long enough period to transport entrained larvae that entire distance. In fact, it was after observing *Okenia rosacea* spawning during early winter 2015 at Scott Creek, and then checking the surface flows recorded by CeNCOOS, that we predicted the occurrence of *Okenia rosacea* and other southern nudibranchs in southern Oregon by mid-2015 and first contacted colleagues there to be on the lookout for them.

With a strong El Niño developing on the heels of the 2014 warm anomaly (Climate Prediction Center/NCEP 2015), we expect that nudibranchs currently reproducing in their new northerly ranges (e.g., *Okenia rosacea* and *Anteaeolidiella chromosoma*) will be transported (as larvae) even farther north in the coming year. Some, including both specialists like *O. rosacea* and relative generalists like *Triopha maculata* and *Dirona picta*, will find abundant encrusting prey, formerly beyond their geographic reach. Local recruitment and reproduction of subsequent generations, combined with the accelerating rise in ocean temperatures owing to global warming (Blunden and Arndt 2015; Gleckler et al. 2016), may then result in long-term persistence of some of these species in their new ranges, a contrast to the ephemeral appearances associated with previous warm-water events, particularly El Niños (reviewed by Lluch-Belda et al. 2005). The effects of these newly arrived, specialized, fast-growing predators will then gradually ripple through the benthic epifauna, altering species interactions and potentially changing community composition as they consume large patches of their prey, some of which, such as sponges, can be very long-lived.

All of the species listed above have free-swimming, planktotrophic larvae [Schmekel and Portmann 1982 (for *Placida cremoniana*); Goddard 2004; Goddard & Hermosillo 2008; Goddard & Green 2013; JG and BG, unpublished data], and most, if not all, were carried northward and onshore into their new ranges as larvae. However, with no records of the widespread sacoglossan *Placida cremoniana* from between Santa Catalina Island and La Paz, Mexico, we cannot rule out a human-mediated introduction of this species to southern California, nor for that matter be certain of its region of origin. Therefore, excluding *P. cremoniana*, the average northward range shift for the nudibranchs found at new northernmost localities in 2015 was 151 km (SD = 113 km, n = 8). This includes *Flabellina cooperi* moving north from Elkhorn Slough to Santa Cruz, but not to Coleman Beach, where it was found in 2009-10.

Notably absent from the 30 species listed above is *Phidiana hiltoni*. The northward spread, starting in 1977, of this large aeolid nudibranch from Monterey appears to have been stalled since 1992 by a combination of oceanographic and geographic features in the vicinity of Duxbury Reef and Point Reyes and the short duration of its lecithotrophic larval stage (Goddard et al. 2011). Further spread north of this species should be closely monitored and may depend on a different mechanism, such as chance rafting of adults or egg masses on drift macro-algae or other floating substrata supporting growths of it hydroid prey.

Goddard (1987) surmised that the rarely observed dorid nudibranch *Crimora coneja* "may... be primarily sublittoral, with rare intertidal outbreaks." Its appearance intertidally in northern California and Oregon in 2015, especially at new sites, combined with the timing of much of its historical occurrence at Cape Arago (see Results), is consistent with increased onshore transport during warm-water events driving larval recruitment from subtidal populations, part of the overall mechanism driving intertidal recruitment of the southern nudibranchs we observed in this study. The same may apply to *Emarcusia morroensis*, another rare species, which prior to this year, had to our knowledge never been observed on open coast rocky shores.

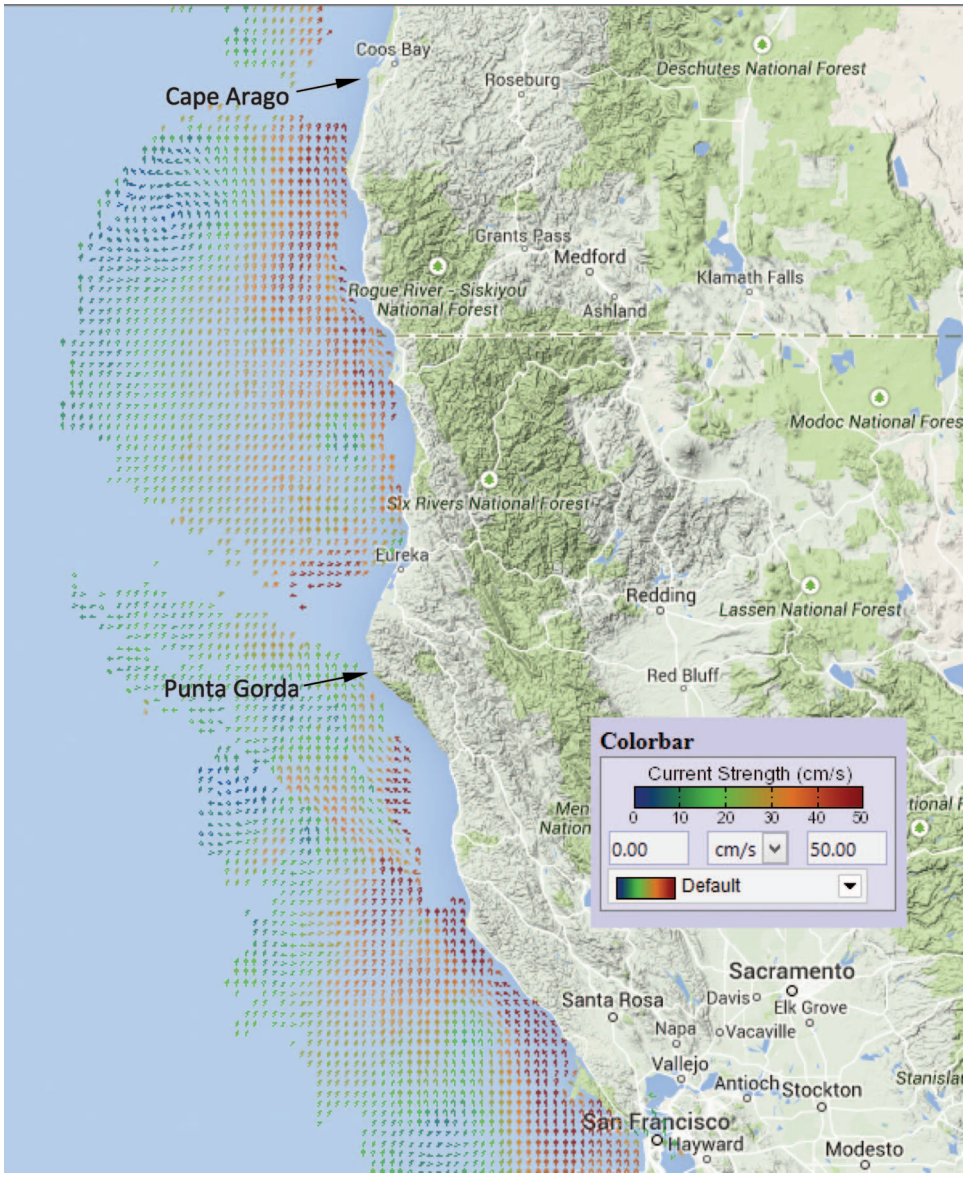

Fig. 9. Surface current flow, 6 February 2015, San Francisco, California to Cape Arago, Oregon. Source: Coastal Ocean Currents Monitoring Program (COCMP).

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