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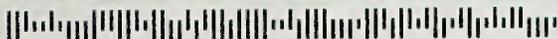
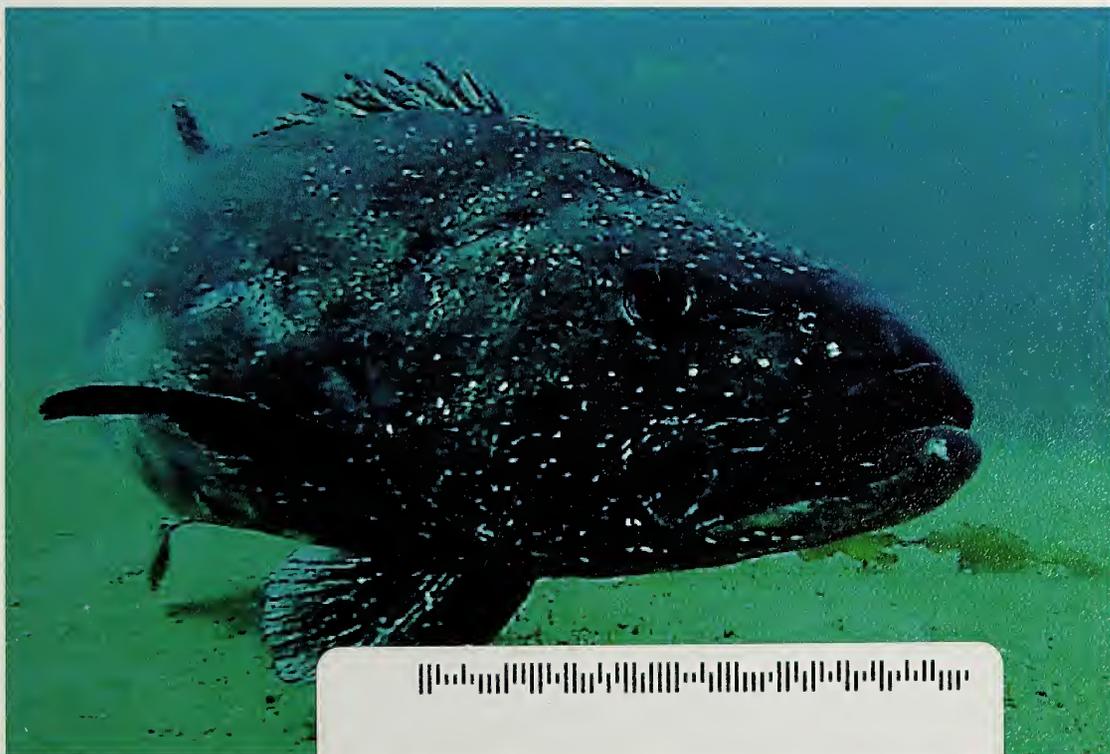
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The Return of the King of the Kelp Forest: Distribution, Abundance, and Biomass of Giant Sea Bass (*Stereolepis gigas*) off Santa Catalina Island, California, 2014-2015

Parker H. House*, Brian L.F. Clark, and Larry G. Allen

California State University, Northridge, Department of Biology, 18111 Nordhoff St.,
Northridge, CA, 91330

Abstract.—It is rare to find evidence of top predators recovering after being negatively affected by overfishing. However, recent findings suggest a nascent return of the critically endangered giant sea bass (*Stereolepis gigas*) to southern California. To provide the first population assessment of giant sea bass, surveys were conducted during the 2014/2015 summers off Santa Catalina Island, CA. Eight sites were surveyed on both the windward and leeward side of Santa Catalina Island every two weeks from June through August. Of the eight sites, three aggregations were identified at Goat Harbor, The V's, and Little Harbor, CA. These three aggregation sites, the largest containing 24 individuals, contained a mean stock biomass of 19.6 kg/1000 m² over both summers. Over the course of both summers the giant sea bass population was primarily made up of 1.2 - 1.3 m TL individuals with several small and newly mature fish observed in aggregations. Comparison to historical data for the island suggests giant sea bass are recovering, but have not reached pre-exploitation levels.

The giant sea bass (*Stereolepis gigas*) is the largest teleost to inhabit nearshore rocky reefs and kelp forests in the northeastern Pacific (Hawk and Allen 2014). Though previously taxonomically classified as a sea bass (Serranidae), the giant sea bass is actually a wreckfish, in the family Polyprionidae (Shane et al. 1996). Unlike most wreckfishes, they are a relatively shallow water species, inhabiting depths from 3 - 40 m. Their historical range is from Humboldt Bay, CA to Baja Mexico (Point Abrejos) and into the northern Gulf of California. However, they are primarily found south of Point Conception. Although, the giant sea bass is the largest member of the southern California rocky reef and kelp forest fish community, very little is known about its basic biology and life history (Allen and Andrews 2012). These fish have been documented to grow over 250 kg (Domeier 2001) and live up to 76 years old (Hawk and Allen 2014). However, there are reports of giant sea bass living as old as 90 - 100 years and over 270 kg (Fitch and Lavenberg 1971), and even possibly reaching sizes of 360 kg as noted by author Charles F. Holder at the turn of the twentieth century (Holder 1910). These early reports of giant sea bass size and age remain unverified.

Along with being a long-lived and slow growing species, with the exception of growing rapidly within the first year of life (Hawk and Allen 2014), they are also relatively late to mature. It is believed that giant sea bass mature between 11 - 13 years of age (Fitch and Lavenberg 1971). However, there have been no studies explicitly confirming age at sexual maturity. To maintain their large body mass, giant sea bass feed on a wide variety of demersal and conspicuous rocky reef fishes as well as cephalopods and crustaceans. They have been documented to feed on rays, guitarfish, skates, flatfish, small sharks, barred sand bass, kelp bass, blacksmith,

* Corresponding author: parker.h.house@gmail.com

ocean whitefish, sargo, sheephead, octopus, spiny lobster, cephalopods and squid (Domeier 2001, Love 2011). They are likely capable of feeding on nearly any species inhabiting nearshore rocky reefs and kelp forests off southern California, as they are the apex, tertiary megacarnivore of this system (Cross and Allen 1993, Horn and Graham 2006).

Like many slow growing, late maturing, large bodied marine predators worldwide (Pauly et al. 1998, Jackson et al. 2001, Dayton et al. 2002, Myers and Worm 2003), the giant sea bass population has historically been depleted due to overfishing and has been rare off southern California (Domeier 2001, Pondella and Allen 2008). During most of the twentieth century, they were highly sought after throughout the Southern California Bight and Mexico by both commercial and recreational fishermen. During the early twentieth century, the commercial fishery which began using hand lines had switched to gill nets providing peak landings during the early 1930's at over 114 mt before the crash of the commercial fishery off southern California in 1935 to under 10 mt (Crooke 1992). The commercial fishery of giant sea bass taken from Mexican waters had greater landings and durability than those off southern California. Peaking in the early 1930's at over 362 mt with a steady decrease throughout the 1960's (Crooke 1992). The recreational fishery for giant sea bass off southern California peaked in 1963, and in Mexico in 1973. That these peaks in recreational landings were after the crash of the commercial fishery is due to the later development of the recreational fishery, and not the population size itself (Domeier 2001). By the mid 1970's, several boats would target presumed spawning aggregations sites throughout the month of July off southern California and Mexico, consistently landing high numbers (Crooke 1992) and in one case up to 255 fish in three days (Domeier 2001). Likewise, during the 1960's and 70's the practice of spearfishing grew in popularity. The gregarious and bold disposition of giant sea bass did not help this apex predator against the increasing numbers of spearfishers, as they were easy targets and landed at high frequencies (Fitch and Lavenberg 1971, Crooke 1992).

This combination of various fishing pressures led to their near disappearance during the 1970's (Pondella and Allen 2008), and by 1981 both southern California and Mexico landings dropped below 5 mt (Crooke 1992, Domeier 2001). In 1981, a law was passed prohibiting the take of any giant sea bass off California, with the exception of two fish per vessel trip for commercial fishermen using gill or trammel nets, and the moratorium was put into effect in 1982. This law was later amended in 1988, allowing one incidental fish per commercial fishing trip off California waters. However, though this amendment limited the number able to be sold in California by commercial fishermen, it still allowed fishing via gill and trammel nets over nearshore rocky reefs and kelp forest habitat (Pondella and Allen 2008). These nearshore habitats that were targeted are those used by giant sea bass, especially during aggregation months from May - October, and the incidental bycatch of giant sea bass was discarded at sea (Crooke 1992, Domeier 2001), or rumored to be shared among commercial fisherman. Due to concerns over the viability of the giant sea bass population off southern California, this species was red listed in 1996 by the International Union for Conservation of Nature (IUCN) as a critically endangered species (Cornish 2004).

It is rare to find evidence of a long-lived, slow growing, and late maturing species recovering after being strongly affected by overfishing (Hutchings 2000). However, after the gill net fishery was banned within three nautical miles of the mainland and one nautical mile of the islands with Proposition 132 in 1994, the population began to recover (Pondella and Allen 2008). After being seldom seen in southern California from the 1970s - 1990s (Domeier 2001), and not being observed in quarterly surveys by the Vantuna Research Group of Occidental College off the Palos Verdes coast between 1974 - 2001, giant sea bass began to be observed in 2002, and have been seen to the present day (Pondella and Allen 2008). Likewise, incidental commercial

catch and CPUE from the Ocean Resource Enhancement Hatchery Program (OREHP) scientific gill net surveys showed a significant positive increase from 1995 - 2004, an increase that was not correlated to fluctuations in environmental factors (Pondella and Allen 2008). These findings allude to a nascent return of giant sea bass within the Southern California Bight.

Giant sea bass frequented yearly site-specific aggregations for presumed spawning purposes in the past, as fishermen targeted and depleted these areas during the 1970's (Crooke 1992). Due to the elimination of previous spawning aggregations and the majority of the southern California giant sea bass population, modern day locations of aggregation sites are largely unknown. For conspicuous aggregation sites to reappear it is likely that population numbers would have to reach a certain abundance (Domeier 2001). However, anecdotal reports by the recreational dive community today suggests that historical spawning aggregations are returning primarily off La Jolla, Santa Catalina Island, and Anacapa Island, California. Surveying spawning aggregation sites allows for a unique opportunity to access a larger percentage of the reproductive population that would otherwise be spread over a greater geographic distribution (Johannes et al. 1999, Whaylen et al. 2004, Heppell et al. 2012). Furthermore, with information on a spawning aggregation biomass, through a length-weight relationship for the species and an estimate of total abundance, the spawning stock biomass of a species can be estimated (Jennings et al. 1996).

Our study applies underwater visual censuses (UVC) using length calibrated lasers for more precise size estimation (Gingras et al. 1998, Colin et al. 2003, Heppell et al. 2012) to provide the first population assessment of the endangered tertiary carnivore, the giant sea bass, of the rocky reefs and kelp forests off southern California at Santa Catalina Island, CA. The objectives of this study were to 1) identify and document spawning aggregation sites and peak aggregation periods throughout the summers of 2014 and 2015; and 2) establish baseline mean densities, stock biomass, and length/biomass distribution frequencies to compare with historical fish surveys.

Materials and Methods

Study Sites

Eight sites were surveyed off Santa Catalina Island, CA during the summer of 2014 (6/9/14 to 8/13/14) and 2015 (6/11/15 to 8/11/15) (Fig. 1a). In an attempt to get both a windward and leeward representative sample for the island, the eight sites were located at Johnson's Rock (33°28'37.08" N lat. 118°35'22.57" W. long.), Little Geiger (33°27'27.62" N lat. 118°30'51.03" W. long.), Empire Landing (33°25'59.96" N lat. 118°26'52.44" W. long.), between Twin Rocks and Goat Harbor (33°25'04.49" N lat. 118°23'38.24" W. long.), Italian Gardens (33°24'39.92" N lat. 118°22'32.50" W. long.), Casino Point (33°20'58.68" N lat. 118°19'30.56" W. long.), The V's (33°18'45.94" N lat. 118°22'11.38" W. long.), and Little Harbor (33°23'08.10" N lat. 118°28'48.94" W. long.). Sites averaged a distance of 7 km apart. Each of the eight sites contained habitat presumed suitable for giant sea bass aggregations based on characteristics of the Long Point State Marine Reserve (SMR) put into effect to protect the best known site for giant sea bass in southern California (CA MLPA South Coast Project 2009). Each site consisting of deep (>18 m) rocky reefs, and reef edges, where *Macrocystis* kelp forests were present. Of the eight sites, four are thought to be possible giant sea bass aggregation sites based on historical records and reports from the recreational diving community (The V's, Casino Point, Italian Gardens, and Goat Harbor). The Vs site was not surveyed in 2015 due to high surge and low visibility throughout the season.

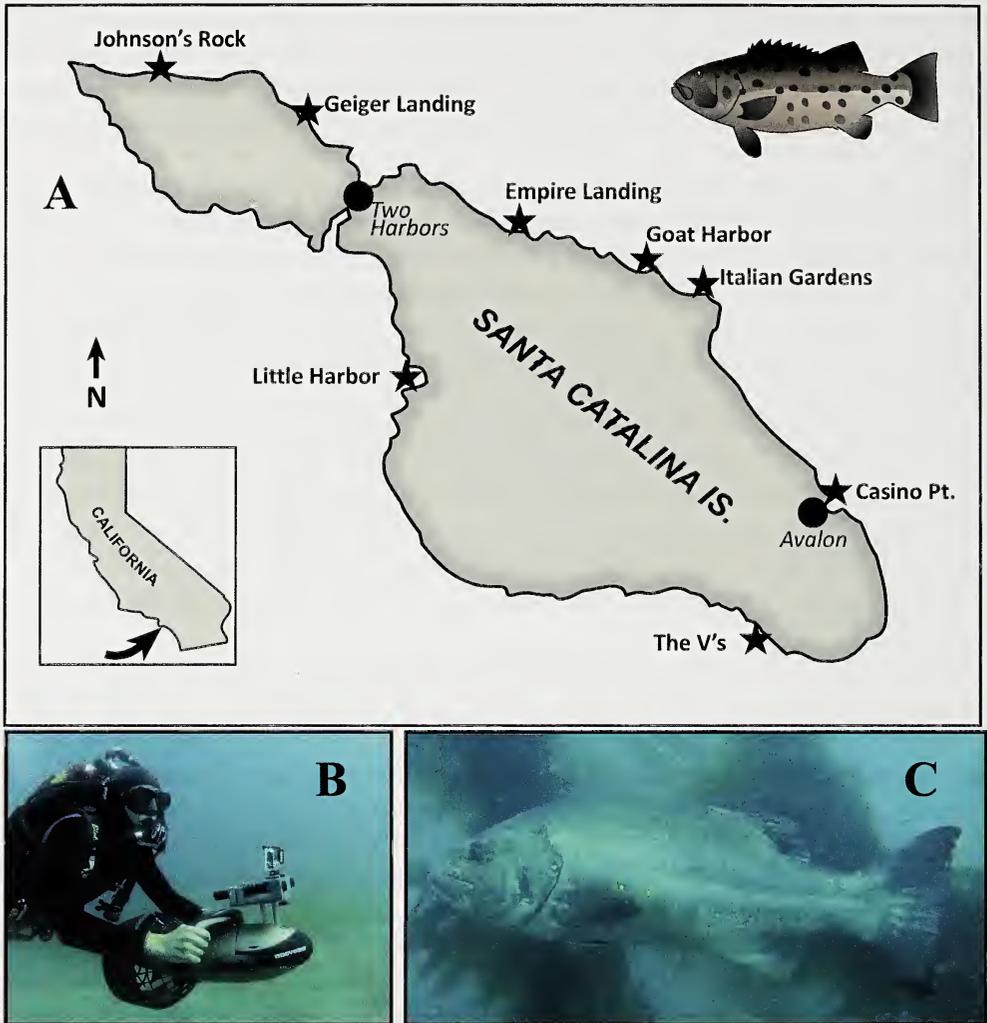


Fig. 1. Sampling sites and methods: A) Location of the eight sites surveyed off Santa Catalina Island, CA in the summers of 2014 and 2015; B) Image of a dive propulsion vehicle (DPV) with mounted length calibrated lasers and GoPro Hero 3 Black Edition video camera used for giant sea bass surveys; and C) Image of a giant sea bass showing broadside length calibrated laser markings at 10.2 cm.

Survey Methods

Surveys at each site were conducted every two weeks for two months in 2014 and 2015 for a total of 64 survey days. Each visual survey was conducted from 10:00 to 14:00 and consisted of five, three-minute, 100 m x 10 m SCUBA transects (1,000 m²) using Sea Doo Vs Supercharged Plus Sea Scooter diver propulsion vehicles (DPVs). DPVs were outfitted with two parallel waterproof length-calibrated lasers, set at 10.2 cm apart, and a mounted GoPro Hero3 Black Edition video camera (Fig. 1b). Before surveys began, divers trained using the DPVs in combination with timed fin kicks to cover 100 m in three minutes. The five timed transects per site were spaced at least 50 m apart with each transect randomly stratified in depth from 28 - 6 m to extensively survey the reef at each site. Along each transect, giant sea bass occurring in front of divers and within the transect area were counted, and their size estimated to the nearest 25 cm. Surveys for giant sea bass covered a large area during a short amount of fixed time to

aid in reducing biases that may arise during non-instantaneous UVC of large mobile fishes (Ward-Paige et al. 2010, McCauley et al. 2012). In addition, transects were video recorded to help identify separate individuals between sampling periods by size, differences in morphology, physical markings, and spot patterns.

Upon the conclusion of each transect, size-surveys were done by video recording individuals observed at a 90° angle to the video camera with the parallel lasers spaced 10.2 cm apart (Gingras et al. 1998, Colin et al. 2003, Heppel et al. 2012). To reduce possible size estimation error, giant sea bass recorded during size surveys were measured within 2.5 - 3 m of the individual fish. Images of fish from the size-survey videos that displayed broadside and perpendicular to the video camera with visible measurement laser markings (Fig. 1c) were digitally captured and length (cm SL and TL) were estimated using the software program ImageJ (<http://imagej.nih.gov/ij/>). The lengths obtained from the size surveys were used to validate size estimations taken during transects.

Lengths were converted to biomass (kg/1000 m²) using the length-weight relationship recently published for this species: $kg = (0.0000001) * (SL \text{ mm})^{2.8173}$ (Williams et al. 2013). Age of sized individuals was back-calculated using the inverse of the published von Bertalanffy growth curve (von Bertalanffy 1938) for giant sea bass: $l_t = 2026.2(1 - e^{-0.044(t-0.345)})$ (Hawk and Allen 2014). The 2014 surveys were conducted during 6/9 - 6/24, 6/28 - 7/12, 7/15 - 8/2, and 8/4 - 8/13/2014 while the seven sites in 2015 were conducted during 6/11 - 6/20, 6/22 - 7/10, 7/11 - 7/31, and 8/4 - 8/11.

In order to provide a historical perspective on the population off Santa Catalina Island, giant sea bass recorded on subtidal surveys conducted from 1965-2013 by the Channel Islands Research Program (CIRP) were generously provided by Dr. Jack Engel (UCSB). CIRP surveys consisted of divers visually surveying the reef between 4 - 21 m in depth for all algae, macro-invertebrates, and fishes within a timed period. Organisms were identified and abundances were estimated on a relative scale from 1 (rare) to 4 (abundant). On surveys where giant sea bass occurred the number of individuals was noted.

Statistical Analyses

The abundance (#/transect) and biomass (kg/1000 m²) estimates of giant sea bass included many zeros and did not fit the assumptions of normality required for parametric analyses. Numerical and biomass densities of giant sea bass for Site (fixed factor: 8 levels), Year (fixed factor: 2 levels), and Sampling Period (fixed factor: 4 levels) were compared using permutational analysis of variance with PERMANOVA+ for PRIMER-E ver. 6 (Anderson 2001, Anderson and Millar 2004) with individual transects used as samples. The Dwass-Steel-Chritchlow-Fligner Test for All Pairwise Comparisons was then used to test for differences between sites. For length frequency and biomass distribution analysis, lengths (mm TL) were grouped into 100 mm increments to investigate the length, biomass, and age class frequency distributions of the surveyed giant sea bass population off Santa Catalina Island for both the summer of 2014 and 2015. Length Frequencies of giant sea bass encountered in 2014 and 2015 were compared with a Non-parametric Kolmogorov-Smirnov Test using SYSTAT 13 (SYSTAT Software, Inc).

Results

Giant sea bass numerical densities (no. fish/1000 m²) were not statistically significant among the four sampling periods ($Pseudo-F=0.92$, $P(perm)=0.48$). Despite this lack of significance, total number of individuals observed during surveys in 2014 peaked in late-July and in early July in 2015 (Figure 2) Similar to numbers, biomass (kg/1000 m²) was not statistically different

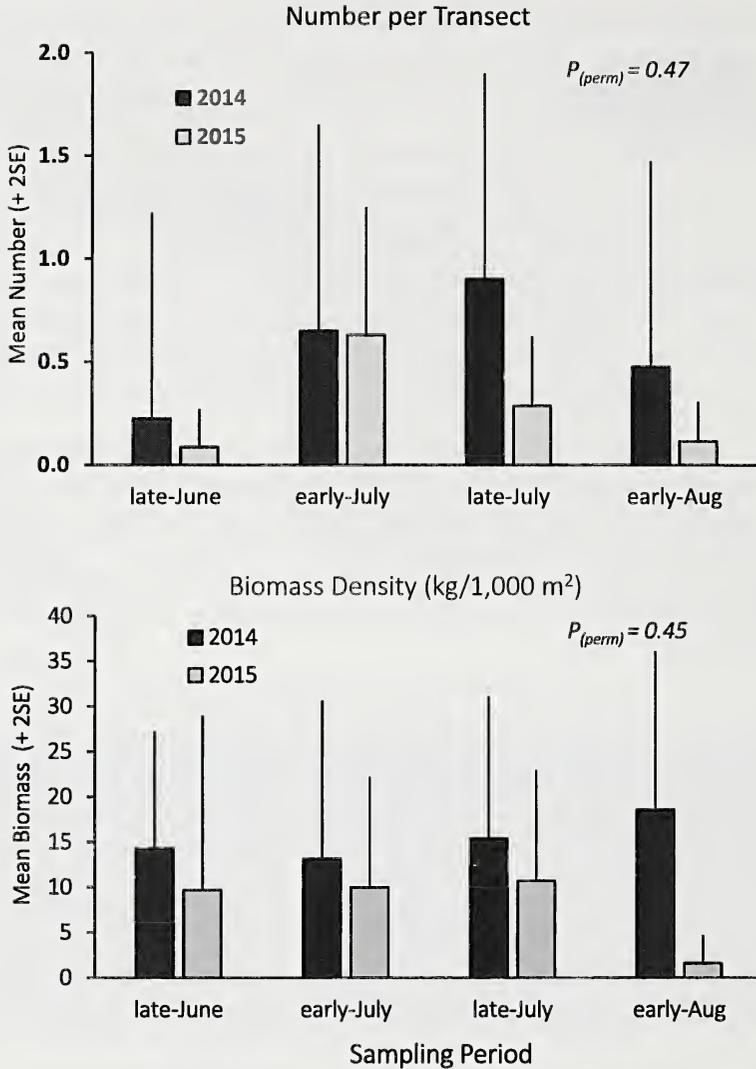


Fig. 2. Mean number of giant sea bass per two-week sampling period (top), and (bottom) mean spawning stock biomass densities (kg/1000 m²) of giant sea bass per two-week sampling period. Error bars represent 2 standard errors. No significant differences ($P_{(perm)} = 0.47; 0.45$) were found in temporal distribution of giant sea bass numbers or biomass in either year.

among the four sampling periods in either year ($Pseudo-F = 0.92$, $P_{(perm)} = 0.45$). However, biomass density (Fig. 2) was consistent among the survey periods in both years with the exception of early August when biomass density peaked in 2014 and decreased in 2015.

Giant sea bass were observed at seven of the eight sites around the island (Little Geiger, Empire Landing, Goat Harbor, Italian Gardens, The V's, and Little Harbor). No giant sea bass were observed at Johnson's Rock. Numbers (Figure 3: $Pseudo-F = 5.88$; $P_{(perm)} < 0.001$) and biomass (Fig. 3: $Pseudo-F = 5.87$; $P_{(perm)} < 0.001$) differed significantly among sites over both summers of sampling. In the summer of 2014, aggregations were found at Goat Harbor, The V's, and Little Harbor. The site containing the largest number of giant sea bass was The V's, where 23 were seen on the second sampling and 24 on the third sampling in 2014. Little Harbor and Goat Harbor had the next highest numbers and spawning stock biomass.

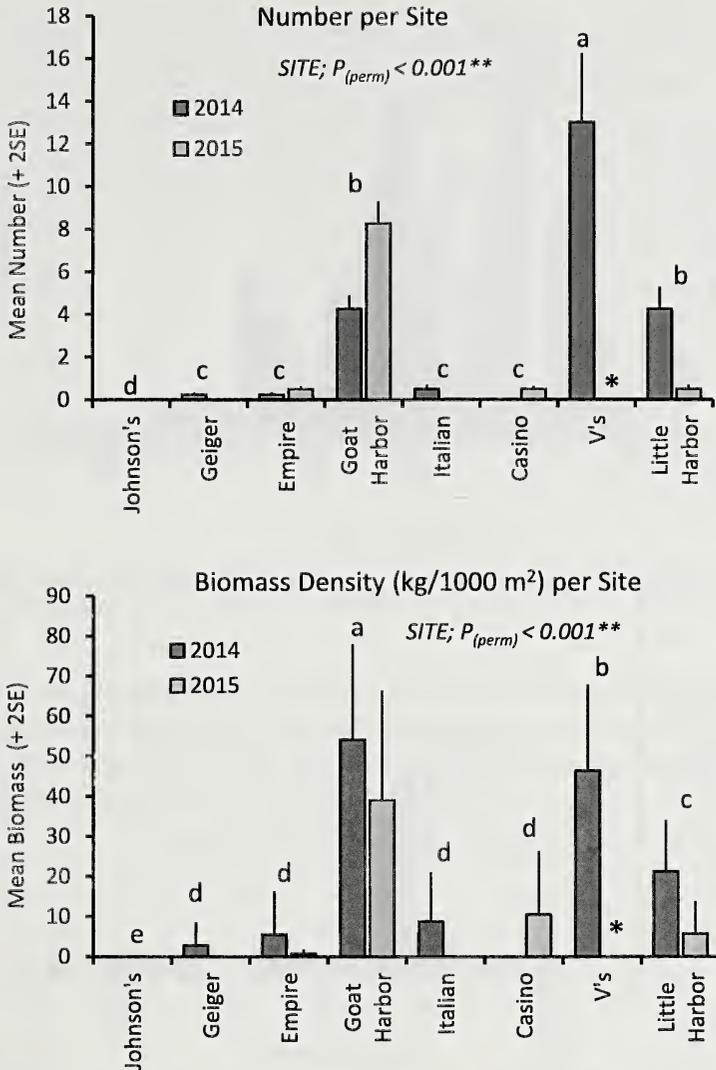


Fig. 3. Mean number of giant sea bass per transect at each sampling site (top) and (bottom) mean spawning stock biomass densities (kg/1000 m²) of giant sea bass per site during the summers of 2014 and 2015. Sites are arranged the NE end clockwise around the island. Letters (a-e) denote sites not statistically different from one another. (* – no transects conducted in 2015 at the Vs).

An aggregation of ten fish was observed on transects at Little Harbor, while at Goat Harbor an aggregation of six was found. Mean biomass was higher at Goat Harbor (81.2 ± 29.8 kg/1000 m²) than Little Harbor (34.0 ± 18.67 kg/1000m²) due to larger individuals aggregating at Goat Harbor. In 2015, Goat Harbor was the only site to contain an aggregation. The Goat Harbor aggregation averaged 8 giant sea bass per sampling period (3, 19, 7, and 4 individuals). Biomass density at Goat Harbor ranged from 11.03 to 66.67 and averaged 39.67 kg/1000 m² in 2015. The remaining sites where giant sea bass were surveyed contained solitary individuals or a single pair.

Size of surveyed giant sea bass ranged from 0.9 - 2.75 m TL. According to the established age-length curve for giant sea bass (Hawk and Allen 2014), the smallest individual (0.7 m TL) was estimated to be 8 years old. The length frequencies of separate individuals that were

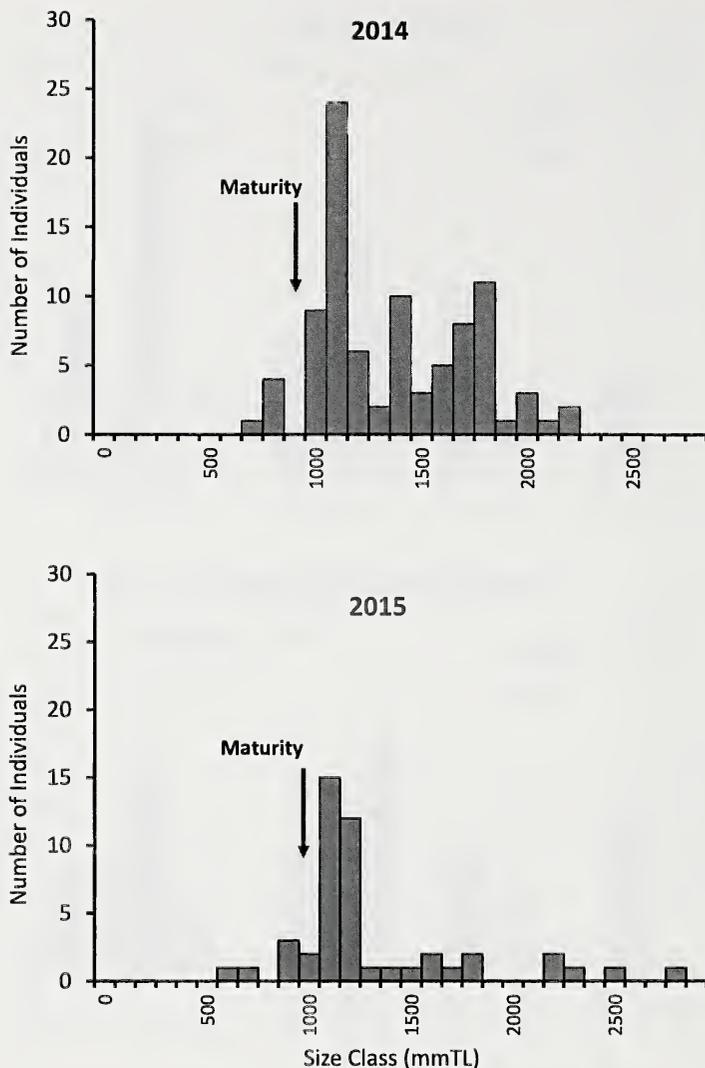


Fig. 4. Length frequencies (mm TL) of separate giant sea bass observed during survey transects in the summers of 2014 and 2015 off Santa Catalina Island. Arrows indicate presumed size at maturity based on estimate size/age estimates from Fitch and Lavenberg (1971).

not significantly different in 2014 and 2015 (K-S test; $p = 0.258$) showed the typical giant sea bass at Santa Catalina Island in 2014 and 2015 to be 1.2 - 1.3 m TL (Fig. 4). However, a large portion (25%) of the population's biomass was found in individuals between 1.9 and 2.1 m TL (Fig. 5). The largest giant sea bass observed occurred in late June in both years. The 1994 to 2003 year-classes dominated the giant sea bass population observed in the summers of 2014 and 2015 (Fig. 6). Based on ages back-calculated from measurements of total length, these eight year-classes constituted 60% of all the giant sea bass observed. Another 16% of the individuals recruited between the years 1982 and 1993 with the remainder recruiting sporadically back to 1954. Overall mean biomass of giant sea bass off Santa Catalina Island during the summer was 25.14 ± 6.57 kg/1000 m² in 2014 and 11.96 ± 6.28 kg/1000 m² in 2015, with an overall mean biomass of 19.57 ± 4.64 kg/1000 m² for both summers. The historical CIRP survey

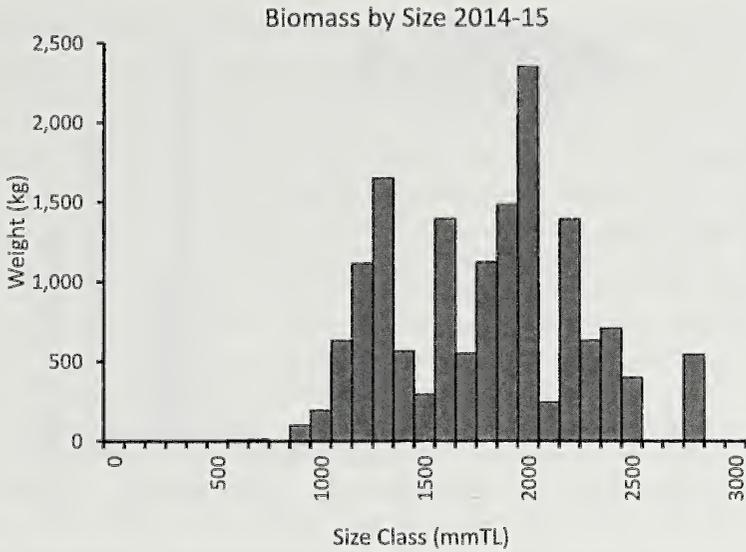


Fig. 5. Total biomass (kg) distribution per size class (mm TL) of giant sea bass observed during survey transects in the summers of 2014 and 2015.

data from 1965-2013 (Figure 7) show one giant sea bass being observed during surveys in 1966 with a 29-year absence until 1996. After 1996, giant sea bass were observed in 1997, 2000, 2001, 2002, 2003, 2006, 2007, 2010, and 2011. The highest number of giant sea bass on CIRP surveys occurred in 2001 with 11 individuals observed.

All Giants by Year Class, 1950-2015

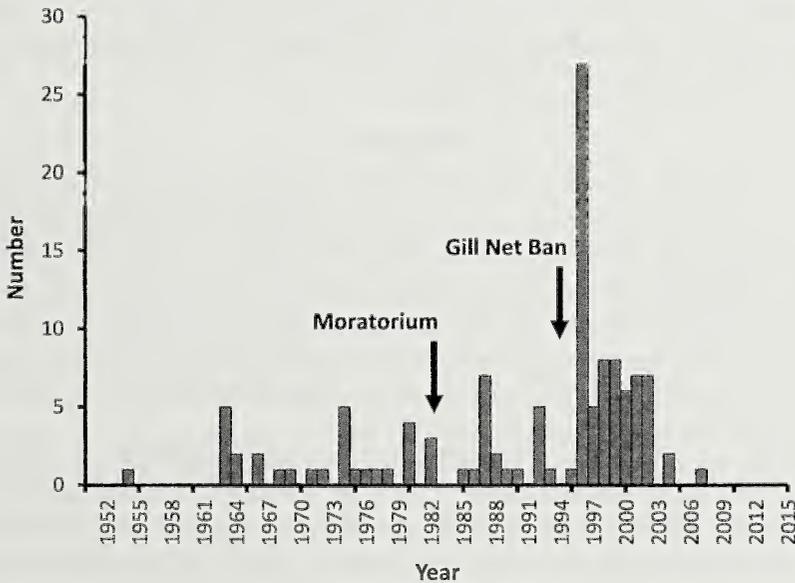


Fig. 6. Year-class strength for giant sea bass for 1950 to 2015 back-calculated from *in situ* measurements of total length converted to age after (Hawk and Allen 2014). Arrows indicate the year that the fishing moratorium was declared (1982) and the year of the Proposition 132 Gill Net Ban (1994) from coastal waters in southern California.

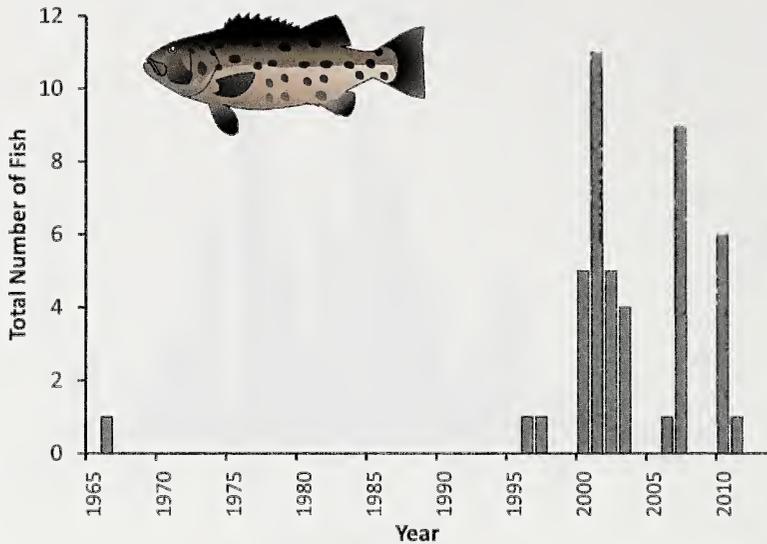


Fig. 7. Giant sea bass observed on SCUBA fish surveys conducted by the Channel Islands Research Program (CIRP) at Catalina Island from 1965-2013. Data courtesy of Dr. John Engle (UC Santa Barbara) funded by the Tatman Foundation.

We observed 44 separate individuals on transects in 2014 and 32 in 2015 based on differences in size, morphology, physical markings, and spot patterns of giant sea bass. If we assume the estimated numerical densities per m^2 are accurate over the depth range of the eight established sites, then about 87 linear km (86,905 m) of coastline around Santa Catalina Island held about 49 giant sea bass in the summer of 2014 and about half that number, about 24, in summer 2015. Similarly, biomass densities estimated that 2.1 metric tons (mt) of giant sea bass occurred around Catalina in 2014 with about 1.0 mt occurring in 2015. The number of individual giant sea bass identified by divers and the number of giants estimated from transect densities were remarkably similar in both years of the study.

Discussion

Altogether, this study provides evidence of the return of giant sea bass to the rocky reefs and kelp forests off Santa Catalina Island, and possibly the Southern California Bight, by documenting new spawning aggregation sites, considerable stock biomass, newly mature individuals recruiting to aggregations, and a large community presence at the island. Overall, abundance and biomass of giant sea bass did not differ greatly among the four sampling periods in 2014 and 2015. The large variation in numbers and biomass during the four sampling periods for both years can be largely attributed to the patchy distribution that resulted in the high number of transects where no giant sea bass were observed.

Of the eight sites, at least three were identified as giant sea bass aggregations off Santa Catalina Island, CA. These sites were located on both the leeward (Goat Harbor) and windward (The V's and Little Harbor) side of the island. Goat Harbor is the only of these three sites where aggregations were encountered in both years of this study. Goat Harbor is also the only aggregation residing in a Marine Protected Area (MPA) as of 2012. The placement of the Long Point State Marine Reserve (SMR) was to protect the best-known aggregation area for giant sea bass off southern California from Long Point to Goat Harbor (CA MLPA South Coast Project 2009), and is a popular site for recreational divers. However, though this site had a consistent

aggregation during each of the four sampling periods, it did not possess the largest giant sea bass aggregation. The largest suspected spawning aggregation was found at the V's in 2014 with a total of 23 and 24 individuals occurring on transects during the second and third sampling period at 18 m depth. The individuals at the V's were typically larger, 1.2 - 2.3 m TL. Throughout the summer of 2014 human presence was minimal at this site, as the V's is located in a more remote area of the windward side of the island. However, commercial squid fishing vessels were observed in close proximity to the reef where the giant sea bass aggregation was observed (P.H.H., personal obs.). Unfortunately, the V's site was largely inaccessible to our divers in 2015. The third aggregation site was located on the reefs just outside and west of Little Harbor. The consistency of this aggregation varied. On the third and fourth sampling periods during 2014, 6 and 10 giant sea bass were observed respectively. The aggregation at Little Harbor in 2014 consisted primarily of smaller individuals (eight individuals under 1.2 m TL) compared to the other two aggregation sites at Goat Harbor and the V's. No giant sea bass were seen during surveys at Johnson's Rock in either summer. The Little Geiger and Empire Landing sites contained solitary individuals that were observed sporadically over the two years. Italian Gardens which is also inside the Long Point SMR had either solitary individuals or a single pair of giant sea bass that were likewise only observed sporadically.

If the giant sea bass population off southern California is indeed recovering, then there is likely to be a larger proportion of smaller and younger fish within the population, which could manifest as a positive skew in length frequencies of the population (Heppell et al. 2012). In the case of a spawning aggregation, smaller size classes represent newly mature fish entering the reproductive population. Our results do not show a strong positive skew as the majority of reproductive giant sea bass off Santa Catalina Island were ~1.3 m TL and were estimated to be 18 - 19 years-old. However, smaller individuals were observed during surveys in presumed spawning aggregations off the island. These individuals were estimated to be 10 - 11 years old. Age at sexual maturity has not been adequately explored for giant sea bass, however, Fitch and Lavenberg (1971) estimated sexual maturity to begin between 11 and 13 years of age. Our findings of young giant sea bass within presumed spawning aggregations support the Fitch and Lavenberg (1971) estimates. Based on year-class strength estimates (Fig. 6), these young fish are likely new recruits to the reproductive population off Santa Catalina Island that were born after the 1994 Proposition 132 gill net ban in coastal waters. Our results also suggest that these young individuals were able to find site-specific suspected spawning aggregations that were likely once decimated by overfishing.

Although a large portion of the presumed reproductive population censused in the present study was made up of individuals 1.2 - 1.3 m in total length, this size class did not account for the largest portion of the stock biomass. The size class with the peak biomass was older (estimated to be 32 - 35 years old) and larger (1.9 - 2.0 m TL) individuals. This skew in total biomass distribution toward the larger size classes was also due to several behemoth individuals. In 2014, the largest individual on transect was measured at 2.3 m TL (1.9 m SL) with a back-calculated age of 67 years old and 177.9 kg. However, this was not the largest giant sea bass measured in 2014. An individual that was measured during underwater observations, but did not occur within a survey transect was seen at Goat Harbor and measured 2.70 m TL (380 kg). Similarly in 2015, at the same site (Goat Harbor) and sample period (late June) an individual was measured at 2.75 m (381 kg), and was observed on transect. It is possible that these two observations in 2014 and 2015 could either be of the same individual or two separate individuals. In either case, these would be the largest giant sea bass ever measured, and supports early, unverified accounts of much older and larger giant sea bass (Holder 1910). Giant sea bass in this size range are over the Loo presented in Hawk and Allen (2014). Although their

age cannot be predicted accurately, it is not inconceivable that fish of this size are over 100 years of age.

Similar to Pondella and Allen (2008), fish survey data collected by the Channel Islands Research Program (CIRP) beginning in 1964 suggests a similar trend to the Palos Verdes coast in number of giant sea bass sightings off Santa Catalina Island. From the CIRP surveys only one giant sea bass was observed until the late 1990's and early 2000's to present day. However, although these data suggest a recent return of giant sea bass, historical accounts document fisherman consistently taking 70 - 100 giant sea bass from summer aggregations (Domeier 2001), suggesting that present day aggregation densities are still well under historical levels. The two aggregation sites containing the highest abundance (the V's) and younger individuals (Little Harbor) of the three spawning aggregation sites are currently in unprotected areas where fishing is allowed.

Pre-exploitation biomass for the entire southern California population of the giant sea bass has been estimated to be 1,179 mt (Ragen, 1990). For comparison, our biomass estimates of 2.1 mt and 1.0 mt of standing stock biomass off Catalina Island in 2014 and 2015 were a full three-orders of magnitude lower. If our current estimates of biomass of Catalina Island are extrapolated to the entire southern California coastline, it appears that the current standing stock of the giant sea bass population off southern California, although returning, falls far short of what the natural stocks were prior to exploitation. As others have often cited (cf., Domeier, 2001), it may well be decades before the giant sea bass population recovers to levels appropriate for renewed commercial exploitation.

Despite giant sea bass being a protected species they are often susceptible to barotrauma when caught incidentally. Schroeder and Love (2002) estimated how incidental catch and release mortality of giant sea bass could affect population sizes. Their estimates suggest that 100 giant sea bass, at a standard catch and release mortality rate of 20%, could be completely eradicated through incidental catch and release in just 16 years assuming no immigration. With the aggregation sizes found in our study, the largest being an aggregation of 24 fish, this incidental catch and release mortality rate could decimate the reproductive population off Santa Catalina Island during the summer spawning months. Seasonally established MPAs at identified giant sea bass spawning aggregation sites, similar to those set in place to protect Nassau grouper spawning aggregations in the Caribbean, could aid in reducing the incidental catch of giant sea bass near these areas. Furthermore, monitoring of aggregations after baseline estimates would allow temporal tracking of numerical densities, biomass, and population dynamics of giant sea bass off Santa Catalina Island and other sites within the Southern California Bight. Our study provides an effective way to survey these aggregations, and further surveys of the kelp forest community are needed to document what potential influences a return of a long absent top predator may have to the dynamics of this ecosystem.

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

Jeffrey H. R. Goddard,^{1*} Nancy Treneman,² William E. Pence,³ Douglas E. Mason,⁴
Phillip M. Dobry,⁵ Brenna Green,⁶ and Craig Hoover⁷

¹Marine Science Institute, University of California, Santa Barbara,
CA 93106-6150

²Oregon Institute of Marine Biology, Charleston,
OR 97420

³Alameda County Office of Education, Hayward,
CA 94544

⁴Science Department, California High School, San Ramon,
CA 94583

⁵California State University, East Bay, Hayward, CA 94542

⁶Department of Invertebrate Zoology and Geology, California Academy of Sciences,
San Francisco, CA 94118-4503

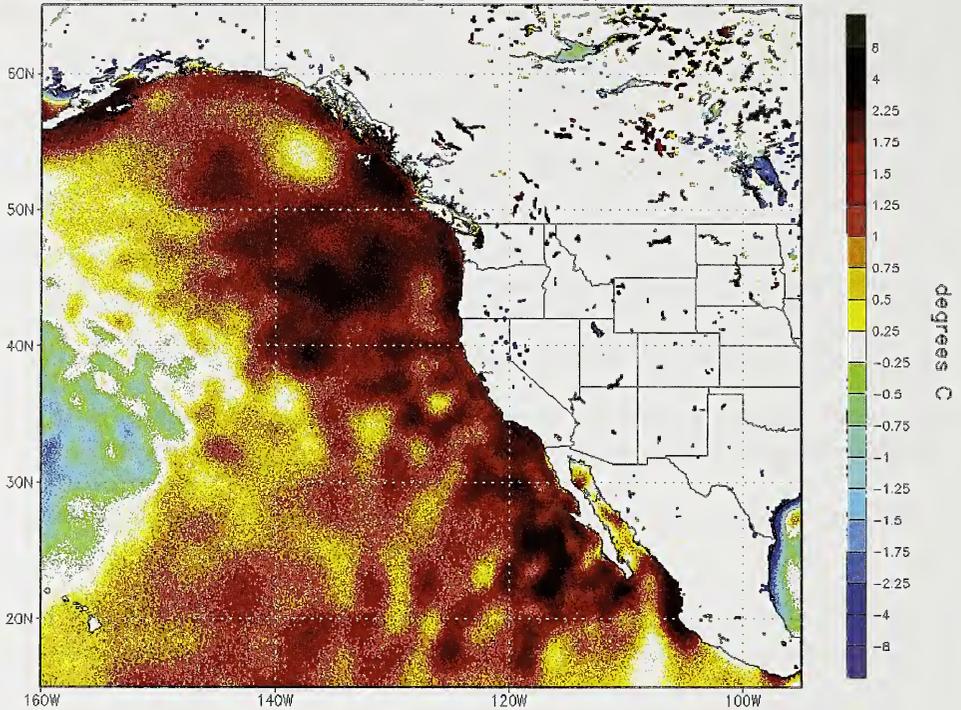
⁷Biological Sciences Department, California State Polytechnic University, Pomona,
CA 91768

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. barbarendis*, *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.

* Corresponding author: goddard@lifesci.ucsb.edu

NOAA/NWS/NCEP/EMC Marine Modeling and Analysis Branch Oper H.R.

RTG_SST_HR Anomaly (0.083 deg X 0.083 deg) for 01 Feb 2015



SUN FEB 1 2015

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 barbarentis* 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
Tar pits 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 Island¹ 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 OIMB⁸, 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 2015⁹.

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

^aData from: R. Agarwall (<http://www.inaturalist.org/observations/1156561>)

¹Data 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 individual¹⁰ 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 County¹¹.

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 Head¹².

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>

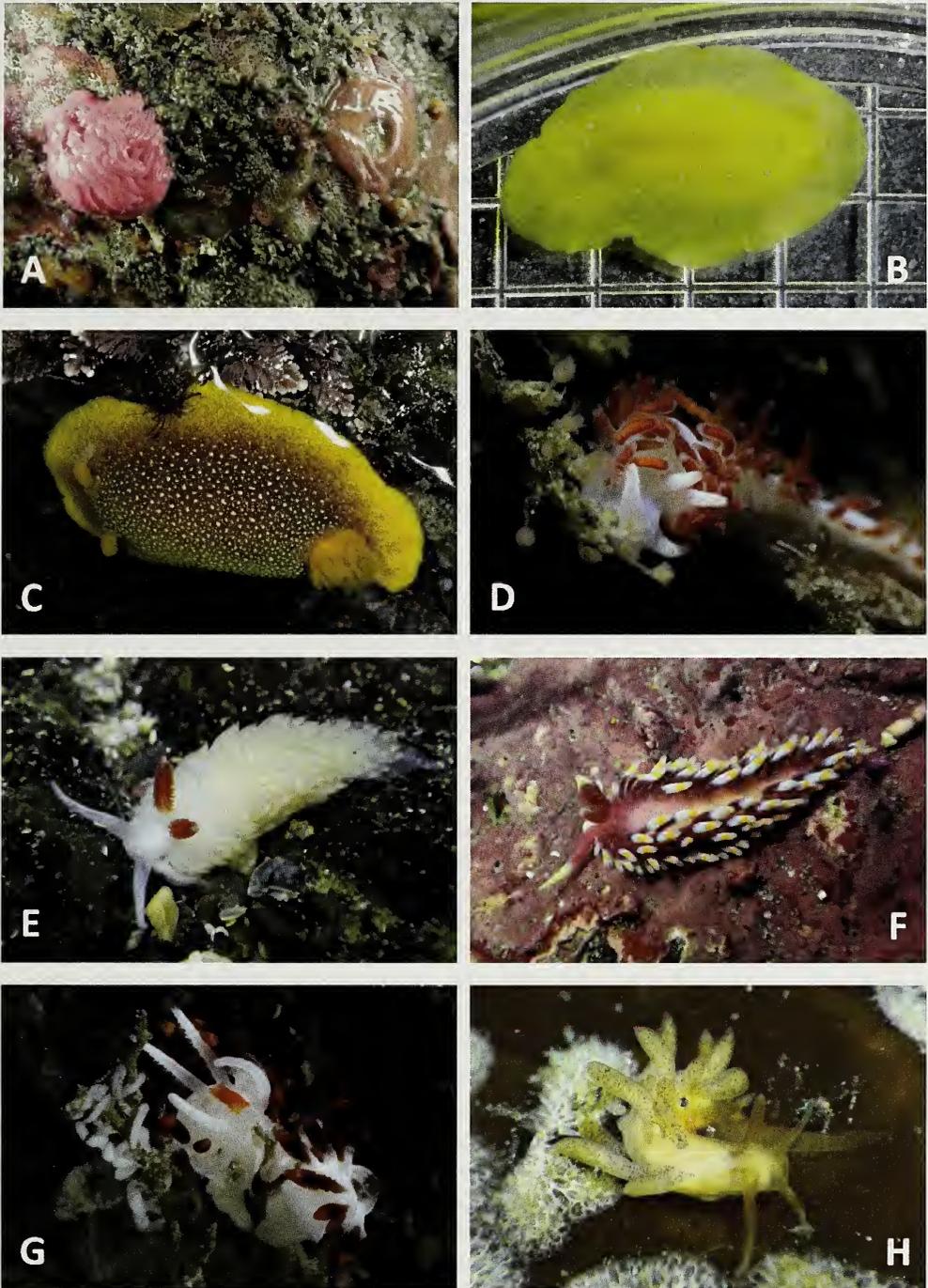


Fig. 3. Selected nudibranchs found in 2014-15 north of their usual geographic ranges. **A** *Okenia rosacea* and egg ribbons, Lone Ranch, Oregon, 18 July 2015. Image by NT. **B** *Doriopsilla fulva*, Whiskey Creek, Oregon, 16 June 2015. Image by NT. **C** *Doriopsilla gemela*, Tarpits Reef, Carpinteria, 19 May 2015. Image by CH. **D** *Flabellina bertschi*, Big Fishermans Cove, Santa Catalina Island, 2 January 2015. Image by CH. **E** *Antaeolidiella 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.

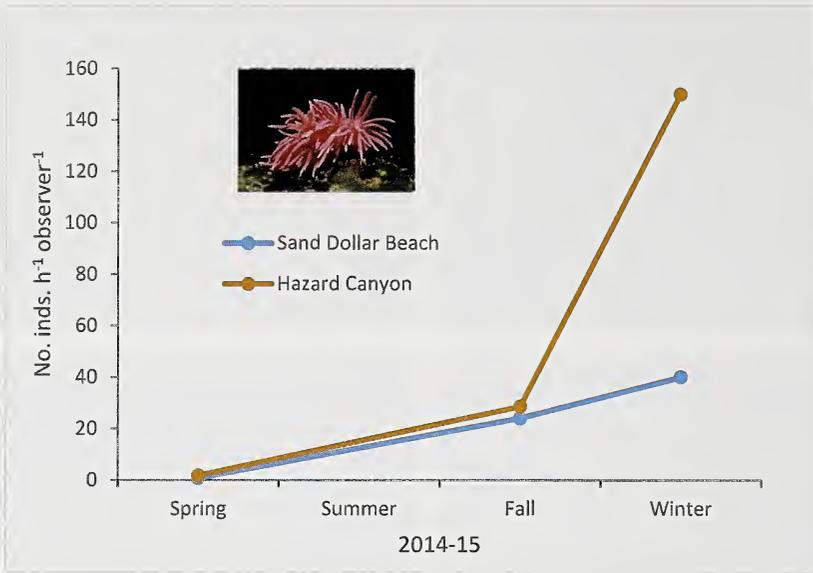


Fig. 4. Increase in abundance of *Okenia rosacea* at two sites in central California, spring 2014 to winter 2015. Sites were not sampled in summer. Image of *O. rosacea* by Gary McDonald.

(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 County¹³. 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 County¹⁶. 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 Grattan¹⁷, (2) Pillar Point by Matt Knoth¹⁸, and (3) Palmer's Point, Humboldt County by Cassidy Grattan, who on 2 August reported 10 specimens from Trinidad¹⁹. Since these reports additional specimens have been found at Pillar Point²⁰, 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/;](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

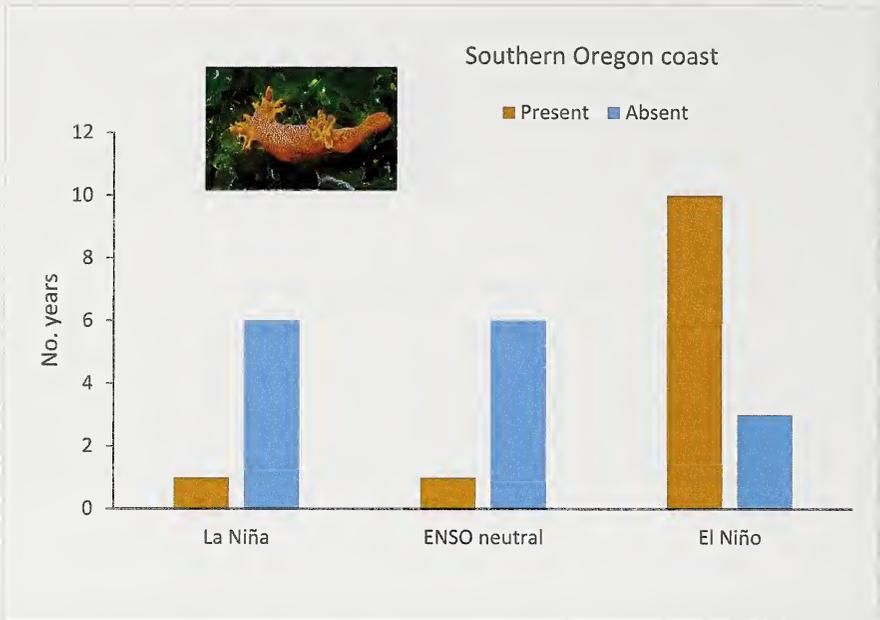


Fig. 5. Number of years *Triopha maculata* present or absent on the southern Oregon coast by phase of ENSO, 1980-98 and 2006-2014. Data for Whiskey Creek, Cape Blanco, and all three coves of Cape Arago combined, from Goddard (1984) and JG and NT (unpublished data). Image of *T. maculata* by Gary McDonald.

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 County²¹. 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 Peninsula²².

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, Bahía 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 Bahía 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 specimen²³ on 7 July 2015, and two more²⁴ 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 Beach²⁵. 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 (Jaekle 1984). NT found an additional specimen, 11 mm long, at Lone Ranch on 15 August 2015, and we found another specimen²⁶, 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 years²⁷.

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) Jaekle'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 specimen²⁸ 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 County²⁹, and on 2 August 2015 Spencer Dybdahl-Riffle found a specimen, 5 mm long, at Trinidad³⁰.

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 Point³¹. 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 Tar pits 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. barbarendis* 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 barbarendis* (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 Bay³³, a day after

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

³²Goddard, 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 Harbor³⁴, where she had first sighted one on 15 October 2014³⁵. On 11 September 2015 Shawn Brumbaugh and Chris Kwan found a *J. barbarentis* 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 locality³⁶.

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 Harbor³⁸ 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>

³⁶Sones, 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 communication 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 Bay⁴⁰, Coleman Beach (J. Sones personal communication to JG, 23 May 2015), and Trinidad, Humboldt County⁴¹. *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 Trinidad⁴².

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 Bay⁴³, and on 25 August 2015 found two specimens and their egg masses in San Francisco Bay⁴⁴. 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

⁴⁰Sones, 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>

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

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

⁴³<https://www.inaturalist.org/observations/1767403>

⁴⁴<https://www.flickr.com/photos/30314434@N06/20876669342>

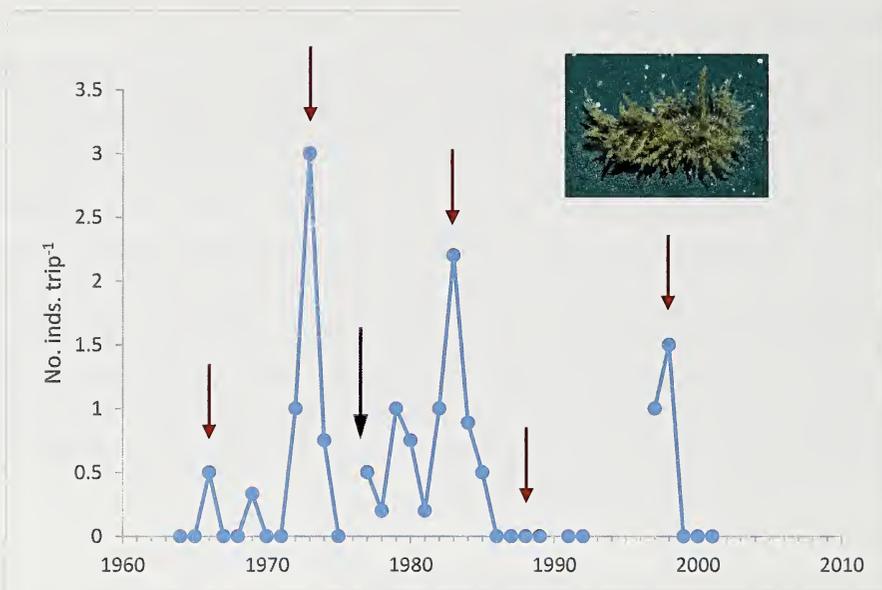


Fig. 6. Number of *Janolus anulatus* observed per sampling trip, La Jolla, California, 1964-2001. Red arrows indicate strong El Niños, and black arrow indicates 1976-77 climate shift. From data collected by James Lance and colleagues during 51 total sampling trips to intertidal sites at South Casa and 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 Beach⁴⁵.

On 20 May 2015 the senior author found six specimens intertidally on the south side of Point Dume, Malibu⁴⁶. Robin Agarwal found a specimen in Morro Bay in September 2014, and another on 26 July 2015 in the Monterey Harbor⁴⁷. 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 Agarwal⁴⁹.

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 County⁵⁰.

⁴⁵Kopp, 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>

⁵⁰http://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 Bay⁵¹, 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 Harbor⁵².

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 (Percy 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>

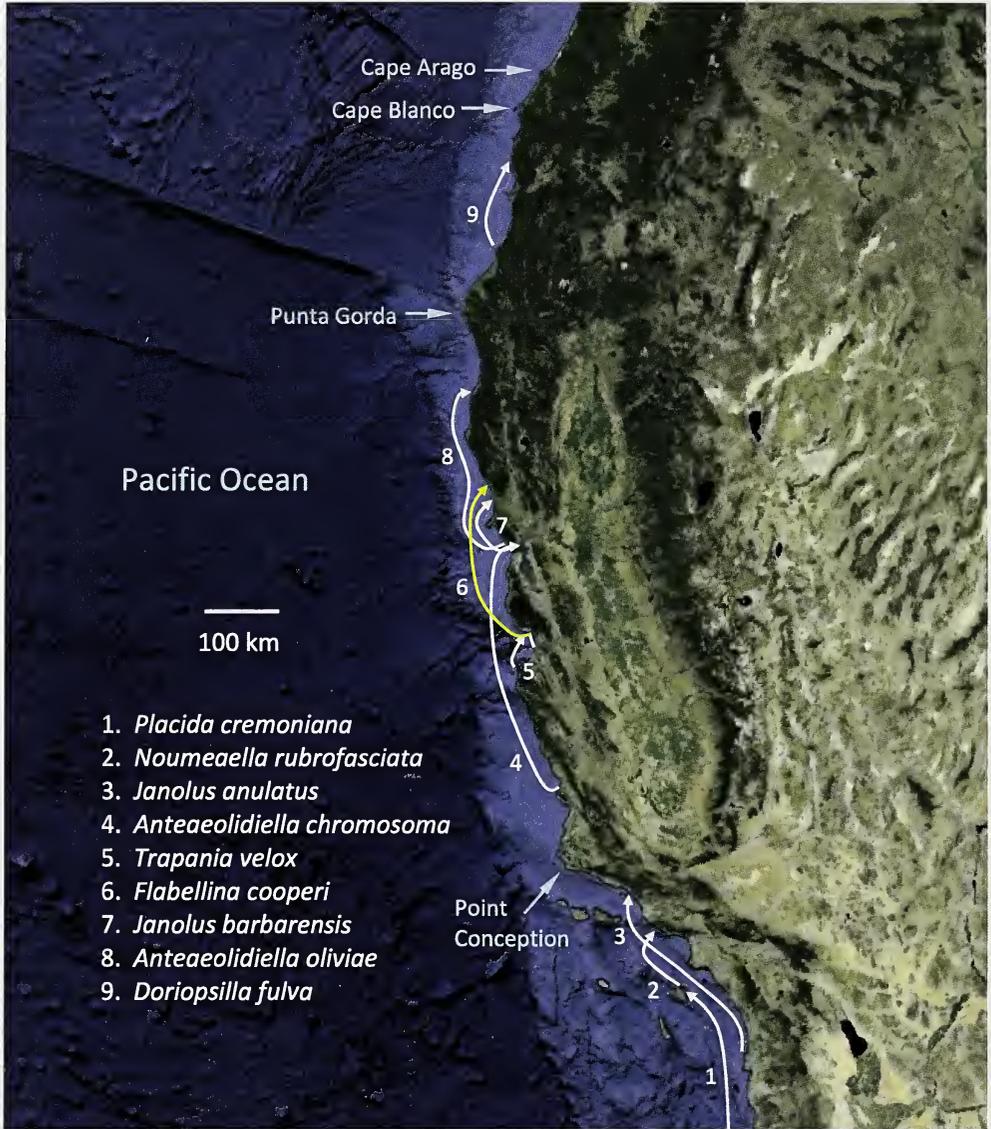


Fig. 7. Range extensions in 2014-15 from previous northernmost known localities of the sacoglossan *Placida cremoniana* and eight species of nudibranchs in the NE Pacific Ocean. The previous northernmost locality at La Paz, Mexico for *P. cremoniana* is not shown, and the yellow part of the line for *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. roseacea* 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

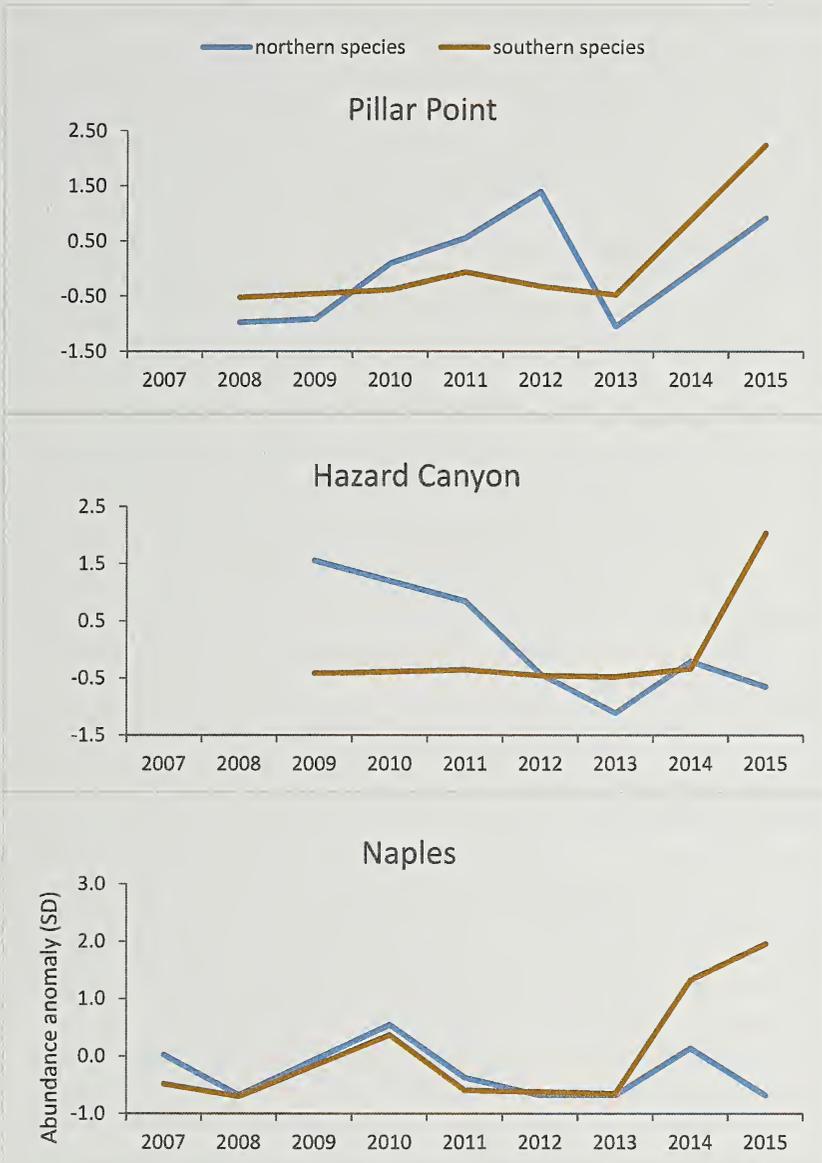


Fig. 8. Total abundance of southern and northern species of nudibranchs at three intertidal sites in California, winters only, 2007-15. Data plotted as anomalies (deviation from mean over years shown, in units of standard deviation). Missing values (2009 at Naples, 2010 at Hazard Canyon, and 2014 at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

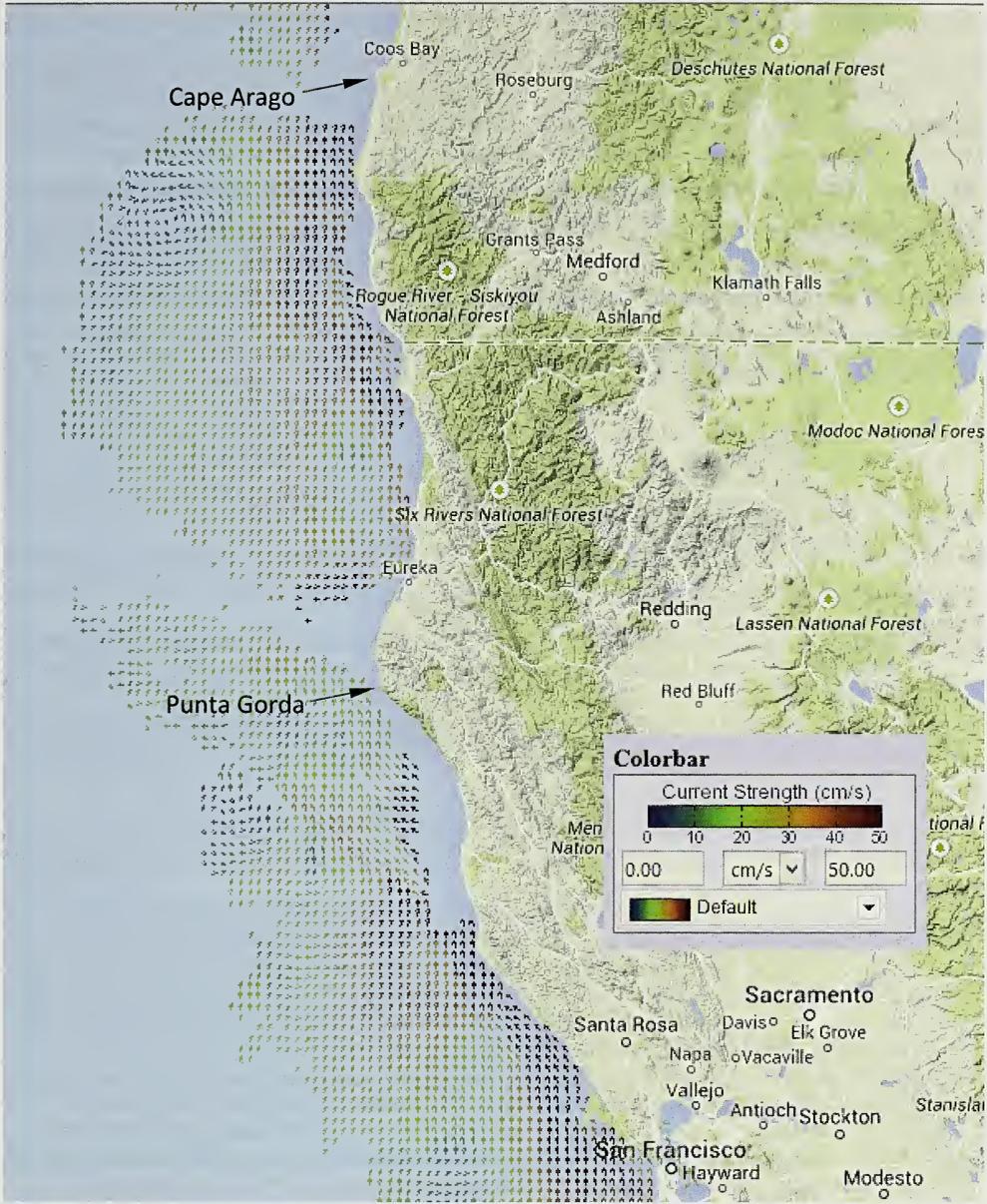


Fig. 9. Surface current flow, 6 February 2015, San Francisco, California to Cape Arago, Oregon. Source: Coastal Ocean Currents Monitoring Program (COCMP).

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Seed Collection and Germination Strategies for Common Wetland and Coastal Sage Scrub Species in Southern California

Michelle L. Barton^{1*}, Ivan D. Medel², Karina K. Johnston², and Christine R. Whitcraft¹

¹California State University Long Beach

²Santa Monica Bay Restoration Commission

Abstract.—There is a need for a consolidated source of information on native vegetation seed collection and germination strategies in southern California. Published literature on these methods is often experimental, species-specific, and widely scattered throughout online and print media. Planting and restoration strategies may need to be site-specific; however, similar methodological approaches are often utilized allowing for the development of general strategies for seed collection, storage, and germination methods. A better understanding of species-specific seed attributes and growth processes will help restoration ecologists collect high-quality, viable seed, thereby increasing the potential success of the restored vegetation community by reducing plant mortality, project costs, and effort. This paper synthesizes seed collection and germination strategies for native vegetation common to southern California estuarine wetland, coastal dune, and coastal sage scrub systems.

Current estimates affirm that over 70% of coastal wetlands in the Southern California Bight have been lost since the 1800's, with estimates increasing to over 95% for highly urbanized areas, such as Los Angeles County (Stein et al. 2014). The magnitude of these losses and the continued degradation of coastal wetland systems, and adjacent upland and coastal sage scrub habitats, threatens the ecological integrity and sustainability of these habitat types and their watersheds. To address these issues, a number of restoration and mitigation projects aimed at restoring lost ecosystem services, increasing biodiversity, boosting resilience, and in the case of mitigation, creating new wetland habitat, are currently in the planning process in southern California (Noss 2000, Zedler 2000). The majority of wetland restoration or mitigation projects develop a site-specific framework of protocols and management strategies outlining a planting and re-vegetation strategy.

Planting strategies designed to establish self-sustaining plant communities identify both the species to be included in the restoration and the source of plant material (i.e. nursery stock or local seeds) (Zedler 2001). Restoration plant palettes should be designed to mimic reference or historic site diversity and be composed of an appropriately broad range of species (Zedler 2001, Johnston et al. 2012). Because of their unique location in the landscape as the connecting habitat between marine, terrestrial, and freshwater ecosystems, coastal wetland complexes naturally support a variety of salt marsh, brackish, and freshwater plant species (Lichvar et al. 2014). Species from each of these habitat types should be incorporated into an appropriate plant palette. Evidence also suggests that the wetland-upland ecotone should be considered an extension of wetland habitat for conservation and restoration purposes (James and Zedler 2000, Wasson and Woolfolk 2011). Thus, coastal sage scrub, dune, and transitional species commonly found in the wetland-upland ecotone should be considered in wetland restoration re-vegetation strategies.

* Corresponding author: mlbarton14@gmail.com

Once a restoration plant palette has been developed, species-specific plant material (e.g. seeds and seedlings) acquisition and propagation methods must be determined. While plant material can be obtained from local nurseries, collection and propagation of native seed from local sites is considered the most cost-effective and ecologically-sound method of sourcing germplasm for restoration and mitigation projects (Zedler 2001, Broadhurst et al. 2008). Site-specific or nearest neighbor collections are preferred to distant collections and use of nursery stock, as locally-collected individuals are better adapted to community environmental conditions, maintain local genetic integrity, ensure persistence of local eco-types, prevent unintended gene flow, may improve the long-term sustainability of the site, and may enrich the diversity of the wetland plant community (Guerrant 1996, Montalvo et al. 1997, Bowler 2000, Zedler 2001, Mitsch and Gosselink 2010, Vander Mijnsbrugge et al. 2010). Non-local genotypes may be maladapted to local site conditions, leading to improper establishment, or negative impacts to plant and animal communities through competition or species hybridization (Bischoff et al. 2006, Vander Mijnsbrugge et al. 2010). The retention of local eco-types and genetic information is gaining importance in the field of restoration biology, reflected by the recent inclusion of required onsite and/or near neighbor collections by regulatory agencies overseeing restoration and mitigation work (Bowler 2000). It is also important to note that making collections in many nature preserves requires permits and/or express permission from the regulating agency.

A number of techniques exist to propagate plant material for wetland, coastal sage scrub, and dune species. Seeds are often the primary means of reintroducing native plant species to restoration sites in a number of habitat types (Montalvo et al. 2002, Merritt and Dixon 2011). Restoration sites may be seeded using a variety of techniques (e.g. broadcast seeding, drilling, imprinting, or hydroseeding) or collected, cultivated in a greenhouse, and transplanted to the site (Bowler 2000, Montalvo et al. 2002, Merritt and Dixon 2011). Simple seeding experiments generally are performed with limited success, especially at lower elevations or within tidal wetland habitats, as seeds often fail to germinate or float away with rising tides (Broome et al. 1988, Zedler 2001). Techniques like hydroseeding that involve mixing seed with water and either mulch, soil, or organic matter prior to application, tend to work well for many wetland and coastal sage scrub species [e.g. *Salvia mellifera* (black sage) and *Eriogonum fasciculatum* (California buckwheat)] and may enhance seedling establishment (Zedler 2001, Montalvo et al. 2002, Montalvo and Beyers 2010).

Transplanting greenhouse-grown seedlings is an effective re-vegetation strategy that may increase the potential establishment success when compared to direct seeding for some species. In one experiment, survivorship of 2-4 month old marsh seedling transplants was over 95% for all but one treatment, much higher than the success rate of direct seeding (Zedler 2001). Seedlings of a variety of halophytic marsh species including *Suaeda esteroa*, estuary seablite, and *Salicornia bigelovii*, dwarf pickleweed, and a variety of coastal sage scrub species like *Atriplex canescens*, four-wing salt bush, have been successfully grown in greenhouses and transplanted for restoration purposes (Zedler 2001, Francis 2009). While use of seeds and seedlings has been successful for many species [e.g. *Achillea millefolium* (common yarrow) and *Astragalus tener* var. *titi* (coastal dunes milk vetch)], effective propagation techniques are species-specific and other species, like *Batis maritime*, saltwort, do not readily grow from seed and require use of alternate methods (Zedler 2001).

Other common approaches to generate plant stock include use of cuttings, root division, and direct transplantation of seedlings or mature plants to the site of interest (Zedler 2001, Baskin and Baskin 2014). Direct transplantation of coastal sage scrub seedlings [e.g. *Artemisia californica* (California sagebrush), *Salvia mellifera*, *Encelia californica* (California brittlebush), and *Eriogonum fasciculatum*] and mature plants salvaged from donor sites have been used with

great success in mitigation efforts (Bowler et al. 1994, Bowler 2000). Similarly, use of transplants, sod, and small plugs of wetland soil, have been effective in introducing a number of wetland species, including *Spartina foliosa*, California cordgrass, to sites (Trnka 1998, Zedler 2001, Mitsch and Gosselink 2010). Use of cuttings is documented to work well for other species; cuttings of *Salicornia pacifica*, common pickleweed, for example, have been successfully propagated by Tree of Life Nursery in San Juan Capistrano, California. While each of these approaches has merit, the discussion in the remainder of this paper (and the accompanying appendices) focuses on the use of seeds and greenhouse-grown seedlings to target a data gap in peer-reviewed literature.

While general techniques for successfully establishing common wetland and coastal sage scrub species described in the preceding paragraphs are understood (Broome et al. 1988), the field of restoration biology is still developing and could benefit greatly from additional research. More specifically, the field could benefit from research regarding species-specific collection and propagation techniques because cultivation and planting strategies are often species-specific, highly variable, proprietary, or experimental. Information for many native species of interest does not exist, or is not publically available, forcing restoration managers and ecologists to rely on general information about the genus or costly and time-intensive exploratory studies (Dreesen and Harrington 1997). Publically available sources are scattered throughout a variety of peer-reviewed and non-peer-reviewed resources. With over a dozen wetlands in southern California considered candidates for large-scale wetland restoration projects, a compilation of literature summarizing re-vegetation strategies for the region is needed (SCCWRP 2001). This paper synthesizes basic seed characteristics, as well as collection and germination strategies for vegetation species common to estuarine wetland and adjacent upland habitat types, specifically coastal salt marsh and coastal sage scrub habitats in southern California.

Materials and Methods

Common seed collection, germination, and propagation techniques are described in the text of this paper. General species information (e.g. scientific name, common name, and habitat type) is included in Appendix I. Detailed species-specific data and recommendations are included in Appendix II, which summarizes available information for 66 native plant species commonly used in southern California coastal restoration projects. Species-specific details were compiled using available literature. While the majority is derived from peer-reviewed publications, some non-peer reviewed literature was included to fill data gaps in published information. As many data gaps exist, and gray literature was used throughout the article text and the accompanying appendices, the authors have chosen not to distinguish gray literature with footnotes and this was approved by the editors. Instead, these sources are listed, with all peer-reviewed sources, in the Literature Cited section. In instances where duplicate information was identified, the source with the most extensive experimental results was cited. Field observations from the Ballona Wetland Ecological Reserve, Los Angeles, CA, were used to determine some seed collection windows. Appendix II is not intended to be comprehensive; instead, it focuses on common coastal wetland and upland species in southern California for which there was available literature. Priority was given to information specific to southern California coastal habitats, but species-specific information from other geographic areas was included as needed for completeness. Implementation of specific methods may vary slightly by site or project. A number of resources exist that provide general species profiles of the plants described in Appendices I and II. Three websites in particular, S&S Seeds (<http://www.ssseeds.com>), the Theodore Payne Foundation (<http://theodorepayne.org>), and Tree of Life Nursery

Table 1. Suggested field, lab, and greenhouse equipment for seed collection, cleaning, and germination.

Field equipment	Lab/greenhouse equipment
Collecting bins/paper bags	Sieves of varying sizes (500 μm –2 mm)
Ziploc bags	Paper envelopes
Pens/pencils/markers	Freezer
Paper clips/binder clips	Refrigerator
Field data collection sheet	Oven
Clipboard	Growing medium*
Background documentation (recommended)	Sterile petri dishes*
Mesh screens/sieves ⁺	Hydrogen peroxide (H_2O_2)*
Tarp(s) ⁺	Nail clippers*
Gloves ⁺	Mothballs*
Gardening shears ⁺	Ethylene (ethephon or sliced apple)*
Jepson manual ⁺	

* = species specific

+ = optional

(<http://www.californianativeplants.com>), are recommended for supplemental information relating to life history and planting recommendations.

Materials

Equipment and supplies needed for seed collection, cleaning, and germination are highly variable based on the specific vegetation species. Recommended field, laboratory, and greenhouse equipment are listed in Table 1. In addition to the field equipment listed, available background information (e.g. reports, vegetation maps, taxonomic keys) should be brought into the field to aid correct taxonomic identification of species.

Seed Collection

Seeds should be collected within seed zones, geographic zones in which genetic exchange naturally occurs. Practitioners are advised to use life history traits, landscape context, and available genetic studies to correctly determine seed zones (Krauss and He 2006). It is important to note that due to extensive urbanization and fragmentation in southern California, historic areas of seed exchange have been diminished. In addition to considering provenance of seeds, care should be taken to ensure that seed collections contain sufficient genetic diversity (Vander Mijnsbrugge et al. 2010) as diversity safeguards against disease, environmental fluctuations, and inbreeding depressions (Smith et al. 2007). To maximize the range of genetic diversity represented in the collection, seed should be collected from 10-50 individuals per population (Lippitt et al. 1994, Vander Mijnsbrugge et al. 2010). Local adaptations and site-specific variability should also be taken into consideration, but site-specific recommendations are outside the scope of this product. When collecting seeds, less intense and more frequent seed harvests are preferable to infrequent and intense harvests (Wall 2009). Negative impacts on the seed source population must be considered (Krauss and He 2006). A general safe harvesting recommendation is to take no more than 5% of seed from a given species and geographic area (Zedler 2001).

Once plant identity has been confirmed, carefully examine the seeds to assess maturity. Avoid collection of immature seed, as premature collection may result in low seed viability (Bonner and Karrfalt 2008, Baskin and Baskin 2014). In general, it is good practice to begin collecting seeds around the time that natural dispersal begins (Baskin and Baskin 2014). Seeds are considered ripe if seed capsules are dry and tan or brown in color, rather than yellow or green (Lippitt

Table 2. General seed collection method based on plant anatomy (Wall 2009).

Fruit/seed type	Collection techniques
Moist fruits/berries	Hand-pluck fruits.
Dehiscent species	Collect entire inflorescences prior to dispersal. Alternatively, secure cloth bags around ripening stalks to capture dispersed seed.
Inflorescences	Strip inflorescences.
Seed heads	Shake ripe seed directly onto a tarp or collection bag underneath the target plant.
Seed clusters	Remove entire seed cluster from plant.

et al. 1994, Bonner and Karrfalt 2008, Baskin and Baskin 2014). Frequent visits to collection sites are suggested to repeatedly assess seed stage within the recommended collection time window. For species with insufficient published seed collection data or information, e.g. *Artemisia douglasiana*, detailed field notes are essential to pinpoint the ideal collection window and successfully collect seeds.

Once the seeds of target species are deemed ripe, the collection process can begin. Collection/isolation of seed varies based on plant anatomy. Observe the plant and note if the species has berries or dry fruits, dehiscent or indehiscent seeds, and note if seeds are in seed heads or seed clusters as collection methods vary for each category (Table 2). Additionally, if a species is known to be dioecious [e.g. *Croton californicus* (California croton), *Baccharis* spp., *Salix* spp.], care should be taken to ensure that sufficient seed quantities are collected from both male and female plants (Clarke et al. 2007). Vouchering specimens from collected seeds is a good practice and should be considered during the planning phase.

Seed Cleaning

Seed cleaning removes floral parts, seed coats, pods, fleshy fruit material, and other debris from seeds (Jorgensen and Stevens 2004). Machinery, including aspirators, hammermills, fanning mills, and blowers, exists to aid large-scale seed enterprises. Hammermills, fanning mills, and blowers help isolate seed and remove chaff and floral parts (Shaw 1975, Jorgensen and Stevens 2004). Although seed cleaning machinery is useful, cleaning for small-scale projects can be efficiently performed by hand (Bonner and Karrfalt 2008). To isolate seeds and remove excess chaff, remove seeds from branches and large floral parts. Then, rub remaining seeds and floral parts over a sieve. Once seeds are isolated from chaff, only retain seeds that look healthy and ripe (i.e. dark brown/tan in color, fully-formed). For some species, chaff does not present a huge problem, and it may be more efficient to seed with some chaff. Discard seeds that appear sickly or deformed. If the seed is contained in a capsule, gently crush the capsule by hand or with a rolling pin. Removal of woody capsules, as seen in *Abronia* spp., may also be aided with the use of generic nail clippers (P.M. Drennan, personal communication).

Seed Storage

For the greatest germination yield, storage time should be minimized, and use of newer seeds should be prioritized. While native seed longevity varies by genus and species, a number of seeds are known to be short-lived. For example, seeds of *Lycium californicum*, California box-thorn, are viable for up to one year at most. While seeds of other species [e.g. *Atriplex* spp., *Astragalus* spp., and *Lupinus chamissonis* (dune bush lupine)] will remain viable for much longer (i.e. 4-10 years), the germination rate of seeds in long-term storage will likely decline over time. In addition to reducing germination rate, long-term storage will often induce seed coat or embryo dormancy, and stored seeds may need to be treated prior to planting. For example, the hard seed coat of *Astragalus tener* var. *titi* seeds may require scarification,

or mechanical scraping with sandpaper, a file, or a knife, to initiate germination if stored for an extended period of time (Baskin and Baskin 2014, USFWS n.d.)

The longevity of certain seeds can be increased if best management practices for storage are followed for the species and/or general seed storage procedures are applied. Most dry seeds should be stored at low temperatures, 10-15.6°C (50-60°F), and low humidity, less than 40% relative humidity (Jorgensen and Stevens 2004, Recon Native Plants Inc. 2015). Substandard storage in conditions with fluctuating temperatures or high humidity may result in significant seed loss (Merritt and Dixon 2011).

Germination Considerations

Successful propagation of southern California coastal plant species requires a thorough understanding of seed germination ecology. Seed germination is dependent upon a number of evolutionary and ecological factors which generally must be observed, and often replicated, in the laboratory or greenhouse to successfully grow propagules. These, often species-specific, factors include, but are not limited to: germination timing/seasonality, environmental conditions, such as temperature, soil texture, soil moisture, soil salinity, light availability, presence of smoke, and seed age, and dormancy state, both at the time of maturation and dispersal (Baskin and Baskin 2014).

Germination Timing

Seeds are adapted to germinate under favorable environmental conditions (Deberry and Perry 2000). An understanding of natural germination timing is helpful in determining the environmental conditions that best promote germination of a particular species in the greenhouse or laboratory. This is particularly true, as in both the greenhouse and laboratory, environmental conditions can be manipulated to mimic natural seasonal variation. Temperature, moisture, and light are generally controlled for this purpose (see 'Temperature' and 'Light' sections below) (Noe and Zedler 2001).

Temperature

Understanding germination timing under natural conditions will often indicate what range of temperatures best promote germination. Temperature influences germination directly through regulation of enzymatic reactions, or indirectly by controlling the synthesis of hormones that alter seed dormancy. While temperature is an important determinant in the regulation of both germination and dormancy, response to temperature in freshwater wetland species seems to be dependent on habitat, not phylogenetic relatedness. Temperature interplays with other environmental conditions to promote germination (Brändel 2006). Further, the germination rate of certain species is enhanced with simulated temperature fluctuations, rather than constant temperatures. While response to fluctuating temperatures depends both on specific species and habitat, a few generalities exist. Both small-seeded species and forbs tend to respond well to fluctuating temperatures while larger-seeded and graminoid species do not show as marked a preference for temperature fluctuations (Liu et al. 2013).

Soil Texture

To grow seedlings, clean, viable seeds should be planted in mixtures of sand, top soil, and peat moss or vermiculite (Broome et al. 1988). To achieve the greatest germination rate, the exact composition of the mixture should be tailored to the individual plant species of interest. Life history and preferred habitat of the species should be considered when determining optimal

soil conditions. For instance, *Abronia maritima*, which naturally occurs on sandy dunes, should be sown in soil consisting largely of sand, or other coarse grains.

Soil Moisture

Soil moisture must also be considered when sowing seeds (Noe and Zedler 2000, Noe and Zedler 2001). Most mature seeds must imbibe in the early stages of germination to activate enzymes (Deberry and Perry 2000). After seeds imbibe, sufficient, and relatively constant soil moisture is needed to ensure proper germination (Bonner and Karrfalt 2008). Most species in southern California salt marsh systems germinate well in moist soil at low salinity (Zedler 2001). Experiments suggest that *Distichlis spicata* grows best with a fluctuating inundation regime, where inundation was varied over time, but the soil surface was never completely dry (Elsey-Quirk et al. 2009). Germination of other high marsh plant species is highest with 41-51% soil moisture (Zedler 2001).

It is important to note that while seeds of wetland species are adapted to wet conditions with limited oxygen, coastal sage scrub and upland transition species are more sensitive to inundation. For these species, excessive exposure to water can be problematic, causing seeds to become waterlogged (Fenner 1992, Deberry and Perry 2000). Following germination, water regimes, that specify both the quantity and frequency of water application, both in the greenhouse and in natural environments, may influence growth rates and should be carefully considered.

Soil Salinity

Another major factor that influences germination is soil salinity (Noe and Zedler 2000, Noe and Zedler 2001). Certain halophytic species, like *Salicornia bigelovii*, germinate to higher percentages under somewhat saline conditions (0.05-0.09 M). In general, although halophytes are salt-tolerant, high percentages of halophyte seeds will germinate in distilled water. Results of salinity experiments suggest that seeds will often germinate to higher percentages in distilled water, as seeds tend to be sensitive to salt concentrations, and exposure to excessive salt can drastically decrease germination yields. Still, much variation exists in the germination of halophyte species in saline environments (Baskin and Baskin 2014).

Light

Light is another environmental factor that affects germination. Exposure to light is often required for germination to occur. Exposure to light has been documented to improve germination rates for certain species [e.g. *Eriogonum fasciculatum* (California buckwheat), *Baccharis salicifolia* (mule fat)] (Zedler 2001, Bonner and Karrfalt 2008). Still, exposure is not always sufficient to ensure the successful occurrence of germination mechanisms. Duration of exposure to light (i.e. day length or photoperiod) also plays an important role in seedling emergence and growth of southern California natives (Sprague 1944, Noe and Zedler 2000, Greiner and Köhl 2014). For instance, long-day conditions (16 hours of light for every 8 hours of darkness) are necessary to successfully culture *Oenothera* species (Greiner and Köhl 2014). Photoperiod may also influence other processes, such as flowering. *Melica imperfecta* and *Stipa lepida* have been shown to flower 10-20 weeks faster with constant light (i.e. 24-hour photoperiod) when compared to an 8-hour photoperiod (Ashby and Hellmers 1959).

Smoke Treatments

Southern California, like most regions with Mediterranean climates, is subject to frequent and intense wildfires, and certain species have adapted to be fire-tolerant (Keeley and

Fotheringham 1998, Crosti et al. 2006). Germination of fire-tolerant species is generally enhanced by exposure to fire or smoke (Crosti et al. 2006, Baskin and Baskin 2014). Smoke-stimulated germination, via exposure to liquid or aerosol components of smoke, may be useful for many coastal sage scrub species. For instances, exposure of *Salvia mellifera* seeds to smoke or other components of fire, like charred wood or potassium nitrate (KNO_3), may help stimulate germination (Montalvo and Beyers 2010).

Other Considerations

In some instances, information regarding the necessary conditions or procedures to promote germination is not readily available for a particular species. In such situations, it is advisable to consult local experts that may have species-specific knowledge. Alternatively, simple tests or experiments manipulating a variety of the environmental factors discussed above may be performed.

Germination Testing

If a seed lot requires germination studies, it is preferable that they are conducted shortly after seed collection, within 7-10 days, to ensure seeds are viable and have not entered seed dormancy. Germination trials can test outcomes of various pre-treatments and/or growing conditions. They are often also used to express the quality of a seed lot (Lippitt et al. 1994). The results of germination trials are typically reported as percentage germination or germination rates. Percentage germination is the percentage of seeds that germinate under the specified set of conditions. Comparing germination rates of a variety of treatments allows easy determination of the most effective combination of germination conditions.

While germination rates are useful, the industry will often use other terms to describe the percentage of seed that will germinate under a given set of conditions. Pure Live Seed (PLS) is a common way to express viability. PLS is calculated by multiplying the percentage of pure seed by the percentage of total viable seed and dividing the product by one hundred (S&S n.d., Showers 2010). Other measures include specification by purity, bulk pounds, or PLS pounds (S&S).

Dormancy Considerations

Seeds for a number of wetland plants are known to be dormant. In these species, seed dormancy must be broken to promote growth and germination (Baskin and Baskin 2014). The process is generally moisture and temperature dependent, but varies both with species and type of dormancy. Three types of dormancy should be considered: physical (or seed coat) dormancy, internal dormancy, and morphophysiological dormancy. Seeds with physical dormancy have seed coats or other structures that are impermeable to water and/or oxygen (Lippitt et al. 1994, Baskin and Baskin 2014). This form of dormancy is generally broken by penetrating/opening the seed coat or specialized structure that excludes water or oxygen. This can be achieved through scarification, cold and warm stratification, or exposure to dry heat, charate, fire, acid, and light. Internal dormancy, caused by a physiological mechanism that inhibits germination, is generally broken through use of warm and/or cold stratification. Morphophysiological dormancy is similar to physiological, but seeds with this type of dormancy also have an underdeveloped embryo. A variety of methods can be used to break morphophysiological dormancy, including: scarification, submersion in hot water [82-93°C (180-200°F)], treatment with dry heat, exposure to fire, acid, mulch treatment, cold stratification, warm stratification, and exposure to light (Emery 1988, McClure 1997, Baskin and Baskin 2014). Common dormancy breaking methods are detailed in Table 3).

Table 3. Detailed methodology for techniques commonly employed to break seed dormancy.

Method	General description
Scarification	Mechanically scar seed coat with sandpaper, knives, files, or clippers. Alternatively soak seed in acid or hot water (Emery 1988, Lippitt 1994, Bonner and Karrfalt 2008).
Hot water treatment	Place seeds into hot water (180-200°F) and leave them to soak as the water cools (Emery 1988, Bonner and Karrfalt 2008).
Dry heat	Expose seeds to 180-212°F heat. Use of an incubator, rather than oven, preferred (Emery 1988).
Charate	Expose seeds to ash from burned plants. This may neutralize germination inhibitors in species that naturally germinate when exposed to fire (Emery 1988, Baskin and Baskin 2014).
Fire	Expose seeds to direct flame. This may be effective as a means to spur germination in species that naturally germinate when exposed to fire (Baskin and Baskin 2014).
Water	Soak seeds in water to leach out water-soluble inhibitors (Baskin and Baskin 2014).
Cold stratification	Store seeds in cold conditions (35-41°F) for 1-3 months to simulate winter conditions (Bonner and Karrfalt 2008, Elsey-Quirk et al. 2009, Baskin and Baskin 2014).
Warm stratification	Store seeds in warm conditions (65°F or higher) (Baskin and Baskin 2014).

Unfortunately, as indicated by the variety of conditions listed above, there is not one prevailing standardized method to break seed dormancy. Again, methods vary based on the life history of the species. Species-specific life histories, available at the growers' websites listed above, can be a good indicator of the required conditions for that species. For example, species that typically germinate in early spring after a cold and/or rainy winter, such as *Platanus racemosa*, western sycamore, often require cold, moist stratification mimicking natural wintering to break dormancy. Other species, such as *Acmispon glaber*, common deerweed, require heat treatment to break dormancy which also correspond with the life history of that species; *A. glaber* does particularly well after wildfire events. However, treating seeds to break dormancy is not enough to guarantee germination. Germination requirements must also be considered. Methods and information should be supplemented by experimentation when necessary.

Mycorrhizae

Establishing functional ecosystems also requires consideration of subsurface components of the system. Many plants have symbiotic relationships with soil-inhabiting microorganisms, yielding root systems that are more effective at extracting water and nutrients from the rhizosphere (i.e. soil profiles influenced by root secretions and soil fauna). The fungus-root system is called mycorrhizae (Gerdemann 1968, Tree of Life Nursery n.d.). Research has shown that mycorrhizae can increase plant growth and are essential in successfully establishing vegetation during restoration and mitigation projects (Reeves et al. 1979, Allen and Allen 1980, Cooke and Lefor 1990). If planting areas are severely disturbed and lack a healthy rhizosphere, steps should be taken to ensure presence of mycorrhizae, or to increase the potential for natural development. As the presence of mycorrhizae is important in establishing many wetland and coastal sage scrub species, container plants are often inoculated prior to planting (Cooke and Lefor 1990, Bowler 2000). Seedlings can be inoculated with a spore suspension or via introduction of small amounts of collected soil from sites with a healthy rhizosphere to a sterile soil (van de Voorde et al. 2012). Starter-cultures are also available commercially.

Discussion

Southern California has lost a significant portion of its coastal ecosystems due to urban development, agriculture, invasive species, and in the case of coastal estuarine wetlands, severely

modified hydrology resulting from both channelization and deposition of fill sediments (Westman 1981). Loss of these ecosystems is concerning because they provide valuable ecosystem services including supporting important fisheries, filtering water, sequestering carbon, and providing habitat for a diversity of plant and animal life, including a number of threatened and endangered species. Wetlands are buffered by transition habitats, and many wetland-associated species also require adjacent upland habitat areas to breed, roost, or to have the highest likelihood of survival. Plant species in Southern California also display a high degree of endemism and the Southern California coast is considered a global biodiversity hotspot (SCCWRP 2001).

Although wetlands in southern California have attained protected status and efforts are being made to restore degraded habitats throughout the Southern California Bight, the increasing human populations along the California coast will continue to impact these coastal ecosystems (Callaway and Zedler 2004). To preserve the spectrum of ecosystem services coastal wetlands and their adjacent upland habitats provide, managers throughout the southern California region need to work collectively to conserve remaining high quality coastal wetland habitat and to restore lower quality, degraded habitats.

Clearly, there is a significant and ongoing regional need for restoration projects to recover lost habitats and preserve the unique communities. Increased reliance on ecological restoration of vegetation assemblages emphasizes the need for sound, scientifically-tested techniques to ensure the successful reestablishment of plant communities. While this document is not comprehensive, and there is still a practical need for land managers to compile detailed site information and evaluate site-specific experiments prior to implementing a restoration scheme, this literature review compiles available seed collection and germination information for the southern California region and provides an initial assessment of published methods for common wetland, dune, and coastal scrub plants. Many unknowns remain in restoration ecology theory, and understanding of the most effective restoration practices remains incomplete. Knowledge gaps regarding the collection and germination requirements of integral species [e.g. *Hazardia squarrosa* (saw-toothed goldenbush)] and other species with limited research available [e.g. *Elymus triticoides* (creeping wild rye)] precluded their inclusion in this review. Planners are encouraged to conduct regular site monitoring and employ adaptive management strategies. In this way, progress can be evaluated and unexpected outcomes and shortcomings can be corrected.

Still, there is a regional need for additional research regarding seed phenology and maturation of southern California species. Although a number of wetland, dune, and coastal sage scrub restorations are planned in southern California, information regarding seed collection and germination for many naturally occurring species is not readily available. Therefore, the field of plant community restoration could benefit greatly from additional research regarding seed phenology and maturation, both in the form of species-specific experimentation and literature and broader-scale, regional or ecosystem-based reviews. Filling in existing knowledge gaps and developing a better understanding of seed processes will help restoration ecologists collect high quality, viable seed, thereby increasing the potential success of the restored vegetation community by reducing seed/seedling mortality, restoration cost and human effort.

Perhaps more importantly, the region could benefit from the development of a coordinated network of restoration ecologists. Compilation of this literature review suggests that information regarding the restoration of wetland plant communities is abundant, but it is dispersed, produced by various sources, and often proprietary. Intentional withholding of information by nurseries or private environmental consulting firms inevitably leads to duplication of efforts by groups working in the southern California region and surely impacts both the overall quality of restored habitats and project efficiency. Engagement and cooperation of existing private industry groups

and public sector regulators with a vested interest in restoring coastal wetland plant communities would be a major victory and a tangible step forward for the threatened coastal ecosystems in the region.

While establishing vegetation in restored wetlands is a vital component to the overall restoration scheme, it is just a small part of the overall restoration process. Restoring wetland ecosystems is complex; plans must incorporate vegetation, hydrology, substrate, and marine and terrestrial animals. To fulfill restoration aims, well-informed, inter-disciplinary approaches that incorporate ecologists, engineers, managers, lawyers, and practitioners from other technical fields are needed (Zedler 2000, Kiehl 2010). Inter-disciplinary approaches will best foster creativity and progress knowledge and understanding in the field of restoration.

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Appendices

Appendix I. Species-specific habitat associations for wetland, coastal sage scrub, and upland transition species common in southern California. This table includes scientific and common names from Jepson eFlora (<http://ucjeps.berkeley.edu/>, accessed June 4, 2015). Habitat association information is derived from Jepson and further refined with information available from the Manual of California Vegetation (2nd edition), the S & S Seeds Plant Database (www.sseeds.com/plant-database), and the species-specific literature cited in Appendix II (Baldwin et al. 2012, Sawyer et al. 2009, S&S Seeds, n.d.).

Scientific name	Common name	Low marsh	Mid marsh	High marsh	Salt pan	Low transition	High transition	Grass	Scrub	Fresh water	Salt tolerant
<i>Abronia maritima</i>	Red sand verbena						x				x
<i>Abronia umbellata</i>	Pink sand verbena						x				x
<i>Achillea millefolium</i>	Common yarrow						x	x			x
<i>Acmispon glaber</i>	Deer vetch						x	x			x
<i>Ambrosia psilostachya</i>	Western ragweed								x		
<i>Artemisia californica</i>	California sagebrush										
<i>Artemisia douglasiana</i>	Mugwort					x					x
<i>Artemisia tridentata</i>	Big sagebrush							x			x
<i>Arthrocnemum subterminale</i>	Parish's pickleweed	x	x								x
<i>Astragalus pycnostachyus</i> var. <i>lanosissimus</i>	Ventura marsh milk vetch		x	x	x						x
<i>Astragalus tener</i> var. <i>itif</i>	Coastal dunes milk vetch			x	x						x
<i>Atriplex californica</i>	California orach			x					x		x
<i>Atriplex canescens</i>	Fourwing saltbush								x		x
<i>Atriplex lentiformis</i>	Big saltbush										x
<i>Atriplex prostrata</i>	Fat-hen			x							x
<i>Atriplex watsonii</i>	Watson's saltbush			x							x
<i>Baccharis pilularis</i>	Coyote brush						x				x
<i>Baccharis salicifolia</i> subs. <i>salicifolia</i>	Mule fat								x		
<i>Baccharis sarothroides</i>	Broom baccharis								x		
<i>Batis maritima</i>	Saltwort		x	x	x						x
<i>Cressa truxillensis</i>	Alkali weed										
<i>Croton californicus</i>	California croton						x				x
<i>Distichlis littoralis</i>	Shore grass			x							x
<i>Distichlis spicata</i>	Salt grass		x	x							x
<i>Encelia californica</i>	California brittlebush							x			
<i>Eriogonum fasciculatum</i>	California buckwheat								x		
<i>Frankenia salina</i>	Alkali heath		x	x	x						x

Appendix I. Continued.

Scientific name	Common name	Low marsh	Mid marsh	High marsh	Salt pan	Low transition	High transition	Grass	Scrub	Fresh water	Salt tolerant
<i>Spartina foliosa</i>	California Cord grass	x									x
<i>Stipa cernua</i>	Nodding needle grass							x	x		
<i>Stipa lepida</i>	Foothill needle grass							x	x		
<i>Suaeda esteroa</i>	Estuary seablite		x	x							x
<i>Suaeda nigra</i>	Bush seepweed										x
<i>Suaeda taxifolia</i>	Woolly seablite										x
<i>Triglochin maritima</i>	Common arrow-grass	x	x	x							x
<i>Pulpia microstachys</i> var. <i>microstachys</i>	Small fescue							x	x		x

Appendix II. Detailed, species-specific seed collection, seed germination, and seed storage information for wetland, coastal sage scrub, and upland transition species native to southern California. Information is sorted alphabetically by scientific name.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Abronia maritima</i> (Drennan 2008, Baldwin et al. 2012)	May	Aug	Winged fruit 10-14 mm long. Fruit contains single-seeded achenes.	Plants seed throughout the year, majority of seed production occurs in late spring/summer. Removal of woody capsules aided with the use of generic nail clippers.	In the most successful trials, achenes removed from anthrocarp. Place achenes on filter paper in sterile petri dishes with ethephon or other 10-100 umol ethylene source. Incubate achenes in a chamber with alternating 12 h periods of light (27°C) and dark (20°C). Requires a sandy substrate.	3
<i>Abronia umbellata</i> (Drennan 2008, Baldwin et al. 2012, Center for Plant Conservation 2015.)	May	Aug	Winged fruit 6-13 mm long. Fruit contains single-seeded achenes.	Plants seed throughout the year, majority of seed production occurs in late spring/summer. Removal of woody capsules aided with the use of generic nail clippers.	In the most successful trials, achenes removed from anthrocarp. Some seed lots require cold pre-treatment. Germination requirements may differ year to year. For best results, sow clean seeds in the top 1" of a sandy growing medium.	3
<i>Achillea millefolium</i> (Baskin and Baskin 2002a, Baldwin et al. 2012)	Aug	Oct	Oblong fruit, usually 2 mm in length, contains brown disk achenes. Seeds mature in late summer-early fall.	Cut entire inflorescences, collect in paper bags. Clean seeds with a hammermill, screen, and fanning mill.	Lightly cover seeds with growing medium (milled sphagnum, peat, perlite, vermiculite w/ osmocote). 90-100% germination rate.	3-5
<i>Acmispon glaber</i> (Montalvo and Beyers 2010c)	May	Jul	Narrow, bean-shaped, curved seed pods 1-2 mm long. Indehiscent pods ripen in 4-6 weeks. Mature pods are dry and brown or olive green.	Strip ripe seed pods from stems by hand. Avoid breaking seeds during thrashing. Rub pods with wooden block over #16 (medium) screen. Remove seeds from pods. Remove excess chaff with seed blower.	Heat or mechanical scarification needed to break dormancy. Soak seeds in boiling water or heat in 120°C oven for 5 minutes for highest yield.	Long-lived
<i>Ambrosia psilostachya</i> (Pavek 1992, Baldwin et al. 2012)	Oct	Dec	Brown bur 3-4.5 mm long contains tiny achenes.	Strip brown inflorescence by hand.	Seeds will germinate when fresh. Stored seeds need to be exposed to light and may require cold stratification. Other sources imply that pre-germination treatment is not necessary.	3-5
<i>Artemisia californica</i> (Hauser 2006, Young-Mathews 2010, Baldwin et al. 2012)	Oct	Feb	Fruit 0.8-1.5 mm long. Very small achenes, generally mature in early fall or winter; wind dispersed.	Strip brown inflorescence by hand.	Seeds will germinate when fresh. Stored seeds need to be exposed to light and may require cold stratification. Other sources imply that pre-germination treatment is not necessary.	2-5

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Artemisia douglasiana</i> (Elkhorn Slough National Estuarine Research Reserve 2001, Shultz 2014)			<1 mm, glabrous fruit. Small, ellipsoid, hairless achenes without ribs or angles.	Seed is ready to harvest when it can be easily removed from the heads by shaking. Clip seed stalks and air dry in a paper bag. To thresh seeds rub the inflorescence through a screen. Remove chaff with a blower.	Germinates naturally at relatively cool temps.	2-5
<i>Artemisia tridentata</i> (Elkhorn Slough National Estuarine Research Reserve 2001, Baldwin et al. 2012, Tilley et al., n.d.)	Sep	early winter	Fruit glandular or hairy, 1-2 mm in length. Very small achenes, generally mature in early fall or winter.	Seed from genus is ready to harvest when it can be easily removed from the heads by shaking. Clip seed stalks and air dry in a paper bag. To thresh seeds rub the inflorescence through a screen. Remove chaff with a blower.	No pre-germination treatment necessary.	2-5
<i>Arthrocnemum subterminale</i> (Zedler 2001, Clarke et al. 2007, Baldwin et al. 2012)	Oct	Dec	Stems have tiny flowers that occur below the tip of the stem and contain brown, vertical seeds with hard seed coat, 1-1.4 mm in length.	Best to collect in November. Collect inflorescences and air dry. When dry, shake seeds from stalks.	Seeds are highly germinable. Germination promoted by low salinities.	3-5
<i>Astragalus pycnostachyus</i> var. <i>lanosissimus</i> (McCue 2010, Baldwin et al. 2012, U.S. Fish and Wildlife Service, n.d.)	Jul		Fruit ovate and inflated, 6-11 mm long and 3-6 mm wide. Seeds are smooth, compressed with a small notch at attachment site. 2 or more seeds/fruit.	Other plants in genus, specifically <i>A. sinuatus</i> , have seeds that mature in late July.	Hard seed coat may require scarification.	Long-lived
<i>Astragalus tener</i> var. <i>titi</i> (Showers 2010, Baldwin et al. 2012)	May		Fruit 6-50 mm long and 1.7-3.5 mm wide. Seeds are smooth, compressed with a small notch at attachment site. 2 or more seeds/fruit.	Endangered species. Extract seeds from fruits by hand. Thresh seeds over sieve large enough to let set seed pass through. Run seeds through seed blower to remove parasitized or aborted seed.	If stored for an extended period of time, hard seed coat may require scarification to initiate germination. 95% germination success rate on 0.5% agar plates with 11 hours light at 20°C and 13 hours dark at 12°C.	Long-lived

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Atriplex californica</i> (Young 2001a)	Sep	Oct	Mature fruit is an utricle with 1 seed. Seeds are black, shiny, hard, round, and flat; 2 mm at maturity.	Gently seeds rub over #18 sieve. Remove as much chaff as possible with a seed blower.	Pre-planting: soak in water for 24 hours, rinse. 86% germination rate after sowing in peat moss, perlite, nutrients, gypsum, and dolomitic lime. Germination occurs after 10 days.	10
<i>Atriplex canescens</i> (Springfield 1970, Baldwin et al. 2012)	Oct	Apr	Cream-colored 4 winged utricle, 5-23 mm wide. Seeds 1.5-2.5 mm long with brown, papery inner seed coat. Species has high percentage of empty seed. Smaller fruits tend to have higher percentages of filled seed.	Strip seeds from branches by hand. If available, use a hammermill and a fanning mill to de-wing and clean seed. Collections made later (Dec-Apr) tend to have higher germination rates.	Germination is inhibited by lack of aeration, but improved with de-winging. Sow in medium with high substrate moisture at low temperatures, ideally at 18-24°C in California. Early collections may benefit from a 60 min. soak in sulfuric acid or a pre-chill at 5°C for 12 weeks.	5-7
<i>Atriplex lentiformis</i> (Young et al. 1980, Baldwin et al. 2012)	Sep	Jan	Produces large amounts of dark brown, 1.5 mm long seeds.	Diocious.	Maximum germination between 10-25°C.	3-6
<i>Atriplex prostrata</i> (Khan and Ungar 1984, Zedler 2001, Baldwin et al. 2012)	Sep	Oct	Two types of seeds: brown, 1-2.5 mm long, and black, 1-1.5 mm long.	Fully mature fruit can be shaken or hand stripped from branches. Seeds will often remain on bushes until April, so late collections are possible.	Readily propagated from seed. In the field, germinates in late spring.	10
<i>Atriplex watsonii</i> (Zedler 2001, Bryant 2004)	Jun	Sep	Seeds light brown, about 1 mm long.		Readily propagated from seed, germinates and establishes easily in field.	10
<i>Baccharis pilularis</i> (Bonner and Karrfalt 2008, Montalvo et al. 2010b, Baldwin et al. 2012)	Aug	Dec	Single-sex white flowers. Glabrous, ribbed fruit 1-2 mm long, pappus 5.5-9 mm long. Mature seeds are tiny, dark brown achenes with ring of long, unbranched pappus bristles.	Diocious. Collect seed heads by hand into open breathable bags. Alternatively shake branches over a tarp. Fruit should be spread out to dry in a well-ventilated room or in the sun. Rub dried heads between palms or over a screen to remove the pappus and phyllaries.	Seeds germinate without pre-treatment. Cool temperatures yield highest germination percentage.	1

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Baccharis salicifolia</i> subs.	May	Jul	Glabrous, ribbed fruit 0.8-1.3 mm long, pappus 3-6 mm long. Tiny achenes with a bristly pappus.	Dioecious. Collect ripe fruits by hand or by shaking seeds onto carvasses/tarps. Dry seeds at room temperature. Once dry, rub seeds over a screen to remove the pappus.	No pre-treatment necessary. Light necessary for germination.	1
<i>Salicifolia</i> (Bonner and Karrfalt 2008, Baldwin et al. 2012)						
<i>Baccharis sarothroides</i> (Bonner and Karrfalt 2008, Baldwin et al. 2012)			Glabrous, ribbed fruit 2-2.6 mm long, pappus 2-3 mm long. Tiny achenes.	Dioecious. Seeds can be collected by hand or branches can be shaken above tubs/tarps.	Germinates well in wet soils.	1
<i>Batis maritima</i> (Zedler 2001, Marcone 2003, Francis 2009, Leonard et al. 2011)	Oct	Nov	Hard-walled lenticular or oblong seeds. 1 mm in length.	Collect when fruits mature and turn from green to white. Extract seed from fruit. Dried fruits should fragment easily, exposing seed	Difficult to grow from seed. Marcone had success exposing seeds to natural light conditions and using a nutrient-enhanced potting medium. No known dormancy requirements.	2+
<i>Cressa truxillensis</i> (Elkhorn Slough National Estuarine Research Reserve 2001, Zedler 2001)	Jul	Aug	Fruits are small hairy capsules, 1/8" long. Seeds pinkish in color, broadly egg-shaped.	Produces mature seeds from late summer into early autumn.		2
<i>Croton californicus</i> (Young 2001b, Baldwin et al. 2012)	Jul	Nov	Flowers develop into compact, greenish seed pods. Mature seeds are smooth, round, and brown with tan spots. 3.5-5.5 mm in length.	Dioecious. Collect July 15th-November 17th. Remove chaff by hand. Remove seeds from pods.	Pre-planting: soak seeds for 24 hours in water, cold stratify for 30 days. Should germinate 30 days after sowing.	3
<i>Distichlis littoralis</i> (Zedler 2001, Clarke et al. 2007, Baldwin et al. 2012)	Jun	Sep	Spikelets, 8-13 mm in length, generally concealed by leaves. Seeds are quite small and remain in flowers until senescence.	Dioecious. Strip flowers with seeds from inflorescences.		4-5

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Distichlis spicata</i> (Baskin and Baskin 2002b, Elsey-Quirk et al. 2009, Baldwin et al. 2012)	Sep	Nov	Spikelets 6-20 mm long. Seed likely dormant at time of dispersal.	Dioecious. Seed is 2 mm long and brownish-gray at maturity. Rub seeds over #18 sieve to clean.	Seed germination highest after wet stratification/ a fluctuating inundation regime and with low salinity (Elsey-Quirk, 2009). Soak in water for 24 hours before sowing. Establishes well at restoration sites. To break dormancy, pre-soak seeds in water.	4-5
<i>Encelia californica</i> (Bonner and Karrfalt 2008, Baldwin et al. 2012)			Fruit 5-7 mm long, slightly longer with pappus. Seeds dark brown at maturity.	Achenes are wedge-shaped and densely compressed. Edges are long-ciliate and faces are glabrous or short-hairy. Collection timing is critical as achenes are easily blown from plant after reaching maturity. Best to collect from Jun-Jul.		2-5
<i>Eriogonum fasciculatum</i> (Zedler 2001, Montalvo and Beyers 2010a, Baldwin et al. 2012)	May	Aug	Glabrous fruit 1.8-2.5 mm in length.	Collect inflorescences as they begin to turn rusty brown. Push seeds through a screen to remove chaff.	Seeds germinate well in flats. Light improves germination rate. Sow in fall-early winter.	2-5
<i>Frankenia salina</i> (Young 2001k)	Sep	Oct	Ellipsoid seed capsules (8 mm) contain 1 mm long, brownish black seeds. Ovarial in shape with pointed tips.	Collect: September 16th- October 21st. Collect mature flowers and rub over #25 sieve. Use gloves when handling, the plant can be spiky.	Seeds need no pretreatment. Germination naturally promoted by low salinity and high temperatures in spring.	0-2
<i>Grindelia camporum</i> (Zafar and Shah 1994, Bliss 2012)	Jun	Oct	Small, long, and flat achenes. Wind-borne, dandelion-like achenes with feathery tufts.	Harvest seed in June and again in October. Clip seed heads or shake/rub mature seeds from seed heads into a collection bag. To clean, rub seed heads over sieve. Remove chaff using additional sieves or an air separator. Air dry in oven at 203 °F.	Soak in water under continuous light OR use two-stage cold stratification at 32°F and 59°F in the dark (Zafar 1994) to pre-treat.	3-5

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Hazardia squarrosa</i> (Keil et al. 2013)			Fruit: 5–8 mm, 5-angled, glabrous; pappus 7–12 mm, white to red-brown in color. Oblong to lanceolate seeds.			0-1
<i>Heteromeses arbutifolia</i> (Bonner and Karrfalt 2008, Baldwin et al. 2012, Gordon 2014, Recon Native Plants Inc. 2015)	Oct	Jan	Large, smooth brown seeds. 2–3 seeds per pome.	Clip or strip fruits from branches when bright red. Soak berries in water to ferment (over-soaking can be damaging). Pulp should float, making it easier to separate seeds from pulp. Alternatively, pulse berries in blender and then rub mixture over a screen to isolate fruit. Dry seeds before storing. RECON suggests keeping fruit intact. Seed easily removed when stalks are hand stripped. No additional cleaning required.	Fresh seeds germinate readily. Chill stored seeds for 3 months at 3–5°C prior to sowing. Seeds germinate well 23°C.	2
<i>Hordeum brachyantherum</i> (Elkhorn Slough National Estuarine Research Reserve 2001, Young 2001d)	Jun	July	Mature inflorescences are light brown.			4-5
<i>Isocoma menziesii</i> (Zedler 2001, Wall and Macdonald 2009, Montalvo and Beyers 2010b)	Sep	Nov	Tan-colored achenes, longer than wide, wider on the plumose end, with lengthwise striations. The top of the achene has a ring of white bristles. Seeds mature when the pappus becomes fluffy and achenes detach easily from the receptacle.	Collect achenes golden in color, as seeds are usually eaten by time achenes turn brown. Shake ripe heads over open containers to collect achenes. Alternatively, remove ripe heads and keep in porous bags. For <i>I. acradenia</i> , Wall and Macdonald recommend rubbing flowers over a large screen, using a seed blower, and sieving over a #18 screen to separate seeds from bracts.	No pre-treatment required. Sow seeds in May. Seeds should germinate 21 days after sowing. Germination rate: 60%. No pre-treatment required. Seeds germinate well in flats.	1+

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Iva axillaris</i> (Montalvo et al. 2010b)			1-2 seeds/head. 2 mm long, tumip-shaped, light, and buoyant.	Strip seeds by hand or beat into a hopper/open container. Rub flower material over a screen and run through a blower to remove chaff.	Generally exhibits low germination rates. Scarification is not effective. Cold stratification may be (studies needed).	Short-lived
<i>Jaumea carnosa</i> (Young 2001e)	Jul	Oct	Seeds are linear achenes with longitudinal stripes.	Collect seed while fruits are swollen and green. Rub seeds over #12 sieve to clean.	Seeds germinate readily in moist soil.	1
<i>Juncus acutus</i> subs. <i>leopoldii</i> (Zedler 2001, Baldwin et al. 2012)	Aug	Nov	Shiny brown capsules contain multiple irregularly shaped seeds. Seeds can be narrowly winged.		Grows readily from seed in moderate salinities. Clones can be dug entire and transplanted.	2-5
<i>Juncus bufonius</i> (Zedler 2001, Baldwin et al. 2012)	Mar	May	Ovoid or elliptic seeds. Seeds generally 0.3-0.6 mm long.	Seed capsules dehisce; seeds should be collected quickly after plant death. Shake mature flowers to collect tiny seed.	Seeds germinate readily in low salinity soils.	2-5
<i>Limonium californicum</i> (Young 2001f)	Sep	Nov	3 mm long narrow ellipse, dark brown/red at maturity.	Collections made in October are best. Collect entire flower heads, which should detach easily when ripe. Rub flower heads over #20 sieve.	Sow in April. Propagates readily from seeds or plugs.	1
<i>Lupinus chamissonis</i> (Young 2001g)	Apr	Jun	Hairy legume pods 2.5-3.5 cm long. Mature seeds are dark brown and speckled and 3-4 mm in length.	Remove seeds from receptacles, no further cleaning required.	Scarify using sandpaper for 5 minutes. Then, soak in hot water over night (repeat for seeds that do not imbibe). Sow in growing medium mid-October. Should germinate after 3 days.	Long-lived
<i>Lycium californicum</i> (Zedler 2001, Baldwin et al. 2012)	Jan	Feb	3-6 mm red berries. 2 oblong seeds per berry.	Pick by hand. Berries best collected within 2 weeks of appearance, otherwise birds will eat majority. Extract seeds from berries within a week, before berries begin to mold.	Soak seeds in water for at least 12 hours, then transferred to moist soil. Reported germination rates are low, 5-10%.	1

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Melica imperfecta</i> (Ashby and Hellmers 1959, Emery 1988, Young 2001h, Baskin and Baskin 2002c)	Apr	Jun	Mature inflorescences are brown; mature seeds are tan.	Strip inflorescences.	Plant has irregular germination patterns and a low documented germination rate, 30%. Literature inconsistent, certain sources suggest soaking seeds overnight in fresh water and cold stratifying for 2 weeks in peat. Conversely, Emery 1988 feels no pre-treatment necessary. Constant light (i.e. 24-hour photoperiod) exposure is documented to speed flowering.	4-5
<i>Mimulus aurantiacus</i> (Young 2001c, Baldwin et al. 2012)	Jun	Aug	Mature capsules are brown and contain tiny, black seeds less than 1 mm in length.	Rub seed capsules over a sieve.	Sow seeds in August. No pre-treatment needed, 50% germination rate.	2-5
<i>Oenothera elata</i> (Greiner and Köhl 2014, B & T World Seeds 2015, Dave's Garden 2015a, Kleinman, n.d.)			Seeds are irregularly shaped, stacked in small, brown, woody capsules with four chambers each with two rows of small seeds.	Collect seed from spring cultivars in October and from winter cultivars in September. Bag seed heads and allow them to dry on plant or collect early and allow to ripen in paper bags.	Surface sow (1 mm deep) to ensure sufficient light. Long-day conditions (16 hours of light/ 8 hours of darkness) should be simulated in the greenhouse. Should germinate after 15-30 days.	3-5
<i>Peritoma arborea</i> (Lippitt et al. 1994, Borders et al. 2008, Baldwin et al. 2012)			Capsules 3-6 cm long and 1-2.5 cm wide. Mature fruits will often split at the seam, revealing seeds. Dark-colored seeds tend to be more viable than light-colored seeds.	Flowers several times/year (except Dec-Jan). Ready for collection when capsules turn brown and are crisp. Strip mature fruits from plants by hand. Break apart pods by hand or with a hammermill or coater blender.	Species does not require high soil moisture to germinate.	2-5
<i>Phacelia ramosissima</i> (Baldwin et al. 2012)			Capsules contain 8-12, 1-2 mm long pitted seeds.	Collect seed when flowers are dry and brown. Strip seed from mature inflorescences directly into collection bag.		2
<i>Plantago erecta</i> (Galmon 1992, Montaivo et al. 2010a, Baldwin et al. 2012)	Apr		2-2.5 mm long.	Dehiscent, ballistic seed dispersal. Collect inflorescences into a paper bag and let dry. Use sieve to clean.	Non-dormant, no pre-treatment needed. With ample water, will germinate from Sep-Dec with varying temperatures.	3
	Jun	Spring				2

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Platanus racemosa</i> (Bonner and Karrfalt 2008)			Chestnut brown seed pods at maturity, many are empty. Achenes are 2-2.5 mm in length and have small tuft at base.	Collect seedpods after they have turned brown. The task is easiest after leaves have fallen. Seedpods remain on trees into spring. Cut seedpods directly from tree. Crush dried seedpods to open. Remove dust and fine hairs.	Cold moist stratification needed to break dormancy.	
<i>Populus fremontii</i> subs. <i>fremontii</i> (Gulmon 1992, Stettler, 1996, Clarke et al. 2007, Kleinman, n.d.)	Mar	Aug	Capsules contain seeds with long, silky hairs.	Diocious. Collect seed as it is released from capsules during dehiscence or collect entire catkins prior to dehiscence. Separate cotton fibers from seed.	Germination is most successful at 20-30°C with adequate moisture. Seed should not be covered with soil.	1
<i>Potentilla anserina</i> subs. <i>pacifica</i> (Walker 2005, Stevens, n. d., Baldwin et al. 2012)			Fruits are oval, flat, and reddish-brown and about 2 mm in length.	Let seeds dry on plant prior to collection.	Non-dormant. Seeds should be planted in full sun in lightly packed soil. Keep soil moist.	Short-lived
<i>Pseudognaphalium californicum</i> (Keeley and Keeley 1987, Nesom 2013)			Oblong fruits with bristly, tuft-like projections (shed at maturity).		Germination stimulated by presence of charred wood or aqueous extracts of charred wood.	
<i>Rosa californica</i> (Young 2001i, Lady Bird Johnson Wildflower Center 2007)	Jul	Sep	Mature fruits (rose hips) are bright red. Each hip contains multiple seeds.	Collect hips as soon as they are ripe. Extract seeds by hand from dried hips. Alternatively, macerate hips in water; remove floating seeds.	Soak seeds in water overnight prior to sowing. Seeds germinate slowly, cold stratification helps speed process.	2-4
<i>Salicornia bigelovii</i> (Glenn et al. 1997, Zedler 2001, Baldwin et al. 2012)	Sep	Nov	1-1.5 mm curved, hairy seeds.	Entire inflorescences should be collected and air-dried. When dry, strip seeds from inflorescences.	Irrigate with seawater. Root zone salinity (top 15 cm of soil) should be kept at a salinity of 70-75 g for high yields.	1

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Salicornia pacifica</i> (Khan and Weber 1986, Young 2001j)	Oct	Nov	Mature seeds pinkish white, puberulent, and 0.5-1 mm long. Sequentially hermaphroditic.	Collect inflorescences when plant tips are purple. Dry seeds on a screen for up to 3 months.	Variety <i>S. utahensis</i> grows best at 5% NaCl treatment and under temperature regime of 15-5°C.	2+
<i>Salix exigua</i> subs. <i>exigua</i> (Young and Clements 2003, Anderson 2006, Clarke et al. 2007)	May	July	Glabrous ovular capsules. Small seeds with pappus. Normally dispersed via wind or water.	Diocitous. Harvest when catkins are yellow-brown and capsules begin to open. Shake catkins to remove dried seeds.	Seeds are non-dormant. Optimal germination temperatures: 2-15°C.	3-4
<i>Salix lasiotepis</i> (Bonner and Karfalt 2008, Don 2014)	May		Glabrous ovular capsules.	Diocitous. Hand-harvest catkins when they begin to turn yellow/brown. It is recommended to wait until capsules open. Separate seeds from cotton.	Sow near soil surface. Exposure to light increases germination rate.	3
<i>Sabia apiana</i> (Stevens 1994, Montalvo and Beyers 2010d, Baldwin et al. 2012, Native Plant Database 2015)	July	Aug	Shiny, light brown fruit. Fruits are 2.5-3 mm in length.	Collect seeds as capsules begin to dry, before seeds are dispersed. Shake seeds from seed heads. Use a sieve to isolate seeds.	Scarification and possibly stratification needed to break seed dormancy. Sow seed in early fall. Seeds may respond to light, so plant in surface soil (1/8-1/4" deep). After planting, soak flats in water.	2-4
<i>Salvia mellifera</i> (Montalvo and Beyers 2010e)	Jun	Aug	Dry calyces are gravity dispersed. Up to 4 seeds/calyx. Seeds are 1 mm by 2 mm.	Collect after inflorescences with calyces are dry and brown. Collect mature seeds by clipping, stripping, or shaking seed heads. Seed should be dried and passed through a sieve. Use of a blower is recommended.	Physiological dormancy. Exposure to light or components of fire (charred wood, smoke, KNO3) may stimulate germination.	1-2
<i>Schoenoplectus acutus</i> var. <i>occidentalis</i> (Lacroix and Mosher 1995, Johnson 2004, Baldwin et al. 2012, Baskin and Baskin 2014)	Aug	Sep	Wide, smooth fruits with 2 or 3 distinct sides. Fruit 2-3 mm long and 1.2-1.7 mm wide.	Because they are easily dispersed by wind, it is important to collect seeds close to the time of maturity. Seeds must be	Physiological dormancy. Cold stratification breaks dormancy. Germination rates are low for the species due to the thick pericarp of the achene. Germination rates increase with overwintering in a pond or water source.	2

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Schoenoplectus californicus</i> (Stevens 2003, Baldwin et al. 2012)			2-sided, smooth fruits. Fruits 1.8-2.2 mm long and 1.3 mm wide.	separated from the panicle and cleaned.	Pre-treat seed with 0.05% solution of sodium hypochlorite 5 days prior to sowing. Seeds germinate to a higher percentage when grown in light.	
<i>Spartina foliosa</i> (Zedler 2001, Baldwin et al. 2012)	Sep	Nov	10-25 mm spikelets.	Harvest seed by hand from seed heads. Alternatively, use shears to clip entire seed heads from plant. Clean seeds. Multiple harvests may increase probability of collected good seeds prior to dispersal or herbivory loss.	Plant seeds 1/4" under the soil surface. Keep soil surface moist and at a temperature of 100°F. Best success after cold storage in freshwater.	4 months
<i>Stipa cernua</i> (Laude et al. 1952, Amme 2003, Herrera et al. 2006)	Jul	Aug	Linear, smooth, glabrous seed.	Harvest by hand or with a flow-vac or combine at maturity. Collection possible for 2-3 weeks.	Overheating can kill seedlings.	
<i>Stipa lepida</i> (Ashby and Hellmers 1959, Elkhorn Slough National Estuarine Research Reserve 2001, Amme 2003, Dave's Garden 2015b)			Brown fruit. Dark seeds 4-7 mm in length.	Seeds mature in spring. Allow seed to mature on plant. At maturity, harvest seed. Clean prior to storage.	No pretreatment needed. Constant light (i.e. 24-hour photoperiod) exposure is documented to speed flowering.	
<i>Suaeda estrova</i> (Zedler 2001, Baldwin et al. 2012)	Oct	Dec	Two types of seeds: seeds can be lenticular, black, and shiny (0.8-1.7 mm in length) or horizontal and matte (1-1.5 mm in length).	Best to collect in Nov or early Dec. Cut whole inflorescence or strip inflorescence. After cleaning, seeds should be dried.	Seedlings establish well at restoration sites.	2+
<i>Suaeda nigra</i> (Borders, n.d.)	Sep	Oct	Small, lenticular, shiny black seeds 0.5-2 mm long. Seed coat can be smooth, finely	Collect when seeds are hard, black, and shiny when calyces will be brown and crumbly. Strip seeds from stalk by hand.	Pre-chill recommended.	3

Appendix II. Continued.

Scientific name	Start	End	Fruit/seed characteristics	Seed collection details	Seed germination	Longevity (yrs.)
<i>Suaeda taxifolia</i> (Zedler 2001, Baldwin et al. 2012)	Jun	Jul	1-2 mm horizontal or vertical seeds. Seeds are shiny, lenticular and range from black to brown.	Pass seed through a hammer mill or a sieve prior. Seeds should be spread out to dry before being processed/stored. Strip inflorescence by hand.	Seeds germinate readily with freshwater irrigation.	3
<i>Triglochin maritima</i> (Young 2002, Baldwin et al. 2012, Recon Native Plants Inc. 2015)	Jul	Sep	Mature inflorescences are brown. 1 seed/fruit. Seeds of genus usually linear. Seeds can be flat or angled.	Collect seeds between July 17-Sept. 23rd. Rub dry fruits between fingers to extract the seeds.	No pre-treatment required.	3-5
<i>Vulpia microstachys</i> (Young and Young 1986, Howard 2006, Baldwin et al. 2012)			5.5-10 mm spikelets contain 4-6 mm long fruits.	Unknown exactly when seeds from S. California plants mature (intermountain varieties mature late July- late September).	Seeds germinate w/o pretreatment. Heating and litter do not increase germination.	4-5

*In instances where published information is insufficient to fill-in portions of the table, cells are intentionally left blank.

*Seed longevity data from Recon Native Plants Inc. used to supplement information found in the literature where necessary

Redescription of *Bathygyge grandis* Hansen, 1897 (Crustacea, Isopoda, Bopyridae) from Southern California with Erection of a New Subfamily, Bathygyginae

John C. Markham

Arch Cape Marine Laboratory, Arch Cape, Oregon 97102-0133, jmarkham@seasurf.net

Hansen (1897), dealing with only fragmentary material, erected the genus *Bathygyge* with *B. grandis* as its type-species as one of the earliest bopyrid species known from the eastern Pacific Ocean. *Bathygyge grandis* was first recorded as a parasite of the deep-water crangonid shrimp *Glyphocrangon spinulosa* Faxon from off the coast of Acapulco, Mexico. It has since been reported from several different localities worldwide as a parasite of other species of *Glyphocrangon*, but it has never been properly described. Material that recently became available from near the type-locality has made it possible to correct that situation.

Order Isopoda Latreille, 1817
Suborder Cymothoidea Wägele, 1989
Family Bopyridae Rafinesque-Schmaltz, 1815
Subfamily Bathygyginae, subf. n.

Genus *Bathygyge* Hansen, 1897
Type-species, by monotypy, *Bathygyge grandis* Hansen, 1897
Bathygyge grandis Hansen, 1897
Figs. 1–2

Bopyrus – Faxon, 1895: 140 [Type-material later described].

Bathygyge grandis Hansen, 1897: 122-124; pl. V, figs. 2-2c [Pacific Ocean, off Acapulco, Mexico, 21°15'N, 106°23'W, 676 fm (= 1236m); infesting *Glyphocrangon spinulosa* Faxon, 1893].—Richardson, 1899a: 869.—Richardson, 1899b: 338.—Bonnier, 1900: 48, 221, 291-292, 381; fig. 53.—Richard, 1900: 71.—Townsend, 1901: 527.—Richardson, 1905: 537-539; fig. 581.—Stebbing, 1908: 57-59; pl. XXXIII [Off Cape Point, South Africa, 800-900 fm (= 1463-1646m); infesting *Glyphocrangon sculpta* (S. I. Smith, 1882)].—Stebbing, 1910: 436.—Nierstrasz and Brender à Brandis, 1923: 86.—Barnard, 1940: 494, 721.—Danforth, 1963: 33, 37, 91, 92; pl. 5, figs. 1, 2.—Şadoğlu, 1969: 197.—Schultz, 1969: 312; fig. 496.—Danforth, 1970: 9, 43, 57-58, 149; fig. 5D, E.—Holthuis, 1971: 285.—Wenner, 1978: 1058-1061 [On continental slope of Middle Atlantic Bight; infesting *G. sculpta* and *G. longirostris* (S. I. Smith, 1882)].—Bourdon, 1979: 510.—Markham, 1979: 771-772.—Markham, 1985: 19, 131 [Atlantic Ocean, off coast of Virginia, USA: infesting *G. longirostris*].—Markham, 1986: 155, 156; fig. 4B.—Kaufmann et al., 1989: 1882; tab. 4 [Magellan Rise, NE Pacific, 07°05'N, 176°55'W - 176°50'W, 3100m; infesting unspecified host, probably *G. vicaria* Faxon].—Salazar-Vallejo and Leija-Tristán, 1989: 429.—Leija-Tristán and Salazar-Vallejo, 1991: 1.—Markham, 1992: 3; tab. 1.—Espinosa-Pérez and Hendrickx, 2001: 50.—Román-Contreras and Soto, 2002: 279.—An, 2006: Abstract [on unnumbered p.], 73-74, 114, 117, 123, 131; fig. 28 [East China Sea, 26°10'N, 126°00'E; infesting *Glyphocrangon* sp.].—An et al., 2007: 1002, 1003; fig. 1 [Same material as An, 2006].—Yu and An, 2008: 691.—Stebbins, 2012a: 2.—Stebbins, 2012b: 2, 6, 16; 4 unnumbered figs.

- ?*Gigantione bouvieri*.—Bourdon, 1967: 857 [Canary Islands; infesting *Glyphocrangon* sp., hyperparasitized by *Cabirops serratus* Bourdon, 1967. Probably not *Gigantione bouvieri* Bonnier, 1900].
- ?*Bathygyge* sp.—Bourdon, 1967: 857 [Same material tentatively called *Gigantione bouvieri* above].—Bourdon, 1979: 510 [Azores, 1590–1665m; infesting *Glyphocrangon longirostris*].—Lemos de Castro, 1970: 2.—Holthuis, 1971: 339.—Restivo, 1971: 71; tab. 1.—Restivo, 1975: 153; tab. 3.—Bourdon et al., 1981: 498.—Rybakov, 1990: 415.—Román-Contreras, 2008: 91.
- ?“bopyrid parasites.”—Holthuis, 1971: 339 [Off Atlantic coast of Nigeria, 04°15'N, 04°27'E–04°12'N, 04°28'E, 1280–1320m; infesting *Glyphocrangon longirostris*].
- Munidion* sp.—Wicksten, 1979: 222 [San Clemente Basin, California, infesting *Glyphocrangon vicaria* Faxon, 1896: material examined herein, described below].—Wicksten, 2009: 168.
- ?“branchial bopyrid.”—Chace, 1984: 11 [West of Halmahera, Indonesia, 00°16'30"N, 127°30'00"E, 497m; infesting *Glyphocrangon faxoni* de Man, 1918].
- Bathygege* [sic] *grandis*.—Campos and Campos, 1989: 33; tab. 2.
- ?“Bopyrid isopod”—Moore et al., 2003: 368 [Bear Seamount, northwestern Atlantic, 39°55'N, 67°30'W, 1100 m; infesting “*Glyphocrangon*” {probably = *G. sculpta*}].
- ?“bopyrid isopod.”—Ahyong, 2006: 68 [Tasman Sea, 32°04'S, 159°53'E, 1920–1934m; infesting *Glyphocrangon dimorpha* Komai, 2004].—Han and Li, 2007: 550 [East China Sea, 09°29'N, 123°41'E, 2000–2150m; infesting *Glyphocrangon megalophtalma* de Man, 1918]

Material Examined

Infesting *Glyphocrangon vicaria* Faxon, 1896. R/V *Agassiz* Station M-7 Sta. 3, San Clemente Basin, eastern Pacific off California, USA, 32°28'N, 118°08'W, 1792m, 16 September 1971, 40-foot otter trawl. 2♀, 2♂, SIO (Scripps Institute of Oceanography) C3100.

Redescription of Female

Length 12.7 mm, maximal width 9.3 mm, head length 1.3mm, head width 2.8 mm, pleonal length 3.9 mm. Distortion 115° sinistrally. Body outline broadly ovate, widest across pereomere 5. All body regions distinct, pereomeres distinct but pleomeres medially fused; pleon strongly torsioned (Fig 1A, B).

Head deeply embedded in pereon, its anterior margin overreached by second oostegites. No eyes. Antennae (Fig. 1C) not extending beyond margins of head, first of 3 articles, second of 6 articles, setation obscure. Barbula (Fig. 1D) with pair of unornamented slender falcate projections on each end, slightly sinuous margin medially. Maxilliped (Fig. 1E) of irregularly pentagonal anterior article bearing subterminal articulating triangular palp (Fig. 1F) densely setose along medial edge; and smaller subtriangular posterior article produced into long slender plectron (Fig. 1G) directed anteromedially.

Pereomeres separated dorsally by sinuate margins. Coxal plates well-developed on pereomeres 1–4, those of first two pairs reflexed medially over dorsal surfaces of pereomeres (Fig. 1A, J), other two pairs completely covering lateral margins of pereomeres. Pereomeres 5–7 lacking coxal plates but their lateral regions expanded and flat. Oostegite 1 (Fig. 1H, I) slightly longer than broad, with nearly parallel sides; internal ridge lacking ornamentation; posterolateral projection about 1/3 width of posterior margin of oostegite, rather short and broadly rounded, turned slightly medially. Oostegites 2–5 of both pairs large and completely enclosing vaulted brood pouch. Pereopods (Fig. 1K, M) all tiny, though slightly larger posteriorly, arrayed along lateral margins of pereon and extending little beyond those margins, pereopods 1 and 2

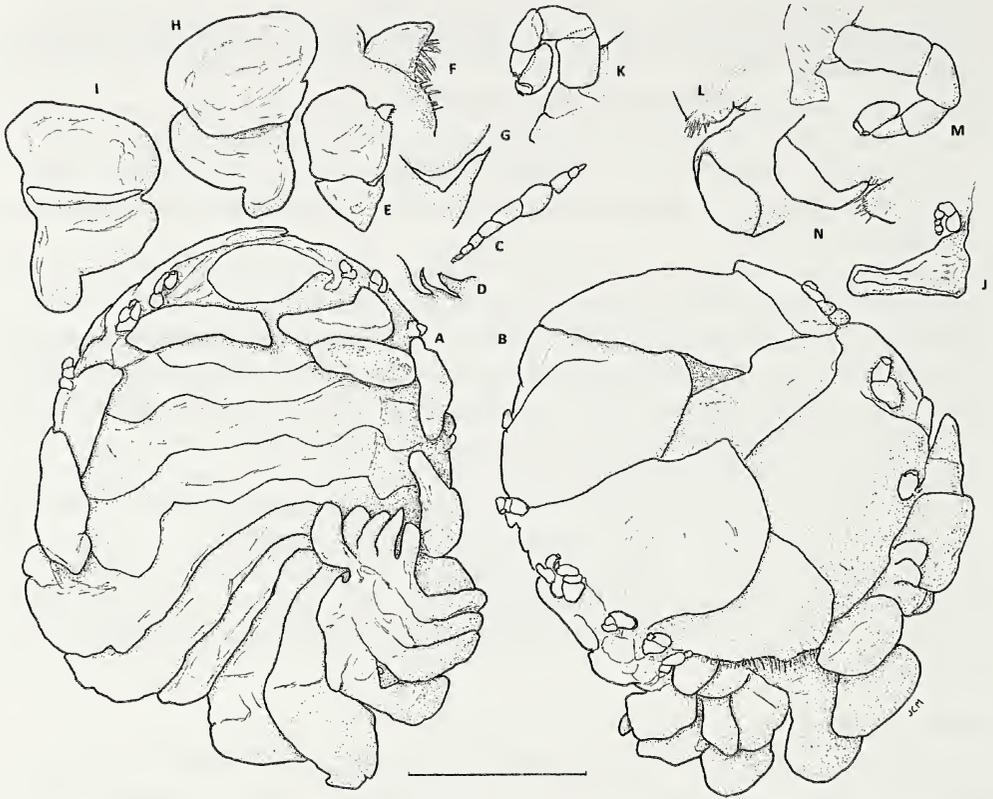


Fig. 1. *Bathygge grandis* Hansen, 1897, reference female. A. Dorsal view. B. Ventral view. C. Right antennae. D. Barbula, right side. E. Right maxilliped, external view. F. Palp of same. G. Plectron of same. H. Oostegite 1, external view. I. Same, internal view. J. Right pereopod 1 and attached coxal plate. K. Left pereopod 1. L. Dactylus and end of carpus of same. M. Left pereopod 7. N. Dactylus and end of carpus of same. Scale: 4.00 mm for A, B, D, E, H, I, J; 1.43 mm for K, M; 1.00 mm for C, F, G; 0.29 mm for L, N.

clustered closely together, and pereopods 6 and 7 similarly clustered on both sides; all articles of all pereopods separate, dactyli reduced and blunt anteriorly (Fig. 1L), bases (Fig. 1M) longer and dactyli (Fig. 1N) longer and sharper posteriorly.

Pleon (Fig. 1A) strongly torsioned and reflexed over pereon, so right (longer) side facing forward, of 6 pleomeres, final four pleomeres incompletely separated. Pleomeres 1-3 produced into broad blunt lateral plates on longer side. Pleomeres 4 and 5 produced into slender lateral plates on both sides. Pleomere 6 bearing widely separated uniramous uropods of structure and shape similar to that of lateral plates. No pleopods on any pleomeres.

Other female quite similar. Distortion dextral, with pleon torsioned to left side. Length 10.5mm, maximal width 8.2mm. Reflexed coxal plates on left (shorter) side of pereomeres 1-3, on opposite sides of pereomeres 1-2. Pereopods 1-4 with long dactyli, those of pereopods 5-7 smaller.

Redescription of Male

Length 6.8 mm, maximal width 1.6 mm, head length 0.6 mm, head width 1.1 mm, pleon length 1.8 mm, pleon width 1.2 mm. Head, pereomeres and pleon distinct. Sides of pereon parallel from pereomere 2-6. No pigmentation (Fig. 2A).

Head roundly quadrate, abruptly narrower than first pereomere and extending forward from it; anterior and posterior margins straight across, former somewhat shorter. No eyes. Antennae (Fig. 2B) of 3 and 7 articles respectively, minutely setose distally.

Pereon narrowest across pereomeres 1 and 7, its sides nearly parallel between; all pereomeres separated by deep notches laterally, slightly ridged middorsally. No midventral tubercles. Pereopods (Fig. 2C, D) with all articles distinct, larger anteriorly; carpi sparsely setose on anteromedial corners; all propodi enlarged, each produced into proximal lobe with socket receiving tip of reflexed dactylus; long sharply pointed dactyli on pereopods 1–5, shorter and blunter dactyli on pereopods 6–7.

Pleon long and extended, markedly narrower than last pereomere, as truncated oval, its sides nearly parallel, posterior margin broadly rounded. No trace of segmentation. No appendages.

Other male very similar, its antenna 2 of 8 articles. Length 12.7mm, maximal width 3.8mm, head length 0.7mm, pleon length 1.5mm.

Bathygyginae, new subfamily

Diagnosis. Branchially-infesting bopyrid. Female: Body outline roughly circular, with no straight margins. Head oval, much broader than long, deeply embedded in first pereomere and overreached by second oostegites. Maxilliped with subterminal triangular palp and slender pointed plectron. Barbula bearing two long slender projections laterally, bare medially. All pereomeres distinct dorsally, their margins irregularly curved. Pereopods all present, reduced. Coxal plates of pereomeres 1, 2 and/or 3 extending medially over dorsal surface of body. Oostegites 2–5 on both sides well-developed and completely enclosing enlarged brood pouch. Pleon of 6 incompletely separated pleomeres, its central axis greatly rotated to one side, posterior-most point of body side of pleomeres 1 and 2, pleomeres bearing blunt lateral plates but lacking all pleopods and uropods. Male: Body about 4 times as long as broad, fusiform in outline. Head narrower than first pereomere and distinct from it. Pereomeres deeply divided. Pereopods all with enlarged propodi with sockets receiving tips of sharply pointed dactyli. Pleon separated from last pereomere, suboval, bulbous, completely lacking all traces of segmentation or appendages. Only one genus and species known, *Bathygyge grandis* Hansen, 1897.

With a complete description of *Bathygyge grandis*, it now becomes possible to assess its systematic placement. Characters unique to *B. grandis*, which indicate that it should be in a subfamily of its own are: Female: Second oostegites extending beyond anterior margin of head; coxal plates of first and second pereomeres extending medially over dorsal surface of pereon; pleon strongly torsioned and pointing forward over pereon. Male: All pereopodal propodi bearing sockets into which tips of sharply pointed dactyli retract. Unusual characters (though in rare instances known from members of other subfamilies of the Bopyridae) are: Female: Body broadly oval, almost circular; head lacking frontal lamina; pereopods proportionately tiny. Male: Body very long relative to width; pleon completely lacking all traces of segmentation and all appendages. Hosts: All known in genus *Glyphocrangon* A. Milne-Edwards, 1881 (Caridea, Crangonoidea, Glyphocrangonidae).

Hansen (1897), whose description of *Bathygyge grandis* Richardson (1905) quoted verbatim and whose illustrations she reproduced, had “[o]nly a male, and the posterior part of a female.” He did not figure the female at all but remarked on it thus: “Abdomen: It is turned to the left in a startling degree...” That extreme rotation of the pleon, figured and described herein, is unique for bopyrid females. The present male closely matches the description and figures of the type-male by Hansen (1897) (reproduced by Richardson, 1905). The only illustration prepared of *Bathygyge grandis* since the original description is that of An (2006), of Chinese material in a dissertation, which has limited accessibility because it is entirely in Chinese and unpublished;

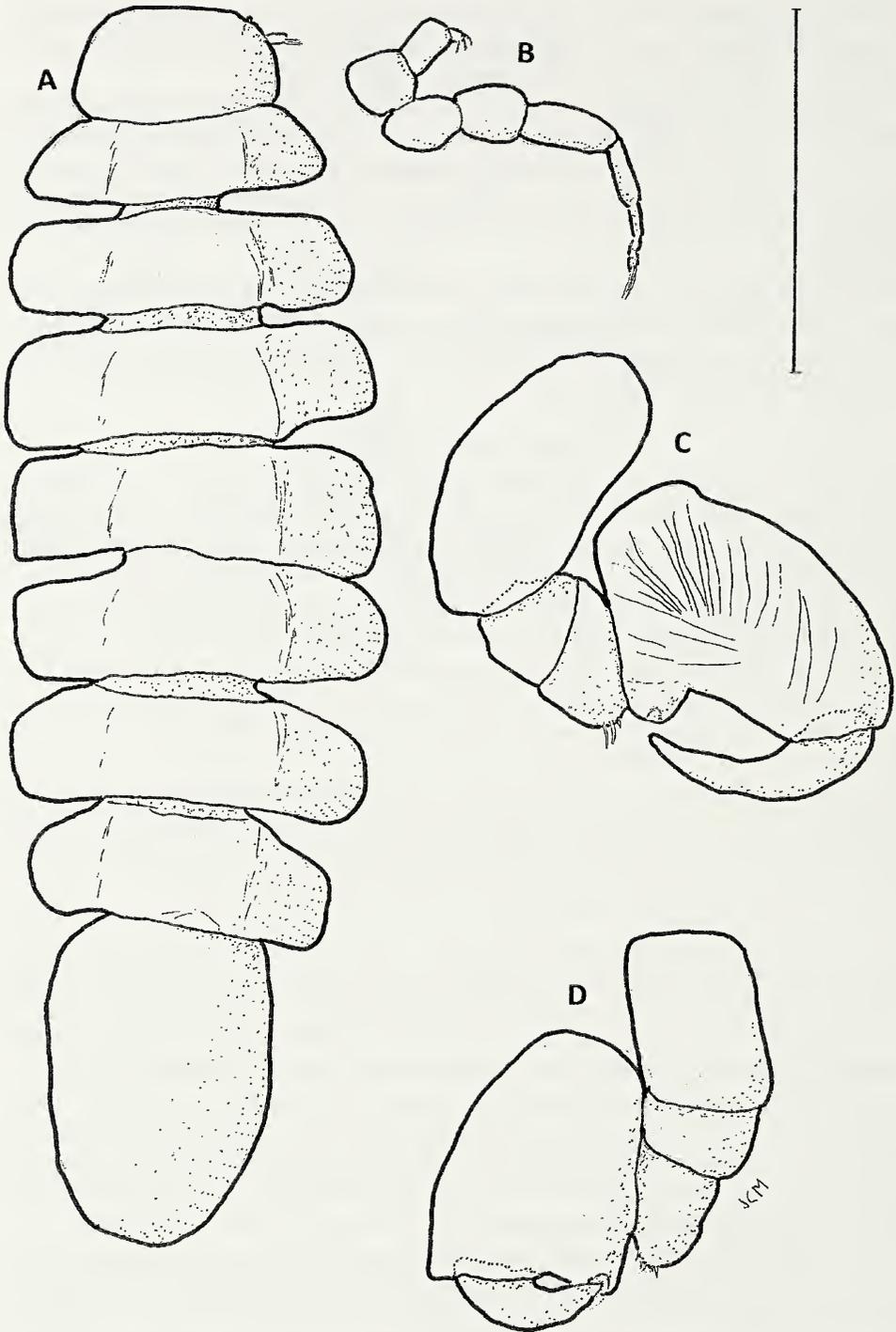


Fig. 2. *Bathytyge grandis* Hansen, 1897, reference male. A. Dorsal view. B. Left antennae. C. Left pereopod 1. D. Right pereopod 7. Scale: 2.00 for A; 0.45 mm for B-D.

it only recently came to my attention. In her figure 28, she presents detailed drawings, the first known, of both sexes. Both the female and male illustrate the diagnostic characters of the species: the medially extending coxal plates of the first two pereomeres, the reduced pereopods and the strongly torsioned pleon of the female; and, in the male, the strongly separated head, pereomeres and pleon; prominent proximal lobes on the propodi of the pereopods of the first pair; and complete lack of segmentation and appendages of its pleon. There are however, several differences between the material herein described and that from China. In the Chinese female, the body is more nearly circular; the maxilliped's palp does not articulate, and its spur is much reduced; the first oostegite has a slightly more slender and longer posterolateral point, which is setose along its lateral margin; the posterior pereomeres bear tergal plates distinctly separated from the segments; and the lateral plates of the pleomeres are quite sharply pointed. In the Chinese male, the body is slightly curved; tiny colorless eyes are present next to the posterior edge of the head; and the pleon is attached to the last pereomere by a narrow peduncle. It is uncertain whether the propodi of that male's pereopods bear sockets receiving the tips of the dactyli, as in the male herein described. An et al. (2007), who published mention of the same material as An (2006), included a photograph (their fig. 1) of the parasite in place on its host but did not present drawings of the specimens themselves. Few specimens assigned to *Bathogyge grandis* have been examined in detail (only the male in the type-collection, only two females and two males in the present collection and a single one of each sex in the report from China). Thus there remains some doubt whether the distinctions cited here are consistent among the populations from opposite sides of the Pacific Ocean. If they are, the individuals from China should quite probably be considered representatives of a separate undescribed species. The status of specimens reported from elsewhere in the world is also uncertain. For now, however, I am retaining all of them in the synonymy of *B. grandis* presented above.

Branchial bopyrid parasites of caridean shrimps are most commonly members of the subfamily Bopyrinae, whose species are not known to infest any hosts but carideans. The small subfamily Argeiinae contains exclusively caridean-infesting parasites. In the large subfamily Pseudioninae, whose many species are typically parasites of anomurans, are a few species found as parasites of deep-water carideans. *Bathogyge* clearly does not belong in the Argeiinae, whose females, among other contrasting characters, have large rear-extending pleons of a very different shape. It has been dubiously assigned to the Bopyrinae (Shiino, 1965) or Pseudioninae (Markham, 1974) but does not fit well into either of those subfamilies for various reasons. Stebbins (2012a, 2012b) expressed doubt about its proper assignment to subfamily. Its unique placement, emphasized by the present erection of a new subfamily, may be a reflection of its occurrence as the only known bopyrid species infesting any member of the family Glyphocrangonidae, of which *Glyphocrangon* is the sole recognized genus.

Wicksten (1979) mentioned infestation of *Glyphocrangon vicaria* and called its parasite "*Munidion* sp." without any descriptive notes and later (Wicksten, 2009) repeated that record. I found her label in the container with the material herein redescribed, thereby confirming that I was dealing with the same specimens.

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The Reef Cornetfish, *Fistularia commersonii* Rüppell, 1838, New to the California Marine Fish Fauna

Milton S. Love

Marine Science Institute, University of California, Santa Barbara, CA 93106,
love@lifesci.ucsb.edu

I report here on several sightings in southern California of the reef cornetfish, *Fistularia commersonii* Rüppell, 1838. These records mark the first time this species has been reported from California marine waters.

Mr. Bill Powers reported an unverified sighting on 7 November 2015 at Little Flower Reef, San Clemente Island (32°50.399'N, 118°22.136'W). Mr. Powers was diving over a sand-shell hash slope adjacent to a vertical rock wall in about 12 m of water. The approximately one-meter-long fish was more or less motionless and Mr. Powers was able to observe it for several minutes, eventually approaching and touching it. Mr. Powers reports that the fish was green in color with blue spots and stripes and had a long filament extending from its caudal fin. This fish was not photographed.

A second sighting was made by Ms. Sandy Dildine on 12 November 2015 within Crescent Bay, Laguna Beach (33°32.7'N, 117°48.3'W) in 7 m of water with surface water temperature at this site of about 20°C. This approximately one-meter-long fish was slowly swimming just above the bottom. Photographs and videos of this fish taken on 12 and 13 November 2015 show a green fish with blue spots and stripes. Ms. Dildine noted that when the fish was more or less motionless it had a series of dark bars along its body as well as bright, light blue spots and stripes (Fig. 1). When actively swimming, the bars of this individual quickly disappeared and the stripes and spots became darker (Fig. 2). Ms. Dildine also observed what was likely the same individual within the same circumscribed area (of about 10 m) on 19, 20, and 22 November 2015. In these instances, the fish was associated with an aggregation of blacksmith, *Chromis punctipinnis* (Cooper, 1863).

Three cornetfish species live in the Pacific Ocean: *Fistularia commersonii* Rüppell, 1838, reef cornetfish; *Fistularia corneta* Gilbert & Starks, 1904, deepwater cornetfish; and *Fistularia petimba* Lacepède, 1803, red cornetfish. All range widely in the Indo-Pacific (*F. petimba* is also found in the Atlantic Ocean). In the eastern Pacific, *Fistularia corneta* occurs as far north as Huntington Beach, southern California (Curtis and Herbinson 2001) and southwards to Callao, Peru (Chirichigno and Vélez 1998), including the Gulf of California (Fischer et al. 1995) and Islas Galápagos (Grove and Lavenberg 1997). *Fistularia petimba* is absent from the eastern Pacific (Nakabo 2002). Of these taxa, *F. commersonii* is the only species that is green with blue spots and stripes (Thomson et al. 2000, Robertson and Allen 2015) as *F. corneta* is orange or brown with pink dorsal, anal, and caudal fins (Robertson and Allen 2015) and *F. petimba* is red to orange-brown (Kells and Carpenter 2011). Thus, based on color and pattern, it is highly likely that the San Clemente Island and Laguna Beach individuals are *F. commersonii*.

These California sightings extend the eastern Pacific range to southern California. The previous northernmost range was Bahia Magdalena (Thomson et al. 2000) to Iquique, northern Chile (Sielfeld et al. 2010), including the Gulf of California (Fischer et al. 1995) and Islas Galápagos (Grove and Lavenberg 1997). They have been reported from surface waters to depths of 132 m (Mundy 2005). This species reaches a maximum length of 1.6 m (Fischer et al. 1995).

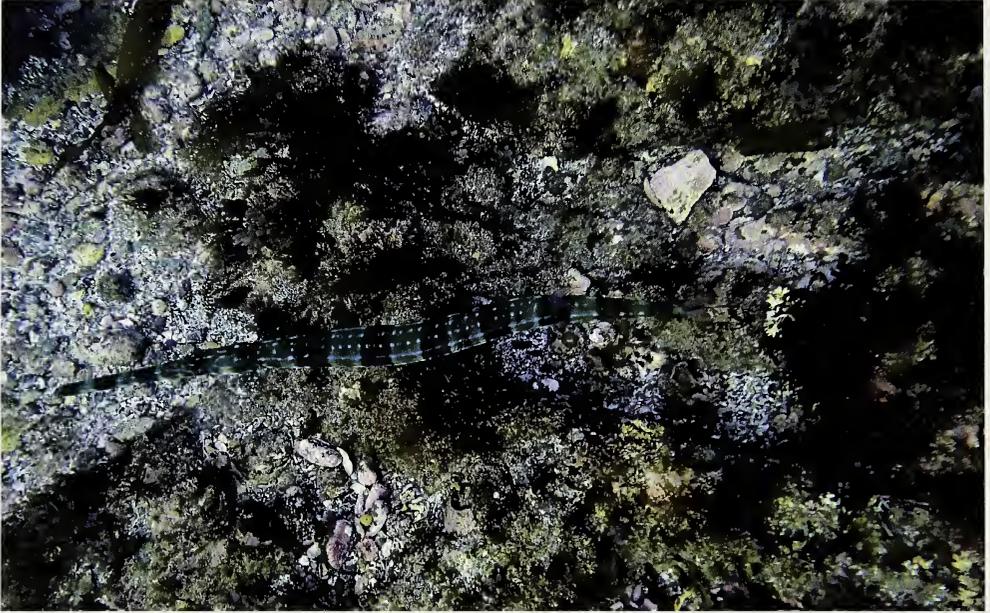


Fig. 1. Dorsal view of a stationary reef cornetfish, *Fistularia commersonii*, showing dark bars and lighter spots and stripes. Photographed on 13 November 2015 off Laguna Beach, southern California, by Ms. Sandy Dildine.

These fish were observed during a very strong El Niño and were part of a wave of tropical reef fish species (including cardinalfishes and damselfishes) that were observed in southern California during 2015. It is interesting to note that the southern-most capture of *F. commersonii*, in northern Chile, also took place during an El Niño (Sielfeld et al. 2010) and that the



Fig. 2. Dorsal view of a swimming reef cornetfish lacking bars and having darker spots and stripes. Photographed on 13 November 2015 off Laguna Beach, southern California, by Ms. Sandy Dildine.

Huntington Beach records of *F. corneta*, based on the capture of two small fishes, occurred during the waning months of the 1997–1998 El Niño (Curtis and Herbinson 2001).

Notes Added in Proof: On 6 December 2015, Mr. Mike Couffer observed and photographed a small (4 cm TL) *F. commersonii*, swimming near the sea floor just south of the Newport Pier, southern California (33°36'N, 117°56'W). Similar to the San Clemente Island and the Laguna Beach individuals, this individual was identified based on its green color and blue spotting on the back. This specimen represents the northernmost record for this species.

A paper by Jackson et al. (2015) postulates, based on *F. commersonii*'s rapid recent colonization of the entire Mediterranean Sea via the Suez Canal, that this species may be particularly well adapted to expand its geographic range when opportunities arise.

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