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# Biogeography of the Pacific Coast Brittle Star, Ophioplocus esmarki (Lyman, 1874) Occurrence Patterns and Environmental Correlates

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This paper presents abundance and distribution patterns of the smooth brittle star Ophioplocus esmarki (Lyman, 1874) along the Pacific Coast, with observations on environmental correlates. The three main objectives of this study are: (1) to test the accuracy of existing published range limits for O. esmarki via field sampling and museum records, (2) to determine its distribution, and (3) to identify important environmental correlates to O. esmarki's presence along the Pacific Coast. Smooth brittle star abundance and distribution along the Pacific Coast were sampled along with substrate and water chemistry. Patterns of species abundance were analyzed according to depth and latitude. Substrate and water chemistry data were investigated by univariate and stepwise logistic regressions in order to determine which variables were significant correlates of O. esmarki occurrence. I found that this elusive brittle star is indeed much more common and widespread than was previously thought. Ophioplocus esmarki's new northern and southern range limits (50°N and 23°N) are documented and cited in this paper. In field surveys, O. esmarki individuals were found from 36°N at Santa Cruz, California south to 27°N in Bahia Asunción, Mexico The most substantive conclusions are that populations are denser in the intertidal than the subtidal, exhibit the abundant center distribution, and large abundances of O. esmarki correlate with coarse sand and water temperature ranging 15.2-16.8°C. This offers new data on O. esmarki's ideal habitat and can be used for conservation efforts to predict the brittle star's response to climate change, anthropogenic impacts, and to interpret other near shore ophiuroids abundance patterns

KEYWORDS: abundance, distribution, environmental correlates, Ophiuroid, Ophioplocus esmarki, Pacific coast, range limits, subtidal.

A fundamental datum in biogeography is the species range, and many studies attempt to delimit and identify environmental correlates with range limits (Terborgh 1971; Root 1988; Carpenter et al. 1993; Miller 1994; Jones and Gladkov 1999; Skov 2000; Scott et al. 2002; Peterson and Kluza 2003,). Accurate accounts of species ranges, their limits, and correlated environmental factors are valuable conservation tools useful in assessing impacts from humans, climate change, habitat fragmentation, natural selection, and extinctions (Root and Sneider 1993; Barry et al. 1995; Brown and Lomolino 1998; Parmesan et al. 1999; Hellberg et al. 2001; Thomas et al. 2001; Karban and Strauss, 2004).

In addition to information from range limits, species abundance and geographic distribution within a range often reveals patterns about important biological and environmental factors (Brown 1984; Brown et al. 1996; Brown and Lomolino 1998). In marine biogeography, research on the abundance and distribution of near shore species has yielded important findings about feeding ecology (Gaymer et al. 2001), dispersal and microhabitats (Gosselin and Chia 1995), substrate selection (Zimmerman et al. 1988), and geographic isolation (Scheltema 1971).

This paper presents abundance and distribution patterns of the smooth brittle star *Ophioplocus* esmarki (Lyman, 1874) (Fig. 1) along the Pacific coast, with observations on environmental correlates. Brittle stars are ophiuroids, a large and understudied class of echinoderms. Sampling for ophiuroids requires focused, intensive searching. Many intertidal and subtidal surveys commonly do not include them as a search objective, obtain them as a search outcome, or deposit them in museums. *O. esmarki* is as under-studied as other ophiuroids, but was chosen for study because information on its abundance, geographic distribution, and environmental correlates would likely be applicable to the biogeography of other closely related, ecologically similar species.

*Ophioplocus esmarki* has a latitudinally broad (Tomales Bay to San Diego, California) but bathymetrically narrow (to depths of 70 meters) range (Johnson and Snook 1955; Austin and Hadfield 1980; Ricketts et al. 1998; Etchemendy and Wood 2000), which simplifies field sampling. Information on *O. esmarki*'s biogeography is timely because it is a rare and endangered species in Canada (Darling 2000), and research suggests that declining *O. esmarki* populations may indicate their vulnerability to anthropogenic pressure (Addessi 1991; Eckert et al. 2000). In addition, the brooding reproductive strategy of *O. esmarki* may geographically isolate metapopulations, thus creating a patchy distribution (Gaarde and McClenagan 1982).

The three main objectives of this study are: (1) to test the accuracy of existing published range limits for *O. esmarki* via field sampling and museum records, (2) to test Gaarde and McClenagan's patchy-distribution hypothesis, and (3) to identify important environmental correlates with the species presence along the Pacific coast. I hypothesize that the range of *O. esmarki* is larger than is published, especially in the southern direction because San Diego is not a marine zoogeographic boundary. Because *O. esmarki* is a brooder, I agree with Gaarde and McClenagan that populations likely exhibit a patchy distribution. I also expect that, as with other benthic species, there are important physical environmental correlates with *O. esmarki*'s presence that contribute to ideal habitat conditions and their abundance and distribution patterns (Mezquita et al. 2000; Freeman and Rogers 2003).

The following clarifications should facilitate understanding of terminology used in this paper. I define *species range* as a geographic area where an organism has been located, and the *range limit* as the location where a species, "population density over large areas declines to zero" (Brown 1984; Gaston 1996). *Abundance* refers to local population density (number of species per unit area), and I use *distribution* to indicate geographic distribution of a species. The term *environmental correlates* refers to the abiotic variables measured in this study. I use the term *correlative factor* to refer to abiotic factors that are (statistically) significant correlates with *O. esmarki*'s presence.

#### METHODS

Smooth brittle star abundance and distribution along the Pacific coast were sampled in addition to recording information about local substrate and water chemistry. Fieldwork was conducted from Bell Island, Washington south to San Lorenzo Channel, Baja California Sur, Mexico from 2004 to 2006. Fifty-one sites were sampled for *O. esmarki* individuals in intertidal and subtidal waters.

The research sites were selected according to habitat and accessibility. *Ophioplocus esmarki* habitats are typically near shore areas with boulders or cobbles in sandy-mud substrate, generally



FIGURE 1. Ophioplocus esmarki, taken at 18 meters depth off of East Santa Rosa Island, California. Photo by author.

on a low sloping beach with sheltered wave exposure (Austin and Hadfield 1980; Ricketts and Calvin 1998). I located these habitats by analyzing topographic and geologic maps, and aerial photos. Each selected site was divided into intertidal and subtidal zones, all at least 50-meters wide (parallel to the shore). Subtidal zones were seaward from intertidal sites in depths of 3 to 18 meters. Latitude and longitude to the nearest 15 meters were determined at every site using a GPS receiver (Garmin Legend Ltd).

**INTERTIDAL SURVEY METHODS.**— Intertidal zones were searched at low tides less than or equal to -0.4 meters. A 50 meter transect was laid parallel to the water line at the 0.0 mean low water level at slack tide. Ten boulders or large cobbles were overturned within nine randomly selected 3.14 m<sup>2</sup> circle plots (Medeiros-Bergen and Ebert 1995). Each boulder flipped was measured to the nearest centimeter, and the width and length were used to obtain the under rock area as if the rocks were square (Ison and Frerich 1997).

The under-rock substratum was searched for *O. esmarki* individuals, and under each rock surface area coverage of the visibly exposed primary, secondary, and tertiary sediments (Sharman et al. 2002) was estimated from a planar view using a modified Wentworth scale. Identifications were made in the field, and at least two voucher specimens of *O. esmarki* were collected at each site. One water sample was collected and water temperature was measured to the nearest  $0.1^{\circ}$ C (Aqua Temp underwater thermometer) along the transect at each site.

If no *O. esmarki* individuals were found, then an additional 20–30 minute timed survey was conducted, overturning 70–100 cobbles and boulders (Sagarin and Gaines 2002a). If *O. esmarki* 

was located during the timed survey, then the intertidal survey was repeated at a new location and low tide within that site.

**SUBTIDAL SURVEY METHODS.**— Subtidal habitats were searched for *O. esmarki* via SCUBA. A research diver and I descended to a minimum of three meters and proceeded along a compass heading perpendicular to each subtidal site to a maximum depth of 18 meters. Ten boulders or large cobbles were overturned in four to nine randomly selected 3.14 m<sup>2</sup> circle plots according to depth (Kushner et al. 1994; Medeiros-Bergen and Ebert 1995). At each circle plot, data on the total number of *O. esmarki* individuals, as well as surface area coverage of primary, secondary, and tertiary under-rock substrate were collected. At least two voucher specimens of *O. esmarki* were also collected at each site. Water temperature was measured and a water sample was taken at the deepest circle plot. Similar to intertidal surveys, if no *O. esmarki* were found, then a second dive occurred and an intensive timed search (10–20 minutes) was conducted. If *O. esmarki* was located during this timed survey, then the subtidal sampling was replicated in a new offshore location at that site.

**LABORATORY AND DATA ANALYSIS.**— Intertidal and subtidal water samples were analyzed for salinity and dissolved oxygen content. Salinity was measured to the nearest 0.1 ppt using a YSI 3200 Conductivity Instrument (K = 1.030 at  $25.0^{\circ}$ C). Dissolved oxygen was measured to the nearest 0.1 ppm using a Hanna HI 9142 dissolved oxygen meter.

*Ophioplocus esmarki* abundance was estimated by dividing the total number of individuals at each site by the total under-rock surface area searched. Mean under-rock surface area for each circle plot was estimated using the length and width measured for each rock in the field. Specimen counts were standardized by applying the mean under-rock surface area for each circle plot  $(1 \text{ m}^2)$  to allow for comparisons of species abundance (Piepenburg et al. 1997). These calculated abundances were then grouped according to latitude for analysis using JMP IN version 5 statistical software.

Substrate and water chemistry data were investigated using two different analytical approaches. A series of univariate logistic regressions were employed for each group of variables in the forward, backward, and mixed directions in order to determine which variables were significant correlates of *O. esmarki* occurrence. The two data groups were also combined in a stepwise logistic regression in the forward, backward, and mixed directions to verify that the same variables that emerged as predictors in the univariate analysis also were significant in the combined stepwise analysis.

**MUSEUM RESEARCH.**— I visited three museum collections: California Academy of Sciences (CAS), Los Angeles County Museum of Natural History (LACM), and the Royal British Columbia Museum (RBCM) to locate unpublished *O. esmarki* range records. These museums were visited because they contained collections of *O. esmarki*, as determined by their curators. *Ophioplocus esmarki* specimens were verified visually using the key to ophiuroids in Light et al. (1975) and all label data were recorded. Records from the National Museum of Natural History (USNM) and Scripps Institution of Oceanography (SIO) were also analyzed, but the institutions were not visited to verify their collections.

## RESULTS

At the 51 sites sampled in this study, a total of 666 *O. esmarki* individuals was found under 2790 boulders and large cobbles. Each boulder's under-rock area ranged from .04-.42 m<sup>2</sup> ( $M = .10 \text{ m}^2$ , SD = .06), and the total under-rock area searched along the coast was 279 m<sup>2</sup> (Table 1).

**RANGE EXTENSIONS.**— The five museum collections yielded 107 records of *O. esmarki* occurrence dating from 1874 (USNM, catalogue numbers 12644 and 12732) to 1997 (LACM, catalogue numbers 97.42-3 and 97.41-7) along the Pacific coast. According to confirmed museum records,

Research Site	GPS Coordinates	Total #	Area	# O. esmarki	1° Sub-	Water
		O. esmarki	$(m^2)$	$/m^2$	$strate^1$	temp ( $^{\circ}C$ )
Bell Island, WA	N48°35.786 W122°58.932	0	4	0.00	C. Sand	8.1
Turn Island, WA	N48°32.189 W122°58.289	0	4	0.00	C. Sand	8.1
Yachats, OR	N44°18.226 W124°06.494	0	3	0.00	F. Sand	NA
Port Orford, OR	N42°75 W124°50	0	2	0.00	Bedrock	9.1
Ocean Shore, OR	N42°42.765 W124°27.752	0	5	0.00	F. Sand	NA
Trinidad Head, CA	N41°03.416 W124°08.855	0	4	0.00	C. Sand	9.5
Van Damme, CA	N39°16.419 W123°47.438	0	3	0.00	Boulder	9.5
Head Rock, CA	N39°16.419 W123°47.438	0	4	0.00	C. Sand	10.2
Gerstle Cove, CA	N38°33.998 W123°19.916	0	5	0.00	C. Sand	10.6
Ocean Cove, CA	N38°33.241 W123°18.241	0	3	0.00	Pebbles	9
Steamer Lane, CA	N36°57.037 W122°01.591	5	4	1.25	Bedrock	12.7
Lovers Point, CA	N36°37.475 W121°54.985	7	5	1.40	Cobbles	11.7
Montaña DeOro, CA	N35°26.732 W120°85.910	0	1	0.00	Bedrock	NA
Shell Beach, CA	N35°15 W120°65	5	3	1.67	Cobbles	16.5
Refugio, CA	N34°45.849 W120°06.890	50	NA	NA	C. Sand	NA
Emma Wood, CA	N34°17.582 W119°20.356	19	3	6.33	Cobbles	16.8
Cavern Point, CA	N34°03.306 W119°34.000	70	5	14.00	Boulder	16.6
Amphitheater C., CA	N34°03.019 W119°35.372	34	6	8.50	C. Sand	16.2
Leo Carrillo, CA	N34°02.649 W118°56.011	3	6	0.50	Bedrock	15.4
Leo Carrillo, CA	N34°02.649 W118°56.011	0	3	0.00	F. Sand	NA
Las Tunas, CA	N34°02.364 W118°35.940	1	4	0.25	Bedrock	15.8
East Point, CA	N33°56.067 W119°58.301	16	2	8.00	C. Sand	15.2
East Pinnacles, CA	N33°56.150 W119°58.134	50	NA	NA	C. Sand	15.2
Malaga Cove, CA	N33°48.184 W118°23.825	0	6	0.00	C. Sand	18.9
Malaga Cove, CA	N33°48.184 W118°23.825	1	9	0.11	C. Sand	NA
Cabrillo, CA	N33°42.489 W118°17.105	1	4	0.25	C. Sand	14.9
Cabrillo, CA	N33°42.489 W118°17.105	36	9	4.00	Bedrock	NA
Corona Del Mar, CA	N33°35.330 W117°52.088	5	6	0.83	C. Sand	16.2
Corona Del Mar, CA	N33°35.330 W117°52.088	1	9	0.11	Bedrock	NA
Dana Point, CA	N33°27.618 W117°42.570	0	7	0.00	F. Sand	NA
Dana Point, CA	N33°27.618 W117°42.570	0	2	0.00	C. Sand	19.2
Seal Point, CA	N33°25.644 W118°25.419	3	5	0.60	Boulder	19.5
Twin Rocks, CA	N33°25.041 W118°25.53	2	5	0.40	Boulder	19.5
Lower Trestles, CA	N33°22.929 W117°35.308	0	9	0.00	F. Sand	NA
San Onofre, CA	N33°22.469 W117°34.132	0	9	0.00	F. Sand	NA
False Point, CA	N32°48.440 W117°15.987	3	8	0.38	F. Sand	20.6
False Point, CA	N32°48.440 W117°15.987	15	9	1.67	Bedrock	NA
San Miguel,MX	N31°54.077 W116°43.716	47	7	6.71	C. Sand	NA
San Miguel, MX	N31°54.077 W116°43.716	84	8	10.50	C. Sand	NA
Pt. St. Tomas, MX	N31°34.164 W116°41.415	33	5	6.60	C. Sand	15.6
Pt. St. Tomas, MX	N31°34.164 W116°41.415	161	9	17.89	C. Sand	NA
Cuatro Casas, MX	N30°56.017 W116°14.475	9	9	1.00	C. Sand	17.8
San Roque, MX	N27°10.824 W114°23.844	1	4	0.25	C. Sand	NA
B. Asunción, MX	N27°07.475 W114°17.739	0	6	0.00	F. Sand	14.4
B. Asunción, MX	N27°07.475 W114°17.739	4	6	0.67	C. Sand	NA
Pt. Abreojos, MX	N26°43.417 W113°32.765	0	8	0.00	F. Sand	NA
Swanee Reef, MX	N24°23.546 W 110°18.288	0	9	0.00	C. Sand	NA
El Merito, MX	N24°18.024 W110°20.257	0	9	0.00	C. Sand	NA
Pt. Conejo, MX	N24°04.508 W111°00.468	0	7	0.00	Shell	24.4
Pt. Conejo, MX	N24°04.508 W111°00.468	0	9	0.00	C. Sand	NA
San Pedrito, MX	N23°22.011 W110°12.133	0	9	0.00	Pebbles	NA
Totals	51 Research Sites	666	279 m	2 N/A	N/A	N/A

TABLE 1. Names and GPS coordinates for all 51 research sites (ordered from north to south), with abundance, primary substrate, and water temperature data.

<sup>1</sup> Under-rock substrate classified using a modified Wentworth scale: F. Sand <sup>1</sup>/<sub>6</sub>-<sup>1</sup>/<sub>4</sub> mm; C. Sand <sup>1</sup>/<sub>4</sub>-2mm; pebbles 4-65 mm; cobbles 64-256 mm; boulders 256-2048 mm.

*O. esmarki's* published range limits are extended north to Quatsino Sound, Vancouver Island (RBCM, catalogue number 180-52), and south to the San Lorenzo Channel, Mexico (LACM, catalogue number 607-36) see Appendix 1.

**ABUNDANCE AND DISTRIBUTION PATTERNS.**— In field surveys of the 51 research sites, *O. esmarki* individuals were found from 36°N at Santa Cruz, California south to 27°N in Bahia Asunción, Mexico. According to abundance data, *O. esmarki* population densities are highest near

the center of its range (17.89 individuals/m2 at Punto Santo Tomas, Baja California Norte; and 14.00 individuals/m<sup>2</sup> at Cavern Point, California) and decrease both to the north and south. At six of seven sites where both the intertidal and subtidal habitats were surveyed, O. esmarki individuals are more abundant in the intertidal (M = 4.99)individuals/m<sup>2</sup>, SD = 6.77) than in the subtidal (M = 2.11 individuals/ $m^2$ , SD = 3.11) (Fig. 2). Two caveats exist for this data. First, since the sampling sites were pre-

Intertidal vs. Subtidal Population Density



FIGURE 2. At six of seven sites where both the intertidal and subtidal habitats were surveyed, *O. esmarki* individuals were more abundant in the intertidal.

selected for habitat suitability, the measurements of density are biased. Second, since the under-rock areas were treated as rectangles, the abundance data reported here is slightly lower than in the field.

**ENVIRONMENTAL CORRELATES.**— A series of univariate logistic regressions in addition to a combined stepwise logistic regression yielded Chi-squared values for all environmental data. Among all environmental correlates measured, primary under-rock substrate, and water temperature are significant correlative factors of *O. esmarki's* occurrence. The most common primary under-rock substrate type, coarse sand (<sup>1</sup>4–2 mm) is a significant correlative factor for the occurrence of *O. esmarki* ( $\chi^2$  [N = 49] = 0.02, *p* < 05). Secondary and tertiary under-rock substrate are not significant. The occurrence of *O. esmarki* correlates significantly with water temperature ( $\chi^2$  [N = 29] = 0.02, *p* < .05) for temperatures ranging from 11.7°C to 19.5°C (M = 16.4°C, SD = 2.3). Dissolved oxygen ( $\chi^2$  [N = 35] = 0.32, *p* > .05) and salinity ( $\chi^2$  [N = 35] = 0.09, *p* > .05) do not yield significant Chi-square values and, thus, were not significant correlates to the species' occurrence.

Analysis of the eight sites where abundances of *O. esmarki* are greatest (> 6 individuals/m<sup>2</sup>) accents the following about habitat preference: the primary substrate is coarse sand ( $\frac{1}{4}$ -2 mm) (six of the eight sites), dissolved oxygen ranges from 7.9–8.1 ppm (M = 8.01 ppm, SD = .07), salinity ranges 32.8–33.4 ppt (M = 33.23 ppt, SD = .20), and water temperature ranges from 15.2–16.8°C (M = 16.08°C, SD = .67).

## DISCUSSION

**RANGE EXTENSIONS.**— The data collected on species range, abundance, and distribution of *Ophioplocus esmarki* show that this elusive brittle star is indeed much more common and wide-spread than was previously thought. New northern and southern range limits (50°N and 23°N) for *O. esmarki* are documented in this paper. The species is most abundant (M > 6 individuals/m<sup>2</sup>) between 34°N at Cavern Point, California and 31°N at Punto Santo Tomas, Mexico.

This is within the Californian marine zoogeographic province (34°N to 27°N), a zone of mixing where eurythermic species of both southern and northern origin are brought into contact (Briggs 1974; Newman 1979; Kaustuv and Martien 2001; Wares et al. 2001). While *O. esmarki* is not one of the 30% of species endemic to the province, it is found in much lower abundances (0–1.67 individuals/m<sup>2</sup>) north of the province limits, and is not found at all to the south (Briggs 1974). This suggests that *O. esmarki* thrives in the subtropical-temperate waters of the California province.

**ABUNDANCE AND DISTRIBUTION PATTERNS.**— Two additional patterns emerged from the abundance and distribution data: (1) *O. esmarki* is most abundant in the central portion of its range, and (2) *O. esmarki* is more abundant in the intertidal compared to the subtidal.

Abundant center distribution: Although not a statistically significant normal distribution (Shapiro-Wilk W = 0.828077), *O. esmarki's* abundance is greatest (M > 6 individuals/m<sup>2</sup>) at the center of its range (34°N to 31°N) and declines toward the northern and southern range limits (Sall et al. 2005). This pattern follows the "abundant center distribution" (ACD) (see Sagarin and Gaines 2002b), which has been well considered in the literature (Preston 1948; Wulff 1950; Udvardy 1969; May 1975; Gaston and Blackburn, 2000; Sagarin and Gaines 2002a, 2002b). Recent research by Murphy et al. (2006), suggests that this pattern may be better described as the "abundant core distribution" (ACD), with core habitat existing near a range center extending out 60–70% toward the range edges. The ACD has been observed in a wide variety of organisms over a range of spatial scales and is most often attributed to marine invertebrates with a pelagic dispersal phase such as *Fissurella volcano* (Reeve, 1849) and *Tegula funebralis* (Adams, 1854) (Grinnell 1922; Cain 1944; Brown 1984; Sagarin and Gaines 2002a). However, *O. esmarki* is ovoviviparous, its young developing within bursae, and would not be expected to exhibit the ACD.

I hypothesize that *O. esmarki* exhibits the ACD largely due to its rafting capabilities. Similar to *O. esmarki*, *Amphipholis squamata* (Chiaje, 1828) is an ovoviviparous ophiuroid that floats on debris and has a high tolerance for environmental change that contributes to its cosmopolitan distribution (Highsmith 1985; Alva and Vadon 1989). Individuals of *O. esmarki* have been documented rafting on kelp (Bushing 1994), which is likely an important vector for dispersal, especially to offshore islands, and contributed to its ACD.

In our field survey, no *O. esmarki* individuals were located north of 36°N or south of 27° N. I hypothesize this is because populations of *O. esmarki* are rarer toward the edges of its range, as often occurs in other marine species like *F. volcano*, *T. funebralis*, and *Nucella canaliculata* (Duclos, 1832) (Sagarin and Gaines 2002a; Sorte and Hofmann 2004). These data support the hypothesis that *O. esmarki* is best adapted to the subtropical-temperate waters of the California province.

Intertidal vs. Subtidal: The second major abundance pattern is that *O. esmarki* is more abundant in the intertidal than in the subtidal. Although the abundance data for the intertidal and subtidal were not significantly different at the 5% level (p = .33, P > .05), the general pattern is evident (Fig. 1). Ophioplocus esmarki's abundant core is located well within subtropical (defined as 23° to 35°N) waters, and thus follows the pattern along the Pacific Coast that ophiuroids are often more abundant intertidally in tropical and subtropical water (Austin and Hadfield 1980). I hypothesize that *O. esmarki* is more abundant in the intertidal because of the higher concentration of complex substrate (Drolet et al. 2004; Kostylev et al. 2005), benthic food supply, and reduction in mobile subtidal predators such as fish, crabs, and lobster (Rilov and Schiel 2006). Even within the intertidal zone, *O. esmarki* exhibits this pattern (at False Point, California) with higher densities at -.1m tide level (14.55 individuals/m<sup>2</sup>) than at the -.3m tide level (10.75 individuals/m<sup>2</sup>) (Presiado, unpublished data 2001).

ENVIRONMENTAL CORRELATES.— Previous studies illustrate that physical environmental vari-

ables such as substratum, bathymetry, and near bed hydrodynamics are important in structuring benthic habitat and are useful correlates to their geographic distribution (Warwick and Uncles 1980; Rosenberg 1995; Freeman 2001; Freeman and Rogers 2003). As with any rocky shore organism, *O. esmarki*'s occurrence is governed by the availability of suitable habitat. The presence of smaller-grained, coarse sand under-rock sediments significantly correlated with the presence of *O. esmarki*, and the lack of these sediments correlated with *O. esmarki*'s absence. At all eight of the field sites where fine sand was the primary substrate type, *O. esmarki* was not present. This is likely due to anoxic conditions which were observed in the field concurrently with fine sand. However, measurements of under-rock substrate are biased because sampling sites were preselected for substrate suitability and not randomized.

Near-shore water conditions are also an important factor influencing *O. esmarki*'s occurrence. Although dissolved oxygen and salinity are not statistically significant predictors for *O. esmarki*'s occurrence, water temperature is. Water temperatures throughout *O. esmarki*'s geographic range (Quatsino Sound, Vancouver Island, to San Lorenzo Channel, Mexico) were found to range from 8.1°C to 24.4°C. Water temperatures where *O. esmarki* was located in the field (Santa Cruz, California to Bahia Asuncion, Baja California Sur) range from 11.7°C to 20.6°C. However, these temperatures were measured at each site only once and do not account for seasonal or long-term variation. Lower water temperatures within its range predict *O. esmarki* have been collected in locations with water temperatures above and below this temperature range near the northern and southern range edges, therefore the species has possibly evolved greater tolerances to higher temperatures, similar to those seen in *A. squamata* (Alva and Vadon 1989). Further research on populations at or near the fringes of the species' range and on *O. esmarki*'s tolerance to temperature should test this hypothesis.

**ENVIRONMENTAL CORRELATES AND ABUNDANCE.**— A consideration of the eight sites where abundances are greatest (> 6 individuals/m<sup>2</sup>) reveals information about ideal substrate and water chemistry. Large *O. esmarki* abundances correlate with coarse sand as primary under-rock substrate, salinity ranging from 32.8 to 33.4 ppt, and water temperature ranging from 15.2 to 16.8°C. These new data on *O. esmarki*'s ideal habitat preferences could be used to predict the brittle star's response to climate change (Rivadeneira and Fernandez 2005). This information can also be used to delineate potential geographic extent, make comparisons between other ophiuroid and echinoderm habitat preferences, as well as assess *O. esmarki*'s sensitivity to habitat change (Freeman and Rogers 2003).

## **CONCLUSIONS**

This study documents a range extension for *O. esmarki* that illustrates the utility of previously unpublished museum records to document more completely species ranges, especially for understudied marine invertebrates such as ophiuroids. The most substantive conclusions from this research are (1) *O. esmarki* abundances are higher in the intertidal than the subtidal, and (2) populations exhibit the abundant center distribution. The implication is that these abundance and distribution patterns suggest that the California province, range cores, and the intertidal zone may be ecologically important habitats for *O. esmarki* and similar ophiuroids. This study also presents information on ideal under-rock substrate and water temperatures that help refine the description of the ideal *O. esmarki* habitat. This adds to the body of literature on ophiuroid distribution patterns, and may be especially applicable to conservation purposes requiring information on geographic range and distribution, habitat preferences and potential *O. esmarki* sensitivity to climate change and anthropogenic impacts in near shore marine waters.

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### References

- ADDESSI, L. 1991. Human disturbance and long term changes on a rocky intertidal community. *Ecological Applications* 4(4):786–797.
- ALVA V., AND C. VADON. 1989. Ophiuroids from the western coast of Africa (Namibia and Guinea-Bissau). Scientia Marina 53:27–845.
- AUSTIN, W.C., AND M.G. HADFIELD. 1980. Ophiuroidea: The brittle stars. Pages 146–159 in R.H. Morris, D.P. Abbott, and E.C. Haderlie, eds., *Intertidal Invertebrates of California*. Stanford University Press, Stanford. California, USA.
- BARRY, J.P., C.H. BAXTER, R.D. SAGARIN, AND S.E. GILMAN. 1995. Climate related, long term faunal changes in a California rocky intertidal community. *Science* 26:672–675.
- BRIGGS, J.C. 1974. Marine Zoogeography. McGraw-Hill Book Co., New York, New York, USA. 475 pp.
- BROWN, J.H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124 (2):255–279.
- BROWN, J.H., G.C. STEVENS, AND D.M. KAUFMANN. 1996. The geographic range: size, shape, and internal structure. Annual Review of Ecological Systems 27:597–623.
- BROWN, J.H., AND M.V. LOMOLINO. 1998. *Biogeography*, 2<sup>nd</sup> ed. Sinauer Associates Inc., Sunderland, Massachusetts, USA.
- BUSHING, W.W. 1994. Biogeographic and ecological implications of kelp rafting as a dispersal vector for marine invertebrates. Pages 103–110 in W. Halvorson and G. Maender, eds., *The Fourth California Islands Symposium: Update on the Status of Resources*. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.
- CAIN, S.A. 1944. Foundations of Plant Geography. Harper & Brothers, New York, New York, USA. 556 pp.
- CARPENTER, G., A.N. GILLISON, AND J. WINTER. 1993. DOMAIN: a flexible modeling procedure for mapping potential distributions of animals and plants. *Biodiversity and Conservation* 2:667–680.
- DARLING, L.M. 2000. At Risk: Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk. University College of the Caribou, Kamloops, BC. and Ministry of Environment, Lands and Parks, pp. 57–66.
- DROLET, D., J.H. HIMMELMAN, AND R. ROCHETTE. 2004. Effect of light and substratum complexity on microhabitat selection and activity of the ophiuroid Ophiopholis aculeata. Journal of Experimental Marine Biology and Ecology 313:139–154
- ECKERT, G.L., J.M. ENGLE, AND D.J. KUSHNER. 2000. Sea star disease and population declines at the Channel Islands. *Proceedings of the Fifth California Islands Symposium*. Minerals Management Service, 99-0038.
- ETCHEMENDY, S., AND S. WOOD. 2000. Marine Taxonomic Database. Partnership for Interdisciplinary Study of Coastal Oceans. (PISCO) HTML document. <a href="http://www.piscoweb.org/research/community/taxondb">http://www.piscoweb.org/research/community/taxondb</a> (last accessed 7 March 2007).
- FREEMAN, S.M. 2001. Comparison: the value of benthic faunas. Pages 31–36 in DEFRA Technical Report, 105 (786).
- FREEMAN, S.M., AND S.I. ROGERS. 2003. A new analytical approach to the characterization of macro-epibenth-

ic habitats: linking species to the environment. Estuarine Coastal and Shelf Science 56:749-764.

- GAARDE, W. A., AND L.R. MCCLENAGAN JR. 1982. Genetic variability, dispersal, and differentiation in two species of ophiuroids from southern California. *Southwestern Naturalist* 27:255–262.
- GASTON, K. 1996. Species-range-size distributions: patterns, mechanisms and implications *Trends in Ecology* and Evolution II, 5:197–201.
- GASTON, K.J., AND T.M. BLACKBURN. 2000. Pattern and Process in Macroecology. Blackwell Science, Oxford, UK. 377 pp.
- GAYMER, C.F., J.H. HIMMELMAN, AND L.E. JOHNSON. 2001. Distribution and feeding ecology of the sea stars *Leptasterias polaris* and *Asterias vulgaris* in the northern Gulf of St Lawrence, Canada. *Journal of the Marine Biological Association of the United Kingdom* 81:827–843.
- GOSSELIN, L.A., AND F.S. CHIA. 1995. Distribution and dispersal of early juvenile snails: effectiveness of intertidal microhabitats as refuges and food sources. *Marine Ecology Progress Series* 128:213–223.
- GRINNELL, J. 1922. The role of the 'accidental.' Auk 34:373–381.
- HELLBERG, M.E., D.P. BALCH, AND K. ROY. 2001. Climate-driven range expansion and morphological evolution in a marine gastropod. *Science* 292:1707–1710.
- HIGHSMITH, R.C. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. Marine Ecology Progress Series 25(2):169–179.
- ISON, T., AND D. FRERICH. 1997. Using artificial cover as a sampling method of shore crab density. The European green crab (Carcinus maenas) in Oregon: a preliminary survey of Yaquina, Coos, Winchester and Siletz Bays. Oregon State University, Zoology 104., Corvallis, Oregon, USA. HTML document. <a href="http://oregonstate.edu/~yamadas/crab/ch6.htm">http://oregonstate.edu/~yamadas/crab/ch6.htm</a>> (last accessed 7 March 2007).
- JOHNSON, M.E., AND H.J. SNOOK. 1955. Seashore Animals of the Pacific Coast. Dover Publications Inc., New York, New York, USA. 659 pp.
- JONES, P.G., AND A. GLADKOV. 1999. Floramap: a computer tool for predicting the distribution of plants and other organisms in the wild. CD-ROM Series, version 1. Centro Internacional de Agricultura, Tropical (CIAT), Cali, Colombia. 99 pp.
- KARBAN, R., AND S.Y. STRAUSS. 2004. Physiological tolerance, climate change, and a northward range shift in the spittlebug, *Philaenus spumarius*. *Ecological Entomology* 29:251–254.
- KAUSTUV, R., AND K.K. MARTIEN. 2001. Latitudinal distribution of body size in north-eastern Pacific marine bivalves. *Journal of Biogeography* 28:485–493.
- KOSTYLEV, V.E., J. ERLANDSSON, J., M.Y. MING, AND G.A. WILLIAMS. 2005. The relative importance of habitat complexity and surface area in assessing biodiversity: fractal application on rocky shores. *Ecological Complexity*, 2(3):272–286.
- KUSHNER, D., D. LERMA, AND D. RICHARDS. 1994. National Park Service Channel Islands National Park Kelp Forest Monitoring 1994 Annual Report. Channel Islands National Park, Ventura, California, USA.
- LIGHT, S.F., R.I. SMITH, F.A. PITELKA, D.P. ABBOTT, AND F.M. WEESNER. 1975. *Intertidal Invertebrates of the Central California Coast*. University of California Press, Berkeley, California, USA. 446 pp.
- LYMAN, T. 1874. Ophiuridae and Astrophytidae, old and new. *Bulletin of the Museum of Comparative Zoology*, *Harvard College* 3(10):221–272.
- MAY, R.M. 1975. Patterns of species abundance and diversity. Pages 81–120 in M.L. Cody and J.M. Diamond, eds., Ecology and Evolution of Communities. Harvard University Press, Cambridge, Massachusetts, USA.
- MEDERIOS-BERGEN, D.E., AND. T.A. EBERT. 1995. Growth, fecundity and mortality rates of two intertidal brittle stars (Echinodermata: Ophiuroidea) with contrasting modes of development. *Journal of Experimental Marine Biology and Ecology* 189:47–64.
- MEZQUITA, F., A. SANZ-BRAU, AND G. WANSARD. 2000. Habitat preferences and population dynamics of Ostracoda in helocrene spring systems. *Canadian Journal of Zoology* 78:840–847.
- MILLER, R.I. 1994. Mapping the Diversity of Nature. Chapman & Hall, London, UK. 240 pp.
- MURPHY, H.T., J. VANDERWAL, AND J. LOVETT-DOUST. 2006. Distribution of abundance across the range in eastern North American trees. *Global Ecology and Biogeography* 15:63–71.
- NEWMAN, W.A. 1979. Californian transition zone: significance of short-range endemics. Pages 399–416 in J. Gray and A.J. Boucot, eds., *Historical Biogeography, Plate Tectonics, and the Changing Environment*. Oregon State University Press, Corvallis, Oregon, USA.

- PARMESAN, C., N. RYRHOLM, C. STEFANESCU, J.K. HILLK, C.D. THOMAS, H. DESCIMON, B. HUNTLEY, L. KAILA, J. KULLBERG, T. TAMMARU, J.W. TENNENT, J.A. THOMAS, AND M. WARREN. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- PETERSON, A.T., AND D.A. KLUZA. 2003. New distributional modeling approaches for Gap Analysis. Animal Conservation 6:47–54.
- PIEPENBURG, D., J. VOSS, AND J. GUTT. 1997. Assemblages of sea stars (Echinodermata: Asteroidea) and brittle stars (Echinodermata: Ophiuroidea) in the Weddell Sea (Antarctica) and off Northeast Greenland (Arctic): a comparison of diversity and abundance. *Polar Biology* 17:305–322.
- PRESTON, F.W. 1948. The commonness, and rarity, of species. Ecology 29:254-283.
- RICKETTS, E.F., J. CALVIN, AND J.W. HEDGPETH. 1998. Between Pacific Tides, 5th ed. Stanford University Press, Stanford, California, USA.
- RIVADENDEIRA, M.M., AND M. FERNANDEZ. 2005. Shifts in southern endpoints of distribution in rocky intertidal species along the south-eastern Pacific coast. *Journal of Biogeography* 32(2):203–209.
- RILOV, G., AND D.R. SCHIEL. 2006. Seascape-dependent subtidal-intertidal trophic linkages. *Ecology* 87(3):731–744.
- ROOT, T.L., AND S.H. SNEIDER. 1993. Can large scale climactic models be linked with multiscale ecological studies? *Conservation Biology* 7:256–270.
- Root, T. 1988. Environmental factors associated with avian distributional boundaries. *Journal of Biogeography* 15:489–505.
- ROSENBERG, R. 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. *Netherlands Journal of Sea Research* 34:303–317.
- SAGARIN, R.D., AND S.D. GAINES. 2002a. Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypothesis. *Journal of Biogeography* 29:985–997.
- SAGARIN, R.D., AND S.D. GAINES. 2002b. The Abundant Center Distribution: to what extent is it a biogeographic rule? *Ecology Letters* 5:137–147.
- SALL, J., L. CREIGHTON, AND A. LEHMAN. 2005. JMP Start Statistics, 3rd ed. SAS Institute, Ontario, Canada.
- SCHELTEMA, R.S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin* 140:284–322.
- SCOTT, J.M., P.J. HEGLUND, AND M.L. MORRISON. 2002. Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, D.C., USA. 840 pp.
- SHARMAN, L., B. EICHENLAUB, D. VANLEEUWEN, S. CROLL, J.S. GROVER, G. LENHART, AND P. HOOGE. 2002. NPS Alaska Coastal Resources Inventory and Mapping Field Protocol- The Polygon Method- Developed at Glacier Bay National Park and Preserve 1997–1998. Glacier Bay National Park and Preserve, Gustavis, Alaska, USA. HTML document. (Database provided on DVD by L. Sharman, October 2004.)
- SKOV, F. 2000. Potential plant distribution mapping based on climatic similarity. Taxon 49:503–515.
- SORTE, C.J.B., AND G.E. HOFMANN. 2004. Changes in latitudes, changes in aptitudes: Nucella canaliculata (Mollusca: Gastropoda) is more stressed at its range edge. Marine Ecology Progress Series 274:263–268.
- TERBORGH, J.W. 1971. Distribution on environmental gradients: Theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 52:26–36.
- THOMAS, C.D., E.J. BODSWORTH, R.J. WILSON, A.D. SIMMONS, Z.G. DAVIES, AND M. MUSCHE. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577581.
- UDVARDY, M.D.F. 1969. Dynamic Zoogeography. Van Nostrand Reinold, New York, New York, USA. 445 pp.
- WARES, J.P., S.D. GAINES, AND C.W. CUNNINGHAM. 2001. A comparative study of asymmetric migration events across a marine biogeographic boundary. *Evolution* 55(2):295–306
- WARWICK, R.M., AND R.J. UNCLES. 1980. Distribution of macrofauna associations in the Bristol Channel in relation to tidal stress. *Marine Ecology Press Series* 3:97–103.
- WULFF, E.V. 1950. An Introduction to Historical Plant Geography. Chronica Botanica Company, Waltham, Massachusetts, USA. 223 pp.
- ZIMMERMAN, K.M., S.E. STANCYK, AND L.A.J. CLEMENTS. 1988. Substrate selection by the burrowing brittle star *Microphiopholis gracillima* (Stimpson) (Echinodermata: Ophiuroidea). *Marine and Freshwater Behavior and Physiology* 13:239–355.

# Appendix I

### Ophioplocus esmarki museum records from the Pacific Coast from 1874 to 1997

One hundred and seven previously unpublished *O. esmarki* records from the Pacific Coast from 1874 to 1997 from five museum collections: California Academy of Sciences (CAS), Los Angeles County Museum of Natural History (LACM), National Museum of Natural History (USNM), Scripps Institution of Oceanography (SIO), and Royal British Columbia Museum (RBCM). Locality data were taken from specimen labels, catalogs, and unpublished manuscripts. In the table, sites are ordered from north to south. *Ophioplocus esmarki*'s northern most record is at Quatsino Sound, Vancouver Island, whereas the southern most record is from La Playita Beach, Mexico.

Research Site	# of O. esmarki	Depth	Museum	Cat. #	Date	Collector
Quatsino Sound, BC	4	15 m	RBCM	180-52	30 Jun 1980	P. Lambert, B. Emerson
Friday Harbor, WA	1	Intertidal	CAS	111494	1918	Oldroyd
N. Pacific Ocean, CA	3	N/A	USNM	27234	15 March 1891	N/A
N. Pacific Ocean, CA	2	N/A	USNM	E23669	22 Sep 1918	W. Schmitt
N. Pacific Ocean, CA	1	N/A	USNM	E53134	26 Jun 1962	J. McLean
N. Pacific Ocean, CA	1	N/A	USNM	E29247	N/A	H.Kirby
N. Pacific Ocean, CA	1	N/A	USNM	18721	N/A	H. Lowe
N. Pacific Ocean, CA	11	N/A	USNM	26642	N/A	H. Hemphill
Mendocino, CA	2	6 m	CAS	103511	July 1965	T.Chess
Point Arena, CA	N/A	15 m	CAS	122282	20 Sep 1971	B. Laurent
Tomales Point, CA	N/A	N/A	LACM	N/A	10 Jun 1941	N/A
Farallon Isl., CA	3	N/A	CAS	4514	4 Apr 1977	C. Chaffee, B. Bowman
Farallon Isl., CA	1	Intertidal	CAS	N/A	6 Aug 1976	D. Lindberg
Moss Beach, CA	1	N/A	CAS	N/A	29 Jan 1964	E.W. Kirshbaum
Monterey Bay, CA	1	N/A	CAS	104189	N/A	E. Ricketts
Pacific Grove, CA	1	N/A	CAS	104623	4 Jul 1966	R. Setzer
Pacific Grove, CA	4	N/A	CAS	104677	17 May 1915	N/A
Pacific Grove, CA	1	N/A	CAS	104830	4 Jul 1966	R. Setzer
Pacific Grove, CA	3	N/A	CAS	111492	N/A	N/A
Pacific Grove, CA	1	N/A	CAS	121206	4 Jul 1966	R. Setzer
Point Piños, CA	1	Subtidal	CAS	104801	5 Aug 1971	J.E. Sutton
Pescadero Pt., CA	7	N/A	CAS	111491	8 Jul 1925	N/A
Malpaso Creek, CA	1	6–12 m	CAS	108601	22 Jul 1972	J.E. Sutton
Pescadero Pt., CA	3	N/A	CAS	111493	2 Mar 1931	G.E. MacGinitie
Hopkins Marine, CA	N/A	N/A	LACM	N/A	18 Jul 1952	N/A
Point Piños, CA	3	N/A	CAS	6194	22 Jul 1948	E. Friedman
Monterey Bay, CA	1	N/A	CAS	N/A	Jun2 1916	W.K. Fisher
Stillwater Cove, CA	15–20	N/A	LACM	N/A	14 May 1992	A. Summers
Piedras Blancas, CA	1	Intertidal	CAS	108794	22 Jun 1978	Bowman, Chaffee, Drake and Weitbrecht
Diablo Canyon, CA	1	N/A	CAS	122505	11 Aug 1976	D. Gotshall, CF&G
Diablo Canyon, CA	N/A	Intertidal	LACM	97.42-3	22 Jun 1997	G. Hendler
Diablo Canyon, CA	N/A	Intertidal	LACM	97.41-7	22 Jun 1997	G. Hendler
Point Sal, CA	N/A	N/A	LACM	ech 632	N/A	N/A
Coal Oil Point, CA	N/A	Intertidal	LACM	239.12	16 Feb 1970	F. Ziesenhenne
San Miguel Isl., CA	N/A	16 m	LACM	hgk 91-7	15 Oct 1991	H.G. Kuck, C. Meyer
Santa Cruz Isl., CA	2	N/A	CAS	104678	N/A	A.E. Noble
Santa Cruz Isl., CA	N/A	N/A	LACM	239.1	29 Oct 1940	N/A
Santa Cruz Isl., CA	N/A	N/A	LACM	239.1	29 Oct 1940	N/A
Santa Cruz Isl., CA	N/A	N/A	LACM	1189.4	29 Oct 1940	N/A
Santa Cruz Isl., CA	N/A	N/A	LACM	1189-40	29 Oct 1940	N/A

Research Site	# of O. esmarki	Depth	Museum	<i>Cat.</i> #	Date	Collector	
Catalina Isl., CA	N/A	12 m	LACM	N/A	16 Oct 1988	R.A. Ronson	
Catalina Isl., CA	N/A	4.6 m	LACM	N/A	25 Apr 1992	G. Hendler	
Catalina Isl., CA	N/A	9 m	LACM	89-230.1	3 Mar 1989	N/A	
Catalina Isl., CA	N/A	N/A	LACM	ech 630	N/A	G. Hendler	
Gulf of Catalina, CA	2	73 m	USNM	12644	1874	W. Dall	
Gulf of Catalina, CA	1	55–73m	USNM	12732	1874	W. Dall	
Gulf of Catalina, CA	2	N/A	USNM	12930	N/A	W. Dall	
Gulf of Catalina, CA	1	N/A	USNM	4290	N/A	N/A	
Catalina Isl., CA	N/A	Subtidal	LACM	123.3	23 Jul 1993	R. Sherlock	
Catalina Isl., CA	1	N/A	CAS	104877	1 Nov 1972	A.J. Ferreira	
Catalina Isl., CA	1	N/A	CAS	108795	28 Jul 1964	B. Marquardt	
Venice, CA	N/A	N/A	LACM	239.18	N/A	N/A	
Redondo Beach, CA	N/A	Intertidal	LACM	239.13	8 Feb 1947	F. Ziesenhenne	
Palos Verdes, CA	1	N/A	CAS	N/A	N/A	N/A	
Point Fermin, CA	1	N/A	CAS	N/A	21 Apr 1913	N/A	
Point Fermin, CA	N/A	Intertidal	LACM	93-10.3	9 Jan 1993	G. Hendler	
Southern CA	N/A	N/A	LACM	ech 629	N/A	G. Hendler	
Point Vicente, CA	N/A	N/A	LACM	ech 617	N/A	N/A	
Point Vicente, CA	N/A	N/A	LACM	ech 618	N/A	N/A	
Point Vicente, CA	N/A	N/A	LACM	ech 624	N/A	N/A	
San Pedro, CA	N/A	N/A	LACM	ech 628	N/A	N/A	
Point Fermin, CA	N/A	Intertidal	LACM	604	1 Nov 1928	A. Hancock	
Portuguese Bend, CA	N/A	N/A	LACM	1013-39	10 Nov 1939	A. Hancock	
Portuguese Bend, CA	N/A	Intertidal	LACM	N/A	13 Feb 1942	N/A	
Portuguese Bend, CA	N/A	Intertidal	LACM	N/A	26 Jun 1914	N/A	
Portuguese Bend and Redondo, CA	N/A	N/A	LACM	907-38	9 Dec 1938	N/A	
Long Beach, CA	N/A	N/A	LACM	N/A	N/A	N/A	
Corona Del Mar, CA	N/A	N/A	LACM	96-1.5	17 Feb 1996	G. Hendler and F. Nishida	
Laguna Beach, CA	N/A	N/A	LACM	ech 647	N/A	N/A	
Laguna Beach, CA	N/A	N/A	LACM	N/A	N/A	G. Hendler	
Newport Bay, CA	3	N/A	CAS	111490	Jan Feb 1930	G.E. MacGinitie	
Dana Point, CA	N/A	N/A	LACM	200.1	1 Oct 1936	G. Ranokoff	
San Clemente Is., CA	1	Intertidal	LACM	1025-39	25 Nov 1939	A. Hancock	
Point Loma, CA	N/A	N/A	SIO	E-587	26 May 1966	Taylor-Heese	
Point Loma, CA	2	N/A	CAS	104622	31 Jul 1916	C.L. Hubbs	
Point Loma, CA	N/A	N/A	LACM	39.275.2	26 Dec 1939	R. Morrison	
La Jolla, CA	N/A	15 m	SIO	E-1156	17 Nov 1958	R. Kiwala	
La Jolla, CA	N/A	12–14 m	SIO	E-803	25 Sep 1959	C.L. Hubbs	
La Jolla, CA	N/A	N/A	SIO	E-227	19 Nov 1915	N/A	
La Jolla, CA	1	N/A	CAS	15427	April 1942	E. Ricketts	

Research Site	# of O. esmarki	Depth	Museum	<i>Cat.</i> #	Date	Collector	
Bird Rock, CA	N/A	N/A	LACM	42-64.1	Oct 1942	R. J Berman	
False Point, CA	N/A	Intertidal	LACM	96-2.2	Feb 1996	G. Hendler and F. Nishida	
False Point, CA	3	Intertidal	CAS	Na	Jun 1974	A. Muscat	
San Diego, CA	1	N/A	CAS	Na	N/A	N/A	
La Jolla , CA	1	N/A	CAS	JBS 32	1947	T. and A. Stephenson	
False Point, CA	7	N/A	LACM	N/A	19 Mar 1992	M.E. Bergen	
False Point, CA	1	N/A	LACM	N/A	27 Apr 1992	M.E. Bergen	
Point Loma, CA	N/A	N/A	SIO	E-2186	31 Oct 1955	P. Johnson	
Point Loma, CA	N/A	Intertidal	LACM	239.15	26 Dec 1939	F. Ziesenhenne	
Baja CA, MX	1	N/A	USNM	E 26873	N/A	R. Smith	
Ensenada, MX	N/A	Intertidal	LACM	N/A	29 Nov 1963	J.H. McLean, J.H.Dearborn	
Ensenada, MX	12	N/A	CAS	15427	Apr 1942	E. Ricketts	
Todos Santos, MX	4	N/A	CAS	N/A	20 Dec 1930	G.E. MacGinite	
Todos Santos, MX	N/A	N/A	LACM	824	Dec 1927	F. Ziesenhenne	
San Martin, MX	5	N/A	CAS	2949	20 Feb 1975	N/A	
Guadalupe Is., MX	10	Subtidal	CAS	121208	18 Mar 1932	T. Crocker	
San Bentio Is., MX	N/A	Intertidal	SIO	E-1880	26 May 1971	R/V Agassiz	
E. San Benito Is., MX	N/A	Intertidal	LACM	33	4 Jun 1933	A. Hancock	
E. San Benito Is., MX	N/A	N/A	LACM	N/A	4 Jun 1943	A. Hancock	
Bahia Tortugas, MX	N/A	Intertidal	LACM	N/A	24 Feb 1942	J. Garth	
Bahia Tortugas and Bahia Asunción, MX	N/A	2–4 m	SIO	E-1845	4–6 Aug 1980	M. Tegner	
San Bartolome, MX	N/A	Intertidal	LACM	239.17	12 Feb 1954	N/A	
San Bartolome, MX	N/A	Intertidal	LACM	239.19	25 Apr 1961	N/A	
Malarrimo, MX	1	Intertidal	LACM	239.16	17 Apr 1951	F. Ziesenhenne	
San Lorenzo Ch., MX	N/A	N/A	LACM	607.36	21 Mar 1936	N/A	
Thurloe Bay, MX	N/A	Intertidal	LACM	283.34	9 Mar 1939	A. Hancock	
La Playita, MX	N/A	Intertidal	LACM	239.11	8 Apr 1950	F. Ziesenhenne	