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Author(s): Maria P. Polson and Danielle C. Zacherl
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GEOGRAPHIC DISTRIBUTION AND INTERTIDAL POPULATION STATUS FOR THE OLYMPIA OYSTER, *OSTREA LURIDA* CARPENTER 1864, FROM ALASKA TO BAJA

MARIA P. POLSON* AND DANIELLE C. ZACHERL
California State University—Fullerton, P.O. Box 6850, Fullerton, California 92834-6850

ABSTRACT Despite the recently renewed interest by ecologists and government agencies to reestablish historical populations of the Olympia oyster, focus has been limited to projects located at the north of this species' range, with little or no attention to southern California and Baja populations. In addition, historical information on the status of natural populations across the range has been mainly qualitative in nature, with no comprehensive information on the current status of natural populations. The focus of this study was to conduct the first large-scale quantitative biogeographic survey of remnant populations of the Olympia oyster and to identify suitable sites in southern California for future restoration projects. We surveyed intertidal populations at 24 historical sites during spring and summer 2005 and summer 2006, established presence/absence and collected data on densities and percent cover. Average maximum densities ranged from 0.0–36.7 ± 12.1 oysters per 0.25 m^2. In southern California, intertidal populations were present in all bays and estuaries south of Morro Bay and most showed evidence of regular recruitment. Thus, all southern California sites could present favorable opportunities for restoration projects. At the north end of the range, intertidal populations were more often absent from sites, though there was evidence of subtidal populations. Populations were absent from intertidal sites at the northern endpoint of its distribution in Sitka, Alaska. We speculate that the current northern range limit of this species is located in northern British Columbia. Intertidal populations were also absent at two CA sites, Morro Bay, and Big Lagoon; anecdotal evidence further suggests that subtidal populations were also absent. This study represents the first comprehensive biogeographic survey of intertidal populations of the Olympia oyster, *Ostrea lurida*†, and identifies sites in southern California as suitable locations for future restoration projects.

KEY WORDS: *Ostrea conchaphila*, *Ostrea lurida*, native oyster, Olympia oyster, biogeography

INTRODUCTION

The Olympia oyster,‡*Ostrea lurida* Carpenter 1864, is the only oyster native to the west coasts of the United States and Canada (hereafter referred to as West Coast). It was once abundant along its known range, extending from Sitka, AK to Baja California (Dall 1914, Baker 1995). The fossil record indicates that it was present in estuarine and marine deposits in central California as early as the late Miocene and early Pliocene (Baker 1995, Howard 1935). In northern California it was abundant during the late Pleistocene where in some instances it was the most common fossil (Miller & Morrison 1988). Fossil data from Washington and shell midden data in California, Oregon, and Washington, also indicate its once common status (Baker 1995). However, anthropogenic influences on the Olympia oyster, including the utilization by Native American Indians (Bonnot 1935, Elsasser & Heizer 1966, Kidd 1967) and extensive harvesting by modern Americans (Galtsoff 1929, Baker 1995), as well as pollution and degradation of water quality and possibly the unintentional introduction of invasive predator and parasite species, had a negative impact on the species. As a result, by the early 1930s, natural populations from many locations along its range were depleted (Hopkins 1931, Bonnot 1935, Baker 1995, Conte 1996). Because larger and thus more profitable oysters such as the American oyster, *Crassostrea virginica*, and the Japanese oyster, *Crassostrea gigas*, were being imported to the West Coast (Elsey 1933, Shaw 1997), the attention of the oyster industry was diverted away from the Olympia oyster. Subsequent attempts to culture the Olympia oyster were either abandoned or deemed unsuccessful (Barrett 1963, Conte 1996). Currently, commercial harvesting of the Olympia oyster is limited to Washington and Oregon and is only marginally profitable.

In recent years, fishermen, ecologists, government agencies, and nongovernmental organizations have expressed a renewed interest in the Olympia oyster. Fishermen are interested in its potential as a specialty food item (Mark Ballo, Brady's Oyster Farm, Grays Harbor, WA personal communication). Ecologists are focusing on this species because it is the only oyster native to the West Coast and yet little is known about its ecology. Agencies such as NOAA, the Oregon Department of Fish and Wildlife, and The Nature Conservancy have expressed interest in restoring natural populations and restoration projects are underway in California, Oregon, and Washington (West Coast Native Oyster Restoration Workshop 2006). However, these restoration efforts are being conducted with little quantitative information on the status of remnant populations.

Historically, the interest in monitoring the status of Olympia oyster populations was because of the fishery. Most of the historical references on population status were qualitative, mentioning the presence or absence of the species at a site (Barrett 1963, Paul & Feder 1976 and more examples in Table 1), or describing abundances using vague terms such as "little," "large numbers," and "beds" (Fasten 1931, Bonnot 1935 and more examples in Table 1). Some references were more "quantitative" in nature, citing the production of oysters from a

*Corresponding author. E-mail: dzacherl@fullerton.edu

†The taxonomy of the Olympia oyster has been in dispute since Harry (1985) proposed synonymy of *Ostrea lurida* Carpenter 1864 and *Ostrea conchaphila* Carpenter 1857. Polson et al. 2009 provide molecular evidence that the Olympia oyster refers to the nominal species, *Ostrea lurida* Carpenter 1864. In view of their genetic data, and for consistency, the original taxon, *Ostrea lurida*, is used throughout this volume to refer to the Olympia oyster, which is distributed from approximately Baja California (Mexico) to southeast Alaska.

‡The common name as sanctioned by the American Fisheries Society is Olympia oyster, though other names are commonly used including, "native oyster," "California oyster," and "Yaquina oyster."

TABLE 1.

Published data on *Ostrea lurida* at surveyed field sites.

Site	Type of Data	Density	Reference
Sitka, AK	Qualitative	Present	Paul and Feder 1976
Ladysmith Harbor, B.C	Qualitative	Present	Gillespie 1999
Ahmah Island, B.C.	Qualitative	Present	Gillespie 1999
Grays Harbor, WA	Qualitative	Present	Galtsoff 1929
Willapa Bay, WA	Quantitative	101 bushels/acre**	Galtsoff 1929
Netarts Bay, OR	Qualitative	Present	Marriage 1954
Yaquina Bay, OR	Qualitative	Present	Fasten 1931
	Qualitative	Present	Marriage 1954
Coos Bay, OR	Quantitative	201 / m^2	Baker et al. 1999
	Qualitative	Absent	Marriage 1954
Big Lagoon, CA	no data		
Humboldt Bay, CA	Qualitative	Present	Bonnot 1935
	Qualitative	Present	Barrett 1963
Tomales Bay, CA	Quantitative	Present	Kimbro & Grosholz 2006
	Qualitative	Present	Bonnot 1935
Point San Quentin, CA	Qualitative	Present	Packard 1918a
	Quantitative	14 Hauls	Packard 1918b
Bolinas Lagoon, CA	Qualitative	Present	Giguere et al. 1970
Elkhorn Slough, CA	Qualitative	Present	Galtsoff 1929
	Qualitative	Present	Bonnot 1935
	Qualitative	Present	MacGinitie 1935
	Qualitative	Present	Barrett 1963
	Qualitative	Absent	Browning et al. 1972
Morro Bay, CA	Qualitative	Present	Gates and Bailey 1982*
Mugu Lagoon, CA	Qualitative	Present	Bonnot 1935
	Quantitative	Absent	Onuf 1987
Alamitos Bay, CA	Qualitative	Present	Bonnot 1935
	Quantitative	3 animals/total area	Reish and Winter 1954
	Quantitative	Absent	Reish 1961
Newport Bay, CA	Qualitative	Present	Bonnot 1935
	Qualitative	Present	Barrett 1963
	Qualitative	Present	Frey et al. 1970
Aqua Hedionda Lagoon, CA	Qualitative	Present	Bradshaw et al. 1976
Batiquitos Lagoon, CA	Qualitative	Absent	Mudie et al. 1976
Mission Bay, CA	Qualitative	Present	Morrison 1930
San Diego Bay, CA	Qualitative	Present	Bonnot 1935
	Qualitative	Absent	Browning et al. 1973
	Quantitative	5–10% cover	Davis et al. 2002
Bahia de San Quintin, Baja California	Qualitative	Present	Keen 1962
	Quantitative	Present	Barnard 1970
Cabo San Lucas, Baja California Sur	Qualitative	Present	Dall 1914***

* This book by Gates and Bailey (1982) only makes a reference to the presence of native oysters in the bay in the past.
** Yields for the year 1926 in Willapa Bay, WA
*** This report has not been confirmed and could be erroneous

location in hauls (Packard 1918b) or bushels (Galtsoff 1929), but such information makes it difficult to extrapolate the densities and distributions of adult populations at any particular site.

Ongoing and more recent studies on the ecology of this species that do provide quantitative data have been limited to small spatial scales in northern populations (e.g., Baker et al. 1999, Kimbro & Grosholz 2006) occurred at different time scales using various techniques, and making comparisons among sites difficult. In contrast, no surveys of Olympia oyster populations in southern California and Baja California have been conducted in recent decades (examples in Table 1, but see Davis et al. 2002). The most recent references on southern California populations report the absence of the Olympia oyster at 4 sites where they were previously present (Table 1). In the absence of more quantitative data, it is difficult to assess just how much populations have declined at any location, how much populations might have recently grown because of restoration efforts, or how reliable an ‘‘absent’’ finding might be.

In sum, there is no widespread consensus on the current status and density of the Olympia oyster populations across large spatial scales or a quantitative estimate of the magnitude of decline over time. Given the interest in restoration projects along the West Coast, we have updated presence/absence and population density data of remnant populations using a consistent methodology that will provide a useful benchmark against which future monitoring data can be compared. We surveyed a total of 24 intertidal populations (Fig. 1) and determined presence/absence; where populations were present, we collected data on abundance, maximum density and maximum percent cover.

MATERIALS AND METHODS

Study Sites

We selected 24 historical sites throughout the species' range (Fig. 1). Historical sites are sites where previous studies, qualitative and quantitative, indicated that the Olympia oyster existed, as is evident in the primary literature (see Table 1). For British Columbia, Canada (B.C.), Fisheries and Oceans Canada (DFO) provided a list of sites where stocks have been identified (Gillespie 1999). From that list, we narrowed our search to the two most easily accessible sites. Ahmah Island is on the west site of Vancouver Island in Barkley Sound, and Ladysmith Harbor is on the east side of Vancouver Island.

Timed Search to Measure Ranks

We performed 2-h timed searches at each site during negative tides. Because of the large number of sites we visited over a vast geographic range, it was not feasible to visit each site during extreme low tides; thus some lower intertidal and shallow subtidal populations may not have been exposed during our searches (see Table 3, for lowest tide per site during surveys). Importantly, the search was targeted in areas within a site that provided favorable habitat for oysters, in the form of hard substrata both natural and artificial. Hard substrata included walls, pier pilings, floating docks, rip rap, rocks, gravel, sand, and shell fragments on sand or mud flat. The timed-search format allowed us to stop the time when unfavorable habitat was encountered (e.g., mud, silt, sand) and move to different locations within a site. For the larger bays and estuaries, this method provided us with a very robust measure of the overall distribution of intertidal oyster populations within a site.

During the 2-h search, all start and end locations were recorded with a Garmin GPS map 60C GPS device. To get an integrated estimate of species abundance at each site and to allow the completion of our surveys at a broad geographic scale, we quantified abundance using a rapid survey approach (Murray et al. 2006). We paced areas in a zigzag pattern that allowed for a thorough survey from the upper to the lower intertidal distribution of oysters. Approximately every 50 m, we estimated a rank based on the overall density of oysters present (Table 2). At every stop (approximately every 50 m) a waypoint was recorded with the GPS so that the distance covered during the survey could be estimated if needed and the area with the highest rank could be located at a later time. Because the distance covered varied among sites, the total number of 50 m transects also varied among sites (Table 3).

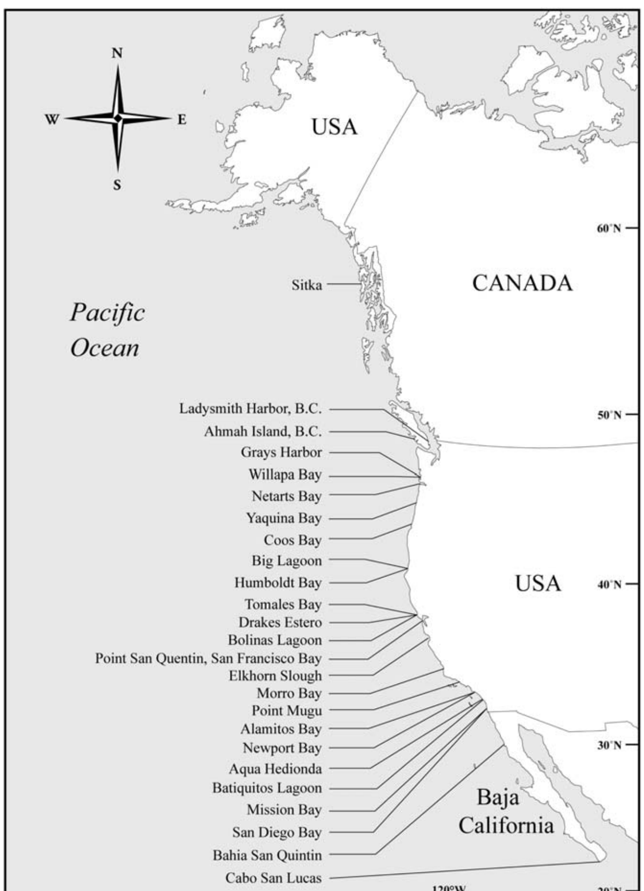

Figure 1. Study sites for the Olympia oyster, *Ostrea lurida*.

Measurements of Maximum Density and Maximum Percent Cover

Because of the interest in restoration of oyster populations, where resource managers often target the most locally abundant populations for restoration, we used our assigned ranks to identify the location within a site that had the highest density of oysters and quantified average maximum density (Sagarin & Gaines 2002) and maximum percent cover within those locations using replicate quadrats ($n = 10$) measuring 0.5 m $\times$ 0.5 m. First, a 50 m $\times$ 4 m transect belt was placed in the middle of the tidal distribution of oysters in the area that received the highest rank at a site. We generated X and Y coordinates using random numbers to place quadrats along the transect and measured maximum density and maximum percent cover within each quadrat. Note that average "maximum" density is not equivalent to average density, but rather represents the average from a targeted search of the most abundant population at a site. This targeted measure of maximum density is expected to be

TABLE 2.

Key to ranks used to estimate oyster density at field sites. Ranks were assigned to areas of approximately 50 m in length.

Ranks	# 0ysters/0.25 m^2	Description
0	0	Not present
1	1–2	Rare
2	3–10	Occasional to frequent
3	11–100	Common
4	>100	Abundant

TABLE 3.

Site names, tidal heights, survey dates, GPS coordinates for locations and transects, average ranks, average maximum densities, percent cover, presence/absence of *Crassostrea gigas*, and presence/absence of multiple size classes of *Ostrea lurida*. At sites where Avg. Rank is zero, GPS coordinates indicate general location of survey. At sites with a recorded Avg. Max. Dens., GPS coordinates indicate the location with the highest rank.

Site	Abbrev.	Tidal Height (m)*	Survey Dates	GPS Coordinates	Avg. Rank ±SE (n)	Avg. Max. Dens. ±SE ($n = 10$)	% Cover[†] ±SE ($n = 10$)	Presence *C. gigas*	Multiple size classes
Sitka, AK§	ST								
Site A		–0.25	07/18/05	N57°03.472′, W135°21.087′	0	0	0	No	No
Site B		–0.55	07/19/05	N57°07.936′, W135°22.276′	0	0	0	No	No
Site C		–0.79	07/20/05	N57°02.740′, W135°12.170′	0	0	0	No	No
Ladysmith Harbor, B.C	LH	–0.91	7/22/05	N48°58.552′, W123°47.845′	1.9 ± 0.25 (11)	2.8 ± 1.5	2.13 ± 0.63	Yes	No
Ahmah Island, B.C.	AI	–0.06	7/25/05	N48°56.814′, W125°04.583′	1 ± 0.40 (4)	0	0	Yes	No
Grays Harbor, WA	GH	–0.27	8/3/05	N46°56.134′, W124°01.716′	0	0	0	Yes	No
Willapa Bay, WA	WB								
Site A		–0.14	08/01/05	N46°42.306′, W123°58.751′	0	0	0	Yes	No
Site B		–0.22	08/02/05	N46°30.098′, W124°01.833′	0	0	0	Yes	No
Netarts Bay, OR	NTB	–0.27	6/10/06	N45°23.660′, W123°56.202′	0	0	0	Yes	No
Yaquina Bay, OR	YB	–0.52	6/12/06	N44°36.577′, W124°00.720′	0.43 ± 0.30 (7)	2.2 ± 0.8	1.45 ± 0.59	Yes	Yes
Coos Bay, OR	CB	–0.51	6/14/06	N33°21.935′, W124°12.730′	1.64 ± 0.24 (11)	19.1 ± 8.6	13.3 ± 5.56	No	Yes
Big Lagoon, CA	BGL	–0.41	08/18/05	N41°09.718′, W124°06.734′	0	0	0	No	No
Humboldt Bay, CA									
Site A		–0.21	08/16/05	N40°50.971′, W124°05.110′	+	ND	ND	No	No
Site B	HB	–0.36	08/17/05	N40°50.716′, W124°6.394′	1.43 ± 0.57 (7)+	18.6 ± 3.7	10.2 ± 2.35	Yes	No
Tomales Bay, CA§	TB				2.74 ± 1.18 (2)**	9.35 ± 12.2**	6.95 ± 4.41**		
Tomales Bay, East		–0.48	06/25/05	N38°11.986′, W122°55.328′	1.57 ± 0.21 (23)	1.5 ± 0.6	1.1 ± 0.46	Yes	No
Tomales Bay, West		–0.56	7/4/05	N38°12.132′, W122°55.366′	3.92 ± 0.08 (13)	17.2 ± 6.9	12.8 ± 5.76	Yes	No
Bolinas Lagoon, CA	BL	–0.36	6/23/05	N37°55.834′, W122°41.343′	0	0	0	Yes	No
San Francisco Bay, CA Point San Quentin	PSQ	–0.48	6/21/05	N37°56.728′, W122°28.897′	2.87 ± 0.22 (8)	36.7 ± 12.1	17.1 ± 5.8	Yes	Yes
Elkhorn Slough, CA	ES	–0.17	7/8/05	N36°50.422′, W121°44.638′	1 ± 0.23 (11)	7 ± 1.6	5.1 ± 1.22	No	No
Morro Bay, CA	MRB	–0.12	7/6/05	N35°20.751′, W120°50.512′	0	0	0	Yes	No
Mugu Lagoon, CA	ML	–0.30	1/26/06	N34°06.375′, W119°05.680′	0.14 ± 0.14 (7)	2.2 ± 1.1	3.5 ± 1.92	Yes	No
Alamitos Bay, CA									
Site A		–0.27	11/04/06	N33°44.857′, W118°06.922′	+	ND	ND	Yes	Yes
Site B	AB	–0.36	11/05/06	N33°45.882′, W118°06.892′	0.5 ± 0.22 (6)+	1 ± 0.3	0.5 ± 0.15	Yes	Yes
Newport Bay, CA	NB	–0.24	4/27/05	N33°37.173′, W117°53.542′	1.6 ± 0.21 (6)	4.8 ± 1.8	1.8 ± 0.71	Yes	Yes
Aqua Hedionda Lagoon, CA	AHL	–0.34	5/27/05	N33°08.579′, W117°19.370′	1.75 ± 0.40 (8)	10.7 ± 3.0	11.3 ± 3.55	Yes	Yes
Batiquitos Lagoon, CA									
Site A		–0.34	12/02/05	N33°5.578′, W117°18.126′	+	ND	ND	Yes	No
Site B	BQL	–0.48	12/30/05	N33°;5.437′, W117°18.105′	2.25 ± 0.25 (4)+	2.6 ± 1.5	1.5 ± 0.97	Yes	No
Mission Bay, CA									
Site A		–0.3	01/13/06	N32°47.528′, W117°12.600′	+	ND	ND	Yes	Yes
Site B		–0.55	1/28/06	N32°46.153′, W117°12.627′	+	ND	ND	Yes	Yes
Kendall Frost	MB	–0.24	2/10/06	N32°47.673′, W117°13.468′	2.06 ± 0.10 (17)+	7.4 ± 2.8	5 ± 1.97	Yes	Yes
San Diego Bay, CA§	SDB				2.57 ± 0.10 (2)**	22.8 ± 2.4**	17.11 ± 2.46**	Yes	Yes

continued on next page

TABLE 3.

continued

Site	Abbrev.	Tidal Height (m)*	Survey Dates	GPS Coordinates	Avg. Rank ±SE (n)	Avg. Max. Dens. ±SE ($n = 10$)	% Cover† ±SE ($n = 10$)	Presence *C. gigas*	Multiple size classes
Harbor Island Exposed site		−0.55	1/28/06	N32°43.449′, W117°12.721′	++	ND	ND	No	Yes
Harbor Island Shelter site		−0.27	3/26/06	N32°43.493′, W117°12.811′	2.69 ± 0.15 (16)++	25.2 ± 3.4	18.4 ± 2.96	No	Yes
Embarcadero Park		−0.3	3/26/06	N32°42.505′, W117°10.260′	2.43 ± 0.14 (14)	20.4 ± 2.7	15.1 ± 1.86	Yes	Yes
Bahia San Quintin, Baja California, Mexico	SQ	−0.22	6/7/05	N30°27.858′, W115°57.834′	3.87 ± 0.1 (15)	20.7 ± 8.4	14.15 ± 5.32	No	No
Cabo san Lucas, Baja California Sur, Mexico	CSL	−0.58	3/31/05	N22°52.918′, W109°54.598′	0	0	0	No	No

* Here we report the lowest tidal height for each site on the day surveyed

** Average of multiple locations within a site. A 2h timed search was performed in each of these locations within a site

\+ Average of multiple locations within a site. A singe 2h timed search was performed among multiple locations

++ Average rank for Harbor Island, San Diego Bay, CA. A 2h timed search was performed at Harbor Island and time was divided between the sheltered site and the exposed site of the island

§ Sites where more than one 2h-timed-search period was conducted at more than one location within the site

† Correlation of % cover and maximum density $y = 0.5746x + 0.6184$

most useful for stakeholders interested in locating areas of maximal oyster abundance.

We further analyzed the range of maximum densities by calculating the coefficient of variation (CV) which is a measure of the dispersion or the spatial distribution of individuals (uniform *vs.* patchy) in a population (Zar 1974).

Qualitative Observations and Other Measurements

Whenever possible, at each area where maximum density and percent cover were measured, the tidal height of the upper and lower distribution of oysters was recorded using a Laser-mark Wizard (57-LM20) rotary laser, a Universal Laser Detector (57-LD120) and a telescopic measuring pole. If there was no reference mark for a known tidal height for a site, a reference mark was determined by taking the average of three low tide mark measurements. We also made qualitative visual assessments of the presence of multiple size classes of the native oyster (Table 3).

Finally, we recorded the presence of the Japanese oyster, *Crassostrea gigas*, because recruitment episodes of this species have been observed in various locations along the West Coast, and the shells of this species are known to provide settlement substrata for the Olympia oyster. Also, resource managers interested in Olympia oyster restoration are typically concerned about whether nonnative oysters are present, and often lack experience in distinguishing these species from one another.

RESULTS

Presence/Absence

Intertidal populations of the Olympia oyster were absent at five sites where they were historically present (Fig. 3, see later), including at Sitka, AK, the northern end point of the distribution of the species. Populations were also scored as absent at Cabo San Lucas, Baja California Sur, Mexico. The other 3 sites where absence was recorded were Big Lagoon, Bolinas Lagoon, and Morro Bay, all in California. Intertidal populations were also absent from our surveys at 3 additional sites, Grays Harbor and Willapa Bay in Washington and Netarts Bay in Oregon. However, Olympia oysters are known to be present in these locations (Mark Ballo, Brady's Oyster Farm, Grays Harbor, Russell Rogers DFW, Alan Trimble, University of Washington, all personal communications) at low intertidal or subtidal depths; we therefore reported presence for those locations (Fig. 3, see later). Specifically, subtidal populations in Willapa Bay are present in Nachotta with some oysters settling on the undersides of floating docks and at lower intertidal to subtidal mudflats. In Grays Harbor, a small population has been seen in shallow subtidal depths during extreme low tides in front of an oyster farm (Mark Ballo, personal communication). We also reported presence for Ahmah Island, located in Barkley Sound, B.C. (Fig. 3, see later); we were able to survey this site and provide rank data, but were not able to record maximum density because of inclement weather conditions.

In California, intertidal populations were present in Elkhorn Slough, Mugu Lagoon, Alamitos Bay, Mission Bay, and San Diego Bay (Fig. 2, Fig. 3), all sites where the most recent surveys of the Olympia oyster reported absence (Table 1).

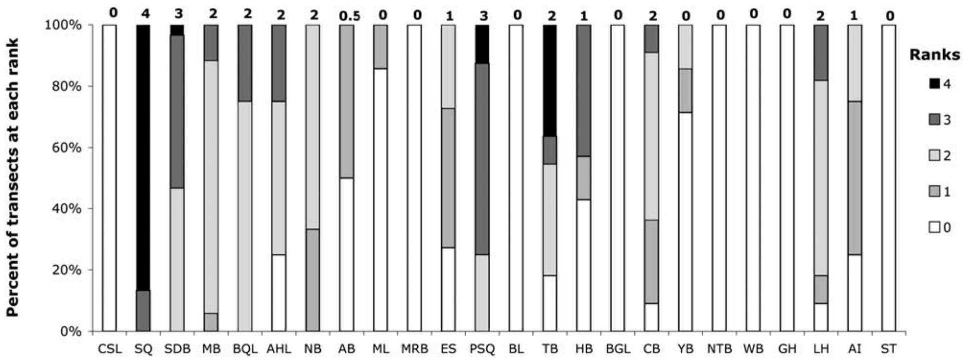

Figure 2. Percentage of transects within each study site that were assigned a particular rank. Refer toTable 2 for rank key. Numbers above bars represent the median rank for each site.

Ranks, Maximum Density, and Maximum Percent Cover

To report the ranks, we used a stacked column approach representing the percent of transects recorded at each rank (Fig. 2) within each site. We also report the average rank (Table 3) and median rank (Fig. 2) for each site. The highest average ranks were at Bahia de San Quintin, Baja California (3.87 ± 0.1), Point San Quentin, San Francisco Bay, CA (2.87 ± 0.22), and Tomales Bay, CA (2.74 ± 1.18). The lowest rank recorded was at Mugu Lagoon, CA (0.14 ± 0.14).

Average maximum densities (Fig. 3) ranged from 0.0–36.7 per 0.25 m^2 and were the highest at Bahia de San Quintin, Baja California (20.7 ± 8.4), San Diego Bay, CA (22.8 ± 2.4), and Point San Quentin, CA (36.7 ± 12.1). Aside from the five localities where absence was reported, lowest maximum densities were recorded in Alamitos Bay, CA (1 ± 0.3), Mugu Lagoon, CA (2.2 ± 1.1) and Yaquina Bay, OR (2.2 ± 0.8). Across all sites, there was a high correlation between maximum percent cover (Table 3) and maximum density ($r = 0.95$). Coefficient of variation ranged from 0.15–1.84 (Fig. 4) for sites where maximum densities were recorded.

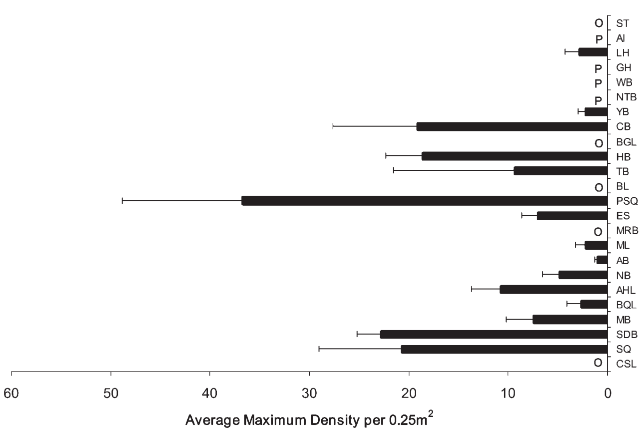

Figure 3. Average maximum densities of oysters per 0.25 m^2. Error bars indicate SE. Maximum densities were recorded at the area within each site assigned the highest rank using 10 replicate quadrats. Sites with "O" indicate absence of intertidal populations. Sites with "P" indicate absence of intertidal populations but where subtidal populations are known to be present. Site "AI" was additionally assigned "P" despite the presence of intertidal populations (seeFig. 2) because inclement weather prevented completion of maximum density surveys.

Qualitative Observations and Other Measurements

Among the seven southern California sites, we observed multiple size classes at Alamitos Bay, Newport Bay, Aqua Hedionda Lagoon, Mission Bay, and San Diego Bay. Multiple size classes were also observed in Point San Quentin, CA, Yaquina Bay and Coos Bay in Oregon (Table 3). Intertidal populations of *Crassostrea gigas* were also observed at most sites surveyed (Table 3). In Ladysmith Harbor and Ahmah Island in B.C. and Grays Harbor and Willapa Bay in WA, *C. gigas* formed extensive reefs in the intertidal zone. Multiple size classes of *C. gigas* were also observed at four southern California sites: San Diego Bay, Mission Bay, Newport Bay, and Alamitos Bay. Apart from Willapa Bay and Grays Harbor in WA, we observed *C. gigas* as an attachment substratum for the Olympia oyster.

DISCUSSION

We have provided the first quantitative data, using consistent methodology, on the status of intertidal populations of the Olympia oyster across a large portion of its geographic range. During our summer 2005 and summer 2006 surveys, across 24 historical sites, we found that intertidal populations of this oyster have persisted or have been re-established over time

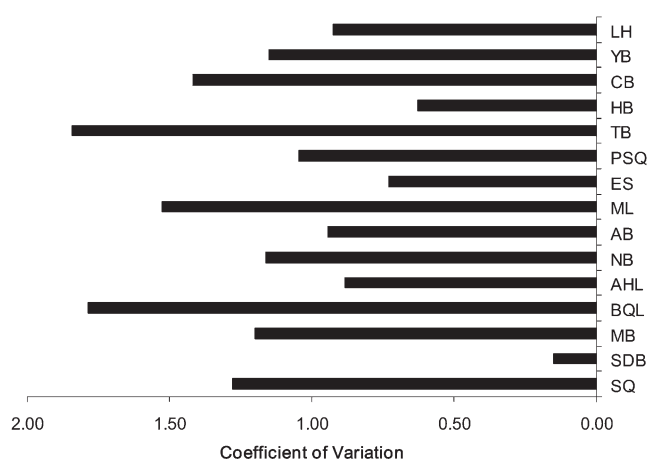

Figure 4. Coefficient of variation (CV) for average maximum density across the transect at each site surveyed. CV was calculated only for sites where presence of oysters was recorded.

throughout much of its range, despite past over-harvesting and continued anthropogenic impacts on bays and estuaries. Putative populations were extinct at only five of the 24 historical sites surveyed.

Absences

For Sitka, AK, where numerous inlets provide suitable habitat for oysters, no specific reference is known for the localities previously surveyed (Dall 1914, Paul & Feder 1976). Thus, we completed 2-h timed searches at each of three different locations. These sites, all inlet/bay habitats, were chosen because the waters were shallow enough for the temperature to reach optimum spawning levels during summer, although the shallow waters are also subject to freezing in the winter. The reported spawning temperature in California is 16°C (Coe 1931), whereas Hopkins (1937) reports that this species requires at least 12.5°C to reproduce. According to Davis (1955), adults cannot withstand freezing and can suffer 100% mortality, even when placed in the subtidal zone. Perhaps if the Olympia oyster was ever encountered in southeastern Alaska, specifically in Sitka, it was from episodic recruitment events from populations further south, e.g., northern British Columbia, and settled oysters likely perished with the first freeze, or failed to reproduce successfully. Alternatively, there might be as-yet-undiscovered localized northern refugia. We carefully searched for shell scars that would indicate past occurrence and encountered none. The current northern range limit for this species is likely located in northern British Columbia, although one cannot eliminate the possibility that it is extremely patchy in this extensive southeastern Alaskan habitat and that our searches simply missed them. However, that possibility underscores the importance of establishing a well-documented baseline data set against which future studies can be compared.

A specific location was also never provided for Cabo San Lucas, Baja California Sur. We surveyed only the bay that serves as the marina of the city, because no other estuarine or inlet sites exist in the immediate area. If Olympia oyster populations do still exist at this site, they are probably located in the subtidal habitat. There is also a possibility that Dall's (1914) locality was erroneous.

The three other sites where we recorded absence were all in California. For Bolinas Lagoon, a Department of Fish and Game report by Giguere et al. (1970) was vague about whether the species was recently present. The report does refer to the Olympia oyster as being historically abundant. At Morro Bay, anecdotal evidence suggests that populations are also absent in the subtidal zone. Long-term studies on fouling organisms in the bay have never yielded settlement of the Olympia oyster (Lisa Needles, UC Santa Barbara, pers. comm.). In addition, this species has not been seen settling on the substratum used to culture *C. gigas* in the bay (Neal Maloney, Tomales Bay Oyster Company, pers. comm.). Although historically present in Morro Bay (Gates & Bailey 1982), this species probably has never re-established following over-harvesting and various negative anthropogenic impacts.

Presence

Like all other locations along the West Coast, natural stocks of the Olympia oyster were depleted in British Columbia, Canada by the early 1930s. Freezing temperatures in 1929 also caused a die-off for much of the stock in Ladysmith Harbor, one of our survey sites. We found oysters at various locations throughout the intertidal habitat, even though average maximum densities at this site were low (2.8 ± 1.5) and multiple size classes were not observed, suggesting a lack of recent recruitment. We also observed that oysters were located exclusively on the underside of rocks or on the shells of the Japanese oyster, which were also abundant throughout the bay.

In Oregon, average maximum densities were low in Yaquina Bay (2.2 ± 0.8), but were relatively high in Coos Bay (19.1 ± 8.6). According to Fasten (1931), the beds of Yaquina Bay were discovered in 1860 and commercially harvested thereafter (also see Groth & Rumrill 2009). Presently, large subtidal beds can be found at various locations throughout the bay and there are restoration attempts underway (David Stick, OSU, personal communication); however, we found very few intertidal populations. In contrast, in Coos Bay, intertidal populations were present in various locations (Groth & Rumrill 2009). Average maximum density in Coos Bay was the highest among the Oregon sites and was among the highest from all study sites. The Olympia oyster was also historically abundant in Coos Bay as is evident in the fossil record and from Indian shell middens, but populations went extinct in the bay prior to the arrival of European settlers (Baker et al. 1999 and Groth & Rumrill 2009). Various attempts to reestablish this species occurred in the early 1900s with little success. Large populations were finally recorded in 1988 at one location in the bay and this re-establishment is attributed to importation of the Olympia oyster as a fouling organism on the shells of the Japanese oyster, which has been cultured in Coos Bay since the 1930s (Baker et al. 1999). It is encouraging for restoration efforts that this species is currently present in this bay with high intertidal population densities and with the observation of multiple age groups (also see Baker et al. 1999 and Groth & Rumrill 2009).

In California, the Olympia oyster was harvested from San Francisco Bay well before the turn of the century (Galtsoff 1929) and, because stocks were depleted by the late 1800s, the Eastern oyster, *Crassostrea virginica*, was introduced to the bay as early as 1870. Even though the Olympia oyster was deemed commercially important and easily cultivated, production was never as high as in Puget Sound, WA (Galtsoff 1929). Despite the anthropogenic impacts on San Francisco Bay, including the loss of intertidal habitat and pollution from domestic and industrial runoff, Galtsoff (1929) and Bonnot (1935) found that the Olympia oyster was not only present but had extended its range within the bay. Bonnot does mention, however, that its growth was hampered to the point that it was not marketable. In recent years, federal, state, and local agencies initiated monitoring and restoration programs for San Francisco Bay. In this study, we chose to survey Point San Quentin, the site of a recent restoration effort that started in the fall of 2005 (Obernolte et al., unpublished data), and also one of the survey stations mentioned in two studies by Packard (1918a, 1918b). Here, we found the highest maximum densities of all the sites surveyed. Most importantly, we observed multiple size classes as well as apparent recruits from the most recent reproductive season. Oysters collected from the site also were brooding larvae. These findings and observations were encouraging signs that restoration efforts are succeeding in San Francisco Bay.

Also encouraging was the presence of the Olympia oyster in Elkhorn Slough in central California, even though densities were low with no evidence of recent recruitment. Although recorded as present in surveys by Galtsoff (1929) and Bonnot (1935), it was not mentioned in a more recent survey by Browning et al. (1972). The same was true for Mugu Lagoon in southern California where Onuf (1987) did not record presence, but where we did find a small intertidal population. We also recorded presence for this species at four other sites in southern California where the most recent surveys reported them as absent, including Alamitos Bay, Batiquitos Lagoon, Mission Bay, and San Diego Bay (Table 1, but see Davis et al. 2002). Although recent restoration efforts have ignored southern California populations, our study revealed that these populations were not only present, but maximum intertidal densities were relatively high (Fig. 3). In fact, intertidal populations in San Diego Bay had some of the highest maximum densities recorded. Finally, the observation of multiple size classes at the four sites suggests regular recruitment. The extrapolation of regular recruitment is corroborated by recent settlement studies on this species in southern California locations (see Seale & Zacherl 2009).

Coefficient of Variation

The coefficient of variation is a dimensionless number that allows comparisons of the within-site dispersion among sites with very different maximum densities. Values >2 indicate high variance and suggest that population distribution of oysters was patchy within surveyed locations. A CV value <1 indicates relatively low variance, or a more regular distribution of oysters. Qualitative observations within sites reflect the CV values. Despite only surveying locations within sites with suitable habitat available, we observed that some sites had patchily distributed oysters upon suitable habitat (e.g., Batiquitos Lagoon, Tomales Bay). This result suggests that in those locations, suitable habitat was not the limiting factor controlling abundance. Quantitative characterization of the availability of suitable substratum, however, goes well beyond the scope of our study. Several authors here (Brumbaugh & Coen 2009, Groth &Rumrill 2009) and elsewhere (Galtsoff 1929 & Bonnot 1937) have noted the importance of understanding how habitat availability affects the persistence of Olympia oyster populations. Even though our data suggest that available substratum might not be a limiting factor for some populations, a definitive test of that hypothesis would require detailed quantitative data on habitat type.

CONCLUSION

To implement a successful restoration project, Brumbaugh and Coen (2009) stressed the importance of determining which factor limits local population densities, whether that is recruitment limitation, habitat limitation, or others. They also noted the complex undertaking of restoration projects in the absence of detailed historic information (no "reference" reefs). We concur with both assertions. First, by constraining our timed searches and maximum density counts to areas with suitable habitat, our CV data suggest that habitat limitation might not be the population bottleneck in at least some locations along the range of the Olympia oyster. Further, our quantitative rank, maximum density data, and detailed notations of survey locations provide an extremely useful benchmark ("reference") against which future studies can be compared. We stress the need to complement our study with detailed quantitative data on both habitat availability and subtidal population density taken with standardized techniques at all locations throughout the range of this species.

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