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Data Paper

The first extensive survey (1970–1971) of intertidal invertebrates of San Francisco Bay, California, USA

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Abstract

There have been few surveys of intertidal invertebrates in San Francisco Bay, California, USA. Most prior intertidal surveys were limited spatially or taxonomically. This survey of the intertidal invertebrates of San Francisco Bay was conducted over 13 months between 1970 and 1971, generating what is now a legacy data set of invertebrate diversity. Specimens were hand collected at land access points at 34 sites around the Bay. In all 139 living species in 9 phyla were collected; 28.8% were introduced species, primarily from the Atlantic Ocean (62.5%) and the Northwest Pacific and Indo-West Pacific Oceans (30%).

Key words: introduced species, cryptogenic, Cnidaria, Annelida, Crustacea, Mollusca

Introduction

Unpublished historical biodiversity data are frequently lost over time. Such data from earlier periods can serve as critical baseline information by which to assess long-term biodiversity shifts and environmental changes. Here we present a data set collected 50 years ago of intertidal macroinvertebrate biodiversity in San Francisco Bay, California.

Published historical data on intertidal macrofauna for most of the shoreline of San Francisco Bay (and its component smaller bays) are scarce. The well-known San Francisco Bay *Albatross* survey of 1912–1913 conducted limited sampling at only a few shore stations (Packard 1918; Schmitt 1921; Anonymous 1921). Filice (1954) sampled intertidal invertebrates in 1951 near a small creek in San Pablo Bay. Painter (1966) reported on intertidal invertebrate samples taken in 1963 at several stations in San Pablo and Suisun Bays. Vassallo (1969) sampled a mudflat north of the San Mateo Bridge in 1967. Wooster (1968) surveyed intertidal shellfish (bivalve) populations, relative to their commercial and recreational value, around the Bay.

In the decades after the work reported here, surveys of intertidal invertebrates continued to be limited. Shimm and Tunzi (1974) re-surveyed some of Wooster's 1967 stations in 1972, and Sutton (1978, 1981) continued

assessments of larger intertidal bivalves of sport shell fishing interest. Chan (1977) studied the recovery of intertidal species at Sausalito, in the central Bay, following a 1971 oil spill. Lindberg (1981) surveyed limpets (acmaeid and lottiid gastropods) at 22 intertidal stations between 1974 and 1981 in the north, central, and south Bay. Thompson and Nichols (1984) and Nichols and Thompson (1985) reported on the invertebrates collected from 1974 to 1983 on a single mudflat in the southwest Bay. Hopkins (1987) studied four intertidal transects in 1983–1985 at two sites (Southampton Bay and northern San Pablo Bay) in the northern Bay and two South Bay sites (Hayward and Palo Alto). Nichols and Pamatmat (1988) provided summaries of aspects of these 1950s–1980s intertidal studies. Remarkably, these studies are the majority of attempts to assess general intertidal invertebrate diversity in San Francisco Bay. No such study as that reported here—a bay-wide survey of intertidal invertebrates—is known to us to have been undertaken before or since.

San Francisco Bay has been a globally important port since the mid-nineteenth century. Estuaries and bays that over the centuries have been converted in part to ports and harbors have become epicenters for the introduction of species transported by ships, both as fouling organisms attached to vessel hulls and other niche areas and as planktonic, nektonic, and other entrained species in ballast water (Cohen and Carlton 1995). The fact that many species were transported long before marine biological studies commenced means that it is at times difficult to distinguish between native and introduced species, resulting in the recognition of cryptogenic species whose historical biogeography and origin remain uncertain or unknown (Carlton 1996). As a result of intensive shipping activity, as well as to the importation of biofouled commercial oysters from both the Western Atlantic Ocean and the Western Pacific Ocean, San Francisco Bay is recognized as one of the most highly invaded estuaries in the world (Carlton 1979; Cohen and Carlton 1995, 1998; Ruiz et al. 2011)

The survey reported here was conducted between 1970 and 1971 when the first author was a student at John F. Kennedy High School in Richmond, California. Samples were brought to the second author, then at the California Academy of Sciences (CAS), San Francisco, to assist with identifications.

Materials and methods

Observations and collections were made at 34 sites (Table 1; missing numbers reflect stations that did not produce fruitful collections) around San Francisco Bay from the Vallejo region on the north shore of San Pablo Bay to the Golden Gate Bridge at the mouth of the Bay and south to East Palo Alto and Newark in the southernmost part of the Bay (Figure 1). Sites were chosen based upon public, land-based access. Access by land to much of the Bay shoreline was at the time, and still is, highly limited due to housing developments, industrial complexes, salt ponds, military reserves, and other barriers. Collections were made over a 13-month period from April 1970 to May 1971.

Table 1. List of collecting stations in San Francisco Bay.

Site 1.	Contra Costa Co., Pinole, west side of Tennet Road.
Site 4.	Contra Costa Co., Richmond, Point San Pablo, former whaling station.
Site 5.	Contra Costa Co., Richmond, beach in front of Point Molate Naval Station.
Site 7.	Contra Costa Co., Richmond, shore beneath Richmond-San Rafael Bridge.
Site 8.	Contra Costa Co., Richmond, Point Richmond, Keller's Beach.
Site 9.	Contra Costa Co., Point Richmond, between Keller's Beach and Santa Fe pier.
Site 11.	Contra Costa Co., northeast side of Brooks Island.
Site 13.	Contra Costa Co., Richmond, half way between Point Isabel and the Albany racetrack (Golden Gate Fields), Hoffman Boulevard
Site 15a.	Alameda Co., Berkeley, beneath Berkeley fishing pier off Berkeley Marina.
Site 15b.	Alameda Co., Berkeley, east shoreline of southernmost point of Berkeley Marina.
Site 16a.	Alameda Co., Berkeley, Frontage Road, just off south side of Berkeley Marina.
Site 16b.	Alameda Co., Berkeley, half way between Berkeley and Emeryville marinas.
Site 18.	Alameda Co., Alameda, Crown Beach Regional Park.
Site 19.	Alameda Co., Alameda, Hester Drive, San Leandro Bay.
Site 20.	Alameda Co., Alameda, Fillmore Street, San Leandro Bay.
Site 23a.	Alameda Co., San Leandro, San Leandro Marina, south side below fishing pier.
Site 23b.	Alameda Co., San Leandro, San Leandro Marina, north side of fishing pier to right of boat ramp.
Site 24.	Alameda Co., Coyote Hills, Newark, 3.2 km north of Dumbarton Bridge
Site 25.	Alameda Co., Coyote Hills Regional Park, near Newark, shoreline 3.2 km across salt ponds.
Site 26.	San Mateo Co., East Palo Alto, Bay Road
Site 28.	San Mateo Co., San Mateo, Coyote Point State Park, north side shoreline.
Site 29.	San Mateo Co., 3.2 km south of the former Candlestick Park, Bayshore Freeway, South San Francisco.
Site 32.	San Francisco Co. San Francisco, below seawall at Fort Point.
Site 33.	Marin Co., Lime Point to south Fort Baker (Figure 2).
Site 35.	Marin Co., Sausalito, Harbor Road, Yacht Harbor between Sausalito and Marin City.
Site 37.	Marin Co., Great Circle Road, 0.4 km north of Strawberry Point, Richardson's Bay
Site 44.	Marin Co., shoreline adjacent to San Quentin Pistol Range, Sir Francis Drake East Boulevard.
Site 45.	Marin Co., Rod and Gun Club, right side of north end of Richmond San Rafael Bridge.
Site 46.	Marin Co., San Pedro Road, 4.8 km south of the San Rafael boundary.
Site 47.	Marin Co., San Rafael, San Pedro Road, 8 km south of the freeway.
Site 50.	Solano Co., 9.7 km west of Guadalcanal Village, Highway 37.
Site 51.	San Francisco Co., South San Francisco, East Grand Avenue, on new fill south of the Fuller Paint Factory.
Site 52.	San Francisco Co., South San Francisco, Oyster Point Road, South San Francisco Marina.
Site 53.	Contra Costa Co., Richmond, 0.4 km north of Stauffer Chemical Company plant.

At each site, approximately 800 meters of shoreline were surveyed. Search time per site was typically between 60 and 120 minutes. Samples of all common invertebrate species larger than 1 mm were collected by hand from the surface of mudflats, rocks, or pilings, and from under rocks, tires, and boards (with the underside of the object and substrate below examined for invertebrates). Limited digging was done when a burrow was visible. Each site was sampled during low tides below a height of +0.91 meters MLLW. A broad range of habitat types was sampled, including mudflats, pier pilings, rock rip-rap and shore rocks, seawalls, and salt marshes. Although observed on occasion, no insects or arachnids were collected as part of this study. Collected specimens were preserved in 3% formalin (soft-bodied specimens) or 70% methanol. Selected specimens were deposited in the CAS Department of Invertebrate Zoology.

Taxa were identified to species level as much as possible. Publications available at the time for species identification included Johnson and Snook (1927), Fitch (1953), Smith et al. (1954), Hedgpeth (1962), Ricketts et al. (1962), Morris (1966) and Hanna (1966). Specimens brought to CAS were

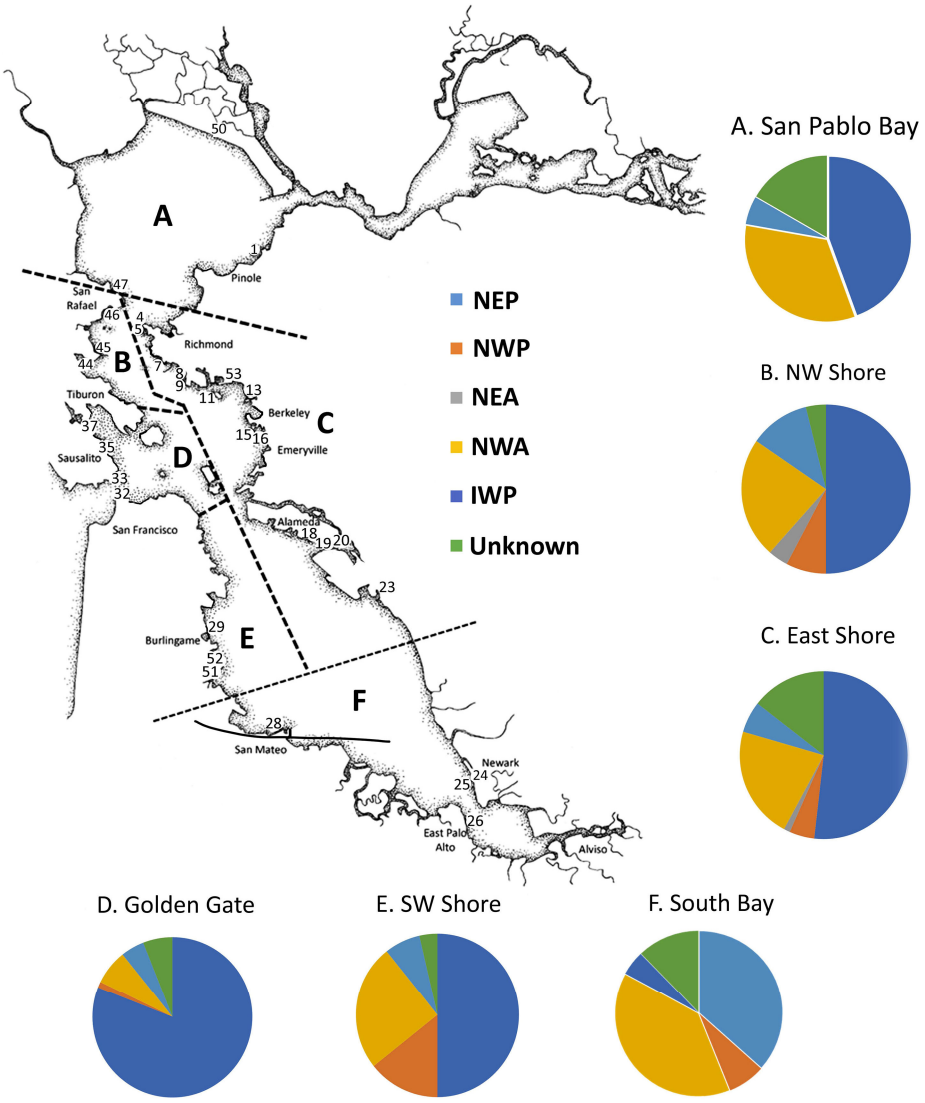

Figure 1. Location of collecting sites (Table 1) in six regions of San Francisco Bay and geographic origins of intertidal invertebrates in San Francisco Bay (NEP = Northeast Pacific Ocean (Pacific coast of North America), NWP = Northwest Pacific Ocean (Japan, Korea, and China), NEA = Northeast Atlantic Ocean (Western Europe and Mediterranean), including amphi-Atlantic; see text), NWA = Northwest Atlantic Ocean (Atlantic coast of North America), IWP = Indo-West Pacific Ocean). Unknown = cryptogenic and undeterminable species. Species numbers for each geographic origin in each region are shown in Table 3.

identified or verified by the second author. Additional identifications were made by Allyn G. Smith (chitons and some additional mollusks), Dustin D. Chivers (crabs), Victor A. Zullo (barnacles), Penny Pinter (Penny Morris-Smith) (bryozoans) and Ernest W. Iverson (isopods).

Based on Cohen and Carlton (1995) and Ruiz et al. (2000), the biogeographic origins of species were assigned to five major regions:

1) Northeast Pacific Ocean (NEP) from Alaska to Mexico, including species that are presumably naturally circumboreal;
2) Northwest Pacific (NWP), including Japan, Korea, and China;
3) Northwest Atlantic Ocean (NWA), from Canada to the Gulf of Mexico;

4) Northeast Atlantic Ocean (NEA), including Europe and the Mediterranean; we include here several species that are considered amphi-Atlantic, but whether native to Europe, North America, or both is uncertain; and,
5) Indo-West Pacific Ocean (IWP), including Australia and New Zealand.

Species from region 1 are considered native, while those from regions 2–5 are introduced. Additional taxa were considered cryptogenic, or were undeterminable relative to their biogeographic status due to the lack of taxonomic resolution.

Nomenclature was updated following Carlton (2007). Post-2007 name changes follow WoRMS (World Register of Marine Species 2020), with a few exceptions, such as the retention of the oyster genus name *Crassostrea* as opposed to *Magallana* (Bayne et al. 2017). In the intervening 50 years, some taxa regarded formerly as one species have been split into two or more. We indicate how we treat these revisions in Supplementary material Table S1.

Results and discussion

Distribution of study sites and species observed

For the purposes of this study, the Bay was divided into six major regions (Figure 1): (A) San Pablo Bay, (B) Central Bay northwest shore, (C) Central-South Bay east shore, (D) the Golden Gate-Richardson Bay region, (E) South Bay southwest shore and (F) South Bay. Station locations are shown in Figure 1 and summarized in Table 1. As noted above, access often dictated collection sites. The most accessible shorelines were along the (C) Central-South Bay east shore, from Richmond to San Leandro, with 17 sites, or 50% of the stations, and (B) the Central Bay west shore, near the Golden Gate (Figure 2) and into Richardson Bay. The remaining regions were represented by three to four stations each. In all, 139 living and five dead taxa were collected (Tables S1, S2, and S3) in nine phyla: Porifera (sponges), Nemertea (ribbon worms), Annelida (polychaete worms), Cnidaria (sea anemones and hydroids), Arthropoda (crustaceans including amphipods, isopods, barnacles, crabs, shrimp, and hermit crabs), Mollusca (bivalves, gastropods, and chitons), Bryozoa (bryozoans), Echinodermata (asteroid sea stars), and Chordata (ascidians, or sea squirts). Polychaetes (19 species), crustaceans (43 species) and mollusks (49) species comprised 80% of the taxa found.

Species frequency

Two near-ocean stations (32 and 33) at the mouth of the Bay account for slightly more than one-third (38.4%) of all native species records – that is, 33 of the 86 native species were found only at these stations. Fifteen (37.5%) of the 40 introduced species were collected at only one station each.

Figure 2. Collecting site No. 33 (Lime Point to south Fort Baker), located near the north base of the Golden Gate Bridge, showing rocky intertidal with riprap deposits. Photograph taken in 1970 by Lynn Siri Kimsey.

Overall, 62 (44.6%) of all 139 species were also found at only one survey station each. Given the frequency of unique occurrences, additional stations would doubtless have added to the overall diversity reported here.

Biogeographic status and origins

We assigned all species to either a native (Northeast Pacific origin), introduced, cryptogenic, or undetermined biogeographic status (Table 2). Eighty-six (61.9%) were considered native, 40 (28.8%) introduced, and two (1.4%) cryptogenic. An additional 11 species (7.9%) were undeterminable as to their origin due to insufficient taxonomic resolution. Of the introduced species, 25 (62.5%) originate from the North Atlantic Ocean, 12 (30%) from the Northwest or Indo-West Pacific. The origins of the three remaining introduced species and of the two cryptogenic species, while likely from either the Atlantic or the Pacific, remain uncertain.

Most prominently represented among introductions were bivalve and gastropod mollusks, with 14 species, comprising 35% of all non-native taxa. Introduced bivalves from the Atlantic coast included the soft-shell clam *Mya arenaria* Linnaeus, 1758, the ribbed marsh mussel *Geukensia demissa* (Dillwyn, 1817), the clam *Limecola petalum* (Valenciennes in Humboldt & Bonpland, 1821) and the gem clam *Gemma gemma* (Totten,

Table 2. Biogeographic status and probable origins of living intertidal invertebrates in San Francisco Bay collected between 1970 and 1971.

Taxon	Biogeographic Status								Total
	Native	Introduced					Cryptogenic	Unknown Origin	
	NEP	NWA	NEA	NWP	IWP	Unknown			
Porifera		2							2
Nemertea	1								1
Annelida	12	2			1			4	19
Cnidaria									
Anthozoa	2	1		1		1			5
Hydrozoa	3	1					2		6
Arthropoda									
Amphipoda	3	3							12
Isopoda	8			1				5	13
Cirripedia	4	1			5				5
Decapoda	13								13
Mollusca									
Bivalvia	12	4							19
Gastropoda	20	6	1	2	1				27
Polyplacophora	3								3
Bryozoa	2	3	1			2		1	9
Echinodermata	2								2
Chordata	1			1				1	3
Total	86	23	2	5	7	3	2	11	139

1834). All of these species were probably introduced when Atlantic oysters (*Crassostrea virginica* (Gmelin, 1791)) were planted in the Bay in the 19th and early 20th centuries (Cohen and Carlton 1995). Two bivalves, the Manila clam *Ruditapes philippinarum* (Adams & Reeve, 1850) and the mussel *Arcuatula senhousia* (Benson, 1842) were from Japan, introduced when Japanese oysters, *Crassostrea gigas* (Thunberg, 1793), were planted in the first half of the 20th century (Cohen and Carlton 1995). The shipworm *Teredo navalis* Linnaeus, 1758, introduced by wooden ships, may have originated in the Indo-West Pacific (Carlton 2009).

Among the introduced gastropods, one was native to Europe (the marsh and riprap snail *Myosotella myosotis* (Draparnaud, 1801)), although it may have been transported to the Bay from the U.S. Atlantic coast). The remaining were all native to the Atlantic seaboard, including the whelk *Busycotypus canaliculatus* (Linnaeus, 1758), the slipper limpets *Crepidula convexa* Say, 1822 and *C. plana* Say, 1822, the oyster drill *Urosalpinx cinerea* (Say, 1822), the mudsnail *Tritia obsoleta* (Say, 1822), and the parasitic pyramidellid *Boonea bisuturalis* (Say, 1822). As with the Atlantic bivalves, all of these may have been introduced during the days of the Atlantic oyster industry (Cohen and Carlton 1995). While ship-mediated invasions are common, San Francisco Bay demonstrates the importance of understanding the role of historical vectors (such as the former importation of commercial oysters) in the transport and introduction of non-native species.

Site physiography and regional frequency of native and introduced species

Native and introduced species were differentially distributed along the Bay's margins, and the proportions of species originating from the Western Pacific or from the Western Atlantic differed as well (Table 3, Figure 1).

Table 3. Number of species by biogeographic origins. Region codes as in text and Figure 1.

San Francisco Bay Region	Biogeographic Origin						Collection Sites
	NEP (native)	NWP	NEA	NWA	IWP	Unknown	
(A) San Pablo Bay	8	0	0	6	1	3	1, 47, 50
(B) NW Shore	13	2	1	6	3	1	44–46
(C) East Shore	41	4	1	17	5	12	4–5, 7–9, 11, 13,15–16, 18–20, 23, 53
(D) Golden Gate	68	1	0	6	4	5	32–33, 35, 37
(E) SW Shore	14	4	0	7	2	1	29, 51–52
(F) South Bay	17	3	0	16	2	5	24–26, 28

San Pablo Bay (Region A) has, in general, the highest levels of freshwater influx and silt coming down from the Sacramento-San Joaquin Rivers. It has extensive fine sediment mud flats and limited rocky shoreline. Most of the shoreline was inaccessible. The majority of the species collected here were either native or originated from the Atlantic coast. The Central Bay northwestern shore (Region B) is rocky, interspersed with sandy mud flats, piers and concrete rubble/landfill. The majority of species collected here were also native or from the Atlantic. The Central and South Bay east shore (Region C) has the most diverse habitats, including sandy beaches, rock shorelines, mudflats and riprap deposits. Slightly more than half of the species found here were native, followed by species from the Atlantic coast.

The Golden Gate region (Region D) shoreline has rocky shores, as well as sand/gravel beaches and piers. This region has the strongest daily currents, influenced by the proximity of the Pacific Ocean. The largest number of native species were found here. Indeed, at the two most exposed stations (32, 33) at the Golden Gate, only one introduced species, the wood-boring isopod *Limnoria tripunctata* Menzies, 1951, was found. South of the Golden Gate, the southwestern shoreline (Region E) consists of a combination of rubble fill, piers and mud flats. Again, half of the collected species were native. Atlantic coast species were significant, and the largest number of species from the northwestern Pacific were found here. The South Bay (Region F) supported salt evaporation ponds and extensive fine sediment mudflats. The majority of species found here were from the Atlantic coast, with a significant number of native species as well.

The clear attenuation of native species as one proceeds into San Francisco Bay away from the Golden Gate may be related to a number of phenomena, including increasingly lower salinities and higher temperatures potentially more conducive to more euryhaline and eurythermal non-native species, to changes in substrate, and to increasingly fewer native estuarine species that might offer competitive resistance. Silva (1979) observed a similar concentration of fully marine native species around the Golden Gate as well, which he suggested was due "in large part" to a salinity gradient. However, the relative roles of physical, chemical, biological, and ecological drivers that may regulate the relative proportions of native and introduced species in the Bay system largely remain to be investigated.

While other introduced species not encountered in this survey were known from San Francisco Bay by 1971 (Cohen and Carlton 1995), clear

patterns in those detected here nevertheless emerge, and the present data may thus serve as a partial baseline for future intertidal surveys in San Francisco Bay. In 1970–1971, introduced species represented increasingly larger fractions of diversity to the north, east, and south of the Golden Gate. Species originating from the Northwest Pacific and the Northwest Atlantic were the primary contributors to the non-native fraction of the biota.

The dearth of long-term, systematic surveys of intertidal invertebrates of San Francisco Bay stands in striking contrast to the critical role of the Bay in the function of California's aquatic ecosystems (Conomos 1979; Cloern and Nichols 1985; Hollibaugh 1996). However, it may be that other historical data sets exist that, if published, could further contribute to our understanding of the Bay's biological and ecological history.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Intertidal invertebrates of San Francisco Bay collected between 1970 and 1971.
Table S2. Living species collected in Regions A–F in San Francisco Bay between 1970 and 1971.
Table S3. Intertidal invertebrate species collected at each survey station in San Francisco Bay between 1970 and 1971.

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