Title:

Down the Up Staircase: Equatorward March of a Cold-Water Ascidian and Broader Implications for Invasion Ecology

Running Head: Equatorward ascidian invasion can alter community structure

ABSTRACT

AIM

While warming temperatures are expected to facilitate the poleward movement of species previously restricted to more equatorial waters, the arrival and persistence of cold-water species in more equatorward waters is relatively unprecedented. The native Northeast Pacific ascidian *Corella inflata* Huntsman, 1912 has spread southward and invaded new regions along the North American Pacific coast, a rare example of a marine species moving toward the equator. Here, we document *C. inflata*’s equatorward movement and potential impact, assess several hypotheses for its spread, and consider implications for invasion ecology.

LOCATION

North American Pacific Coast (Puget Sound to San Francisco Bay).

METHODS

We recorded the southward movement of *Corella inflata* by compiling records from the literature, conducting informal searches, and conducting standardized fouling community surveys at sites from the southern border of *C. inflata*’s native range in Puget Sound to San Francisco Bay. Within San Francisco Bay, we recorded *C. inflata*’s arrival and potential impact by conducting standardized surveys across an 18-year period encompassing the invasion.

RESULTS

First collected outside its native range in Coos Bay, Oregon in 2004, *C. inflata* was subsequently detected 1000 km south of its historical distribution by 2008 in San Francisco and Humboldt Bays, California. At times, this large, conspicuous solitary ascidian became locally abundant in San Francisco Bay fouling communities, which showed significant shifts in species composition and relative abundance at invaded sites concomitant with *C. inflata*’s arrival.

MAIN CONCLUSIONS

The recent southward movement of *C. inflata* runs counter to global warming expectations and may be linked to undetected changes in vessel traffic patterns, rather than natural range expansion. However, an understanding of the one or more processes that would serve to explain the equatorward movement of this cold-water affinity marine species remains elusive.

Keywords:

Invasion, introduction, dispersal, *Corella inflata*, *Corella willmeriana*, San Francisco Bay, fouling community

INTRODUCTION

The poleward range expansions of numerous lower-latitude terrestrial, freshwater, and marine species during the past half century are now well documented (Chen et al., 2011; Bates et al., 2014; Sunday et al., 2015; Canning-Clode and Carlton, 2017). These movements are likely underestimated due to the same challenges that limit the recognition of species invasions, including limited search effort and constraints of taxonomic and biogeographic knowledge (Carlton, 2009). With rare exceptions, these northbound in the Northern Hemisphere and southbound in the Southern Hemisphere range expansions are correlated with warming land and water temperatures. Exceptions may include cases in which new habitat becomes available, suggesting that species' geographic boundaries are in some cases limited by substrate and not temperature. One such example, albeit not a poleward extension, may be the historical southern expansion of the intertidal barnacle *Semibalanus balanoides*, which in the mid-1900s extended south along the North American mid-Atlantic seaboard after the construction of rock groins on long stretches of sandy shores (Carlton et al. 2011); this barnacle is now retreating north with warming temperatures (Jones et al., 2012). Numerous non-native animals and plants may spread both north and south along a coastline after introduction to a new region, a phenomenon typically correlated with a given species' thermal tolerance limits (Reid, 1996; Grosholz, 2010; Epifanio, 2013).

In a steadily warming world, the expansion of a higher-latitude marine cold-water species into warmer temperate waters is unexpected, given that such species are presumably evolutionarily restricted to lower temperature waters for reproduction, settlement, growth, and survival. We consider here the curious case of the native Northeast Pacific Ocean solitary ascidian (*Corella inflata* Huntsman, 1912 (Ascidiacea, Phlebobranchia, Corellidae)), whose southern limit was long recognized as Puget Sound, Washington. Commencing in the 2000s, *C. inflata* began appearing in Oregon and California ports and harbors that had long been under extensive biological scrutiny.

Corella inflata (Figure 1) is a conspicuous, transparent, cuboid species reaching 5 cm in length. It was first described "from between tides to about 10 fathoms" (18.3 meters) from Departure Bay, Nanaimo, British Columbia (Huntsman, 1912). Van Name (1945) mistakenly considered *C. inflata* to be a synonym of the older-named *Corella willmeriana* Herdman, 1898, a larger species reaching deeper waters, believing the former to be smaller specimens of the latter. Based upon morphological and reproductive evidence, Lambert et al. (1981) resurrected *C. inflata*; all literature between 1945 and 1981 thus confused the two species, referring to *C. inflata* as *C. willmeriana.* Lambert et al. (1981) reported the range of *C. inflata* to be from the northern tip of Vancouver Island (Hope Island, Queen Charlotte Strait), British Columbia to Puget Sound, and the usual range of *C. willmeriana* to be nearly identical, from southernmost (southeast) Alaska (Loring) to Puget Sound. A few confirmed specimens of *C. willmeriana* were taken 50 years ago in Monterey Bay, California at depths of 30 and 60 m (Lambert et al., 1981), and were the basis of the comment in Lambert et al. (1995) that *C. inflata* ranges "to central California." This unusual record is presumably the result of a rare transport event of the species from the Pacific Northwest to Monterey Bay, and is unrelated in time or space to the 21st century phenomena that we describe here.

Recently, since the 1990s, *C. inflata* has also been found far to the north in south central Alaska. It was discovered in Prince William Sound in 1998-1999, where it was common in some marina float fouling communities (Hines and Ruiz, 2000a; Lambert and Sanamyan, 2001; Ruiz et al., 2006), and then further west in Kachemak Bay in 2000 (Hines and Ruiz, 2000b). Subsequent reports filled in the range in southeastern Alaska, including Sitka Sound (rare, 2007: Pirtle et al., 2012), Bartlett Cove, Glacier Bay (common, 2010: M. Noble and L. McCann, personal communications, 2012) and Ketchikan (abundant, 2009: Davis, 2010). The report by Bluhm et al. (2009) of "*Corella cf. inflate*" (*sic*) collected in 2004 in the southern Chukchi Sea, near the Bering Strait (65.68° N x 168.30° W) in 49.7 meters, is based upon a species of *Ascidia* (G. Lambert, personal communication, February 2015, who examined USNM specimen 1116525 at our request).

Over the same time period, the congener *Corella willmeriana* was reported similarly from more northward Alaskan stations in the 1990s: Hines and Ruiz (2000a), Lambert and Sanamyan (2001), and Ruiz et al. (2006) reported *C. willmeriana* from Prince William Sound based on the same 1998-1999 collections; Hines and Ruiz (2000b) from Kachemak Bay in 2000; and Pirtle et al. (2012) from Sitka Sound in 2007-2008. Rosenthal et al. (1977) reported "*Corella willmeriana*" earlier from Zaikof Bay, Prince William Sound based upon 1975-1976 collections, but without descriptive or other details; as their report pre-dates the 1981 revision of *Corella* taxonomy, the record (if correct) could represent either *C. inflata* or *C. willmeriana.*

Lambert et al. (1981) remarked that "very extensive collections carried out (north of southernmost Alaska) and the Canadian Arctic have all failed to discover a single specimen of *Corella*." We suggest that the above northern records of *Corella inflata* and *C. willmeriana* likely reflect climate-induced expansions, as would be expected in the latter half of the 20th century, possibly as early as the 1970s, but more certainly during and since the 1990s.

Here, we document the anomalous southward range expansion of *C. inflata* (hereafter, *Corella*). We further examine several hypotheses for this expansion, and report upon possible impacts, including changes observed in community composition and structure in San Francisco Bay after *Corella* appeared.

METHODS

Distribution of **Corella inflata** *South of Puget Sound*

We assessed the known distribution and southward movement of *Corella inflata* along the west coast of North America using three data sources. We compiled records of *C. inflata* occurrence from the literature and from correspondence with workers along the coast from Alaska to southern California. We conducted opportunistic, informal searches of floats and pier pilings for *Corella*, following the discovery of *C. inflata* in Coos Bay, OR in 2004 (see results). This effort focused particular attention on repeated annual observations during the summer months (June to August) beginning in 2004 in Coos Bay, OR, and beginning in 2008 in San Francisco Bay, CA.

These qualitative records complemented results from standardized, systematic surveys of epifaunal communities that we assembled from 28 different bays from 2000-2017 (see results for locations and years), spanning central Alaska to southern California. Standardized surveys were done at least once in each bay, and repeated multiple times in several bays, including San Francisco Bay, which was surveyed for 18 consecutive years.

Initially, *Corella* were identified morphologically from multiple sites along the west coast of North America (Lambert 1981; G. Lambert, personal communication), and the morphology of specimens from Coos Bay, Crescent City Harbor, Humboldt Bay, and San Francisco Bay were identical to this description. Based on these identifications, along with both qualitative observations and standardized surveys, we reconstructed the approximate time course of *Corella*’s range expansion in the 2000s south of Puget Sound, tracking the invasion and evaluating concomitant community changes in San Francisco Bay.

Standardized Fouling Community Survey Methods

We compiled results from standardized three-month panel studies of sessile invertebrate community development at 6 to 10 sites in each of 28 bays along the Pacific coast of North America, including 17 bays south of *Corella*'s original southern range boundary at Puget Sound (see results for locations and years). All surveys were conducted during the summer months (June-September), coinciding with the season of high recruitment, to assess community composition (deRivera et al., 2005; Table 2 in Simkanin et al., 2016; Ruiz and Chang, unpublished data). For these standardized surveys, 14 cm x 14 cm x 0.5 cm square, grey, polyvinyl chloride (PVC) panels were used as passive recruitment collectors. Panels were distributed throughout each site using a stratified-random design. Each panel was lightly sanded, attached to a brick for weight and suspended panel side-down from a rope tied to a dock or buoy. The panels were examined for the presence of benthic marine invertebrates, following standard methods described below for San Francisco Bay. Here we report only on *Corella* presence in these surveys across bays.

As part of a long-term study in San Francisco Bay, we conducted systematic panel-based surveys of epifaunal community composition over an 18-year period (2000-2017) to detect seasonal and interannual changes in community composition (Chang et al., 2018). To study sessile invertebrate community development, three-month panel deployments were conducted at a number of sites during the summer months of June to September each year. In addition, seasonal changes were assessed using two quarterly time series measurements of recruitment and community development from February 2001 to August 2003, and from June 2006 to September 2011. An informal long-term study was performed to help assess *Corella* recruitment, growth, and survival at two sites in San Francisco Bay (San Francisco Marina and Sausalito Marine Harbor) from June 2006 to July 2011.

For each San Francisco Bay survey (summer, quarterly, and long-term), at least 10 panels per site per Timepoint were placed at 1 m depth except for 2004-2010, when at least 5 panels per site per timepoint were used. Surveys for all other bays generally included deployment of at least 5 panels per site at 6 to 10 sites per bay, although replication was lower in reserves and sanctuaries surveyed by deRivera et al. (2005). Losses due to dock maintenance work or vandalism also occasionally reduced replication from the number of panels initially deployed.

In San Francisco Bay, panels were left in place for 12 to 14 weeks (summer and quarterly panels) to record invertebrate settlement on the downward-facing side, then retrieved and replaced with new, blank panels at the same location. Community development as measured here thus encompasses both settlement and post-settlement processes, including mortality, which occurred during the entire deployment period. After retrieval, panels were analyzed for species composition, percent cover, and biovolume. To estimate percent cover of dominant taxa, a grid of 50 to 100 points was placed over each panel and the taxon attached to the panel at each point (i.e. the "primary" cover organism) was identified to the lowest possible taxonomic level using a dissecting microscope. If other organisms were growing on top of the primary cover organism at a point, these "secondary cover" organisms were also identified and recorded. Total percent cover was the sum of primary and secondary cover and could thus exceed 100%. A complete species inventory was then taken and included the removal of organisms from panels to ensure accurate identification if necessary. For a subset of years and sites (2000–2003 at San Francisco, and 2006–2008 at both San Francisco and Sausalito), biovolume, a proxy for biomass, was measured by placing each panel in a bucket fitted with a spigot and measuring the volume of water displaced, then subtracting the volume of a bare panel.

Long-term panels were deployed in June 2006 and photographed approximately annually until July 2011, and examined approximately 2-3 additional times per year in spring and summer.

Environmental Measurements in San Francisco Bay

We monitored temperature at 1 m depth at each site while survey panels were deployed using a combination of Hobo loggers (Onset Computer, Bourne, Massachusetts, USA, models H08-001-02 and UA-002-64) and iButton loggers (Maxim IC Corp., Dallas, Texas, USA, model 1921G-F5). Temperature was measured at 3-hour intervals during the summers of 2001, 2002, and 2003, and at hourly intervals from June 2004 until August 2013. Average temperatures for each panel deployment per site were calculated from iButton and Hobo Pendant logger data.

We recorded salinity levels using a YSI multimeter (Yellow Springs Instruments, Inc., Yellow Springs, Ohio, USA, model 85) to take spot measurements at the beginning and end of each panel deployment interval (generally, every 3 months). Net Delta Outflow, a proxy for freshwater flow entering the San Francisco Estuary (California Department of Water Resources 2016), is highly correlated with salinity levels throughout the Bay and can be used to reconstruct salinity levels for specific sites of interest (Stahle et al., 2001; Chang et al., 2018). We also used publicly-available continuous monitoring records of salinity from three sites near the ocean entrance of San Francisco Bay (Fort Point, Presidio Yacht Harbor, and Alcatraz) (Bodega Marine Laboratory 2016; United States Geological Survey 2016). Average salinity levels for each panel deployment per site were calculated from spot measurement data and continuous monitoring records.

Historical Temperature Data

To examine hypotheses about relationships of *Corella inflata* population dynamics to longer-term temperature changes, we examined records of water temperature data from locations near where we found *Corella* in Friday Harbor, WA, Coos Bay, OR, and San Francisco Bay, CA. We obtained data covering 1993-2016 from continuous monitoring stations operated by the National Oceanic and Atmospheric Administration (NOAA) at Friday Harbor, from Coos Bay at Charleston, OR, and from Fort Point at the mouth of San Francisco Bay (National Oceanic and Atmospheric Administration 2016).

Statistical Methods

In San Francisco Bay, we compared community composition at the two sites (San Francisco Marina and Sausalito Marine Harbor) where *Corella* was eventually observed and for which we had extensive data before and after *Corella*'s appearance. We used one-way PERMANOVA routines performed on Bray-Curtis dissimilarity matrices of square root-transformed percent cover data of the taxa on each panel at every available time point from summer surveys at these sites. *Corella* itself was omitted from the data to examine the impact on the other species in the community; there also was no secondary cover on *Corella*. Square root transformation was used to reduce the effects of extremely abundant taxa while simultaneously emphasizing the effects of rare taxa. The matrices were visualized using non-metric multidimensional scaling (nMDS). We then used SIMPER, a similarity percentage procedure, on Bray-Curtis dissimilarity matrices of square-root transformed percent cover data to ascertain which species were most responsible for community differences after the *Corella* invasion. Separate analyses were performed for each site. Shannon diversity was calculated for each panel.

Community composition on San Francisco Bay survey panels was also compared to environmental parameters using PERMANOVA. We tested for the effect of environmental conditions during community development by using the mean water temperature and salinity during the panel deployment as predictor variables. Because the previous winter's salinity levels have also been shown to significantly impact San Francisco Bay fouling communities (Chang et al., 2018), we also used the mean February-to-May Net Delta Outflow as predictor variables to explain variation in *Corella* presence and abundance on summer and quarterly panels at each site.

We used least-squares linear regression to evaluate the sign and magnitude of annual mean, mean March and mean August water temperature trends in San Francisco Bay and Coos Bay. March and August were selected as comparative months because *Corella* was observed to begin recruiting heavily in March in San Francisco Bay. If summer high-water temperatures limit *Corella* reproduction, trends in August temperatures (when the water is generally warmest in Coos Bay and San Francisco Bay) might be informative.

All analyses were executed in the R Environment for Statistical Computing (R Core Development Team 2016). Multivariate analyses were performed using the vegan package (Oksanen. 2016).

RESULTS

Distribution and Current Status of **Corella inflata** *South of Puget Sound*

Corella inflata was first discovered south of Puget Sound in the fall of 2004 in Coos Bay, Oregon (Table 1) (not 2003, as reported in Simkanin et al. (2016). *C. inflata* next appeared in 2008 in both San Francisco Bay (discussed below) and in Humboldt Bay (Wilson, 2011). In the fall of 2010 it was detected in the northernmost part of California at Crescent City Harbor (J. Chapman, personal communication). As of fall 2017, *Corella inflata* remains present in Coos Bay (Table 1), but has fallen to below-detection levels in San Francisco Bay, where it was last found in 2015, after having sustained populations for nine years.

C. inflata was detected in standardized panel surveys of Coos Bay and Yaquina Bay, Oregon fouling communities in 2004 and 2015, respectively (Table 2; Ruiz et al. unpublished data). While *Corella* has been detected regularly in San Francisco Bay (below), none were found in our surveys of bays to the south (Table 2).

Occurrence and Distribution of **Corella inflata** *in San Francisco Bay, and Post-Invasion Community Changes*

We surveyed a total of 44 sites in the San Francisco Bay Estuary over eighteen years (2000-2017), many of them repeatedly, and found *Corella inflata* at only three sites, all near the Bay's ocean entrance: Sausalito Marine Harbor (first record: June 2008), San Francisco Marina (June 2008), and Presidio Yacht Harbor (January 2014). *Corella* was found in summer surveys and dock collections during subsequent years at Sausalito Marine Harbor and San Francisco Marina. *Corella* was not found at any other sites, nor was it found in extensive surveys throughout the Bay before 2008 (Table 3).

Corella inflata showed considerable interannual variation in abundance (Figure 4), with long-term survey panels showing highest recruitment during spring and early summer (Chang et al., unpublished data). Maximum densities reached approximately 1000 individuals per m^2 and approached 100% cover of primary substrate on summer survey panels, and up to 50% cover on long-term survey panels at Sausalito Marine Harbor and San Francisco Marina.

The presence and abundance of *Corella* were correlated with temperature and salinity conditions at the time of occurrence. *Corella* presence and abundance in summer communities were also significantly related to winter/spring freshwater flow levels, which are a proxy for salinity levels in the bay and vary significantly between years. Greater *Corella* abundance was observed in summer communities following winters with intermediate levels of freshwater flow, corresponding to moderately reduced salinity levels ($F_{2, 82} = 19.0$, $p < 0.001$, Table 4; Figure 5)

Numerous changes to existing communities were observed following *Corella*'s invasion at both Sausalito Marine Harbor and San Francisco Marina. The average biovolume of the community (including *Corella*) increased immediately following *Corella*'s appearance at each site ($t_{4.152,12.44}$, $p < 0.001$ for San Francisco Marina; $t_{3.187,15.90}$, $p = 0.003$ for Sausalito). Average species richness per panel decreased following invasion ($F_{1,\ 172} = 11.7$, $p < 0.001$) and had a weak negative relationship with the percent cover of *Corella* in the community ($F_{1,\ 167} = 3.4$, $p = 0.067$). PERMANOVA analyses showed a significant shift in community composition (not considering *Corella* itself) after the invasion (San Francisco Marina: Pseudo-$F_{1,64} = 2.6277$, $p = 0.003$; Sausalito Marina Harbor: Pseudo-$F_{1,33} = 14.596$, $p = 0.001$; Figure 6). The average Shannon diversity per panel on summer survey panels decreased slightly at both locations (0.38 to 0.25 at San Francisco; 0.28 to 0.26 at Sausalito).

Using SIMPER to examine the species other than *Corella* that were most responsible for community differences after the invasion, we found that the abundances of a wide range of taxa changed, with more pronounced differences at Sausalito Marine Harbor than at San Francisco Marina (Table 5).

Temperature trends in Friday Harbor, Coos Bay, and San Francisco Bay

During the time period tested (1993–2016), annual mean temperatures were 9.65°C ± 1.37°C in Friday Harbor, 11.34°C ± 1.25°C at Coos Bay, and 13.59°C ± 1.86°C at San Francisco Bay (mean ± standard deviation). Mean March temperatures were 8.18°C ± 0.65°C in Friday Harbor, 10.56°C ± 0.88°C in Coos Bay, and 12.25°C ± 0.97°C in San Francisco Bay. Mean August temperatures were 11.53°C ± 0.49°C in Friday Harbor, 12.17°C ± 0.98°C in Coos Bay, and 16.00°C ± 1.01°C in San Francisco Bay. There was no statistically significant trend in annual mean, mean March, or mean August water temperature from either Coos Bay or San Francisco Bay ($p > 0.10$ for all cases). While there were some years when each site experienced cooler temperatures in March, August, and overall, the timing of these years did not coincide with the dates that *Corella* was first observed. In Friday Harbor, there was a significant negative trend in annual mean water temperature ($F_{1,\ 269} = 4.742$, $p = 0.03$), but no trend in mean March or mean August water temperature.

DISCUSSION

Distribution of **Corella inflata** *South of Puget Sound and Potential Vectors of Coastal Dispersal*

Long-term monitoring of repeatedly-surveyed locations along the Pacific coast, including Coos, Humboldt, and San Francisco Bays, permitted the detection of the first appearances of the Pacific Northwest native *Corella inflata* south of its native range. Numerous recent standardized surveys have not detected *Corella* south of San Francisco Bay, thus marking San Francisco Bay as the current southernmost extent of *Corella*'s known range.

Corella inflata retains its embryos in an enlarged brood chamber (Lambert et al. 1995) from which short-lived (minutes to hours) tadpole larvae are released. Natural range expansion from Washington by larval dispersal along the coast for hundreds of kilometers (to Coos Bay) or for nearly 1,500 km (to San Francisco Bay) is improbable, nor has *Corella inflata* been reported in ocean rafting. Moreover, *Corella* has not been reported from many other intermediate embayments between Puget Sound and San Francisco Bay, which would be expected if *Corella*'s recent spread were a result of natural range expansion. Thus, *Corella*'s appearance in southern waters is likely due to human-mediated dispersal.

Corella inflata was most likely transported south attached to the hulls (or other niche areas, including sea chests or internal piping) of vessels departing Alaska, British Columbia or Washington. These vessels may include both larger vessels (such as petroleum cargo tankers and cruise ships) and smaller vessels (such as tugboats, fishing vessels, and recreational craft). Small boats have been shown to be potent vectors for transporting numerous fouling taxa both short and long distances along the North American Pacific Coast (e.g. Davidson et al., 2010; Darling et al., 2012; Ashton et al., 2014). Murray et al. (2012) noted that the relatively low dislodgement velocity (i.e. weak attachment strength) of *Corella* suggested that it "could only be transported on slower-moving boats," which may suggest a greater role for smaller vessels. Alternatively, most vessels have niche areas (including rudders, propeller shafts, bow thrusters, intakes) that are protected from shear forces and offer transport opportunities for a wide range of organisms that cannot persist in more exposed areas with high water velocity (Miller et al., 2018). While we have found no records of *Corella inflata* in vessel hull fouling communities, Frey et al. (2014) report it from the sea chest fouling of a vessel dry-docked in British Columbia.

Switzer (2010) reported that *Corella inflata* was common on commercial oysters (*Crassostrea gigas*) in British Columbia. To our knowledge, no oysters from the Pacific Northwest were imported and planted at any of the sites where *Corella* has been found in Oregon and California, in timeframes compatible with the observations and records that we have compiled.

Distributional Ecology and Community Impact in San Francisco Bay

Starting in June 2008, *Corella inflata* was detected consistently, but at varying abundances, at two sites near the mouth of San Francisco Bay. Given the broad geographic scope and frequent repetition of our surveys within the estuary, it seems likely that *Corella*'s distribution within the Bay remained limited to the general vicinity of areas we first found it. Larvae were observed in the brood chambers of adults each year on quarterly, summer, and long-term panels, with new settlers appearing in spring and early summer (Figure 4).

Corella's incidence and abundance after detection at San Francisco Marina and Sausalito Marine Harbor were strongly correlated with environmental conditions, with greater abundance in slightly lower (but not below 20 ppt) salinity levels. The significantly greater abundance recorded during years with intermediate freshwater flow entering San Francisco Bay suggests a possible preference for slightly lower salinity conditions. The abundance of potential competitors was not significantly greater during drier years (higher salinity conditions), suggesting that competitors were not limiting the abundance of *Corella* during such years. However, *Corella'*s absence from survey panels immediately following a wetter winter (2011) suggests a sensitivity to salinity levels below 20 ppt for longer than a few days.

Our results indicate clear changes in community composition following the invasion of *Corella*, with significant reductions in the abundance and incidence of other species, suggesting that *Corella* may have a strong competitive impact (Table 5; Figure 6). We observed monolayers of *Corella* on quarterly, summer, and long-term survey panels. Young (1988) found that such monolayers could form because *Corella* consume larvae of other species (as well as conspecifics), but have themselves evolved mechanisms to avoid settling on conspecifics. As *Corella* is a solitary ascidian with significant space requirements, the reduction in other taxa post-invasion is also consistent with the effects seen from competition induced by other solitary ascidian species such as *Ciona* spp. and *Ascidia zara* (Blum et al., 2007; ALC pers. obs.). Because the abundance of some non-native solitary ascidians in San Francisco Bay has been shown to be driven by environmental changes (Chang et al., 2018), and since *Corella*'s abundance was also strongly correlated with intermediate freshwater flow, we suggest that a similar process could be at work for *Corella*: salinity levels control the ascidian's survival and recruitment, which in turn determine the magnitude of its competitive impact on the rest of the community. The changes to the rest of the community across the duration of our study were not explained by environmental changes alone – particularly at Sausalito – but do correlate well with the appearance and subsequent abundance fluctuations of *Corella*.

When present in high densities, *Corella* is also likely to significantly alter the local community's filtration capacity, as the community was previously more dominated by branching bryozoans, which have a lower filtration capacity per unit area of substrate occupied (Chang et al. unpublished data.). Byrnes et al. (2009)

have shown that introduced ascidians may significantly affect the filtration capacity of the community. Ultimately, experiments in which the presence and abundance of *Corella* are manipulated directly (as Blum et al. (2007) did for *Ciona robusta*, formerly known as *Ciona intestinalis* Type A) could be used to confirm the impact of *Corella* on community composition and functioning. *Corella* reached high densities further downstream than the other non-native solitary ascidians already present (*Molgula manhattensis, Ciona savignyi, Ascidia zara,* and *Ciona robusta*). *Corella* also largely recruited earlier in the year than these other species – as would be expected from its Pacific Northwest origins – thus fitting into a habitat facies that was poorly occupied by other solitary ascidians.

A Corella Novella: Why A Cold-Water Species Would Colonize Warmer-Temperate Latitudes

We presume that *Corella inflata* has long been transported via ships out of the Pacific Northwest, but was not detected elsewhere along the Pacific coast (or the world) until the beginning of the 21st century, despite possessing a number of attributes associated with colonizing species. *Corella* is a common-to-abundant fouling organism on floats, docks, and piers (Lambert, 1968; Lambert et al., 1981; Cordell et al., 2013; records herein), making it likely to foul vessels. Well before it was resurrected as a distinct species, *Corella* was noted as the "float" or "shallow-water" form of *C. willmeriana* (Lambert et al., 1981). As noted above, *Corella*'s brooding life history includes ovoviviparous reproduction in which tadpole larvae are released and settle gregariously (Lambert et al., 1995), both facilitating colonization and quickly leading to dense monocultures of adults (Figure 1). Individuals can reach sexual maturity in 90 to 120 days at a body length of about 12 mm, with breeding occurring throughout the year (Lambert, 1968, as *C. willmeriana*; Jacobs and Sherrard, 2010). In the warmer, more southerly introduced range, our observations offer tentative support that *Corella inflata* may only reproduce in spring-summer in the introduced range, with warmer temperatures (in late summer-fall) being unfavorable for reproduction but not too warm for survival.

With this suite of traits, *Corella* was poised to be successful if and when transported to new locations, albeit perhaps not to regimes outside of its predicted climatic envelope. Given the conspicuous nature of *Corella* and its absence until recently in repeated surveys of waters south of the Pacific Northwest, we surmise it is unlikely that *Corella* invaded but remained undetected for significant lengths of time. Recent successful invasion, rather than a failure of earlier detection, better explains *Corella*'s recent appearance in southern waters, which have been the focus of extensive surveys and analyses to detect such marine macrofauna over the past 60 years (Carlton et al., 1979, Ruiz et al., 2000, 2011).

We examine four hypotheses for why *Corella* would be successful now, rather than historically, south of its apparent natural southern boundary.

(1) *Increased Abundance in Native Region Increases Probability of Vector Engagement*

Carlton (1992) noted that the invasion of San Francisco Bay by the Japanese semelid clam *Theora lubrica* occurred soon after this species increased in abundance in the Inland Sea of Japan. Clearly, larger populations of a given species in a donor region may provide greater opportunity for vector engagement. In the present case, we have found no data suggesting that *Corella* increased in abundance in the early 2000s or later years in the Pacific Northwest. While *Corella*'s abundance has likely fluctuated over time in northern waters, it did not appear until the early 2000s to the south. We thus find no evidence to support this hypothesis alone, although it could act in conjunction with a change in transport conditions, as described below.

(2) *Increased Turbidity in Bay Mouths South of Puget Sound*

Bingham and Reyns (1999) and Bingham and Reitzel (2000) demonstrated that *Corella inflata*, with a thin, transparent tunic, is found primarily in areas where it is protected from exposure to direct sunlight.

Decreased light penetration in shallow waters due to increased turbidity (due to a number of reasons, such as changes in suspended sediment loads, plankton, or seston) could conceivably increase habitat availability for *Corella*. However, we found no data suggesting that the near-surface waters where *Corella* now occurs south of Puget Sound have become significantly more turbid. Moreover, under-float habitat, protected from ultraviolet radiation, has long been available in Oregon and California bays, but was not previously colonized by *Corella*. We thus also find no support for this hypothesis.

(3) *Decreased Bay-Mouth Temperatures in Oregon and California*

All of the sites where this ascidian has been detected south of Puget Sound are in relatively shallow marina basins close to the mouths of each bay. Coastal water temperatures may cool locally due in part to more intense upwelling in Eastern Boundary Upwelling Systems (e.g. Bakun et al., 2015), which suggests that local near-ocean temperature conditions in Coos Bay and San Francisco Bay could possibly decrease at times toward those more similar to that of *Corella*'s native range in the Pacific Northwest. Indeed, annual mean water temperatures at Friday Harbor showed a decreasing trend from 1993–2016. If warmer temperatures in more southerly regions had previously prevented successful reproduction, then a recent decrease in coastal temperatures might now enable *Corella* to successfully colonize and reproduce, resulting in successful invasion. Our analysis of long-term temperature trends from sites in San Francisco Bay and Coos Bay near where we found *Corella* does not support this hypothesis. Temperature comparisons spanning 1993–2016 indicate no clear trend in Bay environs, despite some evidence of cooling waters offshore and in more northern latitudes such as Friday Harbor. This discrepancy may be explained by higher air temperatures serving to warm up relatively shallow Bay waters, which offsets the cooling trend in offshore waters that enter the Bay. Regardless, the temperatures in locations we have surveyed since 2000 have warmed slightly (A. Chang and G. Ruiz, unpublished data).

(4) *Increased Likelihood of Transport due to Changes in Vector Patterns*

Patterns of coastal shipping traffic, including movements of both larger and smaller vessels, are well known to change over time and could conceivably increase the likelihood that *Corella* would be transported southward. Recreational boat traffic has been implicated as a significant vector for the coastwise spread of non-native species (Floerl and Inglis, 2005; Davidson et al., 2010). Recent studies have demonstrated significant vessel movement along the coast of California (Zabin et al., 2014). More broadly, Iacarella et al. (2019) have noted that the often overlooked coastwise movements of "static" maritime structures, including derelict vessels, barges, dry docks, marina pontoons, and aquaculture equipment, may play a role in the movement of fouling species. In turn, the current and potential future scale of vessel movements of biofouling communities have prompted extensive management attention (Johnson et al., 2007; Galil and McKenzie, 2019). Darling et al. (2012) have demonstrated that recent shipping patterns – including vessel networks that connect Puget Sound, Coos Bay, and San Francisco Bay – have contributed to the contemporary distribution of genetic variation in a non-native ascidian, the Asian *Styela clava* along the Pacific coast. Indeed, if *Corella inflata,* a brooding species, has significant genetic structure from Alaska to Washington, haplotype analyses of southern populations may reveal the source populations that may correlate with specific vessel traffic patterns.

Thus, while we cannot rule out the possibility that the appearance of *Corella* in Oregon and California commencing in 2004 may be linked to as yet undetected changes in vessel traffic patterns, an understanding of the one or more processes that would serve to explain the equatorward movement of a cold-water affinity marine species remains elusive. We demonstrate that this ascidian has survived and reproduced over multiple years in waters well south of its previously known range, revealing a previously little understood breadth of its environmental tolerances and setting the stage for compelling experimental and genetic studies.

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Data Accessibility Statement

Raw data on environmental variation, *Corella inflata* distribution and relative abundances, and fouling community composition and relative abundances from San Francisco Bay are available in Smithsonian's Figshare repository. DOI: 10.25573/serc.c.4820616

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Table 1. North-to-south records, south of Puget Sound, of the ascidian *Corella inflata* compiled from literature surveys, correspondence, informal surveys, and standardized panel surveys (see Tables 2 and 3 for panel result details).

Observation Year and month(s)	**Location**	**Site(s)**	**Observations and References**
2015	Oregon: Yaquina Bay	**South Beach Marina** (near mouth of Bay)	2015 (summer): standardized panel surveys
2004 - 2017	Oregon: Coos Bay	**Charleston** (boat basins, near mouth of Bay)	2004 (summer): standardized panel surveys 2004 (November): common in Inner Boat Basin on floats (R. Emlet and J. Hodder, personal communication) 2005 (July): abundant in Inner Boat Basin on floats (JTC, personal observations) 2010 (May): common in Inner and Outer Boat Basin (R. Emlet, personal communication, 2010) 2010 (October): abundant (Chapman et al., 2011; Figure 1, herein) 2011 (July): present (JTC, personal observations) 2015 (fall) and 2017 (fall): present in Inner Boat Basin (R. Emlet, personal communication, November 2015 and March 2018).
2010 (September)	California: Crescent City Harbor	**Crescent City** (marina docks on northeast side of Harbor)	Present on docks (J. Chapman, personal communication); status in later years not known
2008 (December) – 2015	California: Humboldt Bay	**Eureka** (Eureka Public Marina, near mouth of Bay); **Coast Guard docks** (near mouth of Bay)	Abundant on fouling panels (Wilson, 2011); absent in 2011 (G. Lambert, personal communication); somewhat abundant in standardized panel survey (2015)
2008 (June) – 2015 2014 (January)	California: San Francisco Bay	**Sausalito** (Sausalito Marine Harbor), **San Francisco** (San Francisco Marina) **Sausalito** (Presidio Yacht Harbor), near mouth of Bay	Abundance varying (see text); San Francisco Marina 2008-2009: Marraffini et al., 2017)

Table 2. North-to-south records of *Corella inflata* along the North American Pacific coast, compiled from standardized panel surveys (deRivera et al. 2005; Simkanin et al. 2016; Ruiz and Chang, unpublished data). The total number of panels examined from each bay in a given year is specified in each cell. Shading indicates that *C. inflata* was detected. See text for description of replication and study design.

SITE NAME	Latitude (°N)	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Valdez	61.13	**12**	**14**										**100**						
Prince William Sound	60.69				**100**														
Kachemak Bay NERR	59.60				32	13													
Kodiak Bay	57.79		**101**																
Sitka	57.05		**100**										**46**						
Ketchikan	55.34				**91**														
Prince Rupert	54.31															**13**	**44**		
Dutch Harbor	53.88			**100**															
Padilla Bay NERR	48.49				**26**														
Olympic Coast NMS	48.37				**12**	8													
Puget Sound	47.72	**134**																	
Yaquina Bay	44.62																**77**		
Coos Bay / South Slough NERR	43.37	127			25	**48**													
Humboldt Bay	40.72				101												**100**		
Bodega Harbor	38.33					11									50				50
Tomales Bay	38.17					15	20	20	48	48					50				50
San Francisco Bay	37.62	149	549	317	122	10	10	105	215	**150**	**170**	**202**	**237**	**180**	**99**	**130**	**150**	**150**	**150**
Elkhorn Slough NERR	36.80				41														
Monterey Bay NMS	36.61				16														
Morro Bay	35.37														50				
Channel Islands NMS	34.17					30													
Port Hueneme	34.15																50		
Marina del Rey	33.98																50		
Los Angeles / Long Beach Harbors	33.77				100														100
Newport Bay	33.60																		50
Mission Bay	32.78				12										97				
San Diego Bay	32.73	136			11										84				
Tijuana River NERR	32.56				14														

Table 3. Sites surveyed using standardized panel methods from 2000–2017 in San Francisco Bay, California, including both summer and quarterly surveys. The total number of panels examined from each site in a given year is specified in each cell. Shading indicates that *Corella inflata* was detected. See text for description of replication and study design.

SITE NAME	Latitude	Longitude	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Sacramento Marina	38.565	-121.518													10					
Port of Stockton	37.959	-121.361													10					
Rio Vista Delta Marina	38.150	-121.694																10	10	10
Antioch Marina	38.020	-121.821							10	15	10	5	5	10	10		10	10	10	10
Pittsburg Marina	38.035	-121.883							10	15	10	5	5	9	10		10	10	10	10
Benicia Marina	38.045	-122.156							10	15	10	5	5	10				10	10	10
Glen Cove Marina	38.066	-122.213							10	20	10	5	5	10	10		10	10	10	10
Vallejo Marina	38.109	-122.269												10						
Petaluma Marina	38.230	-122.614												10						
Loch Lomond Marina	37.972	-122.483		10	20				10	20	10	5	5	10	10	10	10	10	10	10
Angel Island--Tiburon Ferry Co.	37.810	-122.323	20																	
Corinthian Yacht Club	37.810	-122.323		9										10						
Paradise Cay Yacht Harbor	37.916	-122.477												10						
Romberg Tiburon Center	37.891	-122.446		10		10														
Sausalito--Bay Model Pier	37.864	-122.494		10																
Sausalito Marine Harbor	37.861	-122.485							10	20	10	15	5	10	10	10	10	10	10	10
Presidio Yacht Harbor	37.833	-122.474							10	20	10	10	5							
Richmond Marina Bay	37.913	-122.352		9	54	10	10	10	10	20	10	31	47	20	10	10	10	10	10	10
Port Richmond Terminal 4	37.909	-122.388		73	30	15														
Port Richmond Terminal 1	37.909	-122.388		7																
Berkeley Pier	37.860	-122.322	20	10																
Berkeley Marina	37.876	-122.318		10						10	10			10						
Emeryville Marina	37.840	-122.313													10					
Southampton Shoal	37.883	-122.400		6																
Treasure Island Pier	37.820	-122.363	19																	
San Francisco Marina	37.808	-122.435	20	72	82	24			10	20	20	30	40	19	10	10	10	10	10	10
Port of San Francisco Pier 23	37.804	-122.399		10																
Port of San Francisco Pier 31	37.808	-122.406													10					
Port of San Francisco Pier 50	37.773	-122.387		10																
Port of San Francisco Pier 80	37.748	-122.384		19																
Port of San Francisco Pier 96	37.742	-122.370		10																
South Beach Harbor	37.780	-122.387												10						
Hunters Point Naval Shipyard	37.716	-122.363	20																	
Oyster Point Marina	37.673	-122.386		10							5			10	10	10	10	10	10	10
Coyote Point Marina	37.588	-122.317	20	73	81	25			5	20	10	30	40	19	10	10	10	10	10	10
Port of Redwood City	37.512	-122.211	20	20																
Redwood City Marina	37.502	-122.213		10										10	10	10	10	10	10	10
Port of Oakland	37.799	-122.323	17	69	25	13									10					
Oakland Yacht Club	37.783	-122.263																10	10	10
Jack London Square Marina	37.795	-122.282		9							5			10	10	10	10			
Jack London Square Fishing Pier	37.802	-122.282		10																
Ballena Isle Marina	37.768	-122.287												10	10	10	10	10	10	10
San Leandro Marina	37.698	-122.191	20	73	25	25			10	20	20	29	40	20	10	9	10	10	10	10
Dumbarton Railroad Bridge	37.500	-122.117	19																	

Table 4. *Corella inflata* abundance is predicted by environmental conditions in San Francisco Bay. Logit-transformed percent cover (e.g. Warton and Hui, 2011) with 0.01 added to avoid undefined logit values at zero percent cover. Year Type refers to classification (dry, moderate, wet) of the previous winter/spring's mean daily freshwater flow entering San Francisco Bay (see Figure 5 caption and Chang et al., 2018).

Response	**Df**	**Sum Sq**	**Mean Sq**	**F**	**p**
Year Type	2	43.01	21.50	18.97	1.69 e-7
Site	1	7.69	7.69	6.79	0.01
Year Type x Site	2	19.42	9.71	8.57	0.0004
Residuals	82	92.95	1.13		

Table 5. SIMPER analysis indicating species most responsible for differences in 3-month old summer (June to September) fouling community composition and species abundance before vs. after the 2008 invasion of *Corella inflata* at Sausalito Marine Harbor and San Francisco Marina, San Francisco Bay, California. See Table 3 for years surveyed.

Sausalito Marine Harbor

Species	Average Abundance Before Invasion	Average Abundance After Invasion	Contribution %	Cumulative Contribution %
Watersipora subtorquata	10	52	14.87	14.87
Bugulina stolonifera	49	10	13.75	28.62
Botrylloides violaceus	11	46	12.36	40.99
Bugula neritina	23	4	7.67	48.66
Botryllus schlosseri	30	25	7.29	55.95

San Francisco Marina

Species	Average Abundance Before Invasion	Average Abundance After Invasion	Contribution %	Cumulative Contribution %
Botryllus schlosseri	28	25	10.32	10.32
Balanus crenatus	16	22	9.79	20.10
Botrylloides violaceus	28	38	9.61	29.72
Diplosoma listerianum	10	15	7.73	37.45
Ciona robusta	7	13	6.33	43.78
Schizoporella japonica	16	3	6.23	50.02

Figure 1. *Corella inflata* fouling a submerged bucket in Coos Bay, Oregon, October 2010 (photograph by Gretchen Lambert).

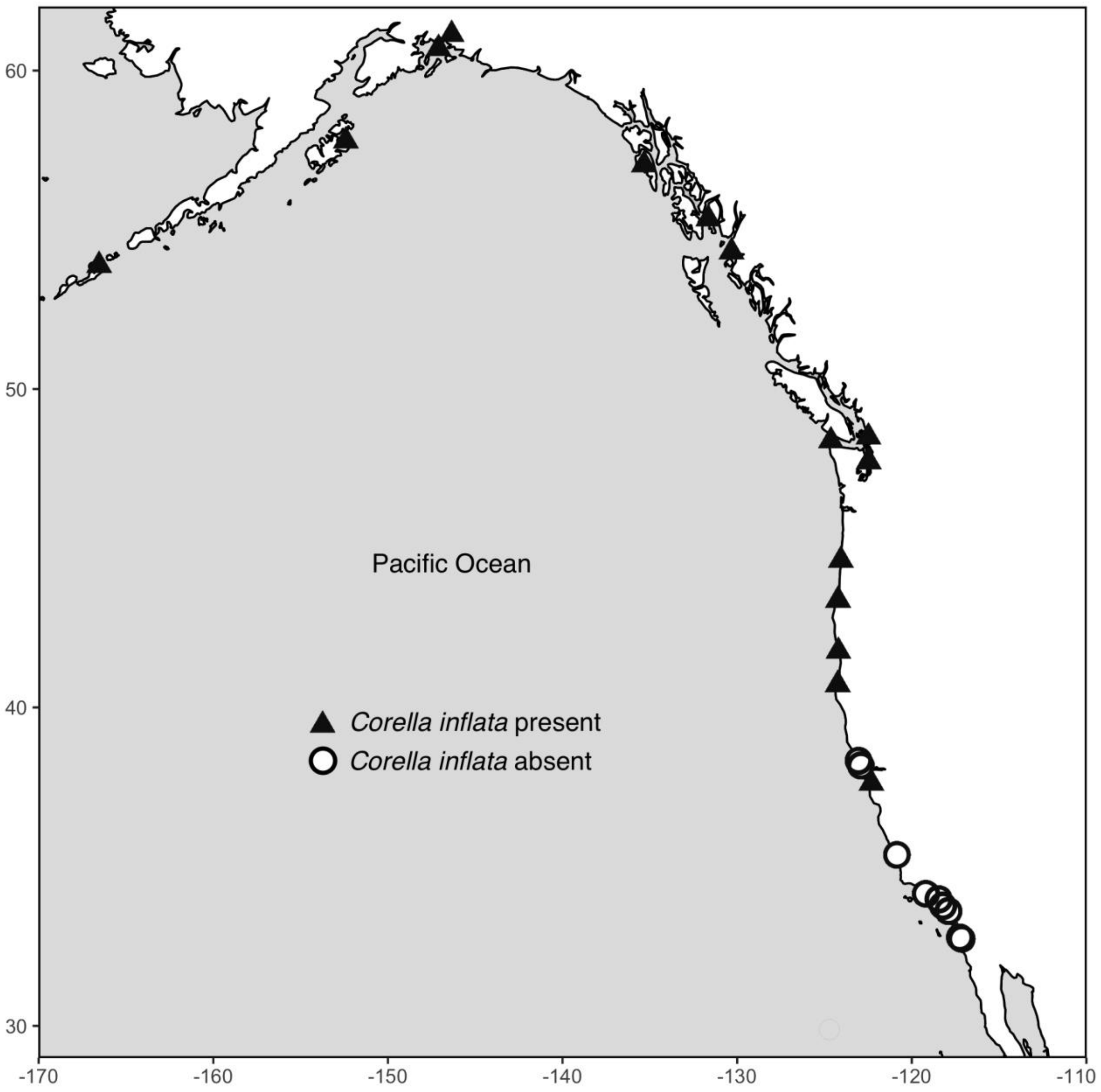

Figure 2. Map of bays showing presence and absence of *Corella inflata*. See Table 2 for list of bays.

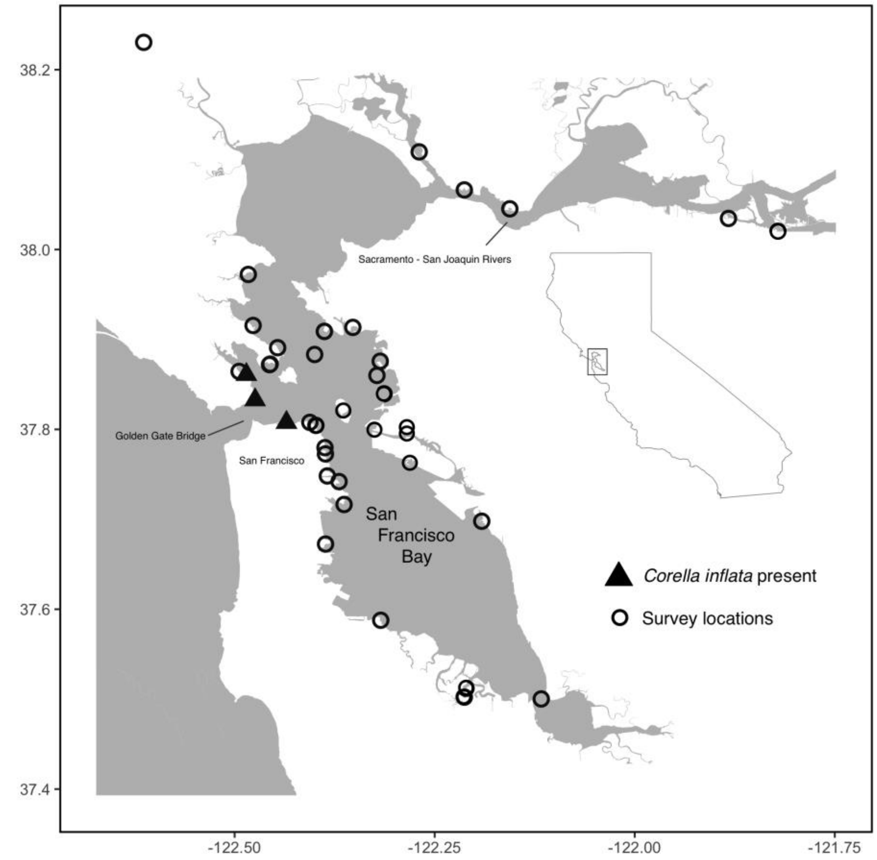

Figure 3. Map of surveyed sites in San Francisco Bay showing locations (coded sites are shown in Table 3) where *Corella inflata* is present (filled triangles) and absent (open circles). Gray-shaded regions represent bay and ocean waters. Sites were surveyed between 2000 and 2017 (see Table 3).

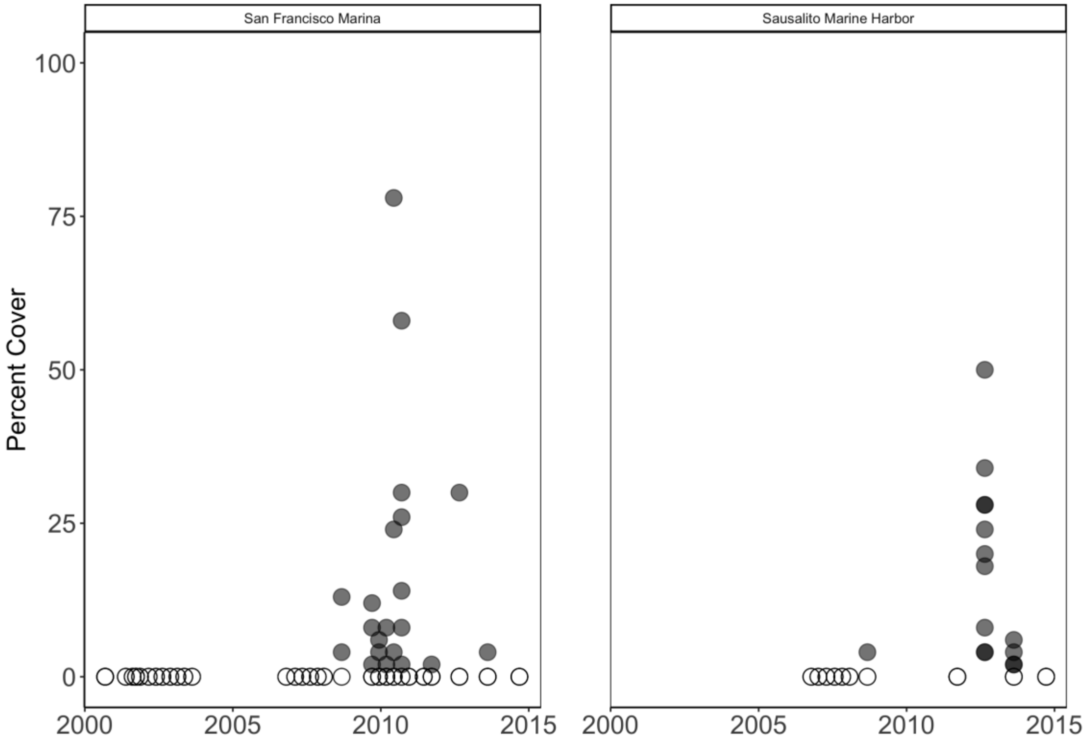

Figure 4. *Corella inflata* abundance per panel from 2000 to 2015 at two sites in San Francisco Bay in quarterly and summer surveys. Survey records are not continuous -- see Table 3 for years each site was surveyed. Open circles represent zero abundance. Filled circles represent > 0% cover, with shading indicating overlapping points.

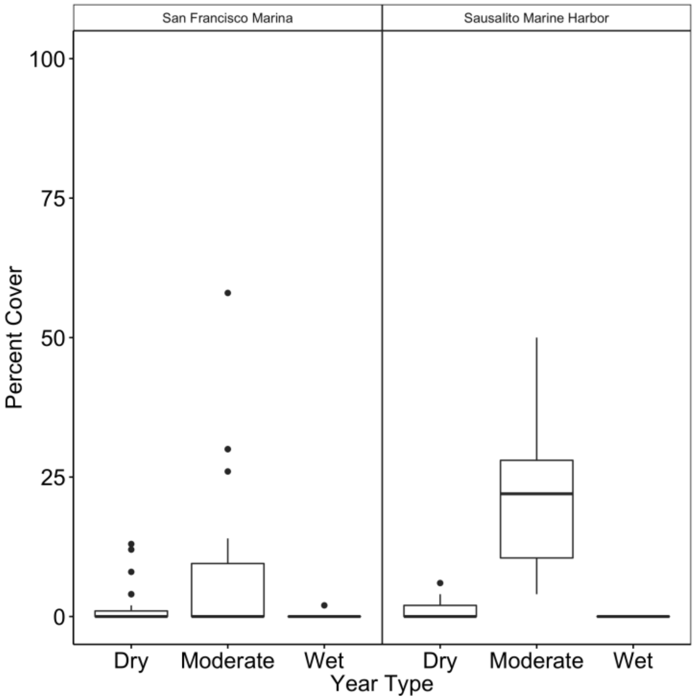

Figure 5. *Corella inflata* abundance as a function of the previous winter's precipitation regime. Year classification type corresponds to average minimum daily salinity regimes of 5 psu (wet), 20 psu (moderate), and 30 psu (dry) (Chang et al., 2018).

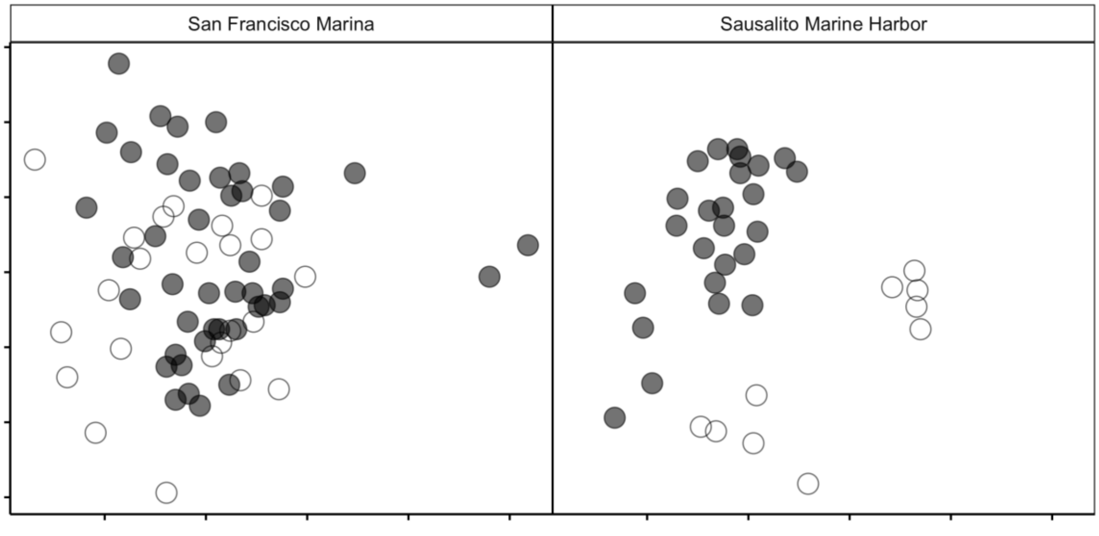

Figure 6. Non-metric multidimensional scaling plot showing change in summer community composition before vs. after *Corella inflata* invasion at San Francisco Marina and Sausalito Marine Harbor. *C. inflata* was omitted from this comparison. Open circles represent communities before *C. inflata* invasion; filled circles represent communities after *C. inflata* invasion.