

Ecological insights into the polyp stage of non-native hydrozoans in the San Francisco Estuary

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Abstract The populations of several invasive jellyfish appear to be increasing around the globe. While data on non-native hydromedusae in the San Francisco Estuary have been accumulating in recent years, little is known regarding their polyp phase. The goal of this study was to gather the first field-derived ecological data for polyp stages of *Blackfordia virginica*, *Moerisia* sp., and *Cordylophora caspia* in the estuary. Monthly fouling plates were deployed at five sites during 2007 and 2008. Settlement data indicate a seasonal presence of *B. virginica* and *Moerisia* sp., with both distribution and abundance correlated with a combination of water quality and physical parameters. *Cordylophora caspia* appeared to be present beyond the time period sampled and may be active in the system year-round. The ability

of polyps to persist month to month was low, likely due to predation by other non-native species and competition for space.

Keywords *Moerisia* · *Blackfordia virginica* · *Cordylophora caspia* · San Francisco Estuary · Hydrozoan polyp ecology

Introduction

Many jellyfish (scyphozoan and hydrozoan medusae) populations appear to be increasing around the world, most likely in response to human-induced alterations of the oceanic environment, such as global warming, eutrophication, and over-harvesting of fish stocks (Mills 2001). However, information on jellyfish biology is limited, especially on the ecology of the polyp phase compared to that of their medusae counterparts (Mills 2001). This disparity is often related to the small size and cryptic nature of the benthic stage, making them difficult to detect in the wild. Yet, knowledge of the ecology of both life stages is crucial to understanding the causes of bloom events (Mills 2001), as well as to being able to predict and manage any resulting impacts.

Four hydrozoan jellyfish, *Maeotias marginata*, *Moerisia* sp. (species indet.), *Blackfordia virginica*, and *Cordylophora caspia* (polyp phase only), have become established within the low-salinity waters of the upper San Francisco Estuary (Mills and Rees

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2000). Originally native to the Ponto-Caspian region, this quartet was likely introduced through ballast water release (Rees and Gershwin 2000). *Cordylophora caspia* was introduced as early as the 1920s (Folino-Rorem et al. 2009), while *B. virginica* has been noted since 1970 (Mills and Sommer 1995). *Moerisia* sp. was first collected in 1993 (Mills and Rees 2000). The cryptic nature of these species may have allowed them to be present, but undetected, in the system even longer. Gelatinous zooplankton are novel predators in this region and increasing trends in medusae abundance may be linked to sharp declines in four planktivorous fish species (Schroeter 2008).

Morphological descriptions of medusae (Mills and Sommer 1995; Rees and Gershwin 2000), diets (Mills and Sommer 1995; Schroeter 2008), and their seasonal trends in the estuary (Rees and Kitting 2002; Schroeter 2008) have been reported in recent years. However, information on polyp biology in the system is largely lacking. Rees and Gershwin (2000) were able to culture the earliest stages of a single *M. marginata* polyp in the laboratory, but it expired before it reached full development. *Moerisia* sp. polyps were successfully reared in the laboratory from a polyp specimen found in a sample bag at the Monterey Bay Aquarium (Mills and Sommer 1995) and also developed from ripe medusae (Rees and Gershwin 2000). Additionally, Mills and Rees (2000) found wild populations of both *Moerisia* sp. and

B. virginica polyps in the Napa River. *Cordylophora caspia* is a global invader that is commonly studied in both laboratory and field (Folino 2000; Jankowski et al. 2008). Ecological information on this species in the San Francisco Estuary, however, is limited.

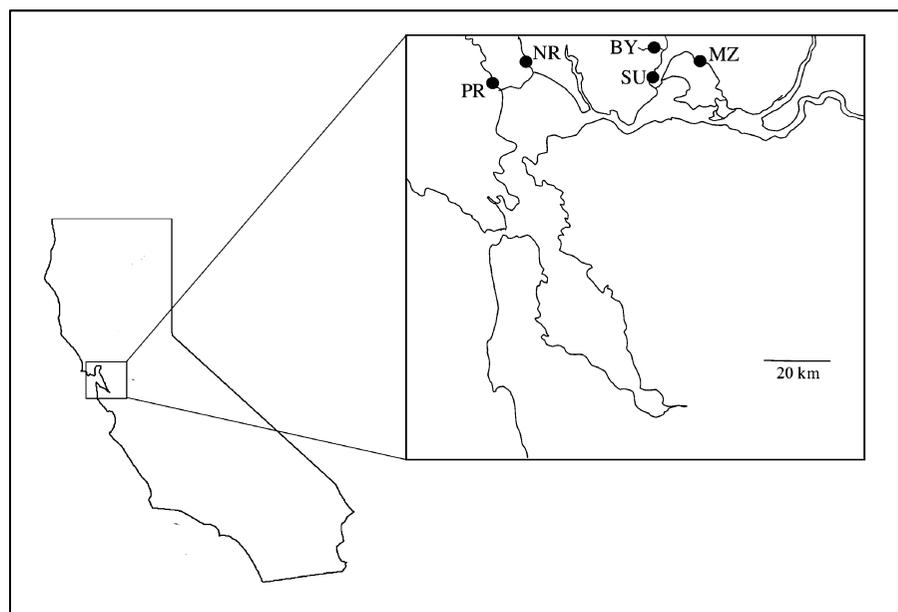
The goal of this study was to gather the first field-derived ecological data for the polyp stages of these hydrozoan species in the upper San Francisco Estuary. Specifically, we aimed to (1) document patterns of recruitment and distribution of polyps within the estuary, (2) identify the abiotic parameters associated with their distribution and abundance patterns, and (3) determine seasonal patterns of persistence of polyps in the estuary. This was part of larger study to develop a solid understanding of the ecology of both medusa and polyp phases of invasive hydrozoans in the San Francisco Estuary in order to determine their impact on the estuarine ecosystem.

Materials and methods

Field collections

Fouling arrays were hung at five brackish water locations within the estuary, with one in each of the Napa and Petaluma Rivers and one in each of three sloughs (Suisun, Montezuma, and Boynton) within Suisun Marsh (Fig. 1). Each array was constructed

Fig. 1 Map indicating sites of settlement array collections in the San Francisco Estuary, *PR* Petaluma River, *NR* Napa River, *BY* Boynton Slough, *SU* Suisun Slough, *MZ* Montezuma Slough



to hang at two levels within the water column, one at 0.5 m below the water's surface and the other 0.5 m above the bottom. Six 100 cm² sheet PVC plates, roughed with an orbital sander on both sides, were suspended from each level.

To assess monthly trends in polyp distribution and recruitment, including settlement of both planula larvae and asexually produced polyps, fouling arrays were deployed during the medusae bloom period from May–November 2007 and April–November 2008. Of the six PVC plates per array level, three were randomly oriented vertically and three were hung horizontally. This was meant to maximize the chance of capturing polyps, because we had no prior knowledge of their environmental preferences for settlement. All plates were replaced monthly, and the collected plates were preserved in 95% ethanol for laboratory work. Additionally, monthly water quality measurements of temperature, salinity, and dissolved oxygen were collected using a YSI meter; water transparency was determined with a Secchi disk.

To examine trends in polyp persistence, fouling arrays were deployed during April 2008, with all six plates per array level hung horizontally. Two randomly chosen plates per level were then collected from each site in June, August, and October 2008 and preserved in ethanol. The sample plates were replaced with new plates to maintain a constant array surface area, but these plates were not used in the analyses.

Laboratory processing

In the laboratory, the polyps were initially identified to species with genetic sequencing using ITS1 primers from Dawson and Jacobs (2001). These regional sequences were then compared to the ITS1 regions, sequenced as noted earlier, of the easily identifiable medusae stages of *Maeotias marginata* ($n = 8$; Genbank accession # GU198208), *Moerisia* sp. ($n = 5$; Genbank accession # GU198209, GU198210), and *Blackfordia virginica* ($n = 5$; Genbank accession # GU198211–GU198213), as well as a positively identified *C. caspia* polyp specimen ($n = 7$; Genbank accession # GU198206, GU19820). No variation was found at the locus within each species, making this a reliable method of species identification. After genetic confirmation, polyp species were classified based on morphology alone and all hydranths were enumerated from the plates.

Analyses

The monthly abundance numbers were standardized to number of days each plate was deployed to yield polyp recruitment rates. The rates were then scaled up to an area of one square meter. Means of these data were plotted by site and by month to allow for visual inspections of distribution and recruitment trends within the estuary.

A canonical correspondence analysis (CCA) was performed with CANOCO (CANOCO ver. 4.0) to examine relationships among monthly recruitment rates of polyps, four water quality variables, and the depth each plate was hung in the water column. The forward selection process was used to build a final model, which was then tested for significance with Monte Carlo simulations ($P < 0.05$, 499 permutations). Collection sites were added to gradients on the resultant ordination plot. The values of each of the model variables associated with the 5th and 95th percentiles of polyp recruitment were then identified to estimate an optimal range of abiotic parameters for each species. In addition, *t*-tests were performed to determine differences in recruitment on plates hung vertically versus horizontally and for top versus bottom sides of the horizontal plates.

To examine persistence of polyps over time, two-way ANOVAs, with month and treatment (monthly vs. persistence) effects, were performed on recruitment data for each polyp species found at each site (when present). These analyses included data for monthly and persistence plates from June, August, and October 2008. Tukey–Kramer HSD *post hoc* tests were then run to pinpoint the source of any variance. The loss of October plates in Boynton Slough precluded a full sample set. Thus, persistence analyses of this site were performed with a one-way ANOVA for each effect.

Results

The fouling arrays were successful at sampling polyp recruitment for all hydrozoan species except *M. marginata*, with cumulative plate totals yielding more than 1 million individuals. Visual plots of mean monthly recruitment data indicate variability among sites, species, and years (Fig. 2). *Blackfordia virginica* was present in the estuary from June through October

and had the greatest recruitment rates at the Napa River site (Fig. 2a, b). Fewer *B. virginica* were collected from the Petaluma River, Boynton, and Montezuma sites, while they were not found in Suisun Slough (Fig. 2a). This species peaked in recruitment in June and July and had higher rates in 2007 than in 2008 (Fig. 2a, b). *Moerisia* sp. recruited to plates at all sites, except for the Napa River, and had the highest rates in Montezuma Slough in 2007 and Boynton Slough in 2008 (Fig. 2c). It was collected between June and November, peaking in August and September (Fig. 2d). *Cordylophora caspia* was found at all Suisun Marsh sites but not in the Napa and Petaluma Rivers (Fig. 2e). It was collected during all sampling months, although recruitment rates were highly variable among months (Fig. 2f). These rates were highest in Boynton Slough during both years (Fig. 2e).

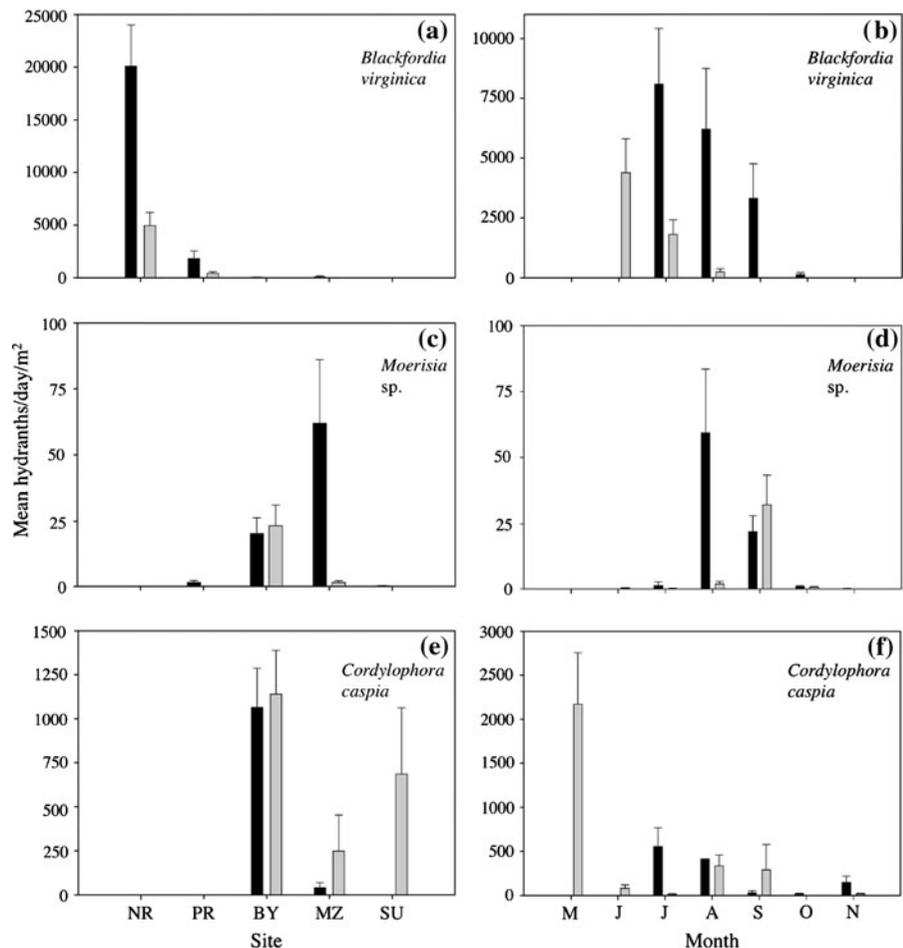
All five environmental variables put through forward selection were retained to build the final

CCA model. The first two CCA axes were associated with 54.9% (48.4 and 6.5%, respectively) of the variability in species recruitment (Table 1). Monte Carlo simulations showed statistical significance on both the first axis ($F = 108.062, P = 0.002$) and the whole model ($F = 27.971, P = 0.002$). The canonical correspondence ordination diagram (Fig. 3) plots the species scores in relation to gradients of the

Table 1 Results of a canonical correspondence analysis relating recruitment of hydrozoan polyps onto settling plates to environmental variables in the San Francisco Estuary

	Axis 1	Axis 2
Eigenvalue	0.732	0.097
Species–environment correlation	0.889	0.408
Cumulative percentage of variance explained		
Species	48.4	54.9
Species–environment relation	88.3	100.0

Fig. 2 Mean recruitment rates of hydrozoans to settling arrays at five sites within the San Francisco Estuary; **a, c, e** by site and **b, d, f** by month; NR Napa River, PR Petaluma River, BY Boynton Slough, MZ Montezuma Slough, SU Suisun Slough; Months: May–November; black bars 2007, gray bars 2008; error bars reflect standard error



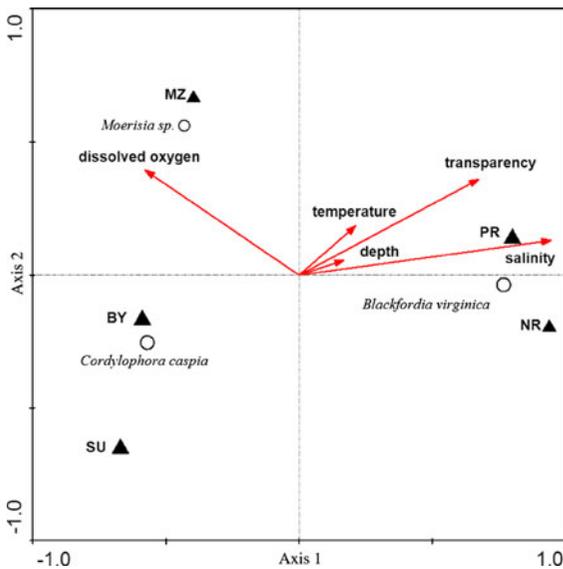


Fig. 3 Canonical correspondence ordination diagram depicting relationships among polyps of three hydrozoan species (circles), sites (triangles), and habitat variables in the San Francisco Estuary; NR Napa River, PR Petaluma River, BY Boynton Slough, MZ Montezuma Slough, SU Suisun Slough

environmental model variables. The length of each environmental variable’s vector represents its relative explanatory power (e.g., salinity explains a high degree of the variability in the species data), while direction of the vector indicates an increase (e.g., salinity is greatest toward the right side of the plot). Relative to other species, *B. virginica* polyps were associated with regions of high salinity, higher water transparency, low dissolved oxygen, high temperatures, and greater depths. *Moerisia* sp. polyps were linked to mid-levels of salinity, water transparency, temperature, and depth, as well as high dissolved oxygen. *Cordylophora caspia* was associated with low salinity, transparency, temperature, and depth, as well as mid-levels of dissolved oxygen. The three

species differed in their correlations with environmental variables measured (Table 2), as indicated by the “optimal ranges” at which they were found, based on 5th and 95th percentiles of recruitment rate (Schroeter 2008).

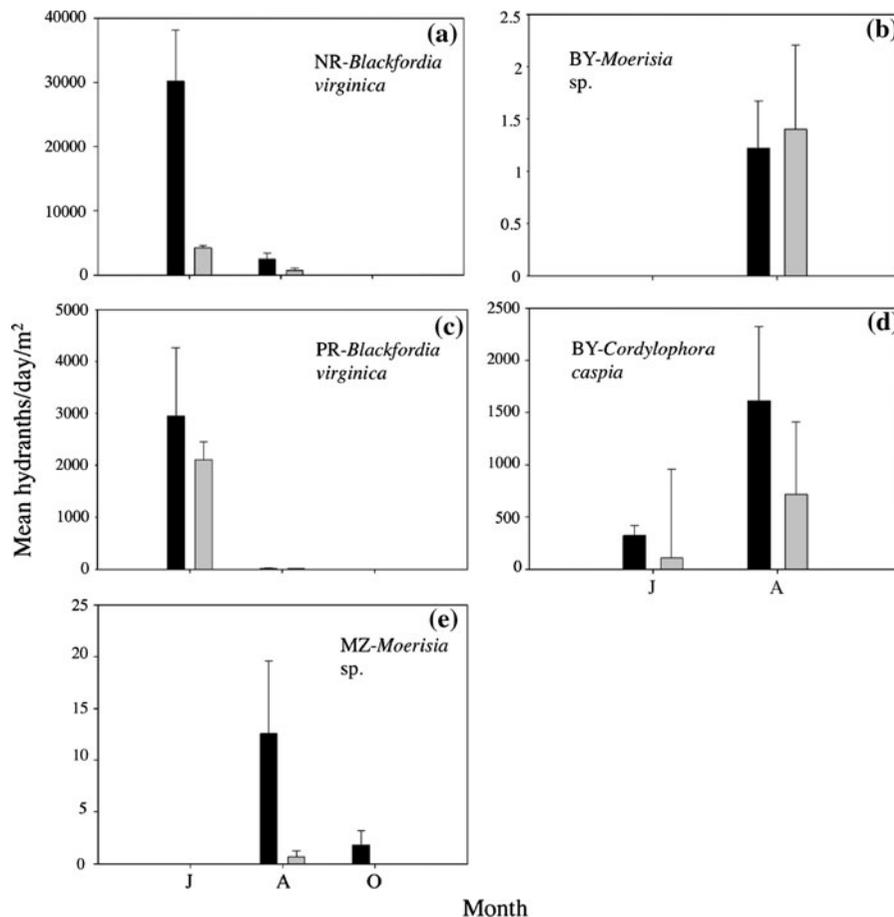
Recruitment patterns, measured as total hydranths settled per day per m², differed among species in response to the physical orientation of the plate. *Blackfordia virginica* showed significantly higher recruitment for horizontal plates ($\bar{x}_{\text{horizontal}} = 331.5$, SD = 487.3) than vertical plates ($\bar{x}_{\text{vertical}} = 113.3$, SD = 198.0; $t = 3.433$, $P = 0.001$). *Moerisia* sp. showed a similar, though non-significant trend ($\bar{x}_{\text{horizontal}} = 2.2$, SD = 4.3; $\bar{x}_{\text{vertical}} = 0.8$, SD = 1.7; $t = 1.979$, $P = 0.053$). Neither orientation was related to recruitment patterns in *C. caspia* ($\bar{x}_{\text{horizontal}} = 43.6$, SD = 78.1; $\bar{x}_{\text{vertical}} = 28.9$, SD = 66.7; $t = 1.186$, $P = 0.238$). An examination of recruitment differences between the top-side of the horizontal plate versus the bottom side, revealed that both *B. virginica* ($\bar{x}_{\text{top}} = 32.0$, SD = 64.1; $\bar{x}_{\text{bottom}} = 310.2$, SD = 454.9; $t = 5.162$, $P = 0.000$) and *Moerisia* sp. polyps were more abundant on the bottom sides ($\bar{x}_{\text{top}} = 0.6$, SD = 0.7; $\bar{x}_{\text{bottom}} = 2.2$, SD = 4.6; $t = 2.160$, $P = 0.037$). *Cordylophora caspia* exhibited no difference in abundance on either side of the plates ($\bar{x}_{\text{top}} = 23.4$, SD = 44.9; $\bar{x}_{\text{bottom}} = 23.6$, SD = 38.2; $t = 0.023$, $P = 0.982$).

Persistence plates did not show the expected cumulative effect of polyps settling over a longer time period, for any species at any site. They did, however, often mirror the monthly trends in recruitment. Two-way ANOVAs of plates collected and replaced monthly showed generally low trends in polyp persistence over time, but the details were related to site and species (Fig. 4). The Napa River, which only had *B. virginica* present in 2008, had significant differences in treatment ($F = 7.3093$,

Table 2 Optimal environmental variable ranges, represented by 5th and 95th percentile, for hydrozoan polyps recruitment onto settling plates in the San Francisco Estuary

Variable	<i>Blackfordia virginica</i>	<i>Moerisia</i> sp.	<i>Cordylophora caspia</i>
Salinity (‰)	14.9–22.2	4.6–21.8	1.4–8.9
Temperature (°C)	20.0–23.1	18.9–22.1	18.1–23.5
Dissolved oxygen (mg/l)	2.3–6.3	5.7–6.9	4.6–7.6
Water transparency (cm)	30.5–91.5	32.0–60.0	12.0–55.0
Plate depth (m)	0.3–2.7	0.3–1.5	0.3–1.2

Fig. 4 Mean recruitment rates of hydrozoans to monthly and persistence settling arrays at five sites within the San Francisco Estuary; *NR* Napa River, *PR* Petaluma River, *BY* Boynton Slough, *MZ* Montezuma Slough, *SU* Suisun Slough; Months: June, August, and October; *black bars* monthly plates, *gray bars* persistence plates; *error bars* reflect standard error



$P = 0.0124$), month ($F = 10.5657$, $P = 0.000$), and their interaction ($F = 6.2854$, $P = 0.006$). Tukey tests revealed that these results were due to extremely high polyp recruitment numbers on monthly plates collected in June. There were no differences among any other monthly or persistence plates. Plates from the Petaluma River that tested solely for *B. virginica* showed an effect of month only ($F = 9.0323$, $P = 0.001$). Multiple comparison tests identified that both monthly and persistence plates had high recruitment in June, compared to other months. Polyps in Boynton Slough, due to the loss of October persistence plates, were analyzed as one-way ANOVAs for the treatment effect for each of the *Moerisia* sp. and *C. caspia* and neither was significant. Montezuma Slough plates, analyzed for *Moerisia* sp. persistence, were also not significant. Persistence plates from Suisun Slough did not contain any polyps and therefore were not compared to monthly plates.

Discussion

Distribution and abundance

The polyp phases of *Moerisia* sp. and *B. virginica* follow the common recruitment pattern in benthic hydroids in temperate waters, showing a peak in productivity during spring and summer, which slows down in fall and winter (Coma et al. 2000). Polyps that appear the following season are likely to be either coming from an existing population of active individuals from an alternate location or re-generating after a period of dormancy. The re-vitalization of polyp colonies when optimal seasonal water quality parameters are reached may be a strong indication of the latter (Calder 1990). Dormancy is a common method of survival until optimal conditions that promote growth are restored and is seen in a variety of marine taxa (Boero et al. 2008). Thus, the closely

related *M. lyonsi* is known to form a durable cyst resting stage that gives rise to the next year's population (Purcell et al. 1999). There is currently no information available about a resting stage of *B. virginica*, but their rapid seasonal reappearance in the Napa and Petaluma Rivers strongly suggests it is likely to be present.

Cordylophora caspia appeared to follow a different recruitment pattern with little seasonal influence. Although our sampling was limited only to the period around medusae blooms, fish dietary studies from Suisun Marsh noted a year-round presence of the hydroid in this system (Matern and Brown 2005). Similarly, a study by Calder (1990) indicates that it also remains active throughout the year in warmer waters along the coast of South Carolina. *Cordylophora caspia* has successfully invaded a broad latitudinal range along the eastern coast of North America, extending from Quebec to the Caribbean Sea (Calder 1990). In extreme salinities (Kinne 1971) and temperatures (Fulton 1962), likely associated with the two ends of such a range, it stops growth and may form diapause stages, known as "menonts," by keeping dormant tissues within stems and stolons (Roos 1979). The year-round presence of *C. caspia* in the San Francisco Estuary indicate that temperature and salinity ranges found in this system remain within this species' tolerance levels.

The reason for lack of *M. marginata* polyps on the plates remains unknown and may be related to polyp size or substrate preference. Schroeter (2008) stated that the extremely rapid increase in abundance of medusae in relation to environmental factors indicates that polyps are present in the system, but information on them is limited. The single early stage polyp cultured by Rees and Gershwin (2000) grew on detritus, rather than the glass of its holding vessel. This may indicate that *M. marginata* polyps prefer soft substrate settlement or it may simply be a lack of preference for glass. Our inability to find this species may also be due to its small, cryptic nature. The single primary polyp reared in the laboratory was only ~0.1 mm in height and lacked tentacles (Rees and Gershwin 2000). This specimen expired before it could develop further. Thus, morphology of the fully mature stage is unknown. A similarity to the primary polyps of the freshwater jelly *Craspedacusta sowerbii* has been noted (Rees and Gershwin 2000) and *M. marginata* has been named as the extant sister

group to freshwater jellies (Collins et al. 2006). Therefore, it is possible that the small, simple polyps of *C. sowerbii* may be similar to *M. marginata* polyps and were overlooked on the plates. Additionally, the ethanol preservative may have shrunk polyps down to an unrecognizable specimen. Future samples may require alternate plate materials and formalin preservation.

Physical correlates

The CCA results demonstrate that water quality factors are strongly correlated with the majority of variation in our polyp data and thus explain a large portion of our seasonal observations. It is commonly believed that temperature is the main driver of seasonal hydroid patterns (Gili and Hughes 1995). In our system, while temperature was a factor of influence, it was salinity that had the most importance. The San Francisco Estuary has a seasonally dynamic salinity regime compared to the more stable marine systems involved in most hydroid research (Boero 1984). Similarly, work in tropical regions with rainy seasons and related salinity shifts has noted salinity as an important variable in seasonal hydroid abundance (reviewed in Gili and Hughes 1995). Salinity also was a major factor for *M. lyonsi* polyps in Chesapeake Bay (Ma and Purcell 2005a, b). Salinity did not appear to dictate a seasonal presence of *Cordylophora*, which may be due to this species' remarkable ability to physically remodel itself under changing saline conditions to maintain effective metabolic function (Kinne 1964).

Surprisingly, dissolved oxygen levels were highly correlated with higher recruitment rates of *Moerisia* sp. and *C. caspia* in this study. While many medusae are well known for their abilities to withstand low oxygen conditions, the limited information about tolerance in the polyp stage for some species suggests otherwise. Reduced abundances of hydromedusae in the Adriatic sea, for example, were hypothesized to result from an intolerance of polyps to depleted oxygen levels in the benthos (Benovic et al. 1987). Similarly, polyps of the scyphozoan *Chrysaora quinquecirrha* had reduced long-term survival and asexual reproduction rates in laboratory treatments with low dissolved oxygen levels compared to those with higher levels (Condon et al. 2001).

Water transparency is a known variable that influences hydroid distribution. *Blackfordia virginica* recruitment was greatest at high (for the estuary) levels of transparency. An increase in water transparency in this system is often related to reduced levels of suspended sediment and detrital matter. This in turn may reduce contact damage to their small, fragile polyps. Increased light levels may also result in an increase in prey abundance. *Cordylophora caspia* showed an opposing trend, thriving in less transparent sites, which could be a behavior associated with the avoidance of filamentous algae substrate competitors (Gili and Hughes 1995).

Some alternative biotic factors that may influence trends of hydrozoan polyps include food availability and strategic temporal staggering of seasonal cycles with those of substrate competitors (Bavestrello et al. 2006). Other species have been known to possess some form of internal clock, going through the motions of seasonality even when kept at constant laboratory conditions (Brinkmann 1964; Brock 1975). Further investigation would be required to test these alternatives.

The interplay of abiotic factors in relation to plate orientation may explain some of the trends observed in this study. For example, the fact that both *Moerisia* sp. and *B. virginica* polyps were at higher densities on plates hung horizontally versus vertically is likely related to water flow. The San Francisco Estuary is a tidally driven system. Many hydroid species will grow perpendicularly to the major direction of flow, with benefits of increased water exchange lending itself to rapid replenishment of oxygen and planktonic prey (summarized in Boero 1984) while also acting to effectively disperse recently budded medusae (Gili and Hughes 1995). The preference of *B. virginica* to settle on the bottom side of horizontal plates may be a strategy to avoid being covered with sediment, because this species is quite small, to reduce competition with filamentous algae, or to expel self-generated waste products from their proximity (C. Widmer, personal communication). The lack of position preference for *C. caspia* colonies may be due to their sets of stacked annular rings at branching points. Similar annuli in *Obelia longissima* were found to significantly reduce local soft tissue damage during flexion (Hunter 1987), such as that induced by water flow.

In terms of settlement substrate, it is clear from this study that *Moerisia* sp., *B. virginica*, and

C. caspia will recruit to a wide variety of substrates including PVC. Calder (1990) collected *M. lyonsi* polyps from the Chesapeake Bay growing on shells of the mussel *Brachidontes recurvas* and on detrital matter. This species was also observed on oyster shells (Purcell et al. 1999). *Blackfordia virginica* was collected in the Napa River on both floating docks and shells of the barnacle *B. improvisus* (Mills and Rees 2000). *Cordylophora caspia* is well known for its ability to settle on a variety of surfaces, including intake screens (Folino-Rorem and Indelicato 2005), rocks, floating, and emergent vegetation (Roos 1979), and even the dorsal surface of a live cyprinid fish, the Sacramento splittail, *Pogonichthys macrolepidotus* (A. Wintzer, unpublished observation)!

Persistence

Like most hydrozoans, the polyp phases of non-native jellyfish in the San Francisco Estuary are exceptional pioneers, settling early on the fresh surfaces of our array plates. Boero (1984) credited the taxa's early establishment success to its predisposition for rapid settlement and growth. High estimates (hydranths/day/m²) for single settling plates in this study included 124,976 *B. virginica*, 1,107 *Moerisia* sp., and 22,998 *C. caspia*. Boero (1984) also noted that, as in this case, after initial settlement, most hydrozoans are then often out-competed for space by more robust species. In the persistence study, polyps were competing, unsuccessfully, for space with a number of other non-native fouling species, including the Australian tubeworm, *Ficopomatus enigmaticus*, the common sea grape, *Molgula manhattensis*, the bay barnacle, *Balanus improvisus*, and a particularly aggressive unidentified bryozoan species.

Polyp persistence may have also been limited by presence of predators commonly associated with the settling plates. Both the shimofuri (*Tridentiger bifasciatus*) and shokihaze (*T. barbatus*) gobies, native to Asia (Moyle 2002), were commonly seen resting on our plates. Gut content examinations of shimofuri gobies in the San Francisco Estuary have revealed that *C. caspia* accounted for 18–23% of diet volume and that it was a prey item consumed year-round (Matern and Brown 2005). Shokihaze gobies were also found to be *C. caspia* predators, but to a lesser degree, with it comprising up to 10% of total gut content weight depending on season (Slater 2005). Several other

species of Suisun Marsh fishes have been found to consume hydroids, but in very small amounts (<1% total weight). These include native Sacramento split-tail and prickly sculpin (*Cottus asper*), as well as non-native striped bass (*Morone saxatilis*) and yellowfin goby (*Acanthogobius flavimanus*) (Feyrer 1999). The low percentages for these species, however, may reflect incidental ingestion while consuming other prey items and suggest that their cropping potential on hydroids is quite low. Finally, dozens of the miniature aeolid nudibranch, *Tenellia adspersa*, were found on our settling plates. Also from the Ponto-Caspian region, this species is known to voraciously feed on benthic hydroids (Mills and Sommer 1995; Chester 1996).

Implications

There is a great need to understand ecological impacts of non-native hydrozoans in the San Francisco Estuary. Fish-monitoring studies have recently revealed sharp declines in populations of delta smelt (*Hypomesus transpacificus*), longfin smelt (*Spirinchus thaleichthys*), age-0 striped bass and threadfin shad (*Dorosoma petenense*) in the upper San Francisco Estuary (IEP 2005, 2006, 2008). A decrease in the abundance of calanoid copepods was also noted for this system (IEP 2008).

Studies are currently underway to examine the trophic implications, through both competition and larvae predation, of the medusae stage on these fishes. This, however, may only be a piece of the puzzle, because in some species the polyps are voracious predators themselves. Gili and Coma (1998), for example, noted that hydroids, which constituted less than 0.5% of biomass in a community, were able to consume 10% of the system's annual algal production. Additionally, polyps of both *Hydra canadensis* and *Craspedacusta sowerbii* can capture and consume larval fishes (Dendy 1978, Elliot et al. 1997). Further investigations will be necessary to understand the polyps' role in the trophic ecology of the estuary, and thus, total impact of these non-native jellyfish on the food web.

The reduced ecological health of the heavily modified San Francisco Estuary has resulted in plans for habitat restoration. As Rees (1999) remarked, knowledge of general habitat use of this suite of hydrozoans, as well as environmental factors that

increase populations, will be advantageous to restoration efforts, in order to minimize creation of conditions beneficial to these unwanted species. An avoidance of the "optimal" abiotic conditions given in Table 2 will negatively influence polyp survival. However, for a more effective restoration strategy, these studies should be paired with field studies on medusae that give an understanding of population dynamics of these species.

Finally, aided by unregulated ballast water transport and global shifts in thermal and salinity regimes, many jellyfish species are increasing their ranges. Each of our study species has now been identified on several continents (Kramp 1961; Paranaguá 1963; Denayer 1973; Santhakumari et al. 1997; Folino 2000; Buecher et al. 2005; Genzano et al. 2006; Bardi and Marques 2009). While some findings from this study can be applied to these systems, a continued effort to study the poorly understood polyp stage is necessary to develop predictive tools for bloom formation, ecological impact, and management decisions, as well as to determine sites vulnerable to future invasions.

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