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RESEARCH

Amazing Graze: Shifts in Jellyfish and Clam Distributions During Dry Years in the San Francisco Estuary

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ABSTRACT

Aquatic invasive species have drastically changed how the San Francisco Estuary functions. During the past 2 decades, the effects of invasive species in the estuary may have increased in response to frequent and severe drought conditions. The invasive overbite clam (*Potamocorbula amurensis*), and the Asian Clam (*Corbicula fluminea*) have well documented consequences on the estuarine food web, but their responses to drought are not well understood. Another invasive species, the jellyfish *Maeotias marginata,* can further affect the food web, but these effects have not been studied. We investigated the population responses of these invasive species to dry years and their potential effects on the pelagic food web using data from the Interagency Ecological Program's monitoring surveys. We found *M. marginata* rapidly moves upstream with changing salinities during dry years, though it sees its highest abundance during high-outflow years in Suisun Bay and Suisun Marsh. Grazing rates of *M. marginata* in the estuary have not been quantified but are potentially high during localized blooms. The two invasive clams overlap in distribution, but have opposite population responses to drought conditions, with increases in *P. amurensis* densities and decreases in *C. fluminea* densities in dry years. With increasing *P. amurensis* densities, the clams' combined annual filtration rates increase during drier years in the confluence and Suisun Marsh. Like *M. marginata*, *P. amurensis* also shifts upstream during droughts, but because adults cannot move immediately with a change in salinity, the population center of distribution shifts upstream the year after a dry year as a result of juvenile recruitment. If multiple dry years occur in a row, and both *P. amurensis* and *M. marginata* move upstream together, their effects on the food web could be compounded, and phytoplankton and zooplankton biomass could steeply decline in the confluence, affecting higher trophic levels in the estuary.

KEY WORDS

Potamocorbula amurensis, Corbicula fluminea, Maeotias marginata, jellyfish, clams, invasive species, benthic invertebrates, gelatinous zooplankton, grazing, drought

INTRODUCTION

Invasive species have drastically altered aquatic ecological systems world-wide, and invasive invertebrates can have sweeping effects on freshwater, marine, and estuarine systems. Filter-feeding invertebrates can vastly alter ecosystem structures by reducing resources available to native species and higher-order consumers. For example, increases in abundance of jellyfish worldwide have caused collapses in fish stocks as a result of competition and predation (Richardson et al. 2009), most notably in the Black Sea where the invasive ctenophore *Mnemiopsis leidyi* caused a crash in planktivorous fish abundance and diversity (Shiganova 1998). Similarly, in the Baltic Sea, invasive cnidaria and ctenophores have been linked to decreased populations of zooplankton and increased chlorophyll concentrations (Schneider and Behrends 1998; Jaspers et al. 2021; Stoltenberg et al. 2021). Jellyfish may form "blooms" that cause far-reaching, short-term effects on estuaries (Lars Johan et al. 2005; Manzari et al. 2015; Amorim et al. 2018; Gueroun et al. 2020), and the collapse of these blooms can negatively affect water quality (Baliarsingh et al. 2020; Guy–Haim et al. 2020).

Invasive bivalves can also have widespread effects on water quality and on benthic invertebrate, phytoplankton, and zooplankton abundance, as exemplified by the zebra mussel (*Dreissena polymorpha*) invasion of the Laurentian Great Lakes (Strayer 2009), as well as many other aquatic ecosystems across North America (Higgins and Zanden 2010; Spear et al. 2022; Lovejoy et al. 2023). In another example, in the Potomac River on the East Coast of the US, the Asian clam (*Corbicula fluminea*) has had sweeping effects on the ecosystem, including water clarity, submersed vegetation, fish, and birds (Phelps 1994), with similar effects on additional aquatic systems in its invasive range (Europe and the Americas) (Crespo et al. 2015; Labaut et al. 2021; Ferreira–Rodríguez et al. 2022)

Consequences of invasive species can be exacerbated by extreme events, such as floods, droughts, and heat waves that allow populations of non-native species to flourish to the detriment of native species. For example, on the Iberian Peninsula, frequent droughts and a heavily managed water system have increased the dominance of wide-spread invasive species that have a high tolerance for disturbance (Ibáñez and Caiola 2013), and droughts in the San Francisco Estuary have been linked with the success and proliferation of invasive aquatic species in this region (Winder et al. 2011). Climate change may also increase invasion success as temperature regimes are pushed to the limits of native species' tolerances (Rahel and Olden 2008). Climate change is contributing to more frequent, prolonged, and severe droughts in the western US (Wetz and Yoskowitz 2013; Williams et al. 2020; He 2022). Understanding how droughts may change populations of invasive species, particularly of benthic and pelagic invertebrate grazers, will be important in determining which invasive taxa will be most problematic for aquatic ecosystems in the future.

In the upper San Francisco Estuary (the Sacramento–San Joaquin Delta, Suisun Bay, and Suisun Marsh, hereafter "estuary"), very high rates of invasions and high percentages of invasive species now dominate the aquatic ecosystem (Cohen and Carlton 1998). At the top of the food web, non-native fishes may predate on smaller fishes and zooplankton (Nobriga and Smith 2020). At the bottom of the food web, invasive submerged aquatic vegetation has significantly altered the community of primary producers (Cloern et al. 2016). At the primary consumer levels, non-native copepods have received extensive study (York et al. 2013; Kimmerer, Ignoffo, et al. 2018), as have clams (Crauder et al. 2016).

Two invasive aquatic species in particular— the clam *Potamocorbula amurensis* and the jellyfish *Maeotias marginata*—are now dominant components of the ecosystem in Suisun Bay and Suisun Marsh (Mills and Rees 2000; Peterson and Vayssieres 2010). These taxa graze on pelagic phytoplankton and zooplankton (Greene et al. 2011; Kimmerer and Thompson 2014), and therefore may compete with native pelagic fishes

for resources, but their response to drought and changes to flow remains under-studied.

Study Species

Maeotias marginata

Research to date has shown that *M. marginata* was present in the estuary as early as 1959, based on unpublished field notes (Mills and Rees 2000), but not officially documented until 1992 (Mills and Sommer 1995), and then quickly increased in abundance and spatial distribution after 1995 (Mills and Rees 2000; Baumsteiger et al. 2018). *Maeotias marginata* has two distinct life stages—the benthic polyp and the pelagic or benthic medusae—and can reproduce sexually or asexually via budding (Mills and Sommer 1995). When conditions are favorable, polyps release larval medusae into the water column, which spawn daily once mature. Time to sexual maturity for *M. marginata* is unknown, however a co-occurring species in the estuary, *Moerisia lyonsi,* can develop within 8 days (Ma and Purcell 2005). *Maeotias marginata* is typically found in salinities of 2 to 9, and its abundance is correlated with high temperatures during summer and fall (Schroeter 2008).

M. marginata also employs different feeding strategies depending on where it is in the water column. When swimming to the surface, *M. marginata* consumes pelagic prey, mostly calanoid copepods and other planktonic organisms, including larval fish (Mills and Sommer 1995; Wintzer et al. 2011). After surfacing, individuals flip over and sink to the bottom where they consume benthic organisms such as amphipods. Employing two feeding strategies increases their chance of finding patchy prey resources (Schroeter 2008; Wintzer et al. 2011). However, despite *M. marginata's* high density and dietary overlap with pelagic fishes—particularly in Suisun Marsh—long-term trends in response to changes in salinity or flow, and how it affects the food web, remain relatively understudied.

Invasive Clams

Two invasive clam species occur in Suisun Marsh and the estuary at abundances high enough to affect the ecosystem: *C. fluminea*, which was first found in the estuary in 1945 (Hanna 1966), and *P. amurensis*, which was introduced in 1986 (Nichols et al. 1990). Both clams filter feed phytoplankton and zooplankton from the water column (Kimmerer et al. 1994; Bolam et al. 2019), shift their distributions based on salinity, and overlap in low-salinity regions (salinity of <2) (FLOAT MAST 2022). There are also distinct differences in environmental tolerance and life history between these two species: *P. amurensis* has a wider salinity range and is more common in brackish water (Paganini et al. 2010), can reproduce 2 months after settling, is less than half the size at maturity, and is shorter lived at a maximum of 2 years vs. 4 to 7 years for *C. fluminea* (Eng 1977; Carlton et al. 1990). As a result, we expect that *P. amurensis* is more likely than *C. fluminea* to rapidly increase in abundance and shift its distribution in response to increasing salinity during droughts.

Another important difference between these species is their filtration (i.e., feeding) rate. *P. amurensis* has ~4x the filtration rate as *C. fluminea* (Cole et al. 1992; Werner and Hollibaugh 1993), and after the invasion of *P. amurensis* in the estuary in 1986, significant decreases in phytoplankton biomass and resulting changes to the food web occurred (Nichols et al. 1990; Brown et al. 2016). The invasion by *P. amurensis* has caused a 5-fold decrease in phytoplankton biomass (Alpine and Cloern 1992), a shift to dominance by smaller-celled phytoplankton (Kimmerer and Thompson 2014), and a decline in diatoms (Kimmerer 2005). Decreases in phytoplankton can affect higher trophic levels (e.g., zooplankton and fish) by decreasing food availability and increasing competition. Thus, zooplankters such as *Eurytemora affinis* and *Neomysis mercedis* have also decreased during this time (Kimmerer and Orsi 1996). The resulting changes to the lower food web have led to food limitation and shifts in diets and distributions of fishes in the estuary, likely contributing to their decline (Bennet and Moyle

1996; Sommer et al. 2007). If the abundance of *P. amurensis* increases, or their distribution shifts upstream during drier years, then overall grazing rates by invasive clams may increase, magnifying their effect on the food web.

In this paper, we utilize several long-term datasets on abundance, distribution, filtration, and grazing rates of *P. amurensis, C. fluminea,* and *M. marginata* to investigate how drought conditions and invasive species may interact to stress the pelagic food web. Specifically, our research questions are:

1. How does the abundance of *P. amurensis, C. fluminea,* and *M. marginata* change during drought conditions?

2. How do the distributions of *P. amurensis* and *M. marginata* shift during drought conditions?

3. Is salinity the best explanatory mechanism behind these changes?

4. What are the implications of changes to *P. amurensis* and *M. marginata* abundance and distribution for the food web during drought conditions?

METHODS

Hydrology

To assess the effect of drought on *P. amurensis, C. fluminea,* and *M. marginata*, we used the Sacramento Valley Hydrological Index (hereafter, "Sacramento Valley Index") and associated classifications to define water year types. This index is based on modeled unimpaired flow in the major rivers of the Sacramento Valley, and each year is classified as "Critically Dry," "Dry," "Below Normal," "Above Normal," or "Wet," depending on the index value. (See CDWR 2022 for details.) It's important to note that in hydrologically modified systems such as this estuary, an index of unimpaired runoff does not directly describe the amount of flow through the estuary. The Sacramento Valley Index relates to the amount of water available to upstream reservoirs, but the management decisions that dictate dam releases

are the final determinant of inflows to the estuary (Brown and Bauer 2010). There is a tight correlation between Sacramento Valley Index and Delta Outflow on an annual basis, but many other hydrologic factors control the flows organisms experience on a daily basis (Bosworth et al., this issue; Hartman et al., this issue).

Density and Responses to Drought Conditions

Jellyfish

Data on *M. marginata* was combined from four long-term monitoring surveys that sample in the Delta, Suisun Bay, and Suisun Marsh between June and October. These surveys were: the California Department of Fish and Wildlife's (CDFW) Summer Townet (STN) Survey, which samples June through August; the CDFW's Fall Midwater Trawl (FMWT) Survey, which samples September and October; the CDFW's San Francisco Bay Study (Bay Study) midwater trawl, which samples year-round; and the University of California–Davis' (UCD) Suisun Marsh Fish Survey (Suisun), which also samples year-round. None of these surveys target gelatinous zooplankton, so most of them did not begin recording gelatinous zooplankton until recent years, and they use varying types of nets and mesh sizes, which, based on size, likely retain jellyfish with varying efficiency. None of these nets have been evaluated for their ability to catch *M. marginata*. Despite this variation in catchability, the data can still provide some insights into *M. marginata* abundance trends and potential correlations with abiotic conditions. These data likely underestimate jellyfish abundance, particularly in the fall when only larger-meshed nets are used, but because the gear types are the same between years, it these data can still allow for inferences into general trends. It These data also provide a starting point to inspire future, directed studies of jellyfish status and trends.

The FMWT and Bay Study have recorded jellyfish catch consistently since 2000, and STN has recorded catch since 2007. *Maeotias marginata* catch for the three CDFW surveys were converted to catch-per-unit-effort (CPUE) by dividing the catch by the volume of water sampled, as
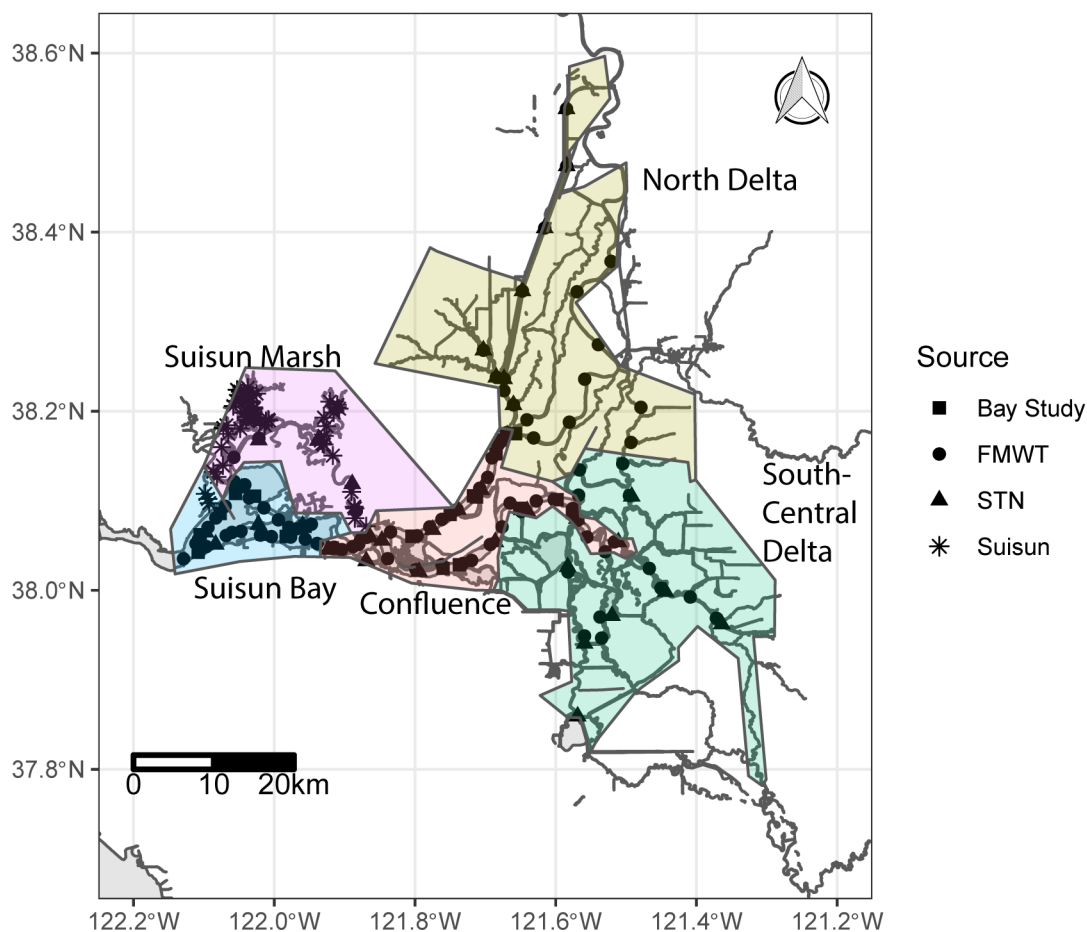
Figure 1 Jellyfish sampling locations from Summer Townet (STN), Fall Midwater Trawl (FMWT), San Francisco Bay Study (Bay Study), and Suisun Marsh Survey (Suisun)

calculated from measurements with a General Oceanics Flowmeter, and multiplying by 10,000 to give us catch per 10,000 cubic meters of water. The UCD Suisun Marsh Study samples using an otter trawl and has recorded *M. marginata* catch since the survey began in 1980. *M. marginata* catch for the Suisun survey was converted to CPUE by dividing the catch by the volume of water sampled, which is calculated based on tow area (distance traveled times width of net, multiplied by the height of the net). This was multiplied by 10,000 to give us catch per 10,000 cubic meters of water. See Appendix A for additional details on sampling locations and net specifications for each survey.

We divided the data to include only June through October of 2007 through 2020, since all surveys

consistently recorded jellyfish catch over these years, and exploratory plots of the data showed that these are the months of the year with consistent catch of *M. marginata*. We further sub-set the data to include stations in the estuary from West Sacramento in the north to Vernalis in the south and Carquinez Straight in the west to Stockton in the east (Figure 1). This comprises the Legal Delta, Suisun Marsh, and Suisun Bay as defined by the Delta Plan (DSC 2013). Data were categorized by regions as shown in Figure 1. We further sub-set the data to include only catches of *M. marginata*, because this species represented 99.25% of jellyfish caught by these surveys in these regions over this period. Other species identified in the region were *Blackfordia virginica* (0.088% of total catch), *Pleurobrachia* sp. (0.56% of total catch), and *Polyorchis* sp. (0.096%

of total catch). Where necessary, we standardized units and accounted for differences in effort by calculating a single, average CPUE per region and month to use for statistical analyses and data visualization.

We excluded catch in November through May for all regions and year types, as well as catch in the North and South-Central regions because of limited or no catch. To assess how drought conditions affect *M. marginata* abundance, we used log-transformed data and used a generalized linear mixed model to test the effect of water year type (WYT) and region on *M. marginata* CPUE using the equation:

$$\log(\text{CPUE}) \sim \text{Region} * \text{WYT} + \text{Random(Year)} \qquad \textbf{Eq 1}$$
$$+ \text{Random(Month)}$$

We included random effects of month and year to account for differences between years, and changes over the course of the season. Year was coded as a factor and Month was coded as a continuous variable. Water year type was included as an ordered factor where Critical < Dry < Below Normal < Wet. No Above Normal years occurred between 2007 and 2020. By including WYT as an ordered factor, the model looked for a linear relationship between the response and the predictors *across* levels, rather than comparing each level to the other levels individually.

The "regions" used for analysis are static, but gelatinous zooplankton respond to dynamic shifts in water quality such as salinity that can vary within regions as a result of drought conditions. Therefore, to test whether changes in abundance across the regions arose from changes in salinity that resulted from drought or the result of other drought conditions, we calculated the observed salinity niche by calculating the catch-weighted mean and standard deviation in salinity. We then sub-set the dataset to include only samples taken in salinities that were +/– 1 SD from the catch-weighted mean salinity. This is the sample region where 68% of the catch occurred. We tested whether catch in this salinity range was sensitive to WYT using the equation:

$$\log(\text{CPUE}) \sim \text{WYT} + \text{Random(Year)} \qquad \textbf{Eq 2}$$
$$+ \text{Random(Month)}$$

All models were fit using the *lmer()* function from the 'lme4' package Version 1.1-31 (Bates et al. 2022) in R version 4.2.2 (R Core Team 2022).

Clams

Clams were sampled by two different surveys, both conducted by the California Department of Water Resources (CDWR). The first survey is the long-running benthic invertebrate survey of the Environmental Monitoring Program (EMP; Wells and IEP 2022), which has sampled monthly at ten sites from San Pablo Bay upstream to endpoints at Clifton Court Forebay, near Stockton, and up the Sacramento River as far as Rio Vista (Figure 2). This survey has occurred at these ten sites from 1996 to present, and from 1975 to 1996 at a smaller subset of those sites along with others since discontinued. The ten EMP sites sampled since 1996 are hereafter referred to as "EMP core sites," and the dataset that encompasses sites sampled since 1975 as "EMP long-term data." See Wells and IEP 2022 for full metadata (Wells and IEP 2022).

The second survey is a spatially extensive survey performed twice a year in May and October from 2007 through 2019 (except for 2013 and 2016), designed to augment EMP data. CDWR staff who designed the survey chose sites in the same geographic range as the EMP survey, using a Generalized Random Tessellation Stratified (GRTS) sampling design (Stevens and Olsen 2004), which stratified site selection by water body type, ensuring adequate sampling effort in habitats with smaller total areas. Staff sampled 175 sites each year from 2007 through 2017 (sampling did not occur in 2013 and 2016), 100 sites in 2018, and only 50 core sites in 2019. Fifty of the sites sampled were the same from year to year (core sites), and additional sites were newly selected each year using the same GRTS design. This survey is hereafter referred to as "GRTS."

The two surveys are complementary in that the EMP survey is temporally intensive but spatially limited (up to ten sites chosen to represent main rivers and bays, done every month), while the
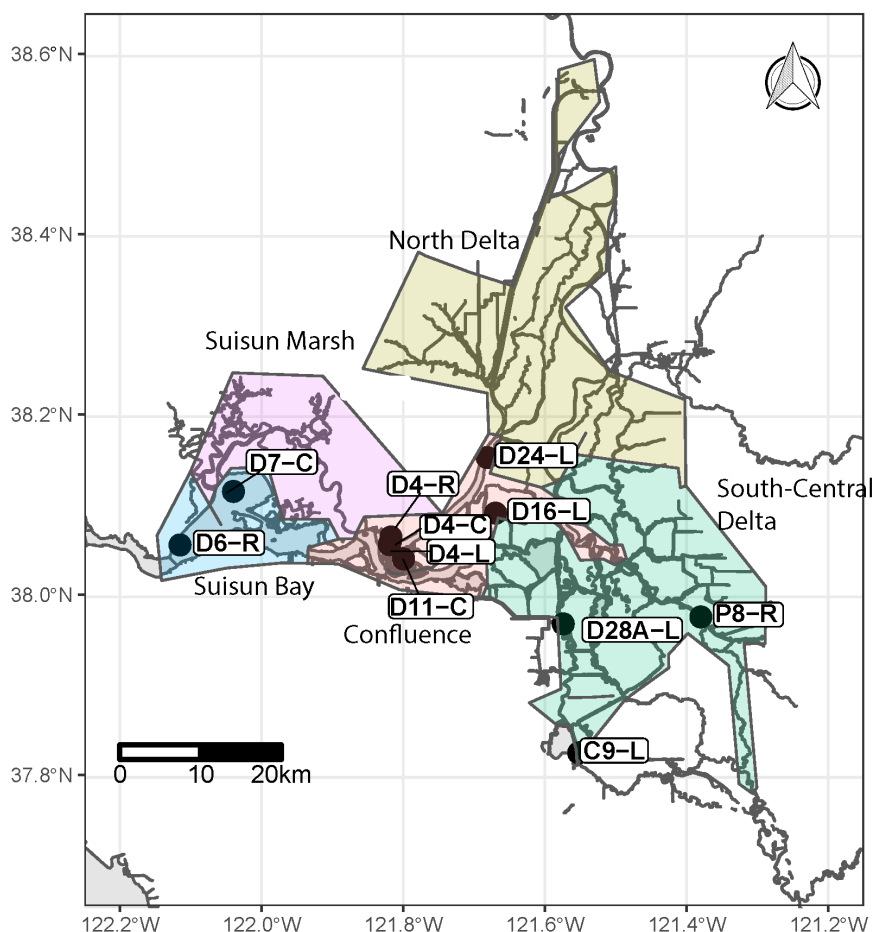
Figure 2 Environmental Monitoring Program's long-term benthic invertebrate sampling locations. Note that there were not sufficient samples in Suisun Marsh or the North Delta for long-term analysis. All but the 50 core GRTS sampling locations were randomly generated each year and are too numerous to display here but covered much of the same area except for the North Delta, which was much less sampled than in the jellyfish surveys.

GRTS survey was temporally limited but spatially intensive (sampling twice a year, at a minimum of 50 and at most 175 randomly chosen sites that extended into smaller water bodies, such as sloughs and canals). Data from these surveys were sub-set to include only stations within the area defined above for the jellyfish data, within the following regions: the North Delta, the confluence, Suisun Marsh, Suisun Bay, and the South-Central Delta (Figure 2).

For each survey, staff used a Ponar dredge to collect 0.052 m^2 of benthic area to a maximum sediment depth of 10 cm at each site. The sample was rinsed over a 0.595-mm sieve and all *P. amurensis* and *C. fluminea* individuals were identified, enumerated, and binned by size

(e.g., 0 to 1 mm, 1 to 2 mm). Staff converted clam densities to individuals m^{-2}.

Staff converted clam counts and sizes into ash-free dry mass using length:biomass regression equations. Staff constructed equations monthly from an additional separate sample taken at nearby EMP sites that contained large numbers of the relevant species of clam. We used the regressions from these "reference sites" for all sites within a region for that year and month. We used unique regressions for each region, year, and month, to account for differences in condition from temperature, food availability, and other factors. A table of all site locations, reference sites, and regressions used is included in Appendix A, courtesy of Dr. Jan Thompson, US

Geological Survey (See Appendix A, spreadsheet "ClamData.xlsx.").

We combined data from GRTS and the EMP core sites sampled during May and October because GTRS only sampled during these months, and from 2007 to 2019 (excluding 2013 and 2016, when GRTS data were not available) to assess effects of water year type on *P. amurensis* and *C. fluminea* population densities and their combined filtration rates across regions (Figure 2). We used combined filtration rates to test the hypothesis that total clam filtration increased during drought conditions.

Clam density data for both species were zero-inflated because of absences across many sampling locations. Therefore, we used zero-inflated negative binomial models with clam counts instead of densities to assess the effects of water year type and region on each species' density. We fit separate models for each species with the *glmmTMB()* function in the 'glmmTMB' R package Version 1.1.5 (Brooks et al. 2022). We tested for an interaction between water year type (as an ordered factor) and region and included a random effect of month. Zero inflation was modeled against region, since most of the zeros resulted from sampling in regions outside of the range for each species. The model for *C. fluminea* was fit using the entire data set, but the model of *P. amurensis* would not converge with the entire data set because of lack of catch in the North and South-Central regions. Therefore, *P. amurensis* data were sub-set to only include Suisun Marsh, Suisun Bay, and the confluence. Species count was modeled using the following set of equations:

$$\text{Count}\sim\begin{cases} \text{Region, Count} = 0/1 \\ \text{Year type} * \text{Region} + \text{Random(Month), Count} > 0 \end{cases} \quad \textbf{Eq 3}$$

Filtration and Grazing Rates

Jellyfish
To develop a rough estimate of how jellyfish can affect the zooplankton community, we conducted a literature review on feeding in M. marginata and similar species. No data on feeding rates are available for *M. marginata*, and feeding

rates in other species vary widely from study to study, depending on prey type, prey density, water temperature, bell diameter, and species (Purcell 2009). Therefore, we used a study of another small cnidarian, *Aurelia aurita* (Moller and Rissgard 2007), because it provided data on feeding in terms of volume of water cleared by individuals of a similar size to the *M. marginata* seen in our study (20 to 50 mm) at a variety of water temperatures (4 to 26 °C) (Moller and Rissgard 2007). *Aurelia aurita* is a scyphozoan whereas *M. marginata* is a hydrozoan, so this is not intended to provide a fully accurate estimate of *M. marginata*'s feeding rates. Instead, the following analysis is designed to provide an order-of-magnitude approximation of the potential effect of *M. marginata*, and highlight the need for further study.

We assumed the average bell diameter of *M. marginata* caught by fish surveys was 40 mm (the upper end of the range of *M. marginata* sizes usually retained in otter trawls; the full range is 20 to 50 mm) (Baumsteiger et al. 2018), and the average summer temperature in the estuary was 20 °C. Using the filtration rates determined by Moller and Rissgard (2007) for *A. aurita* ($F = 1.17e^{0.18T}$, where F is filtration rate in L day^{-1} and T is temperature), we calculated the water column turnover rate in proportion per day by the mean and maximum observed density of *M. marginata* by water year type and region.

To estimate the biomass of prey that *M. marginata* may have consumed, we used zooplankton data collected by long-term monitoring surveys throughout the region. These data have been previously combined by (Bashevkin et al. 2022) and made available on the Environmental Data Initiative data repository (Bashevkin, Hartman et al. 2023). We downloaded data collected in the "mesozooplankton" size range (150- to 160-µm mesh nets) for June through October between 2007 and 2020 and calculated the average biomass of copepods per cubic meter of water sampled for each water year type and region. We multiplied the observed water column turnover rate (proportion per day) by the density of copepods to calculate the potential carbon consumed per

day. This calculation assumes copepods replace themselves once per day. However, actual growth rates may be higher or lower (Kimmerer, Gross, et al. 2018), leading to a different value of total biovolume consumed, so the results should be taken only as a starting point for future experiments and analysis.

Clams

We calculated adjusted filtration rates in $m^{-3} m^{-2} day^{-1}$ for each sample following the method outlined in Crauder et al. (2016), which incorporates biomass, temperature-dependent per-gram filtration rates, and an estimated refiltration proportion to account for boundary layers of water that are refiltered. We summarized the mean filtration rate for each species by region and month, and then added the means of the two species to calculate combined filtration rate. We then fit linear mixed-effects models to test for interactive effects of water year type (as an ordered factor) and region on log(x+1) combined filtration rates.

Models were fit using the *lmer()* function from the 'lme4' package Version 1.1-31 (Bates et al. 2022) in R Version 4.2.2 (R Core Team 2022) with the following equation:

$$Log\ (FR + 1) \sim WYT * Region + Random(Month) \qquad Eq\ 4$$

To compare the potential effect of clams to the effect of jellyfish, we calculated the mean and maximum combined filtration rates by region and water year type, then divided by the average depth per region to calculate the water column turnover rate for the region per day. To obtain grazing rates (i.e., the estimated amount of chlorophyll grazed), we combined the water turnover rates above with data collected by long-term monitoring surveys throughout the region, which have been previously combined and made available on the Environmental Data Initiative data repository (Bashevkin, Perry, et al. 2023), with data from the UCD Suisun Marsh Fish Study (collected for Montgomery 2017; Williamshen et al. 2021) and the Directed Outflow Project (Schultz and Kalmbach 2023). We

then estimated the potential carbon consumed per day by assuming a 32:1 C:Chla ratio (as estimated by Lucas and Thompson 2012), and multiplying carbon density by the water column turnover rates to calculate potential carbon consumed per day. This calculation assumes that phytoplankton productivity keeps pace with grazing rates to lead to the observed chlorophyll concentration. However, actual productivity rates may be significantly higher or lower (Jassby and Powell 1994; Wilkerson et al. 2006), leading to an under-estimate or over-estimate of actual carbon consumed.

Center of Distribution

Jellyfish

To calculate the center of distribution, we first calculated the in-water distance between each sampling location and the Golden Gate (mouth of the estuary) using the *GGdist* function in the 'spacetools' package in R (Bashevkin 2022). This function uses a raster of waterways within the estuary to calculate the shortest distance from each sampling location to the Golden Gate. We then calculated the catch-weighted mean distance from the Golden Gate by month and year as an estimate of the center of distribution within the sampling frame.

Once we had the center of distribution for each month, we fit a linear model of center of distribution vs. net Delta Outflow (Outflow) to model the shift in distribution with dry years. Mean monthly Net Delta Outflow Index (an estimate of tidally filtered flow past Chipps Island) was obtained from the CDWR's Dayflow model (CDWR 2002). The monthly center of distribution was modeled against monthly Delta Outflow using the equation:

$$Distance \sim Outflow + Random\ (Year) \qquad Eq\ 5$$

The random effect of year (coded as a factor) was included to account for year-to-year variability in *M. marginata* populations.

Clams

First, we calculated the distance between each long-term EMP sampling location and the Golden Gate as described above for *M. marginata*. To minimize effects of uneven sampling effort across regions over time, we binned stations into categories by distance, measured in 10-km intervals from the Golden Gate, and calculated the mean density by bin. Using the binned data, we calculated the annual, density-weighted mean distance from the Golden Gate. Exploratory analyses indicated that the previous year's Sacramento Valley Index was a better predictor of the center of distribution than the current year's Index, likely because of changes in clam density and distribution that resulted from the relative success of the previous year's reproduction and recruitment, rather than from movement of individuals (as with jellyfish). Therefore, we used the previous year's Sacramento Valley Index to predict center of distribution. In addition, we found two distinct relationships by sampling period (pre-2000 vs. post-2000) between center of distribution and the previous year's Sacramento Valley Index. Thus, we considered models with and without an effect of sampling period to explain the relationship between *P. amurensis* center of distribution and the previous year's Sacramento Valley Index, and used Akaike information criterion (AIC) model selection to select the best-fit model (Appendix A, Table A1).

The EMP long-term data were used to evaluate how the center of the *P. amurensis* distribution—measured as the distance in km from the Golden Gate—varied with the Sacramento Valley Index from 1987 to 2020. We used the Sacramento Valley Index instead of monthly Delta Outflow (as for *M. marginata*) because we hypothesized benthic clams to respond to drought on an annual time-step instead of a monthly time-step based on their movements only occurring during the pelagic juvenile stage. We did not analyze *C. fluminea* distribution because its range extends well upstream of our sampling area, and all we could meaningfully examine was its downstream extent, while we sample the whole *P. amurensis* range across the same regions where we find jellyfish.

RESULTS

Density

M. marginata was found chiefly in the confluence, Suisun Marsh, and Suisun Bay regions, and was only caught in the South-Central Delta during Dry and Critically Dry years (Figure 3). The highest catches occurred in Suisun Marsh and Suisun Bay during the wet years of 2017 and 2019 (Figure 3; Figure A2 note log scale). Suisun Marsh was the region with the highest average CPUE, then Suisun Bay, followed by the confluence. There was a significant negative relationship between water year type and *M. marginata* CPUE in the confluence, but there was also a significant interaction between water year type and region, such that this relationship was reversed in Suisun Marsh and Suisun Bay (Figure 3; Table 1; Table A2). *M. marginata* CPUE in the confluence was highest during critically dry years and lowest in wet years, whereas in Suisun Bay and Suisun Marsh catch was highest in wet years and lowest in critically dry years.

The CPUE-weighted mean salinity at which *M. marginata* was caught was 5.40 ±2.11, giving an observed salinity niche for *M. marginata* of 3.29 to 7.52. Within this salinity range, wet years had the highest CPUE, but the trend was not significant; the linear mixed-effects model of CPUE vs. WYT with month and year as random effects found no effect of WYT ($t = 0.378$, $p = 0.711$; Figure 4). This suggests that shifts in the population with salinity—rather than water year type *per se*—was the driving factor behind jellyfish abundance.

P. amurensis densities were highest in Suisun Marsh and Suisun Bay, with lower numbers in the confluence, and their densities increased across these regions during dry and critically dry years (Figure 5). In contrast, densities of *C. fluminea* were higher in the North, South-Central, and confluence regions and decreased during drier years (Figure 5). Densities differed significantly by water year type and region, and there was a significant interactive effect of water year type and region, as densities changed more during drier years in regions where clams were commonly found (Table 1; Figure 5; Tables A3 and A4).
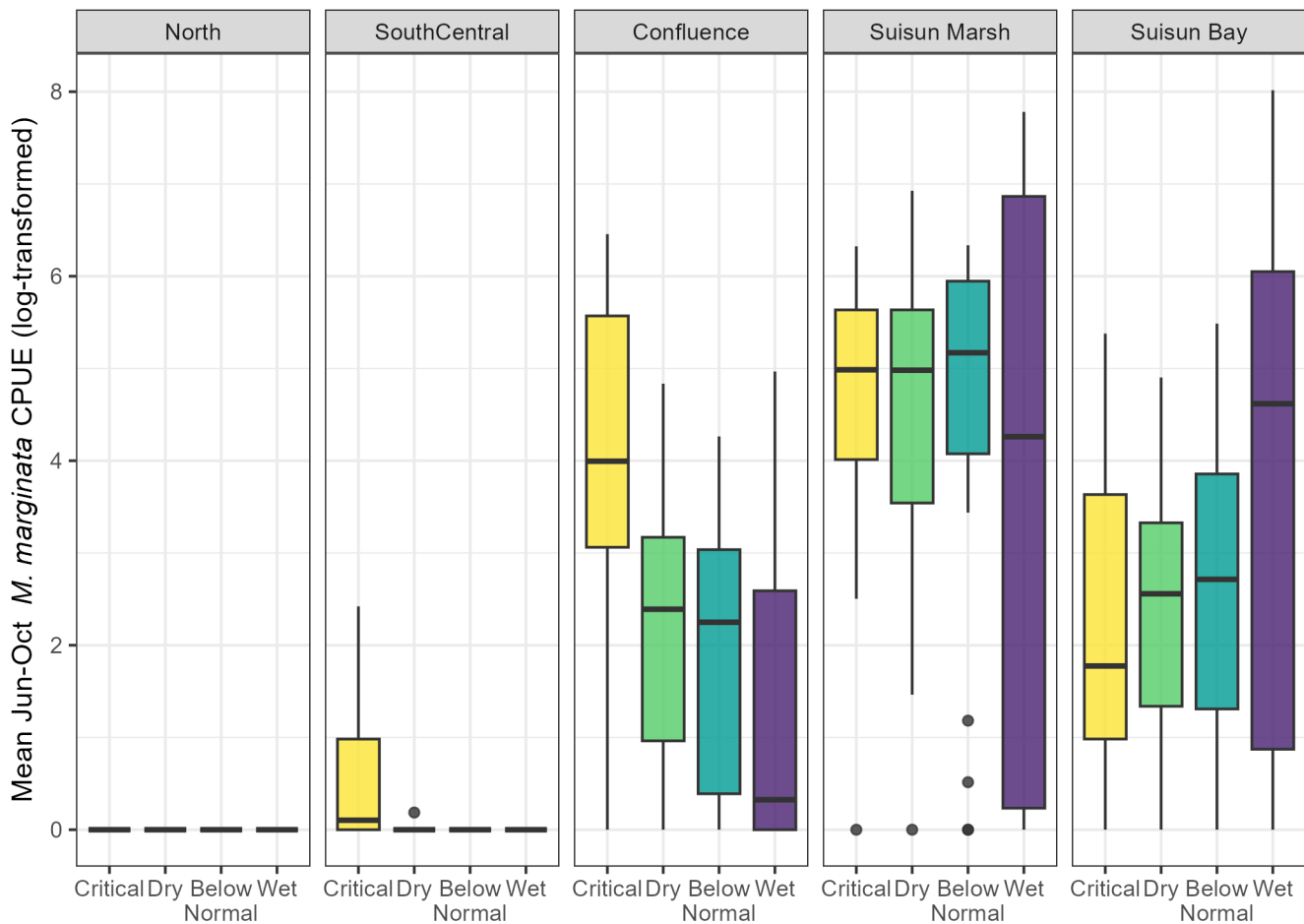
Figure 3 *Boxplots* of monthly mean *M. marginata* CPUE (individuals per 10,000 m³) from June to October by region and water year type for 2007 to 2020. Note: There were no Above Normal water years included in these years.

Table 1 Analysis of Deviance Table of a linear mixed[-effects?] model of log-transformed monthly mean *M. marginata* density vs. the interactive effects of Region and Water Year Type (WYT, as an ordered factor) from 2007 to 2021, and for zero-inflated negative binomial models of *C. fluminea* and *P. amurensis* density vs. the same predictors from 2007 to 2019. Data from 2013 and 2016 were too sparse to include in the models of *C. fluminea* and *P. amurensis*. Sampling month was included as a random effect in all models.

| Species	Model term	Chi-sq	df	Pr (> Chi-sq)
M. marginata	Region	109.8	2	< 0.001
M. marginata	WYT	0.961	3	0.811
M. marginata	Region:WYT	56.077	6	< 0.001
C. fluminea	Intercept	701.139	1	< 0.001
C. fluminea	Region	165.426	4	< 0.001
C. fluminea	WYT	20.684	3	< 0.001
C. fluminea	Region:WYT	48.186	12	< 0.001
P. amurensis	Intercept	316.048	1	< 0.001
P. amurensis	Region	120.658	2	< 0.001
P. amurensis	WYT	136.236	3	< 0.001
P. amurensis	Region:WYT	41.999	6	< 0.001
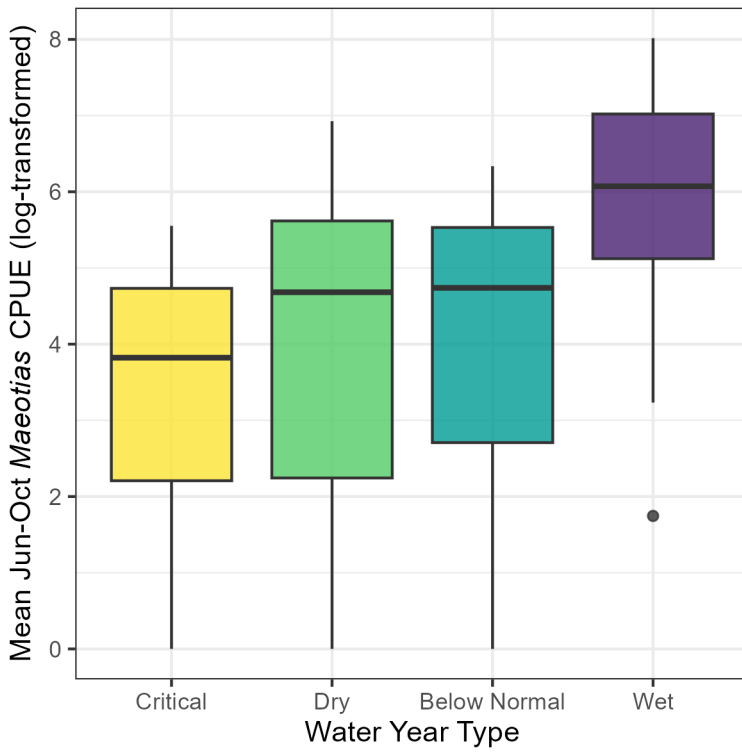
Figure 4 Log-transformed monthly mean *M. marginata* CPUE (catch per 10,000 m3) from June to October when restricted to 3.27 to 7.52 salinity. A linear mixed-effects model of CPUE vs. WYT with month and year as random effects found no effect of water year type (t = 0.378, p = 0.71). No Above Normal years occurred during this period.
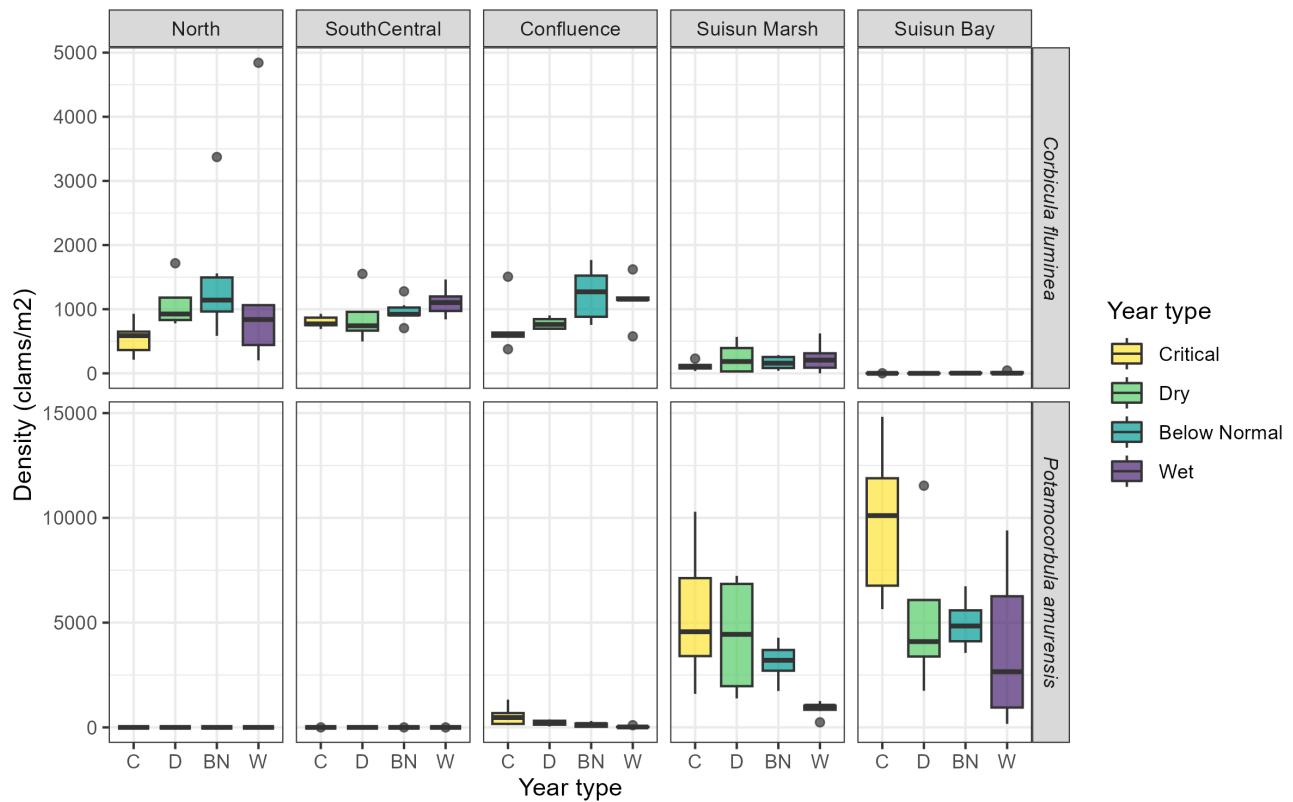

Figure 5 *Boxplots* of mean annual *P. amurensis* and *C. fluminea* density by region and water year type for 2007 to 2019 (omitting 2013 and 2016). No Above Normal years occurred in this time-period.

Center of Distribution

The center of distribution of *M. marginata* showed a very strong relationship with Net Delta Outflow (Table 2; Figure 6), with the center of distribution being closer to the ocean during high-outflow periods.

The center of distribution for *P. amurensis* was best described by a model that included an interaction between the previous year's Sacramento Valley Index and sampling period (1987 to 1999 vs. 2000 to 2020) (Table 2, Table A1). The population shifted upstream from the Golden Gate after dry years (years following a low Sacramento Valley Index), but the relationship between the center of distribution and the previous year's Sacramento Valley Index was much stronger from 1987 to 1999 than ~~in~~ from 2000 to 2020 (Figure 7; Table 2). Post-2000, *P. amurensis's* population center was anchored in Suisun Bay, where densities have increased substantially over time compared to other regions (Figure 9). *C. fluminea* densities did not change dramatically over the same period (Figure 9).

Filtration and Grazing Rates

Combined annual filtration rates of *P. amurensis* and *C. fluminea* did not vary significantly by water year type (Figure 8; Table 3), although filtration rates increased somewhat during drier (Critical, Dry, and Below Normal) years in the confluence and Suisun Marsh (Figure 10). Filtration rates were significantly higher in Suisun Marsh than in other regions (Figure 10; Table 3; Table A5).

The water column turnover rates for clams were much higher than for *M. marginata*. For example, estimated mean turnover rates from clams were 0.14898 day^{-1} in the confluence in a below normal year, but only 0.0005 day^{-1} for *M. marginata*. In Suisun Marsh, mean turnover rates reached 0.28832 day^{-1} in a wet year while *M. marginata* was only 0.0012 day^{-1}. In contrast to *M. marginata,* turnover rates by clams were highest during drier years (Figure 10A).

Potential carbon consumed was higher for *M. marginata* than for the clams in some regions/water year types, despite the generally lower turnover rates, because of the much higher biomass of copepods than phytoplankton (Figure 10B). In particular, the high biomass of copepods in the confluence during critically dry years leads to a potentially higher loss of zooplankton than in Suisun Marsh, where there are more *M. marginata*. Similarly, the high biomass of phytoplankton in the South-Central region (where filtration rates are relatively low) led to higher potential carbon consumption in the South-Central region than in Suisun Bay, where there are higher clam densities (Figure 10B).

DISCUSSION

We found that two different invasive invertebrate filter feeders shift their distributions upstream in response to drier water years, and both have been increasing in abundance over time. The planktonic *M. marginata* responds to changes in salinity within a month, moving with its observed salinity niche from Suisun Bay and

Table 2   Model coefficients for a linear mixed model of monthly *M. marginata* center of distribution (km from the Golden Gate) vs. monthly mean net Delta Outflow Index from Dayflow (cubic meters per second). Year and Month were included as random effects. Data from Jun–Oct only. Model coefficients for a linear model that examined the interaction between sampling period (1987 to1999 vs. 2000 to 2020) and the previous year's Sacramento Valley Index on the annual mean weighted center of *P. amurensis* distribution (km from the Golden Gate).

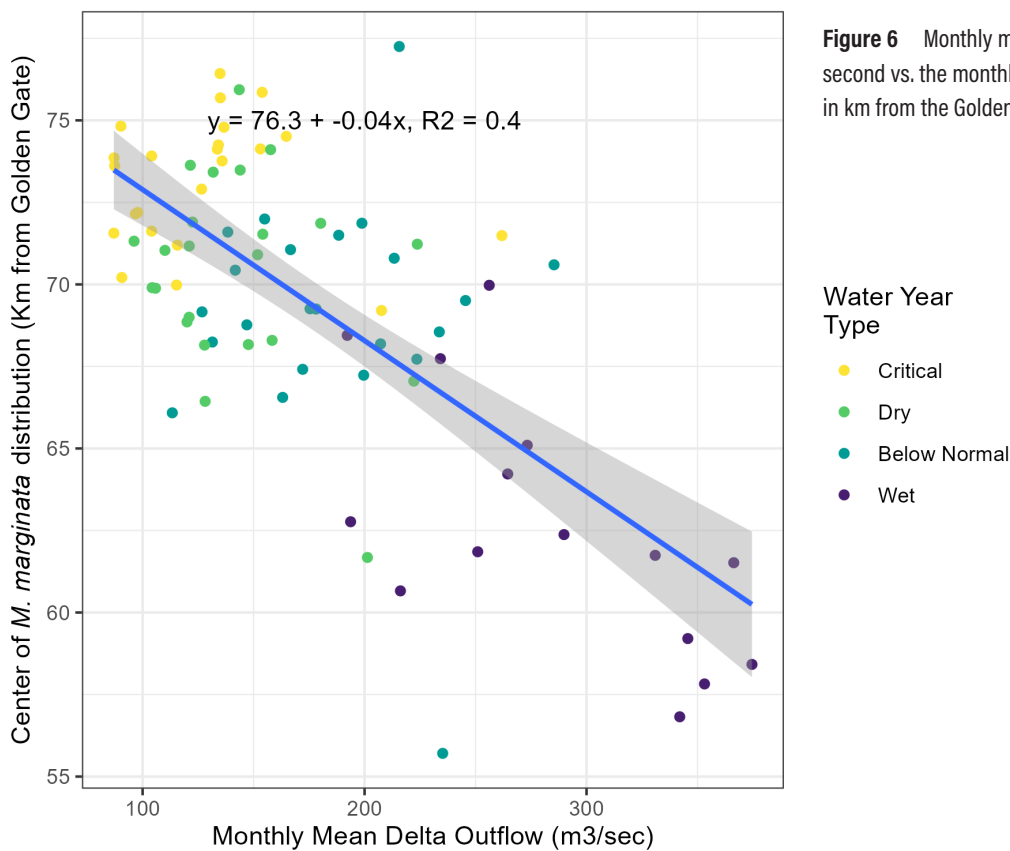| Species	Model Term	Estimate	Std. Error	t value	Pr(>|t|)
M. marginata	(Intercept)	76.335	1.188	64.247	< 0.0001
M. marginata	Outflow	− 0.040	0.006	− 6.616	< 0.0001
P. amurensis	Intercept	81497.6	1448.8	56.251	< 0.0001
P. amurensis	Previous Year's Sacramento Valley Index	− 2192.9	175.8	− 12.471	< 0.0001
P. amurensis	Sampling Period (200– 2020)	− 26410.5	1992.0	− 13.258	< 0.0001

Figure 6   Monthly mean Delta Outflow in cubic-meters-per-second vs. the monthly center of distribution for *M. marginata* in km from the Golden Gate; data from Jun-Oct only

Suisun Marsh into the confluence. It experiences short, high-density blooms that are often largest in the wettest years. *P. amurensis*, in contrast, increases in abundance and shifts its distribution upstream toward the confluence during droughts, chiefly through juvenile recruitment, and thus has a roughly 1-year lag in changes to its distribution. There is a trend (though not statistically significant) toward increasing clam and *M. marginata* filtration in the confluence with drought conditions. The increase in filtration may partially explain reduced zooplankton densities in Suisun during Dry years (Barros et al., this issue). Both *P. amurensis* and *M. marginata* abundance have increased substantially in Suisun Bay over the past 20 years, but the causes and implications of this increase are poorly understood.

M. marginata Responses to Drought

Patterns in *M. marginata* catch followed its observed salinity niche closely, moving from Suisun Marsh and Suisun Bay into the confluence during drier months and years (Figure 3, Figure 4). The observed salinity niche for

M. marginata was between 3.2 and 7.5, which is narrower than previously reported (i.e., 2 to 9; Schroeter 2008). Other biotic and abiotic factors may have also contributed to the observed distribution of *M. marginata*, such as temperature, competition, predation, and prey availability, but salinity was the factor most strongly influenced by dry conditions. Similar responses to changing salinity have been observed in crustacean zooplankton, including *Pseudodiaptomus forbesi* in this estuary (Kimmerer, Ignoffo, et al. 2018) and a variety of other taxa across the globe (Gunter et al. 1964; Roddie et al. 1984; Gao et al. 2008; Telesh and Khlebovich 2010; Marques et al. 2014), including the scyphozoans *Catostylus mosaicus* (Loveridge et al. 2021) and *A. aurita* (Amorim et al. 2018).

As salinity increased, *M. marginata* moved upstream but no other gelatinous zooplankter replaced it in higher-salinity waters. Several salt-tolerant jellies are caught in the more saline reaches of San Francisco Bay (Figure A1, Bay Study, unpublished data). Some, including
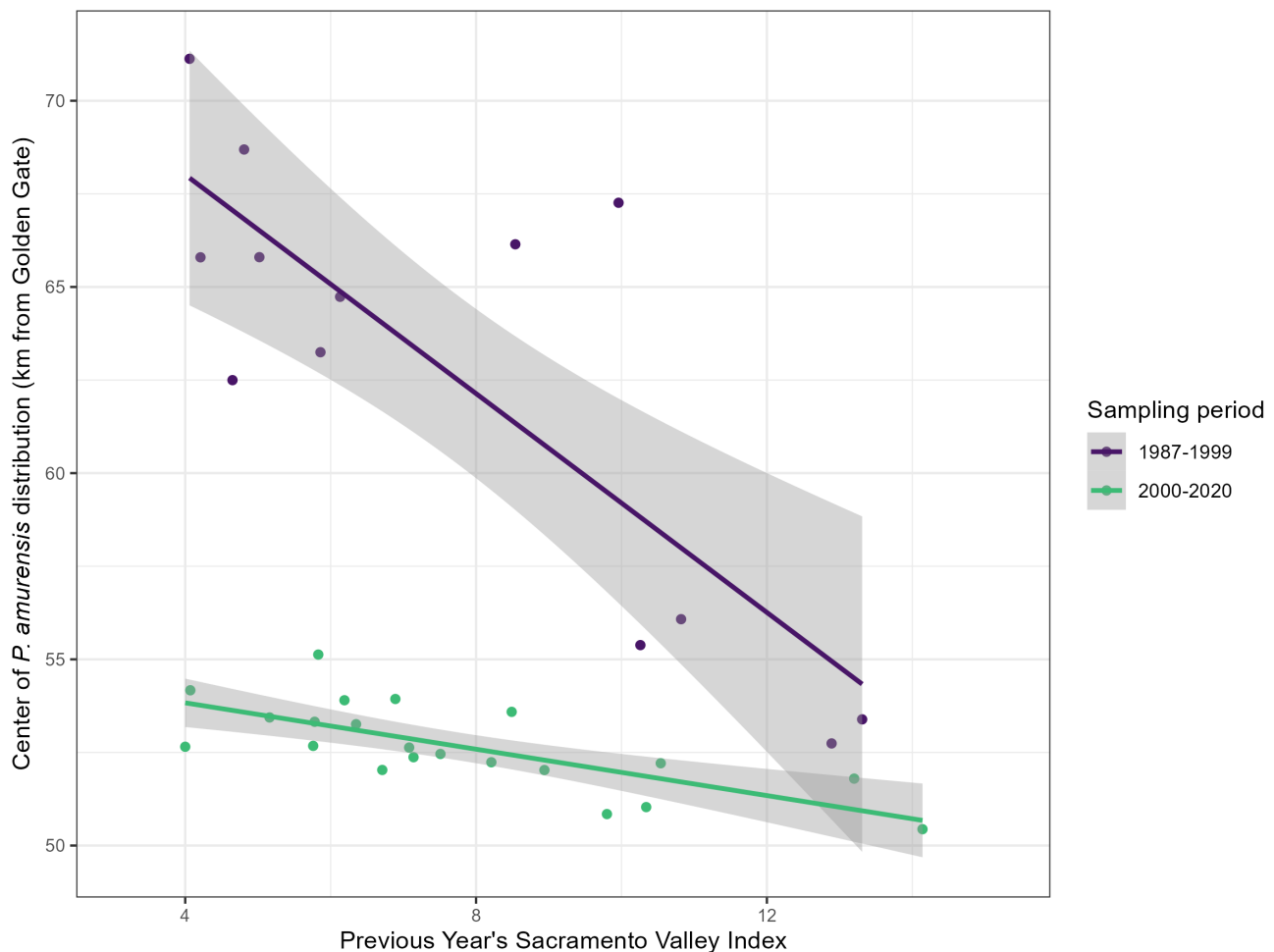
Figure 7   Annual mean weighted center of *P. amurensis* distribution in km from the Golden Gate by sampling period (1987 to 1999 vs. 2000 to 2020) and the previous year's Sacramento Valley Index.

Polyorchis penicillatus and *Pleurobrachia bachei* can be as abundant or more abundant than blooms of *M. marginata*. However, both these species are more abundant in the winter and spring than in summer, so they do not significantly affect the jellyfish community in Suisun Bay during the summer, even in very dry years (Figure A1, Bay Study, unpublished data).

The shift in *M. marginata* distribution with changing salinity during droughts is clear, and a narrow salinity tolerance is a plausible mechanism. What is less clear is why recent wet years (2017, 2019) experienced massive blooms of *M. marginata* in Suisun Marsh and Suisun Bay (Figure 3, Figure A2). Hydrozoans such as *M. marginata* and *Moerisia lyonsi* are capable of

asexually reproducing and establishing polyps when conditions are less favorable (Ma and Purcell 2005; Schroeter 2008). However, we would expect asexual reproduction to result in a decline in abundance during less favorable, wet years when salinity is greatly reduced in the winter and spring, followed by an increase in drier years, as observed in the past for *M. marginata* in Suisun Bay and Marsh (Schroeter 2008). A similar pattern was observed in Guadiana estuary (southwest Iberian Peninsula, Europe), where increased freshwater flows during the winter decrease the frequency and density of *A. aurita* blooms (Amorim et al. 2018), though a contrasting pattern was seen for *Blackfordia virginica* in the same estuary, with decreased flows increasing biomass (Muha et al. 2017).
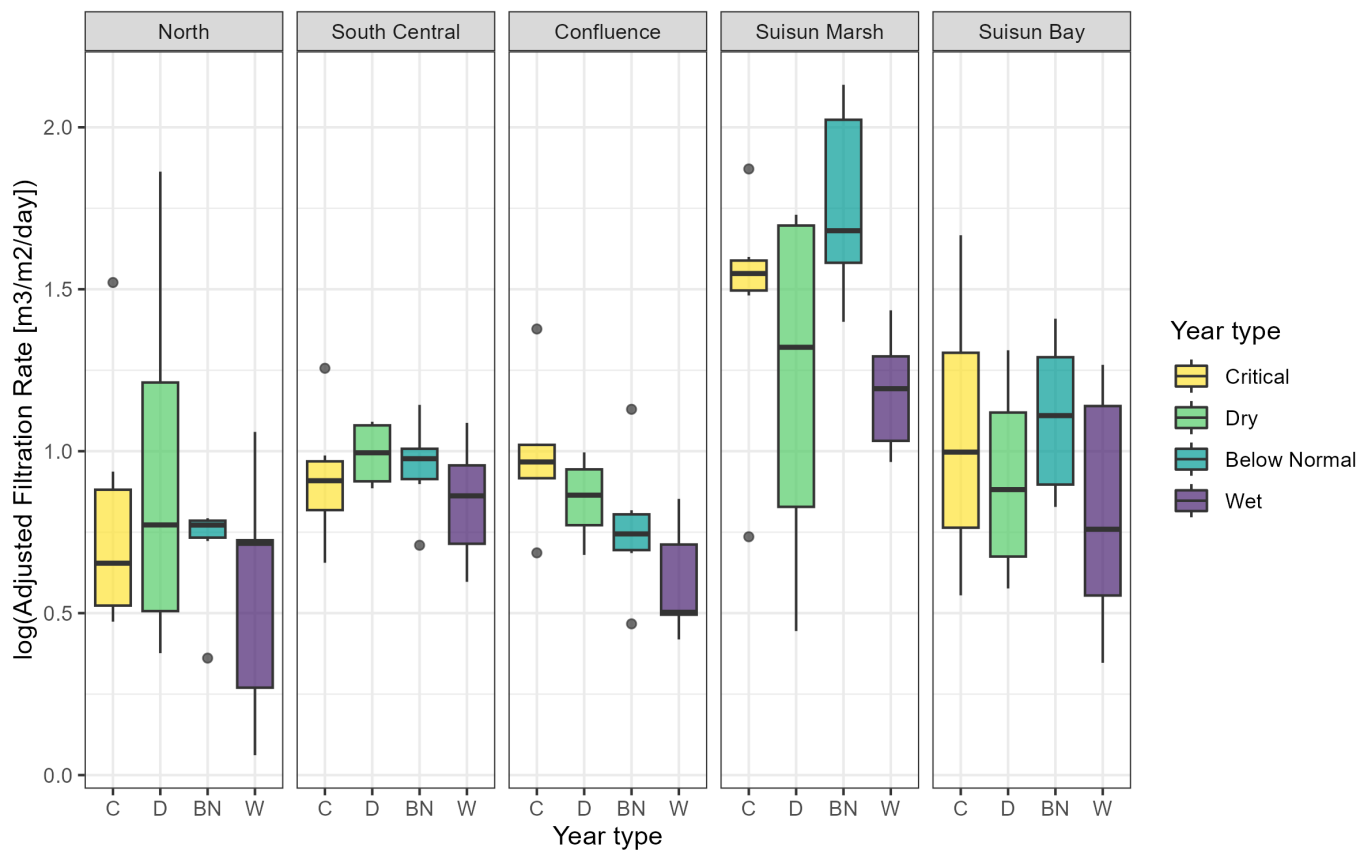
Figure 8 *Boxplots* of mean annual combined adjusted filtration rate (log x + 1) of *P. amurensis* and *C. fluminea* by region and water year type for 2007 to 2019 (omitting 2013 and 2016, when no sampling occurred).

In other estuaries, such as Hiroshima Bay, Japan, freshwater inflow provides additional nutrients that trigger phytoplankton blooms and increase gelatinous zooplankton density (Shoji et al. 2010). This may be the cause of the wet-year blooms in our estuary, since transport of freshwater zooplankton from upstream is a

Table 3 Analysis of Deviance for Type-3 ANOVA testing for interactive effects of region and water year type on (log x + 1)-combined average adjusted filtration rate of *C. fluminea* and *P. amurensis* from 2007 to 2019. Data from 2013 and 2016 were too sparse to include in the model. Month was included as a random effect.

Model term	Chi-sq	df	Pr(>Chi-sq)
Intercept	57.0846	1	<0.001
WYT	4.9785	3	0.173
Region	15.8110	4	0.003
WYT:Region	12.3426	12	0.419

key source of food for fish in the Suisun regions (Kimmerer, Ignoffo, et al. 2018). The calanoid copepod *P. forbesi*, in particular, experiences large increases in Suisun Bay during wet periods when compared to droughts (Barros et al., this issue), and calanoid copepods, which are the dominant prey resource for *M. marginata*, in the summer of 2017 were significantly higher than normal (~200% higher abundance in 2017 than in 2016 or 2018; Barros 2021). Since *M. marginata* relies on random entanglement with their prey to feed (Wintzer et al. 2011), high densities of prey during Wet years could result in increased jellyfish feeding and growth. Further research on feeding behavior, reproduction, and growth of *M. marginata* is necessary to see whether the increase in zooplankton could have caused the blooms of 2017 and 2019.
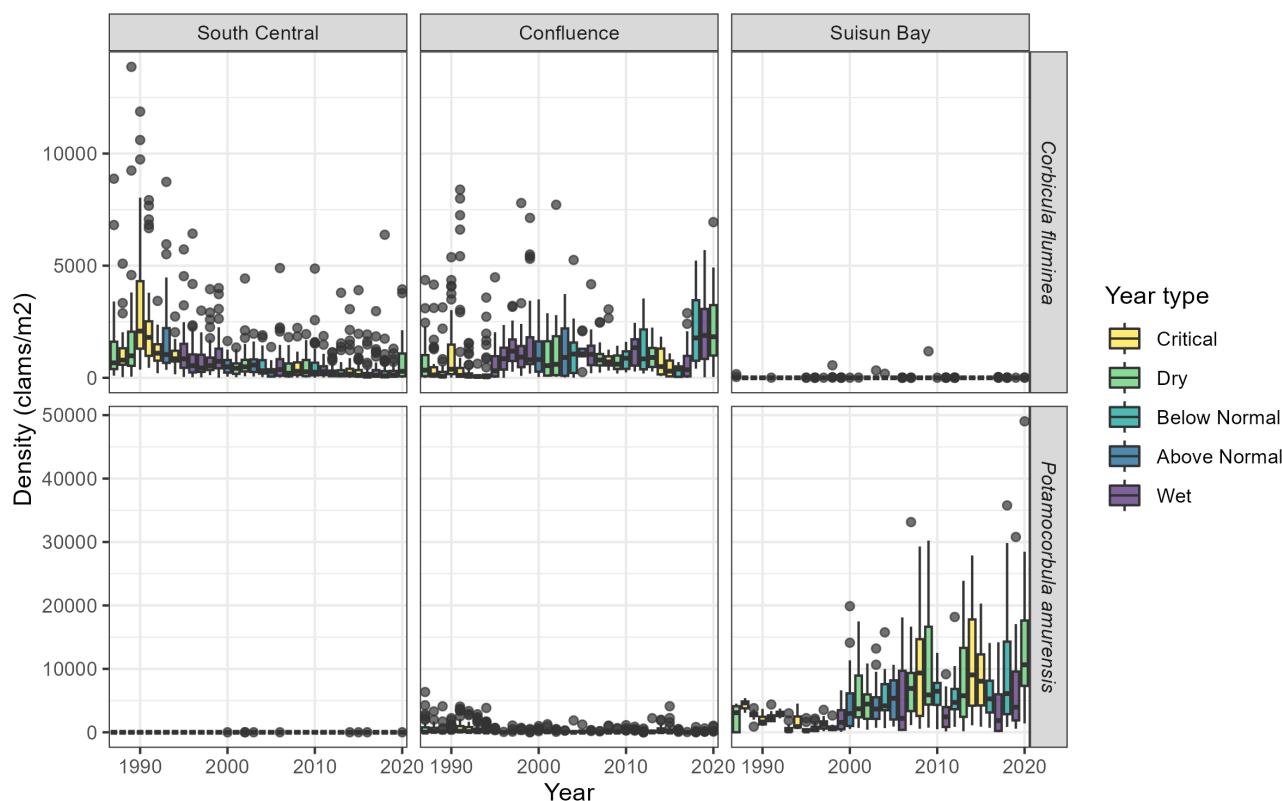
Figure 9 Boxplots of *C. fluminea* and *P. amurensis* density (clams/m²) by region and year from 1987 to 2020

P. amurensis Responses to Drought

Invasive clams have been more thoroughly studied than jellyfish in the upper estuary, and the patterns found in this analysis confirm and extend some of the earlier studies' findings (Parchaso and Thompson 2002; Winder et al. 2011; Crauder et al. 2016; Baumsteiger et al. 2017). *C. fluminea* and *P. amurensis* occupy different salinity regimes: *C. fluminea* primarily inhabits freshwater but has some tolerance for increased salinity during the juvenile phase, while *P. amurensis* is oligohaline with tolerance for both fresher and more saline water (Crauder et al. 2016). The two species overlapped in the confluence and Suisun Marsh (Figure 5), which provided habitat for each clam in varying amounts, depending on the water year type. In wetter years, *C. fluminea* was seen in higher densities in the confluence because of the lower salinity there (Figure 5). After drier years, *P. amurensis* recruitment followed salinity intrusions upstream into the confluence, while

densities decreased during Wet years in the confluence and Suisun Marsh.

As a result of upstream movement (Figure 7) and increasing densities of *P. amurensis* following dry years, and their high species-specific filtration rates per gram of biomass (~ 4x the rate of *C. fluminea*; Crauder et al. 2016; Foe and Knight 1986; Werner and Hollibaugh 1993), there is a non-significant pattern of higher combined filtration rates in Critical to Below-Normal water years (Figure 8). Our analysis of filtration rates included only 11 years of data, and patterns in Figure 8 suggest that with more years of data, we may have found a significant effect of water year type on combined filtration rates. However, in areas where both species are found, drought effects on combined total filtration can be somewhat muted because a decrease in *C. fluminea* can partially temper an increase in *P. amurensis*. Any increase in total filtration rates in the confluence and Suisun Marsh where both species are found is likely the result of the higher species-specific
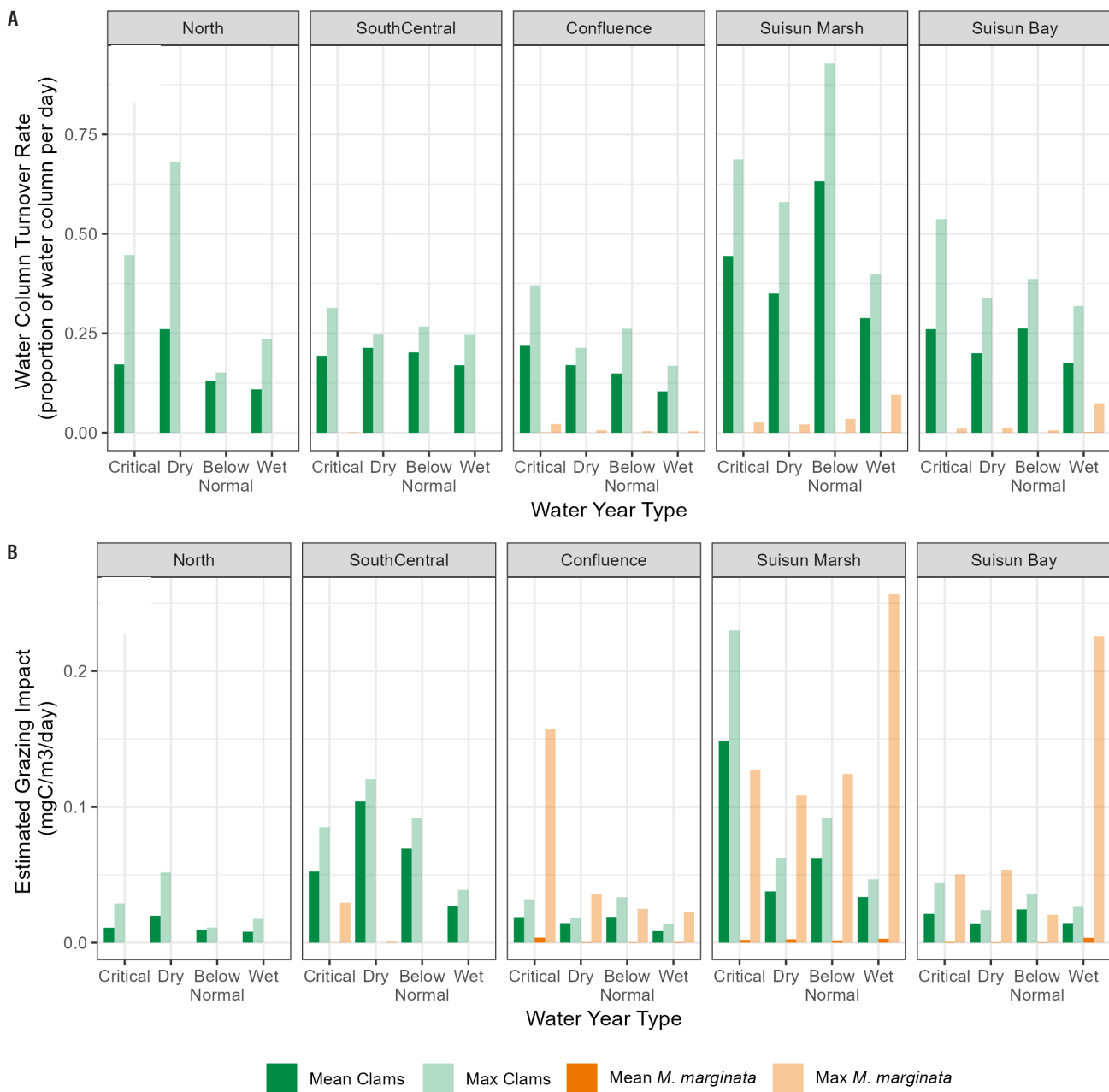
Figure 10   Mean (dark bars) and maximum (light bars) (**A**) water column turnover rates and (**B**) estimated grazing effect (mgC m^{-3} day^{-1}) for clams (*P. amurensis* and *C. fluminea* combined) and *M. marginata* across regions and water year types. Mean turnover rates for *M. marginata* are too low to be visible in comparison with clams' turnover rates. Note that *M. marginata* did not occur regularly in the North or South-Central regions.

filtration rates of *P. amurensis* and the higher salinity and temperature found during droughts (Bosworth et al., this issue), both of which also increase grazing rates (Lauritsen 1986; Paganini et al. 2010). Similarly, Nichols (1985), found that the clam *Mya arenaria* became numerically dominant in Suisun Bay during the 1976–1977

drought, where it may have caused a reduction in phytoplankton abundance.

P. amurensis demonstrates a lagged response to drought (Figure 7) because adults are relatively tolerant of changes while early life stages have a narrower salinity tolerance (Paganini et al.

2010; Thompson and Parchaso 2012). During sequential Wet years, older individuals that inhabited upstream areas of the estuary (e.g., confluence) eventually died off or new recruits failed to establish, whereas recruitment was higher in the same regions during sequential Dry years (Crauder et al. 2016; Baumsteiger et al. 2018; Watkins and Wells 2020), resulting in an upstream shift of the population center of distribution.

There is a discontinuity in the long-term response of *P. amurensis'* center of distribution to salinity. From the introduction of *P. amurensis* in 1987 until 2000, the clam's center of distribution was strongly influenced by the previous water year (previous year's Sacramento Valley Index). After 2000, the total density of *P. amurensis* in Suisun Bay increased dramatically (Figure 9; Table 2), and while the water year type continues to influence their upstream and downstream range edge, the population remains more firmly centered in Suisun Bay regardless of water year type. Parchaso and Thomson (2002) found that *P. amurensis* often has a second recruitment period in Suisun Bay, which could have contributed to the large increase in densities after 2000.

Food Web Implications

The timing of the increase in *P. amurensis* density in 2000 coincides with the Pelagic Organism Decline (POD)—the estuary-wide decline in pelagic fish populations (Sommer et al. 2007; Mac Nally et al. 2010; Thomson et al. 2010), and grazing by *P. amurensis* is hypothesized to have contributed to the POD (Sommer et al. 2007). The post-2000 explosion in *P. amurensis* may have resulted from five consecutive Wet years leading up to 2000 that disturbed the benthic community and released *P. amurensis* from competition, followed by consecutive Dry years that facilitated their recruitment (Figure 9). Previous wet–dry cycles may have allowed *P. amurensis* to proliferate in the estuary as a result of similar mechanisms (Carlton et al. 1990; Nichols et al. 1990; Winder et al. 2011; Chang et al. 2018). Regardless of the cause, the higher *P. amurensis* density in Suisun Bay increased overall filtration pressure and provided a source of clam propagules to lower-salinity areas of Suisun

Marsh and the confluence (Baumsteiger et al. 2017), where filtration intensity increased during drought periods from a combination of higher clam densities, higher salinity, and temperature (Lauritsen 1986; Paganini et al. 2010). Our analysis of estimated carbon consumption (Figure 10B) found that despite the higher filtration intensity in Suisun Bay, there may be greater carbon consumption in Suisun Marsh and the South-Central Delta because of higher phytoplankton densities. However, our analysis did not include consumption of microzooplankton (which may be significant, see Greene et al. 2011) or productivity rates, so actual carbon consumed may be much higher.

M. marginata has not been studied as extensively in the estuary as *P. amurensis,* thus its effect on the rest of the ecosystem is speculative. The medusae phase of *M. marginata* feeds primarily on copepods and other pelagic prey (e.g., barnacle nauplii, mysids), putting them in direct competition with threatened pelagic fishes such as Delta Smelt and Longfin Smelt (Wintzer et al. 2011). Studies of *M. marginata* stomach contents found that all samples examined had full guts, with an average of 37 prey items, and up to 100 prey items per medusa (Mills and Sommer 1995; Wintzer et al. 2011). *M. marginata,* when settled on the bottom, also feeds on benthic prey such as corophiid amphipods, which could result in competition with benthic fishes as well (Schroeter 2008; Wintzer et al. 2011). Mills and Sommer (1995) found that *M. marginata* medusae spend most of their time on the bottom; therefore, the individuals captured in midwater trawls only represent a small proportion of the *M. marginata* population, which likely is far greater than our data shows.

Jellyfish can feed on ichthyoplankton in addition to crustacean zooplankton and could directly predate upon threatened fishes as well as compete with them (Wintzer et al. 2011). The highest abundances of *M. marginata* (which occur in June through September) do not currently overlap temporally with the larval stages of most native fishes in the estuary (which chiefly spawn in January through May; Meng

and Matern 2001), and the only larval fishes documented in *M. marginata* diets in the estuary were gobies (Wintzer et al. 2011). However, increasing temperatures have extended bloom periods (by 4x from 1995 to 2005; Schroeter 2008), so *M. marginata* could expand the spatial and temporal range of its bloom period with climate change, potentially increasing their effects on fishes. In addition, jellyfish in the estuary have no known predators, enabling their populations to increase rapidly under favorable conditions (Rees and Gershwin 2000). In the Chesapeake Bay, one study found that large blooms of the invasive hydrozoan *Moerisia lyonsi* may have been limiting copepod populations (Purcell et al. 1999), and studies in the Baltic Sea have seen significant decreases in zooplankton (Stoltenberg et al. 2021), so similar blooms in *M. marginata* may cause local limitation on zooplankton.

Our rough analysis of the potential effects of grazing on copepods showed that, on average, *M. marginata* turn over less than 1% of the water column per day; however, this can increase to over 9% per day during large blooms (Figure 10A), and this can translate to a higher mass of carbon than that consumed by *P. amurensis* in some circumstances (Figure 10B). Copepod mortality can vary widely, and be quite high, with calculated values for *P. forbesi* in the estuary of between 0.01–0.8 day^{-1}, depending on life stage and location (Kimmerer, Gross, et al. 2018), so jellyfish grazing may not contribute a significant percentage of this rate except in large blooms, but blooms of gelatinous zooplankton appear to be increasing in the estuary and worldwide (Figure A2; Richardson et al. 2009; Osborn and Civiello 2013). Our analysis was based on filtration rates of a different species of jellyfish (*A. aurita*) and did not account for changes in filtration rates with jellyfish size and temperature. Filtration rates also change based on prey density and prey type. Purcell (2009) summarized data from numerous studies of jellyfish trophic ecology and found feeding rates could range from 4 to 20,000 copepods per day within a species (Purcell 2009). Therefore, we do not expect this analysis to represent actual conditions in the field. Instead, we aim to highlight the importance of future

study, especially because the frequency and severity of jellyfish blooms have been increasing.

M. marginata is also not the only—or even the most—abundant brackish-water species in the estuary. Another invasive jelly, *Moerisia lyonsi,* has been found in even higher abundance in Suisun Marsh during the summers of 2004 and 2005 (reaching densities of 1 to 24 individuals per m^3 vs. 0.5 to 2.5 for *M. marginata*) (Baumsteiger et al. 2018). *Moerisia* also consumes copepods and other small pelagic prey, although at a much lower rate than *M. marginata* (1 to 2 copepods day^{-1}) (Purcell et al. 1999). This is because of its smaller size, with *Moerisia* having a bell diameter of up to 8 mm vs. up to 50 mm for *M. marginata* (Wintzer et al. 2011), and is not well captured in fish trawls. If *Moerisia* responds similarly to *M. marginata* to flow, the combined effect of both species on the zooplankton community may be significantly higher than what we estimate here.

Putting aside the limitations in our jellyfish water column turnover analysis, we found that *P. amurensis* filtration usually swamps *M. marginata* filtration by an order of magnitude (Figure 10A). However, because of the larger size of the zooplankters generally consumed by *M. marginata* than the phytoplankton consumed by clams, *M. marginata* had a similar—if not higher—rate of carbon consumed (Figure 10B). The combined effect of both invaders on carbon consumed changes between regions, with the highest combined effect in the confluence in Critically Dry years, the highest grazing in Suisun Bay in Wet years, and a tradeoff between the two organisms in Suisun Marsh, with higher clam grazing in the marsh in Dry years and higher *M. marginata* grazing in the marsh in wet years. Both species increase in the confluence during drier years, when pelagic fish communities are already stressed by increases to harmful algal blooms, increased temperatures, decreased turbidity, and lower flows (Durand et al. 2020; Hartman et al. this issue). Reducing food supply through increased filtration during droughts will only serve to increase the stress on the system.

CONCLUSIONS

P. amurensis and *M. marginata* shift upstream during dry conditions, and clam abundances and filtration rates also increase, though potential carbon consumption varies regionally. Increasing densities of *M. marginata* and *P. amurensis* over time increases stress on the system, particularly when multiple dry years in a row increase the abundance of both species in the confluence. Higher temperatures have already extended the bloom duration of *M. marginata* medusae over the past 2 decades by ~4x, a pattern that will likely intensify with climate change. Moreover, the increase in *P. amurensis* abundance post-2000 may be an under-appreciated contributor to the POD, and the increases in both *P. amurensis* and *M. marginata* in recent years may represent a "new normal" for an estuary with increasing frequency and severity of droughts.

ACKNOWLEDGEMENTS

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