

## Life history and population dynamics of *Moerisia* sp., a non-native hydrozoan, in the upper San Francisco Estuary (U.S.A.)

Alpa P. Wintzer<sup>a,b,\*</sup>, Mariah H. Meek<sup>c</sup>, Peter B. Moyle<sup>a,b</sup>

<sup>a</sup> Center for Watershed Sciences, University of California, One Shields Ave, Davis, CA 95616, USA

<sup>b</sup> Department of Wildlife, Fish and Conservation Biology, University of California, One Shields Ave, Davis, CA 95616, USA

<sup>c</sup> Department of Animal Science, University of California, One Shields Ave, Davis, CA 95616, USA

### ARTICLE INFO

#### Article history:

Received 20 August 2010

Accepted 20 May 2011

Available online 6 June 2011

#### Keywords:

*Moerisia*  
life history  
population dynamics  
hydrozoa  
sexual reproduction  
asexual reproduction

### ABSTRACT

Some populations of gelatinous zooplankton appear to be increasing and causing ecological disruptions during large bloom events. The goal of this study was to investigate the life history and population dynamics of the small, invasive *Moerisia* sp. and its potential ecological impacts in the upper San Francisco Estuary, California. Medusae and polyps were collected from 8 and 2 sites, respectively, during 2007 and 2008. Polyps emerged from a resting stage during June. Asexual reproduction of medusae buds was positively correlated with temperature and negatively related to salinity. The production of polyp buds was positively correlated with dissolved oxygen and water transparency levels. Sexual reproduction, defined by the presence of eggs, was related to the size of medusae. Cessation of reproduction of both polyps and medusae occurred in October, when temperatures dropped below 17 °C. This life history is similar to other hydrozoans and allows *Moerisia* sp. to reach large numbers seasonally in the San Francisco Estuary, possibly contributing to the recent declines of pelagic fish and zooplankton.

© 2011 Elsevier Ltd. All rights reserved.

### 1. Introduction

Blooms (normal, seasonal cycles) of gelatinous zooplankton can have tremendous impacts on trophic interactions and nutrient cycling. Sudden pulses of medusae can significantly reduce numbers of zooplankton prey (Brodeur et al., 2002; Hansson et al., 2005; Smith and Alexander, 2008). Fish abundances may decrease through competition for copepods and other zooplankton prey (Lynam et al., 2005) or direct predation on fish eggs and larvae (Purcell and Grover, 1990; Purcell et al., 1994). Blooms of gelatinous zooplankton may also alter carbon, nitrogen, and other elemental fluxes via large-scale prey consumption, excretion, and mass post-bloom decomposition (reviewed in Pitt et al., 2009). Because the scale and frequency of many blooms appear to be increasing (Mills, 2001), an understanding of each species' life history and population dynamics is needed to predict trends and consequences of these events.

Detailed ecological knowledge of hydromedusae is especially scant, due to their small size and highly seasonal nature (Boero et al., 2008). A yet-to-be-identified hydrozoan species of *Moerisia*,

\* Corresponding author. Center for Watershed Sciences, University of California, One Shields Ave, Davis, CA 95616, USA.

E-mail address: [apwintzer@ucdavis.edu](mailto:apwintzer@ucdavis.edu) (A.P. Wintzer).

believed to be native to the Black Sea region, has recently become established in the low-salinity waters of the San Francisco Estuary (Mills and Rees, 2000). Because of its small size (typically < 5 mm), its effects in the San Francisco Estuary have been little studied. Rees and Gershwin (2000) cultured *Moerisia* sp. in the laboratory and found they exhibited a classic hydrozoan 2-stage reproduction cycle: 1) polyps asexually produce more polyps, and 2) polyps bud dioecious medusae that mate sexually, producing planula larvae, which settle to form more polyps. In the same study, both the medusae and polyp stages were found to be efficient predators, killing and eating *Artemia* nauplii at a rapid rate. A San Francisco Estuary jellyfish survey found the densities of medusae to be relatively low,  $\geq 1/m^3$  (Rees and Kitting, 2002). More recent sampling in the upper estuary, however, yielded density estimates as great as  $197/m^3$ , with this species comprising 71–88% of the total medusae numbers over a 2-year study (Schroeter, 2008).

The goal of our study was to identify trends in the population dynamics of *Moerisia* sp. in Suisun Marsh within the upper estuary, a region identified as key nursery area for many fish and invertebrate species (Meng and Matern, 2001; Schroeter, 2008). Specifically, we aimed to document density, size structure, and biomass of the medusae population over the seasonal bloom period, as well as the biotic and abiotic factors influencing egg production by medusae and asexual reproduction by polyps. Additionally, we considered these data in the context of previous studies.

## 2. Materials and methods

### 2.1. Field sampling

Zooplankton samples, including hydrozoans and their planktonic prey, were collected from eight sites within Suisun Marsh, located in the northeast part of the San Francisco Estuary (Fig. 1) at monthly intervals during the 2007 and 2008 seasonal bloom period of June–November. Collections were made with a horizontally towed conical zooplankton net (230  $\mu\text{m}$  mesh, 0.5 m diameter, 2 m length) paired with a General Oceanics flowmeter to determine water volume sampled. Tows in sloughs less than 15 m in depth were performed at a mid-water column depth. In sloughs greater than 15 m deep, tows were made in the top (approximately 1 m below the surface) and bottom (approximately 1 m above the bottom) halves of the water column. Samples were immediately preserved in 5% non-buffered formalin. A single additional zooplankton tow was performed during August 2009, and the collected medusae were transported fresh to the laboratory for biomass processing.

From April–November of 2008, fouling arrays were deployed at two locations within the study area (Fig. 1) to collect the polyp stage of *Moerisia* sp. Each array hung at two levels within the water column, 0.5 m below the surface and 0.5 m above of the bottom. Six 100  $\text{cm}^2$  roughed PVC plates were suspended from each level. All plates were replaced monthly and the sample plates were preserved in 95% ethanol.

Water quality data, including temperature, salinity (measured using the Practical Salinity Scale), and dissolved oxygen, were measured with a model 30 YSI metre in conjunction each sample collected. Additionally, measures of water transparency were collected using a secchi disk. Mean values of abiotic water quality from all 8 sites were plotted by sample month.

### 2.2. Copepod densities

In the laboratory, subsamples of formalin-preserved calanoid copepods, that contained at least 100 individuals of the most abundant species, were used to determine monthly concentrations. Calanoid copepods were targeted to represent the prey field in this study because they were the most numerous taxa found in the zooplankton samples and they are the most common prey item found in *Moerisia* sp. gut contents (Wintzer, 2010).

### 2.3. Medusae densities and population structure

Preserved *Moerisia* sp. medusae were also subsampled, so that individuals from 1/3 of each sample were counted. Additionally, medusae bell diameters were measured using an SPOT Idea camera and software. Subsamples of medusae and bell diameter values were scaled up using sample volume to estimate monthly totals. Site maps with medusae concentrations and size frequency histograms were created based on these estimates.

A bell diameter-dry weight relationship was developed for the fresh medusae specimens. Sixty fresh medusae were rinsed with freshwater, measured for bell diameter, and initially weighed. They were then left to dry at 25  $^{\circ}\text{C}$ . Specimens were re-weighed every two weeks until a constant value, the dry weight, was obtained. The resulting exponential equation was then combined with the size structure data to develop monthly mean medusa biomass estimates during the blooms.

### 2.4. Medusae egg production

The interradial surfaces of the stomach and lobes of medusae ( $n = 1168$  individuals) were inspected for the presence of eggs

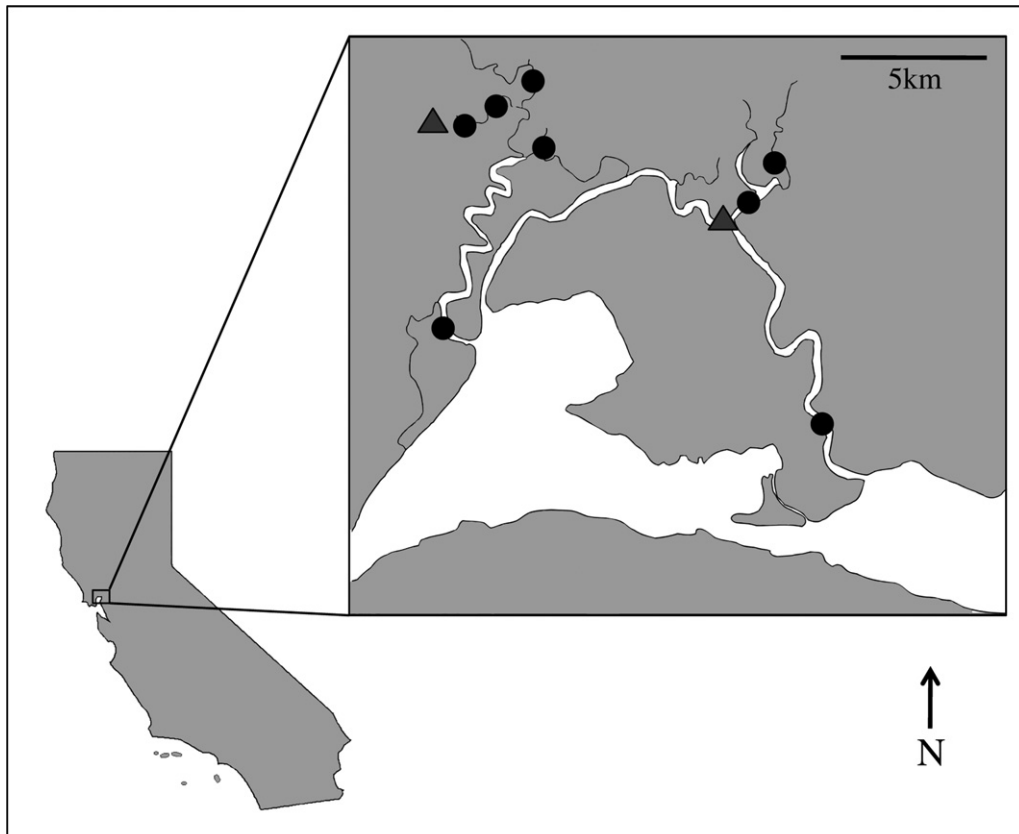


Fig. 1. Sampling stations in Suisun Marsh, California. Black circles = medusae collection sites. Grey triangles = polyp collection sites.

using a dissecting microscope. To examine the factors correlated with presence of eggs in medusae, a forward step-wise regression model was built using temperature, salinity, dissolved oxygen, water transparency, calanoid copepod prey density, hours of daylight, and medusae bell diameter as potential parameters. After selection, a nominal logistic model, utilizing a likelihood-ratio  $\chi^2$  test, was run on the retained variables. We were unable to detect fertile males in our preserved samples.

### 2.5. Polyp reproduction

The presence or absence of medusae buds and polyp buds were noted on polyps ( $n = 198$ ) from the monthly fouling plates. As described for medusae egg presence in Section 2.3 above, regression models were built using the same parameter pool, with the exception of medusae bell diameter, to find factors related to the production of both medusae buds and polyp buds by polyps, and nominal logistic models were then run for each case.

## 3. Results

### 3.1. Monthly water quality and copepod densities

Water temperature data (Fig. 2a) showed typical summer and fall seasonal trends. Temperatures were highest in the summer months (June–August), approximately 21.0 °C during both years, and then sharply declined beginning in August, reaching a low of 11.3 °C in 2007 and 14.8 °C in 2008.

The trend for salinity was generally opposite to that of temperature (Fig. 2b). Salinity was lowest in June of both years: 3.0 in 2007 and 4.3 in 2008. Values increased throughout the summer to a maximum in the fall. In 2007, salinity was highest in November (7.2) and in 2008, salinity peaked in September (8.9) and then fell to 6.6, likely due to earlier rains and freshwater inflow. These trends are typical for this region, which receives little to no rain, and associated increased freshwater inflow, until the fall or winter.

Dissolved oxygen values (Fig. 2c) had a fair amount of variability, but showed an overall increasing trend from July (6.1 mg/l) to September (7.1 mg/l) in 2007 and June (6.0 mg/l) to October (7.3 mg/l) in 2008, in response to the decrease in temperature. Dips in dissolved oxygen are common in Suisun Marsh during fall, as a result of multiple anthropogenic factors, including increased urban runoff and wetland drainage (Schroeter, 2008).

Water transparency generally tracked trends of salinity (Fig. 2d). The sampling period began in June with reduced water clarity (24 cm) in both 2007 and 2008, increasing to maximums of 32 cm and 40 cm in October of 2007 and 2008, respectively. The sharp decrease in transparency seen in November 2008 reflects turbidity associated with increased freshwater flows.

Density estimates for calanoid copepods showed an increasing trend from month to month during the two study years (Fig. 3). The samples for 2008, however, had much greater variability and higher average density values than those for 2007.

### 3.2. Medusae densities and spatial patterns

An estimated 80,000 *Moerisia* sp. medusae were collected during the study. This species exhibited a bloom pattern of low densities in June, with numbers gradually increasing throughout the summer and a rapid decrease by October (Fig. 4). The 2008 densities did appear to increase faster than the previous year, and both sampling years showed extremely high densities of greater than 200 individuals/m<sup>3</sup> at some sites between July and September.

Spatial trends place the first medusae of the bloom in the southeastern-most site sampled. By July, *Moerisia* sp. could be

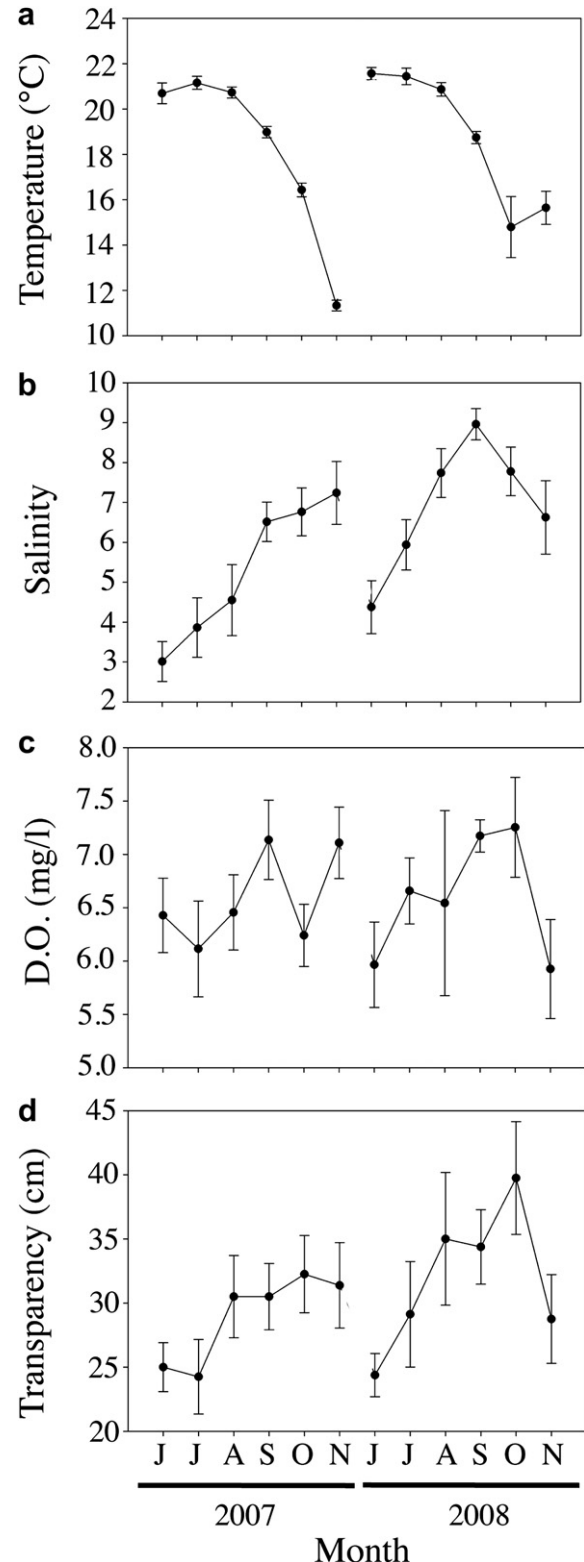
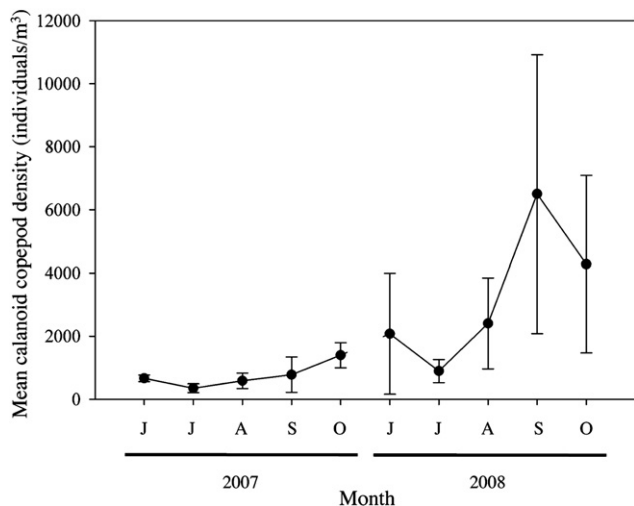


Fig. 2. Monthly temperature, salinity, dissolved oxygen, and water transparency in Suisun Marsh, California during the 2007 and 2008 *Moerisia* sp. seasonal bloom periods. Error bars = standard error.

found throughout the system. The highest concentrations of medusae were found in the northwestern region of the marsh, and the few individuals remaining in October were in the northern reaches (Fig. 4).



**Fig. 3.** Monthly density of calanoid copepods in Suisun Marsh, California during the 2007 and 2008 *Moerisia* sp. seasonal bloom periods. Error bars = standard error.

### 3.3. Medusae size distribution and biomass

Monthly bell diameter histograms revealed a discernable trend over the bloom period (Fig. 5). The few medusae found and measured in June of 2007 and 2008 fell into the smallest size classes, less than 2 mm. Over the following three months, the medusae were found in nearly all of the classes, although individuals greater than 5 mm were not common. The continued representation of smallest size class indicates continuous production of new medusae through October of both years. At the completion of the bloom, the two medusae that were collected were fairly large, greater than 3 mm.

The relationship between bell diameter and dry weight was fit with an exponential curve ( $R^2 = 0.97392$ ) (Fig. 6):

$$y = 0.00002 \exp(0.5362x)$$

Total medusa biomass plots per month show overall trends of initial low values, rising to peaks in September 2007 and August 2008, and then decreasing again by October in both years (Fig. 7). Biomass values for July and August of 2008 are much larger than those for the same months in 2007.

### 3.4. Correlates of egg production by medusae

Medusae carrying eggs were found from July–September during both 2007 and 2008. Only medusae bell diameter was retained as a variable after forward parameter selection. The nominal logistic fit whole model test showed a significant, positive correlation between bell diameter and the likelihood-ratio that medusae were producing eggs,  $\chi^2(1, N = 1168) = 65.34, p < 0.001$ . The range of *Moerisia* sp. bell diameters for medusae that had eggs was 1.9–5.2 mm, while the mean size was 3.3 mm.

### 3.5. Correlates of medusae bud and polyp bud production by polyps

Polyps produced medusae buds from June to October. The variables temperature and salinity were retained by the step-wise regression and integrated into a significant nominal logistic model,  $\chi^2(2, N = 198) = 39.85, p < 0.001$ . Temperatures that correlated to medusae bud production ranged from 16.9 to 25.6 °C, with an average of 22.1 °C. Salinities correlated with medusa bud production were between 1.5 and 7.1, with a mean of 5.2.

Polyp buds were also produced from June to October and were positively correlated with dissolved oxygen and water transparency. The logistic model created with these variables was significant,  $\chi^2(2, N = 198) = 26.16, p < 0.001$ . The production of polyp buds occurred within a dissolved oxygen range of 3.7–7.4 mg/l, with an average of 7.0 mg/l. The water transparency range was broad, from 19 to 60 cm, with an average of 56 cm.

## 4. Discussion

The life history of *Moerisia* sp. in Suisun Marsh has four distinct stages, which correspond to the dynamics of the annual bloom: polyp regeneration, asexual reproduction, sexual reproduction and bloom cessation. These stages are similar to those documented for other cnidarians, especially *Moerisia lyonsi*, the species that *Moerisia* sp. most closely resembles (Rees and Gershwin, 2000). The blooms observed in Suisun Marsh are the result of a sequence of environmental conditions that seasonably favour the different life history stages.

### 4.1. Polyp regeneration

In our study area, *Moerisia* sp. polyps appear during June (Wintzer et al., 2011). Temperature appears to be the principal trigger that initiates regeneration from resting stages in temperate estuarine and freshwater hydrozoans (Dunham, 1941; Calder, 1990; Folino, 2000). While no encysted specimens were recovered, the rapid appearance of medusae implies that local populations of polyps are re-vitalized from a state of dormancy rather than from the immigration of medusae from other parts of the estuary. This is further supported by the lack of medusae collected in the regions surrounding the marsh prior to polyp appearance in this study. The polyps of *M. lyonsi* are also believed to utilize a dormant resting stage, because they were able to repeatedly colonize mesocosm setups even after enduring desiccated conditions (Purcell et al., 1999).

### 4.2. Polyps and asexual reproduction

We found temperature to be positively related to production of medusae buds in *Moerisia* sp., while salinity had a negative correlation. Schroeter (2008) noted that the *Moerisia* sp. medusae blooms appeared at an average temperature of 21.2 °C, and an average salinity of 5.8. These values fall within the ranges of salinity and temperature correlated with bud production, but the early season values from the current study suggest this event may occur at conditions of 25.6 °C and 1.5. The discrepancy may be attributed to a larger collection mesh size (500 µm) of the net used by Schroeter (2008), which would not have captured the earliest, small medusae.

We also found that the production of polyp buds was related to high dissolved oxygen levels. This is in agreement with Wintzer et al.'s (2011) study, correlating water quality variables to polyp distribution and abundance in Suisun Marsh, which found recruitment rate of *Moerisia* sp. polyps is most strongly influenced by dissolved oxygen. Given this, and the lack of a relationship between dissolved oxygen and sexual reproduction in medusae, it is likely that asexual reproduction is the most utilized mode of population increase for the benthic stage in this system. A similar trend has been demonstrated for stolonation by *Chrysaora quinquecirrha* polyps (Condon et al., 2001).

Interestingly, high values of water transparency were also related to polyp bud production. Because water transparency values may be considered to be a crude proxy for light intensity, this trend is the opposite of that found in *Aurelia aurita*, in which polyps are produced at lower light intensities and medusae buds are

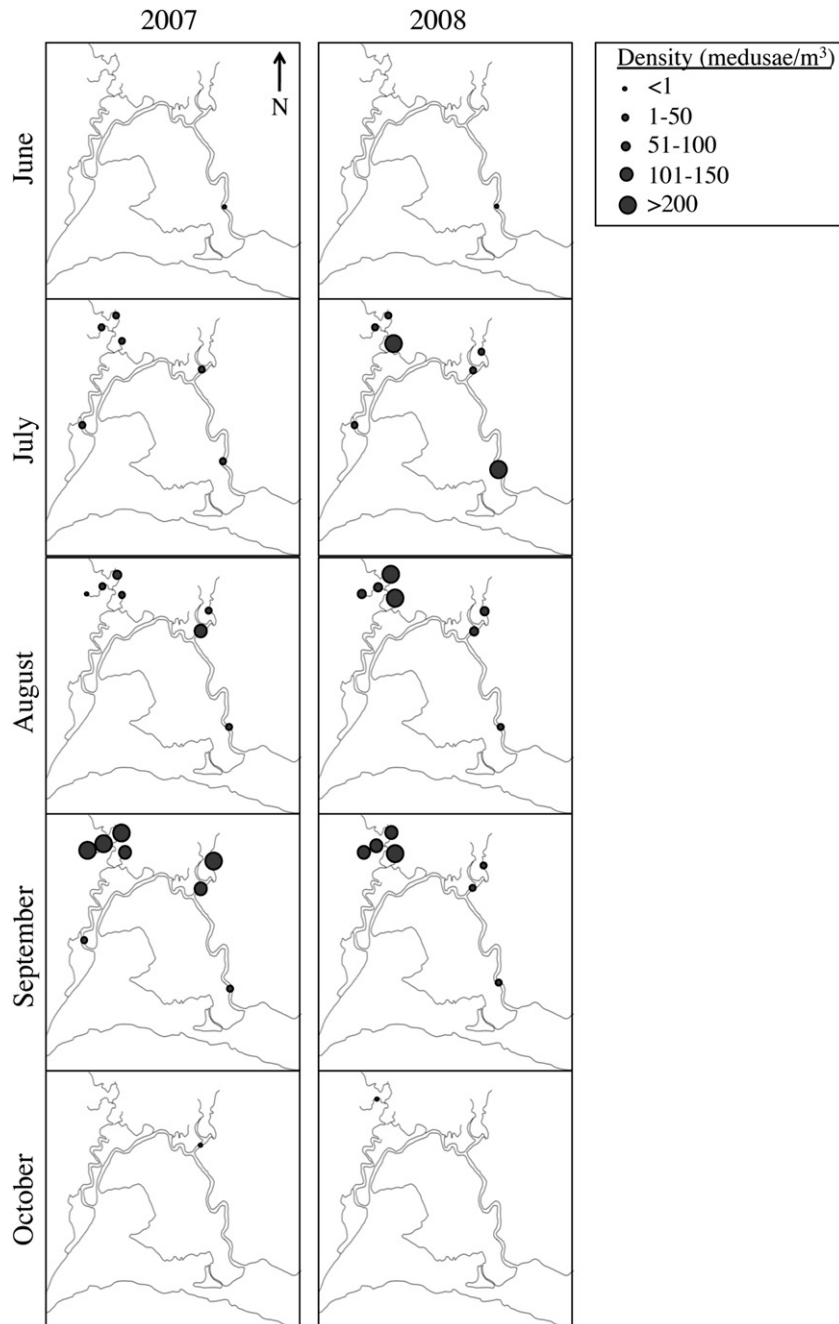


Fig. 4. Monthly medusae densities at sampling stations in Suisun Marsh, California during the 2007 and 2008 *Moerisia* sp. seasonal bloom periods.

formed as this value increases (Liu et al., 2009). The polyps of *A. aurita* settle on the undersides of substrate, which have low light intensities. *Moerisia* sp. polyps, however, recruit to both vertical and horizontal surfaces without significant difference (Wintzer et al., 2011). These variations in settlement behaviour may reflect behavioural differences between these species, which can explain the alternate trends regarding light and polyp production.

It may be that prey availability also impacts rates of asexual reproduction by *Moerisia* sp. polyps. Purcell et al. (1999) found that the creation of *M. lyonsi* polyp buds was related to high food levels, based on treatments of 1–8 copepods/day. The polyp stage of *Moerisia* sp. in Suisun Marsh consumes a variety of small zooplankton and benthic crustaceans (Wintzer, unpublished data), which were not collected during this study.

Once re-established in the estuary, *Moerisia* sp. polyps were collected between June and November, with peaks in August and September (Wintzer et al., 2011). The “optimal conditions” for this life stage (based on the 5th and 95th percentile values of density data) include temperatures between 18.9 and 22.1 °C, a broad salinity range of 4.6–21.8, dissolved oxygen levels of 5.7–6.9 mg/l, and a water transparency range of 32.0–60.0 cm (Wintzer et al., 2011). Recruitment within the system seems to infer high rates of asexual reproduction, with a single settlement plate estimate of 1107 *Moerisia* sp. hydranths/day/m<sup>2</sup> (Wintzer et al., 2011). Purcell et al. (1999) noted that the rapid rate of asexual reproduction in *M. lyonsi* is also striking in relation to the few published data for other cnidarians. As with most hydrozoan polyps, they are well adapted to early colonization of surfaces, but are soon

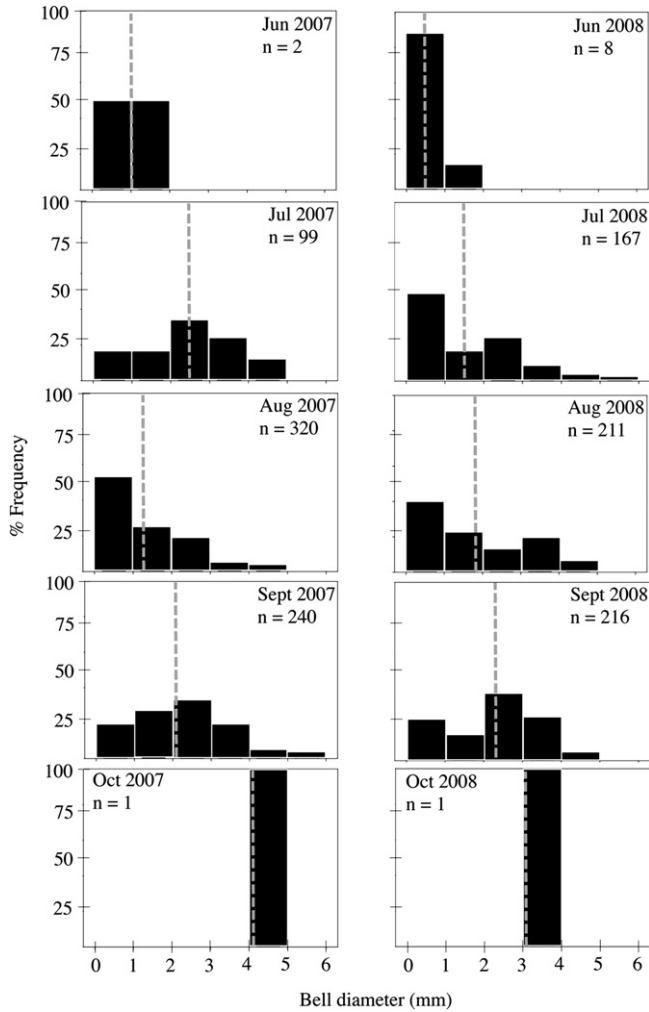


Fig. 5. Percentage frequency histograms of *Moerisia* sp. medusae in Suisun Marsh, California during the 2007 and 2008 *Moerisia* sp. seasonal bloom periods. Vertical dashed line = mean size. *n* = number of medusae examined.

out-competed for space (Boero, 1984). Persistence of polyps was generally poor from month to month, as non-native substrate competitors, including the bay barnacle, *Balanus improvisus*, and predators, such as shimofuri (*Tridentiger bifasciatus*) and shokihaze (*T. barbatus*) gobies reduced their numbers (Wintzer et al., 2011).

4.3. Medusae and sexual reproduction

Fast growth rates have been observed in *Moerisia* medusae post-release from polyps. Under laboratory conditions, Rees and Gershwin (2000) found 10-day-old *Moerisia* sp. medusae ranged in size from 1.5 to 2.5 mm bell diameter and reached 3.5–4.2 mm by day 24. This rate, of approximately 13% growth/day, was slower than the 33% growth/day recorded for laboratory-raised *M. lyonsi* (Purcell et al., 1999), but on par with other species, including field measured *A. aurita* (Hansson, 1997).

The development of eggs in medusae of *Moerisia* sp. was correlated only with bell diameter. The fast growth rate of this species, coupled with its small final size and a high level of available prey may explain these findings. Hamner and Jenssen (1974) found that maturation in *A. aurita* was also dependent upon size of medusae. Mature *Moerisia* sp. females were found during several months of both sampling years, over a period in which water

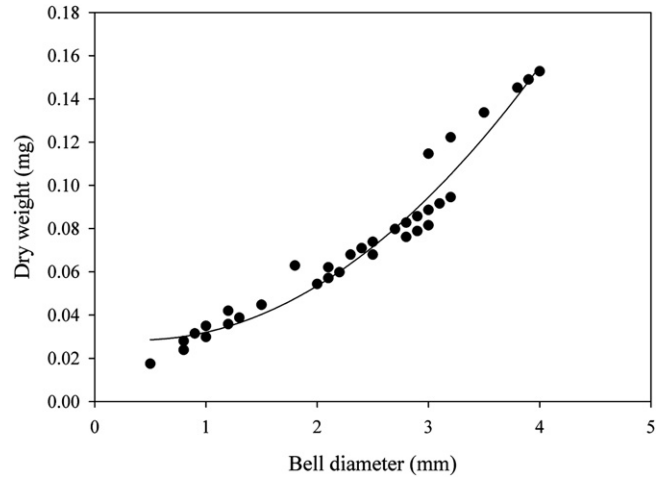


Fig. 6. Relationship between bell diameter and biomass of *Moerisia* sp. medusae in Suisun Marsh, California.

quality varied considerably. During the course of the seasonal bloom, medusae occurrence was greatest under the apparently optimal conditions of 19.5–22.7 °C temperature, 2.8–9.9 salinity, and 4.6–7.8 mg/l dissolved oxygen in 2005 and 15.7–22.0 °C temperature, 3.1–9.3 salinity, and 4.6–7.8 mg/l dissolved oxygen in 2006 (Schroeter, 2008).

Combinations of physical forces (e.g. circulation patterns, thermoclines, etc.) and behaviours commonly influence the distributions of hydromedusae (Arai, 1992). The rapid, wide-spread appearance of medusae in Suisun Marsh during the early months of the bloom is likely a due to polyp regeneration and asexual reproduction, in addition to the movement of the weak-swimming *Moerisia* sp. via tidal motion (Rees and Gershwin, 2000).

4.4. Bloom cessation

Large-scale declines of *Moerisia* sp. polyps were observed during October. A decrease in temperature, and its associated physiological and ecological impacts, is the commonly accepted trigger for dormancy in polyps during the winter (Coma et al., 2000). The

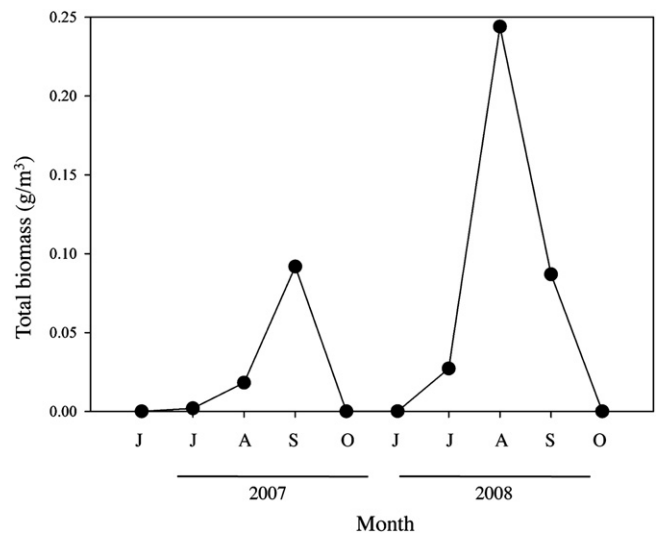


Fig. 7. Monthly biomass densities of medusae in Suisun Marsh, California during the 2007 and 2008 *Moerisia* sp. seasonal bloom periods. Error bars = standard error.

reduction of *Moerisia* sp. polyps occurred with temperatures of 16.9–17.1 °C, which may be the thermal limit for the benthic stage of this species before it enters a diapause stage (Wintzer et al., 2011).

Mortality in medusae may be linked to physiologically intolerable environmental conditions. A minimum temperature of 19 °C was estimated for survival of the medusae stage, explaining their typical reductions in early October (Schroeter, 2008). *Moerisia* sp. medusae were collected at a minimum temperature of 17 °C in this study, suggesting a slightly lower thermal tolerance for this stage. Some mortality in medusae may also be due to natural senescence, which is common after sexual reproduction (Boero et al., 2008). There are no known medusae predators in the upper San Francisco Estuary (Rees and Gershwin, 2000) that would cause a reduction in their population. Additionally, prey limitation is an unlikely contributor to the declines, as there were numerous calanoid copepods present at the end of the bloom.

#### 4.5. Future investigations of *Moerisia* sp.

To date, most data on *Moerisia* sp. come from field studies, and detailed laboratory experiments are required to identify fine-scale patterns of life history and population dynamics. For example, studies on the polyp phase may allow us to identify the exact conditions required for the promotion of polyp regeneration and regression to a resting stage. Additionally, we may gain insight into how temperature, salinity, dissolved oxygen, and water transparency interact to influence the asexual production of medusae and polyp buds. Laboratory experiments with medusae can investigate the factors that promote the maturation of male medusae, as well as the conditions at the physiological threshold of survival for medusae nearing the culmination of the bloom.

#### 4.6. Implications of *Moerisia* sp. blooms

The flexible and rapid reproductive capacities, coupled with the ability to form resting stage “seed banks” during unsuitable conditions, may allow *Moerisia* sp. to have a very large seasonal impact on other pelagic species in the upper San Francisco Estuary, especially via trophic interactions. Perhaps the greatest concern relates to recent precipitous declines in the local populations of four planktivorous fish species, delta smelt (*Hypomesus transpacificus*), longfin smelt (*Spirinchus thaleichthys*), age-0 striped bass (*Morone saxatilis*), and threadfin shad (*Dorosoma petenense*) (Sommer et al., 2007). Large reductions in the number of calanoid copepods, a major prey source for these fishes, have also been documented in the system. *Moerisia* sp. consumes a wide variety of zooplankton, especially calanoid copepods (Wintzer, 2010). Although individuals of this species are small, diet data demonstrate that it rarely has an empty gut and is capable of digesting multiple items at once (Wintzer, 2010). Additionally, laboratory culture has revealed that *Moerisia* sp. leaves many prey items dead, but uneaten (Rees and Gershwin, 2000), likely increasing the level of competition with fishes for food resources.

A second potential trophic impact of *Moerisia* sp. is their alteration of nutrient cycling through the marsh food web. Because there are no known predators of the medusae in the estuary, the nutrients obtained from the pelagic realm are likely not significantly released back into the system until the medusae die off in late fall. This event shunts the energy from the pelagic food web directly to the detrital loop (Schroeter, 2008). Another contribution to the benthos may be from *Moerisia* sp.’s tendency to kill more zooplankton than it consumes (Rees and Gershwin, 2000), allowing this energy source to sink to the bottom of the system. It is

unknown how this alteration may impact the trophic relationships of the estuary.

#### Acknowledgements

We would like to thank Dr. May, B., Dr. Schroeter, R.E., Dr. Grosholz, E.D., Dr. Lawler, S.P., Durand, J.R., Purdy, S.E., and O’Rear, T.A. for their assistance. We are grateful to an anonymous reviewer whose comments greatly improved this manuscript. This research was supported by funding from the CALFED Science Program, UC Davis Biological Invasions IGERT NSF-DGE#0114432, Dr. Nancy Foster Scholarship, Marin Rod and Gun Club Scholarship, Stockton Sportsmen’s Scholarship, and the Giles W. and Elise G. Mead Foundation.

#### References

- Arai, M.N., 1992. Active and passive factors affecting aggregations of hydromedusae: a review. *Scientia Marina* 56, 99–108.
- Boero, F., 1984. The ecology of marine hydroids and effects of environmental factors: a review. *PSZN I: Marine Ecology* 5, 93–118.
- Boero, F., Bouillon, J., Miglietta, M.P., Parsons, T., Piraino, S., 2008. Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series* 356, 299–310.
- Brodeur, R.D., Sugisaki, H., Hunt Jr., G.L., 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series* 233, 89–103.
- Calder, D.R., 1990. Seasonal cycles of activity and inactivity in some hydroids from Virginia and South Carolina, USA. *Canadian Journal of Zoology* 68, 442–450.
- Coma, R., Ribes, M., Gili, J.M., Zabala, M., 2000. Seasonality in coastal benthic ecosystems. *Trends in Ecology and Evolution* 15, 448–453.
- Condon, R.H., Decker, M.B., Purcell, J.E., 2001. Effects of low dissolved oxygen on survival and asexual reproduction of scyphozoan polyps (*Chrysaora quinquecirrha*). *Hydrobiologia* 451, 89–95.
- Dunham, D.W., 1941. Studies on the ecology and physiology of the freshwater jellyfish, *Craspedacusta sowerbii*. Dissertation, The Ohio State University.
- Folino, N.C., 2000. The freshwater expansion and classification of the colonial hydroid *Cordylophora* (Phylum Cnidaria, class Hydrozoa). *Marine Bioinvasions: Proceedings of the First National Conference*, Cambridge, Massachusetts, United States of America, pp. 139–144.
- Hamner, W.M., Jønsen, R.M., 1974. Growth, degrowth, and irreversible cell differentiation in *Aurelia aurita*. *American Zoologist* 14, 833–849.
- Hansson, L.J., 1997. Effect of temperature on growth rate of *Aurelia aurita* (Cnidaria, Scyphozoa) from Gullmarsfjorden, Sweden. *Marine Ecology Progress Series* 161, 145–153.
- Hansson, L.J., Moeslund, O., Kiørboe, T., Riisgård, H.U., 2005. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). *Marine Ecology Progress Series* 304, 117–131.
- Liu, W.C., Lo, W.T., Purcell, J.E., Chang, H.H., 2009. Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. *Hydrobiologia* 616, 247–258.
- Lynam, C.P., Heath, M.R., Hay, S.J., Brierley, A.S., 2005. Evidence for impacts by jellyfish on North Sea herring recruitment. *Marine Ecology Progress Series* 298, 157–167.
- Meng, L., Matern, S.A., 2001. Native and introduced larval fishes of Suisun Marsh, California: the effects of freshwater flow. *Transactions of the American Fisheries Society* 130, 750–765.
- Mills, C.E., Rees, J.T., 2000. New observations and corrections concerning the trio of invasive hydromedusae *Maotias marginata* (= *M. inexpectata*), *Blackfordia virginica*, and *Moerisia* sp. in the San Francisco Estuary. *Scientia Marina* 64 (supp. 1), 151–155.
- Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 452, 55–68.
- Pitt, K.A., Welsh, D.T., Condon, R.H., 2009. Influence of jellyfish blooms on carbon, nitrogen, and phosphorous cycling and plankton production. *Hydrobiologia* 616, 133–149.
- Purcell, J.E., Nemazie, D.A., Dorsey, S.E., Houde, E.D., Gamble, J.C., 1994. Predation mortality of bay anchovy (*Anchoa mitchilli*) eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. *Marine Ecology Progress Series* 114, 47–58.
- Purcell, J.E., Grover, J.J., 1990. Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. *Marine Ecology Progress Series* 59, 55–67.
- Purcell, J.E., Båmstedt, U., Båmstedt, A., 1999. Prey, feeding rates, and asexual reproduction rates of the introduced oligohaline hydrozoan *Moerisia lyonsi*. *Marine Biology* 134, 317–325.
- Rees, J.T., Gershwin, L.A., 2000. Non-indigenous hydromedusae in California’s upper San Francisco Estuary: life cycles, distribution, and potential environmental impacts. *Scientia Marina* 64 (supp. 1), 73–86.

- Rees, J.T., Kitting, C.L., 2002. Survey of Gelatinous Zooplankton (“Jellyfish”) in the San Francisco Estuary: Initial Field Survey, Annotated Species Checklist, and Field Key. Interagency Ecological Program for the San Francisco Estuary, Tech Rep 70.
- Schroeter, R.E., 2008. Biology and long-term trends of alien hydromedusae and striped bass in a brackish tidal marsh in the San Francisco Estuary. Ph.D. thesis, University of California, Davis, unpublished.
- Smith, A.S., Alexander, J.E., 2008. Potential effects of the freshwater jellyfish *Craspedacusta sowerbii* on zooplankton community abundance. *Journal of Plankton Research* 30, 1323–1327.
- Sommer, T., Armor, C., Baxter, R., Breuer, R., Brown, L., Chotkowski, M., Culberson, S., Feyrer, F., Gingras, M., Herbold, B., Kimmerer, W., Mueller-Solger, A., Nobriga, M., Souza, K., 2007. El Colapso de los Peces Pelagicos en La Cabecera Del Estuario San Francisco. (The Collapse of Pelagic Fishes in the Upper San Francisco Estuary). *Fisheries* 32, 270–277.
- Wintzer, A.P., 2010. Ecology of non-native hydrozoans in the San Francisco Estuary: implications for Pelagic Organism Decline fishes. Ph.D. thesis, University of California, Davis, unpublished.
- Wintzer, A.P., Meek, M.H., Moyle, P., 2011. Ecological insights into the polyp stage of non-native hydrozoans in the San Francisco Estuary. *Aquatic Ecology* 45, 151–161.