

## Research Article

## Abundance, size, and diel feeding ecology of *Blackfordia virginica* (Mayer, 1910), a non-native hydrozoan in the lower Napa and Petaluma Rivers, California (USA)

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### Abstract

*Blackfordia virginica* (Mayer, 1910) is a small hydrozoan that has invaded estuaries around the world. In the lower Napa and Petaluma rivers, located within the San Francisco Estuary, *B. virginica* populations followed a classic pulsed bloom event. Medusae monthly bell diameter measurements showed an initial increasing trend with a wide range of sizes, followed by a decreasing average size and narrower size range towards bloom culmination. Biomass was generally greatest in June. Medusae were pelagic feeders, consuming both invertebrates and fish larvae. Copepod nauplii were by far most numerous prey in the guts, followed by cyclopoid copepods and mysids. Further studies of *B. virginica* are needed to understand its potential impacts on estuarine ecosystems, which may be great where it is abundant.

**Key words:** invasive species; gelatinous zooplankton; seasonal bloom dynamics; trophic ecology; size distribution; biomass

### Introduction

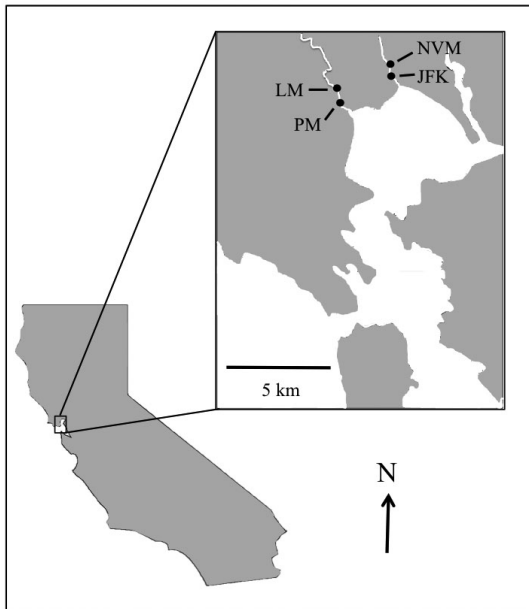
*Blackfordia virginica* (Mayer, 1910) is a small hydrozoan native to the Black Sea (Thiel 1935). Its broad thermal and salinity tolerances (Moore 1987) have allowed it to be easily transported in the ballast water of ships (Kramp 1958) and successfully invade estuaries of North America (e.g. Mayer 1910; Silva et al. 2003), South America (e.g. Genzano et al. 2006; Bardi and Marques 2009), Europe (e.g. Denayer 1973; Ré 1996), Asia (e.g. Zhang 1982; Santhakumari et al. 1997), and Africa (e.g. Beucher et al. 2005).

Blooms of some gelatinous zooplankton are increasing (Richardson et al. 2009) and impacting local food webs (Hansson et al. 2005; Lynam et al. 2005). Compared to other cnidarian taxa, relatively little is known about hydrozoan ecology (Boero et al. 2008). A greater understanding of the biology of *B. virginica* is needed to recognize its effects on estuarine ecosystems and to develop control strategies, if necessary.

*Blackfordia virginica* was first reported in the Napa and Petaluma Rivers, which are part of the greater San Francisco Estuary, in the 1970s

(Mills and Sommer 1995). Their density was noted as approximately 0.02–0.09 medusae/m<sup>3</sup> in the Napa River, and, although no density was reported, they were common in the Petaluma estuary (Rees and Kitting 1999). Mills and Sommer (1995) processed medusae gut contents from a single sample day, revealing a diet restricted to copepods, copepod nauplii, and barnacle nauplii. Mills and Rees (2000) identified polyps of *B. virginica* from the Napa River, and most recently, Wintzer et al. (2011a) studied the polyp phase in a sample area that included the Napa and Petaluma Rivers, among other sites, within the San Francisco Estuary. *Blackfordia virginica* polyps were present during the summer and fall, peaking in abundance during June and July. Monthly persistence of polyps, measured by the presence of hydranths, was low.

The goal of our study was to report abundance, size, and feeding trends for *B. virginica* medusae in the lower Napa and Petaluma Rivers. Specifically, we aimed to test the following hypotheses: 1) Density, size structure, and biomass of the medusae population follow a classic



**Figure 1.** Monthly sampling stations for *Blackfordia virginica* medusae in the lower Napa and Petaluma Rivers. LM=Gilardis Lakeville Marina, PM=Petaluma Marina, JFK=John F. Kennedy Park and NVM=Napa Valley Marina.

hydrozoan seasonal pulse over the bloom period, and 2) during a diel period, *B. virginica* medusae diets are comprised of a variety of prey items which are consumed in proportion to their availability in the environment.

## Materials and methods

### Study area

The Petaluma and Napa Rivers provide water to California's premiere wine-growing regions, eventually discharging into San Pablo Bay in the northwest section of the San Francisco Estuary (Figure 1). The rivers and their estuaries suffer from agricultural and urban pollution, and as a result, they are home to many threatened and endangered species, as well as to a growing number of alien species.

### Monthly field sampling

*Blackfordia virginica* medusae were sampled monthly from the lower reaches of the Napa and Petaluma Rivers during their seasonal bloom from June–November in 2007. These collections inadvertently missed the start of the 2007 bloom period; consequently, sampling was undertaken

from April–November 2008 in the Napa River and April–October 2008 in the Petaluma River to span the entire event. Samples were taken from 2 sites, Gilardis Lakeville Marina (average depth 3.5 m) and Petaluma Marina (average depth 2.3 m), in the Petaluma River and 2 sites, John F. Kennedy Park (average depth 1.4 m) and Napa Valley Marina (average depth 3.5 m), in the Napa River. At each site, sampling consisted of a single vertical haul of a zooplankton net (64  $\mu$ m mesh, 0.5 m diameter, 2 m length) outfitted with a General Oceanics flowmeter (Miami, Florida, USA) to record the volume of sampled. All medusae were immediately preserved in a 5% formalin solution. An additional sample was taken during June 2009 and left unpreserved to derive a dry weight–bell diameter relationship needed for biomass calculations.

Measurements of water temperature, salinity and dissolved oxygen were taken using a model 30 YSI meter (Yellow Springs, Ohio, USA) during each sampling event, approximately 1 m below the surface. Water transparency was estimated with a 20 cm diameter Secchi disc.

### Medusae density and population structure

In the laboratory, all medusae from a tow were counted, and density was expressed as number per  $m^3$  using the volumes derived from the flowmeter estimates. Bell diameters were measured using a SPOT Idea camera and SPOT Basic 4.0 software (Sterling Heights, Michigan, USA). Additionally, the values of each water variable associated with the 5th and 95th percentiles of medusae occurrence data were then identified. This was used to estimate abiotic conditions associated with *B. virginica* presence.

To examine medusae biomass over the bloom, fresh specimens ( $N = 60$  individuals) were rinsed with fresh water, bell diameter measured, and air dried at 25°C. Medusae were weighed every week with a Mettler Toledo balance (Columbus, Ohio, USA) until they maintained a constant weight. The relationship between dry weight and bell diameter was fitted with a power regression. The resulting equation was then applied to size frequency and medusae density datasets to yield biomass estimates (expressed as  $mg/m^3$ , dry mass).

### 24 hour diet study

Diel sampling occurred June 4–5, 2008 at the Petaluma Marina to examine feeding patterns

over a 24-hour period. Specimens were collected by means of vertical tows taken at ~ about 3-h intervals. The sample timing was chosen based on laboratory digestion experiments (Wintzer, unpublished data) to ensure discrete feeding events. Medusae were immediately placed in individual vials and preserved with 5% formalin to minimize net feeding and to contain any prey regurgitation caused by contact with the preservative. The remaining zooplankton from the tow were preserved in 5% formalin and stored for later analysis.

In the laboratory, gut contents of all medusae collected during a sampling interval were identified to the lowest taxonomic level possible. For the same interval, a subsample of zooplankton, obtained using a Folsom splitter until at least 300 individuals were retained, were identified and counted. Feeding selectivity for each interval was estimated using Pearre's selectivity index, with a Yate's correction for continuity (Pearre 1982):

$$C = \pm \left[ \frac{\left( |a_d b_e - a_e b_d| - \left( \frac{n}{2} \right)^2 \right)^{0.5}}{abde} \right]$$

where,  $a_d$  is the number of a prey type consumed,  $a_e$  is the number of that prey in the environment,  $a$  is the total number of that prey type (consumed + environment),  $b_d$  is the number of all other prey consumed,  $b_e$  is the number of all other prey in the environment,  $b$  is the sum of all other prey consumed and in the environment,  $d$  is the total number of prey consumed,  $e$  is the total number of prey in the environment, and  $n$  is the sum of  $d$  and  $e$ . A positive value of  $C$  indicates a high occurrence of that prey type in the diet as compared to the amount in the environment, a value of 0 represents no difference, and a negative value indicates a disproportionately low occurrence in the diet. The statistical significance of each index calculation was tested using a  $\chi^2$  statistic (Pearre 1982):

$$\chi^2 = nC^2$$

where  $n$  and  $C$  are calculated as described above. In order to reduce type 1 error, a Bonferroni correction was also applied to the  $\chi^2$  statistic.

Percent by number (each sample treated as a replicate) and percent occurrence (all individuals combined) in the gut were calculated for each prey item. A one-way ANOVA was used to

detect whether the mean number of prey consumed per individual differed between sampling intervals. Which intervals differed was then identified with Tukey-Kramer HSD tests. Additionally, a nonparametric Spearman's  $\rho$  rank correlation test was performed to examine any relationship between medusae size and the number of prey items consumed.

## Results

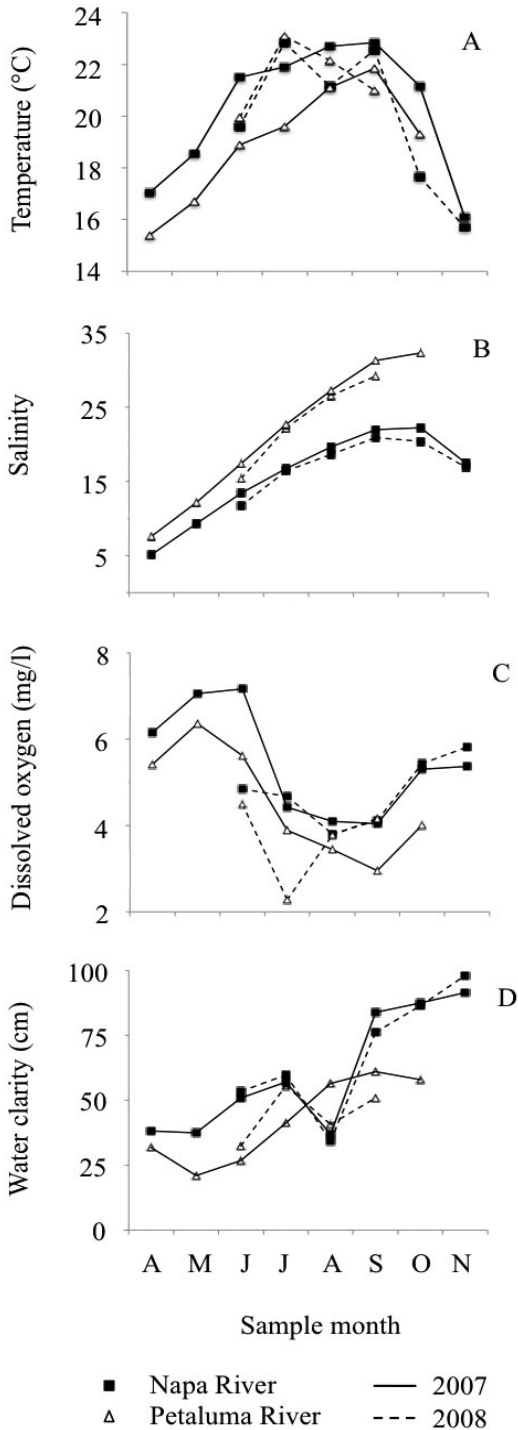
### *Monthly water characteristics*

The Napa River was warmer than the Petaluma River in 2007, but not in 2008. During both sampling years, the maximum temperature was approximately 23°C. By November, temperatures had declined to those observed in the spring (Figure 2A). Salinity showed a steady increasing trend from spring until September-October, with a slight dip in November in the Napa River. November samples were not collected from the Petaluma River. The Petaluma River had higher salinities than the Napa River during both study years (Figure 2B). Dissolved oxygen levels decreased through the summer months before rising again in the fall. The lowest values were noted from the Petaluma River during September 2007 and July 2008 (Figure 2C). Percent oxygen saturation estimates for these sample dates were 54.1 and 48.6%, respectively. The average percent saturation values for the Petaluma River were 56.2% during the 2007 study and 51.2% during the 2008 study period. Water transparency in both rivers typically was low (< 100 cm) (Figure 2D).

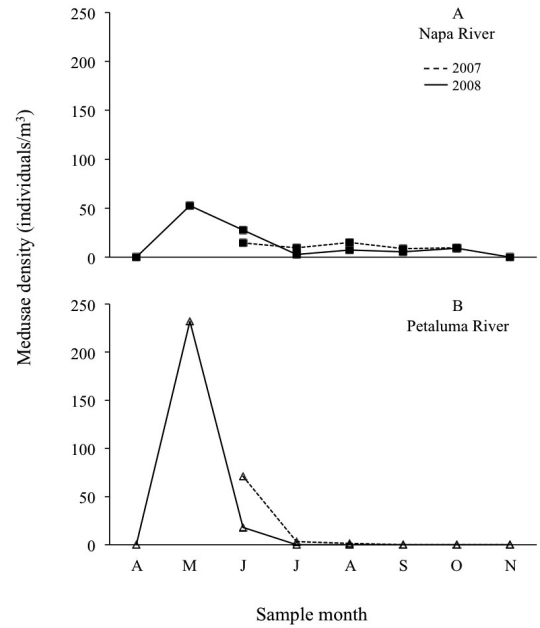
### *Medusae density and population structure*

In 2008, *B. virginica* were collected from the Napa River from May to October and in the Petaluma River from May to June (Figure 3A, B). Medusae may have been present before and after these months but missed due to the single tow sampling method used in this study. Densities appeared to peak in May 2008 for both rivers, with higher values for the Petaluma River. The initial pulse of 2007 was likely missed, but the subsequent data track well with latter portion of the bloom during 2008 for both rivers.

Monthly bell diameter frequency histograms for the Napa River over both sample years indicated a trend of increasing average diameter, with a wide range of size classes represented (Figure 4). This was followed by a period of decreasing average size and narrowing size range



**Figure 2.** Monthly water data from the lower Napa and Petaluma Rivers during the 2007 and 2008 seasonal blooms.



**Figure 3.** Medusae density of *Blackfordia virginica* collected from the lower Napa and Petaluma Rivers during the 2007 and 2008 seasonal blooms.

until the end of the bloom. A similar trend was found in the Petaluma River during 2007, while data for the 2008 bloom lacked the gradual reduction in bell size; instead, medusae abruptly disappear after peaking in June. The June 2008 samples from the Petaluma River had the largest average bell width measured in this study (Figure 5).

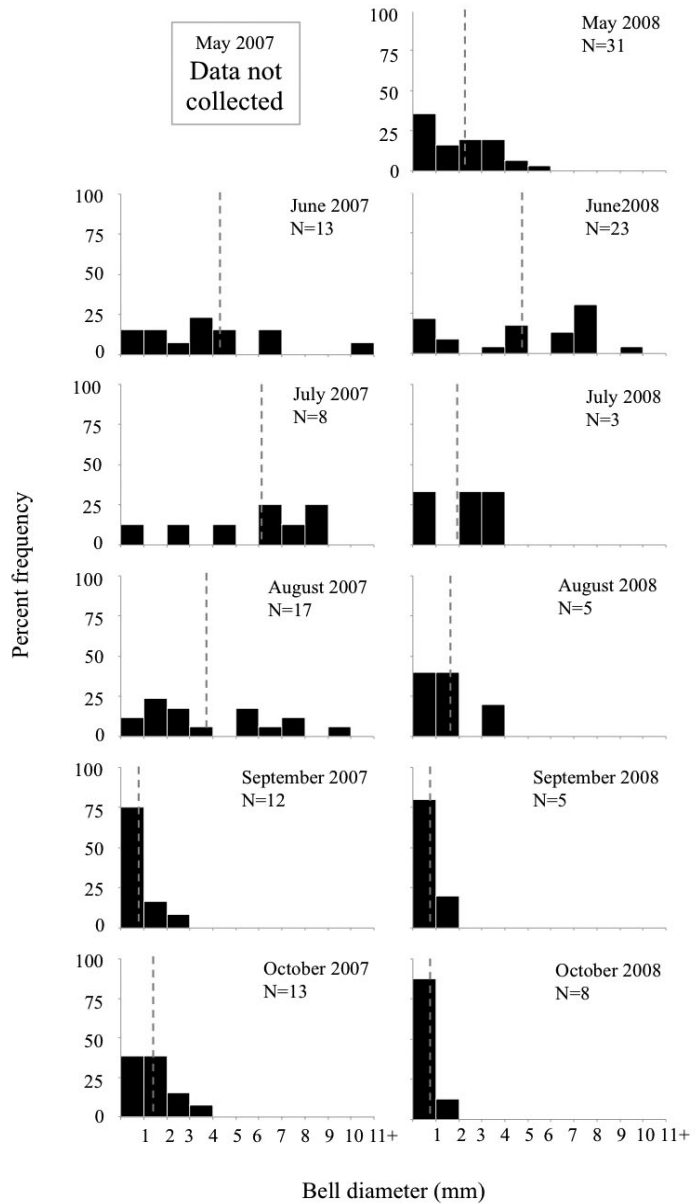
The ranges of occurrence, based on the 5<sup>th</sup> and 95<sup>th</sup> percentiles in which *B. virginica* were found in the Napa and Petaluma Rivers, included temperatures between 16.5–23.0°C, salinities of 10.1–20.6, a dissolved oxygen range of 3.8–6.9 mg/l, and water clarity values of 12.0–75.1 cm.

The biomass relationship between bell diameter and medusa dry weight was:

$$y = (2.785 \times 10^{-5})x^{2.089} \quad n = 60, R^2 = 0.964$$

When applied to the abundance and size-frequency data, it was clear that the density of medusae peaked in May in the Napa River during 2008 but the biomass peaked in June before

**Figure 4.** Percent frequency histograms of *Blackfordia virginica* collected from the lower Napa River during the 2007 and 2008 seasonal blooms. Vertical dashed line=mean size.

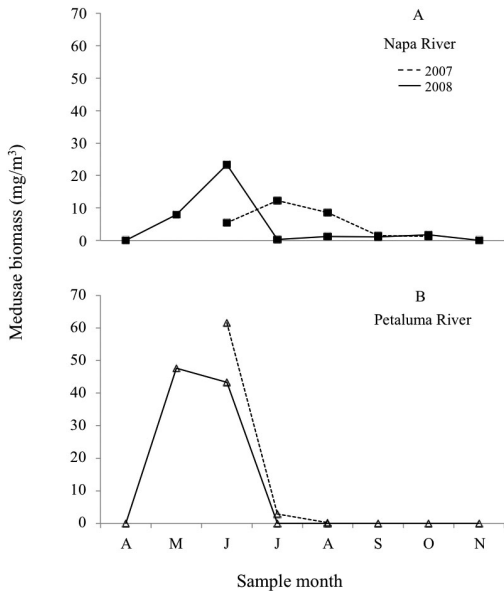
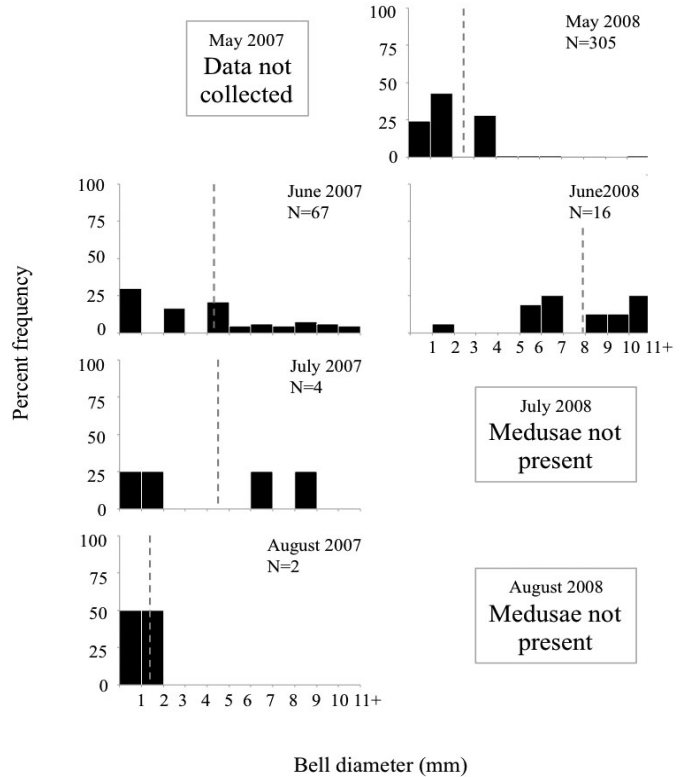


rapidly declining in July (Figure 6A). While incomplete, the 2007 data showed an increasing biomass trend until July, gradually decreasing through October. The Petaluma River's *B. virginica* biomass reached its highest value of the study during June 2007, falling rapidly the next month (Figure 6B). During 2008, the biomass was highest in May, mirroring the density data, however biomass remained high in June, then dropped quickly in July.

*Feeding selectivity, diel diet and feeding periodicity*

Results of the Pearre's selectivity index generally did not differ from zero. The few significant non-zero values were very low (maximum value 0.1) and unlikely to be biologically significant. Therefore, *B. virginica* may be classified as non-selective zooplankton predator (Table 1).

**Figure 5.** Percent frequency histograms of *Blackfordia virginica* collected from the lower Petaluma River during the 2007 and 2008 seasonal blooms. Vertical dashed line=mean size.



**Figure 6.** Monthly biomass estimates of *Blackfordia virginica* in the lower Napa and Petaluma Rivers during the 2007 and 2008 seasonal blooms.

Copepod nauplii were by far the most abundant prey in the guts, followed distantly by cyclopoid copepods and mysids (Table 2). All other prey items constituted less than 1% of the abundance. Percent occurrence calculations for each item further support non-selective zooplankton feeding, with each prey item, except fish larvae, found in at least 50% of the sampling periods (Table 2).

One-way ANOVA results showed a difference in prey consumption numbers between sample times ( $F_{(7,104)} = 66.930, P < 0.001$ ). Significantly more prey were consumed per medusae during the 06:44 and 10:22 morning collection times compared to all others (Table 3). The Spearman's  $\rho$  test found no correlation between medusae size and the number of prey consumed ( $\rho = 0.074, d.f. = 111, P = 0.438$ ). An average of 8.8 prey items, with a range of 0–41, were found per medusa gut.

**Table 1.** Diel selectivity calculations for prey consumed by *Blackfordia virginica* June 4–5, 2008 in the lower Petaluma River using Pearre’s selectivity index. 0.00 values indicate no difference between relative abundance of plankton in the guts and in the water. Bold values=significance with Bonferroni correction ( $\alpha=0.005$ ).

Prey type	Sample time (n)							
	13:13 (18)	16:35 (22)	18:28 (18)	21:05 (11)	12:02 (18)	03:08 (7)	06:44 (14)	10:22 (3)
Barnacle nauplii	-0.01	-0.01	-0.02	0.00	-0.01	-0.02	0.00	-0.01
Calanoid copepods	<b>0.10</b>	-0.01	0.00	-0.01	0.00	-0.01	0.00	<b>0.08</b>
Copepod nauplii	-0.06	0.01	0.04	-0.01	<b>0.08</b>	0.02	0.01	0.00
Cyclopoid copepods	<b>0.10</b>	0.02	-0.02	0.00	0.03	0.00	-0.02	0.00
Cumaceans	0.00	0.00	-0.01	--	-0.01	--	--	--
Fish larvae	--	0.03	-0.04	--	<b>0.06</b>	--	--	--
Gammarid amphipods	--	0.00	-0.01	--	-0.01	0.00	-0.01	--
Harpacticoid copepods	0.00	-0.01	-0.02	0.00	0.05	0.00	0.00	0.00
Mysids	-0.01	0.00	0.02	0.01	<b>-0.08</b>	0.00	0.02	0.00
Ostracods	--	0.00	--	--	0.00	-0.02	--	--
Zoea	0.01	-0.01	-0.01	0.00	<b>0.06</b>	--	<b>0.03</b>	--

**Table 2.** Percent abundance and occurrence of prey items in the diet of *Blackfordia virginica* June 4–5, 2008 in the lower Petaluma River.

Prey type	% abundance in diet ( $\pm$ SE)	% occurrence in diet
Barnacle nauplii	0.72 (0.31)	62.50
Calanoid copepods	1.03 (0.47)	75.00
Copepod nauplii	81.42 (8.00)	100.00
Cyclopoid copepods	9.55 (2.37)	87.50
Fish larvae	0.21 (0.22)	37.50
Harpacticoid copepods	0.92 (0.68)	75.00
Mysids	5.85 (6.33)	87.50
Zoea	0.31 (0.22)	50.00

**Table 3.** Mean number of prey items consumed by *Blackfordia virginica* during June 4–5, 2008. Differences in superscript letters indicate significant difference in prey number.

Time	Mean prey (SE)
13:13 <sup>a</sup>	4.50 (1.45)
16:35 <sup>a</sup>	5.50 (2.84)
18:28 <sup>a</sup>	4.17 (0.96)
21:05 <sup>a</sup>	5.36 (2.59)
12:02 <sup>a</sup>	3.33 (1.33)
03:08 <sup>a</sup>	3.86 (1.77)
06:44 <sup>b</sup>	26.86 (1.91)
10:22 <sup>b</sup>	23.00 (3.20)

**Discussion**

*Population trends*

The medusae of *B. virginica* in the lower Napa and Petaluma rivers followed a seasonally pulsed bloom pattern. Bloom duration varied considerably, from a 6+ month bloom in the Napa River during 2007 to a 2 month bloom in the Petaluma River during 2008. In Suisun Marsh, a

low salinity region of the San Francisco Estuary, the abundance of medusae was positively related to high values of salinity, temperature, and oxygen, but negatively affected by high turbidity (Schroeter 2008, unpublished Ph.D. thesis). The 2008 blooms in the Napa and Petaluma Rivers began as salinity, temperature, and dissolved oxygen increased and turbidity decreased from April to May. However, medusae densities declined after May, even as temperature and salinity continued to increase. Dissolved oxygen levels did fall during this time, which may help to explain the decline in medusae abundance. Three of the four observed blooms culminated between September and October, as temperature, salinity, and water clarity decreased. The ranges of occurrence of *B. virginica* for water variables measured by Schroeter (2008, unpublished Ph.D. thesis) included temperatures of 14.8–22.8°C, salinities of 5.6–10.3, and dissolved oxygen of 5.4–8.0 mg/l. These ranges were more restrictive than in this study, likely because Suisun Marsh represents the upstream edge of the suitable habitat in the system.

*Blackfordia virginica* polyps were reported in the lower Napa and Petaluma Rivers from June-September in 2007 and June-August in 2008 (Wintzer et al. 2011a). However, polyps were most likely present when the medusae appeared in May, as the June samples were not collected on the first day of the month. Additionally, medusae collected from the Napa River towards the end of the blooms may have originated elsewhere in the system, perhaps upstream of this study's sample sites where the salinity remained in the apparent optimal range for the polyp phase (Wintzer et al. 2011a).

The maximum density estimated for *B. virginica* from this study, with non-replicate sampling, was 232 medusae/m<sup>3</sup>. Previous values for this system have been much lower, ranging from 5.0–5.7 medusae/m<sup>3</sup> (Rees and Kitting 1999; Schroeter 2008, unpublished Ph.D. thesis). Other invaded systems around the globe have reported a wide range of densities, including: 10.6 medusae/m<sup>3</sup> in the Babitonga estuary of southern Brazil (Bardi and Marques 2009), 29.5 medusae/m<sup>3</sup> from the Rio de la Plata estuary in Argentina-Uruguay (Genzano et al. 2006), 31.70 medusae/m<sup>3</sup> in the Guadiana Estuary of Portugal/Spain (Chícharo et al. 2009), 66.6 medusae/m<sup>3</sup> in the Mira Estuary of Portugal (Moore 1987) and, 420 medusae/m<sup>3</sup> in the Bombay Harbor-Thana and Bassein Creek estuarine complex of India (Santhakumari et al. 1997).

### Diets

Mills and Sommer (1995) described *B. virginica* as “quiescent in the water column,” likely making this species an ambush predator (Colin et al. 2003). In this study, it consumed a diverse variety of planktonic prey, including fish larvae. The diet breadth was broader than that found by Mills and Sommer (1995), in which 29 medusae from the Napa River fed exclusively on copepods, copepod nauplii, and barnacle nauplii. Their samples were collected on a single day late in the bloom season, which may explain the discrepancy. The ability to non-selectively consume a broad prey base has probably helped *B. virginica* to successfully invade new territories (Richardson et al. 2009), such as the San Francisco Estuary.

Prey consumption by *B. virginica* was greatest during the morning hours, in contrast to many other gelatinous zooplankton. *Chrysaora hysoscella* (Linnaeus, 1767) (Flynn and Gibbons

2007), *Craspedacusta sowerbyi* (Lankester, 1880) (Spadinger and Maier 1999), and various epipelagic siphonophores (Purcell 1981), for instance, all feed more actively at night, often migrating in the water column to follow prey movements. Increased feeding during the day appears to be a lesser-documented phenomenon. Siphonophores *Rhizophysa eysenhardti* (Gegenbaur, 1859) and *Rosacea cymbiformis* (delle Chiaje, 1830) were found to extend their tentacles during lighted laboratory conditions for feeding, regardless of the actual photoperiod (Purcell 1981). *Blackfordia virginica* does not possess obvious light-sensing organs, but may still be responding to light-dark cues, as most gelatinous species are believed to have evolved some form of photoreception (Anderson 1985). Alternatively, the increase in prey consumption during morning collection times may be related to an increase in copepod nauplii densities during these periods.

Because of the wide variety of prey types, including both larger (*i.e.* fish larvae, mysids) and smaller (*i.e.* nauplii) items, we did not find a correlation between prey number and bell diameter, as was found for *Maeotias marginata* (Modeer, 1791) and *Moerisia* sp., two other non-native hydrozoans in the San Francisco Estuary (Wintzer et al. 2011b). However, if diet had been examined as % biomass, large and small prey items may have been equally important in terms of energy acquisition. *Blackfordia virginica* consumed more prey in this study (mean 8.8 organisms per gut, range 0–41) compared with the previous study in this system (mean 1.4 organisms per gut, range 1–3; Mills and Sommer 1995).

### Ecological implications and population limitations

As blooms of some gelatinous zooplankton increase in size and frequency (Mills 2001), fish populations may be affected through competition for prey (Lynam et al. 2005) and/or predation on egg and larval stages (Purcell and Arai 2001; Shoji et al. 2005). The current study demonstrated that *B. virginica* is capable of larval fish predation in the lower Napa and Petaluma Rivers. Additionally, Chícharo et al. (2009) noted decreased zooplankton abundance, including eggs of the European anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), in regions of the Guadiana Estuary where *B. virginica* was present, indicating a potential



competition-predation interaction. Purcell et al. (1987) reported that unfed larval fish were at greater risk of predation by *Aequorea victoria* (Murbach and Shearer, 1902) than those that were fed. If larval fish are consuming less prey due to competitive effects with gelatinous zooplankton, they may then be even more likely to fall to predation, also by gelatinous zooplankton.

The *B. virginica* population in the Napa and Petaluma Rivers has grown since the initial sampling of Rees and Kitting (1999). Biological factors, however, may ultimately control the population (Mills and Rees 1995). Although there are no native predators on medusae in the Napa and Petaluma Rivers, there are several species that may prey upon the polyp stage. These include: the Ponto-Caspian nudibranch *Tenellia adpersa* (Nordmann, 1845) (Chester 1996), a voracious hydroid predator; and (to a lesser degree) a number of native and non-native fishes (e.g. yellow fin goby, *Acanthogobius flavimanus* (Temminck and Schlegel, 1845), striped bass, *Morone saxatilis* (Walbaum, 1792), and Sacramento splittail, *Pogonichthys macrolepidotus* (Ayres, 1854)) from which small amounts of hydroid have been reported in gut contents (Feyrer 1999). Additionally, the polyp population appears to face competition for space by a diverse community of non-native fouling organisms [e.g. Australian tubeworm, *Ficopomatus enigmaticus* (Fauvel, 1923), and the bay barnacle, *Balanus improvisus* (Darwin, 1854)] in the Napa and Petaluma Rivers (Wintzer et al. 2011a). Continued monitoring of *B. virginica* populations will be necessary to gauge true ecological impacts and the population trends of this global invader.

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