

## Trophic ecology of two non-native hydrozoan medusae in the upper San Francisco Estuary

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**Abstract.** Blooms of some gelatinous zooplankton are increasing worldwide, often disrupting foodwebs. Invasions of non-native jellyfish are a growing problem in many estuaries, including the San Francisco Estuary, where at least two species of Ponto-Caspian hydrozoans, *Maeotias marginata* Modeer, 1791 and *Moerisia* sp., are abundant. The present study investigated their trophic ecology, testing the following hypotheses: (1) diets over the bloom and at the diel scale are comprised of a variety of prey items; (2) hydrozoans are generalist feeders; (3) hydrozoans feed on the larvae of declining fish species; and (4) the potential for prey competition exists between the hydrozoans and two declining planktivorous fishes, striped bass (*Morone saxatilis*) and threadfin shad (*Dorosoma petenense*). Both hydrozoans ate a variety of crustaceans, most notably calanoid copepods, which were found in greater proportion in the guts than in the environment. The only fish larvae consumed were gobies. Density of *Moerisia* sp., was negatively correlated with gut fullness for both fishes, and diet overlap was high between shad and hydrozoans, but low for bass. Because of strong spatial and temporal overlap between hydrozoans and shad, competition for zooplankton may be occurring. These hydrozoans have invaded other systems, and should be monitored to assess potential ecological interactions in these locations.

**Additional keywords:** diel, diet, *Dorosoma petenense*, intra-bloom, *Maeotias marginata*, *Moerisia*, *Morone saxatilis*.

### Introduction

Gelatinous zooplankton have proven to be important, yet understudied, predators in marine and estuarine systems. Increases in bloom size and frequency of several jellyfish species, coupled with their ability to consume copious amounts of prey, can dramatically alter pelagic foodwebs, including the initiation of trophic cascades (Greve 1994; Jankowski *et al.* 2005; Pitt *et al.* 2007). Fish populations may be affected through strong competition for zooplankton prey (Purcell 2003; Hansson *et al.* 2005; Lynam *et al.* 2006) or through direct predation on eggs and larvae (Purcell and Arai 2001; Shoji *et al.* 2005).

Several pelagic, plankton-feeding fishes have undergone long-term declines in the upper San Francisco Estuary, with step-declines since 2002, resulting in record low numbers of delta smelt (*Hypomesus transpacificus*), young-of-year striped bass (*Morone saxatilis*), threadfin shad (*Dorosoma petenense*) and longfin smelt (*Spirinchus thaleichthys*) (Feyrer *et al.* 2007; Rosenfield and Baxter 2007; Sommer *et al.* 2007). These trends, combined with declines in zooplankton species, are considered to be part of a general pelagic organism decline in the estuary (IEP 2005).

Three small hydrozoans, *Maeotias marginata* (bell width <40 mm), *Moerisia* sp. (<8 mm) and *Blackfordia virginica*

(<18 mm), all native to the Ponto-Caspian system (Calder and Burrell 1969), have become established in the upper San Francisco Estuary. Hydrozoans are novel predators in this region, resulting in an especially high likelihood of foodweb alteration (Moyle and Light 1996). Schroeter (2008) analysed otter trawl data collected for *M. marginata* from 1981 to 2005 within Suisun Marsh in the upper San Francisco Estuary, and found significant increases in the annual percentage occurrence per site across the system. Of the nearly 29 000 *M. marginata* individuals collected during these years, more than 90% were captured after 1992 and more than 80% after 1998. Long-term data are not currently available for the other two species in the estuary; however, if their populations are following growth trends, such as those found for *M. marginata*, their impact on the system may be substantial.

Preliminary diet studies on *M. marginata* and *B. virginica* have demonstrated that they feed on a wide variety of planktonic organisms, including larval fishes (Mills and Sommer 1995; Schroeter 2008). Studies on the diet of *Moerisia* sp. have never been published. The limited, but compelling, data on these invasive jellyfish species indicate that more information is needed to properly assess their potential role in the declines of zooplankton and pelagic fishes in the upper San Francisco Estuary.

The present study begins to address these data needs by examining the trophic ecology of *M. marginata* and *Moerisia* sp., the two most common hydrozoans in the estuary, to better understand how they might interact with two declining species of fish, namely striped bass and threadfin shad. Specifically, the hypotheses under investigation include the following: (1) the diets of the hydrozoans are comprised of a variety of prey items, both over the bloom period and at the diel scale; (2) the hydrozoans are generalist feeders, consuming prey in relation to their availability in the environment; (3) the hydrozoans feed on the larvae of declining fish species; and (4) the potential for competition for prey exists between the hydrozoans and the two pelagic fishes.

## Materials and methods

### Study area

The present study was conducted in Suisun Marsh (38.1707°N, 121.9736°W), in the upper San Francisco Estuary. Suisun Marsh is a brackish water system, covering 34 0007 ha. Approximately one-third of this area is formed by an array of tidally influenced sloughs, whereas the remainder is a combination of diked seasonal pools and upland grasslands (DWR 1999; Meng and Matern 2001). The system receives the majority of its freshwater input from the Sacramento River, via the Sacramento–San Joaquin Delta to the east, with smaller contributions made by a waste-treatment facility outfall, and a series of small inflowing creeks. Saline water enters the marsh by tidal action from three southerly located bays (Meng and Matern 2001). Water quality (e.g. salinity, temperature, dissolved oxygen) varies both spatially and seasonally, making this a very dynamic system (Schroeter 2008).

### Intra-bloom diets

To investigate the hypotheses that the hydrozoans feed on a wide variety of prey items during the seasonal bloom, prey are consumed in relation to their availability over the bloom period, and that they consume larvae of declining fish species, monthly field sampling during the medusa bloom (July–October) was undertaken in 2007 and 2008. Four sites were sampled for *Moerisia* sp., small-sized *Maeotias marginata* and their planktonic prey by using a zooplankton net (230- $\mu$ m mesh, 0.5-m diameter, 2-m length) coupled with a General Oceanics (Miami, Florida, USA) flowmeter to estimate the towed volume. This mesh size was chosen because it was able to capture both the smallest sizes of medusae as well as the majority of their potential prey items. Samples collected from sloughs less than 15 m in depth were performed at a mid-water column depth, whereas tows in sloughs greater than 15 m deep were performed in each of the top (~1 m below the surface) and bottom (~1 m above the bottom) halves of the water column. All tows were 5 min in length. On retrieval of the zooplankton net, the samples were immediately preserved in 5% formalin to minimise net feeding. Some prey consumption is inevitable for this type of sampling and may have slightly skewed the diet data.

To collect the larger, more mobile sizes of *M. marginata*, an otter trawl (1.5 m  $\times$  4.3 m mouth, 5.3-m length, 35-mm stretch graded to 4-mm stretch mesh at the cod end) was towed at all sites. In the deep sloughs, hydrofoils were fitted to the otter

boards (Trent 1967), and additional trawls were performed to sample the upper half of the water column. All trawls were paired with a flowmeter. The larger mesh size of the trawl precluded net feeding. Medusae were preserved in 5% formalin.

In the laboratory, the bell diameters of up to 20 individuals from each species in each sample were measured using a Leica Z16 APO dissection microscope (Wetzlar, Hesse, Germany) and attached SPOT Idea camera and software (Sterling Heights, Michigan, USA). The medusa gut contents were removed and identified to the lowest possible taxonomic level. In addition, subsamples from the zooplankton samples, commensurate with the total sample density, were identified and enumerated. Zooplankton assemblages and densities from samples taken in the upper and lower portions of a site's water column were found to be similar and were combined for all subsequent analyses.

A Spearman's  $\rho$  rank correlation was performed to identify possible relationships between medusa-bell width and the number of prey items consumed. Non-parametric tests were utilised because data did not meet normality assumptions. Values of percentage occurrence over the four sample months per year were also calculated for each prey item found in the gut contents.

Pearre's selectivity index (Pearre 1982) was used on pooled site data to assess dietary patterns for each species by comparing the proportion of prey items found in medusa guts with the proportion of these prey items available in the zooplankton samples, as follows:

$$C = \pm(((n(|a_d b_e - a_e b_d|) - (n/2)^2)/abde)/a + b)^{0.5},$$

where  $a_d$  is the number of a specific prey type ingested,  $a_e$  is the number of that prey in the environment,  $a$  is the total number of that prey type (ingested + environment),  $b_d$  is the number of all other prey ingested,  $b_e$  is the number of all other prey in the environment,  $b$  is the sum of all other prey ingested and in the environment,  $d$  is the total number of prey ingested,  $e$  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 with the amount in the environment, a value of 0 represents no difference, and a negative value indicates a disproportionately low occurrence in the diet. All calculated indices were tested for significance using a modified  $\chi^2$  statistic (Pearre 1982), as follows:

$$\chi^2 = n \times C^2,$$

where  $n$  and  $C$  are calculated as described for Pearre's selectivity index above. A Bonferroni correction was also applied to the  $\chi^2$  statistic to reduce the risk of Type 1 error.

### Diel diets

Diel sampling occurred on 11–12 August 2008 in a single slough to explore the hypotheses that dietary patterns over a 24-h period involve a broad prey base and that the hydrozoans are generalist feeders. Laboratory studies have shown that the digestion times for several zooplankton species were 1 h, or less for both hydrozoan species (A. P. Wintzer, unpubl. data). Therefore, to collect discrete time series diet data, samples were taken approximately every 3 h, during slack, ebb and flood portions of

the tidal cycle. The zooplankton net and flowmeter were used during collection. In the laboratory, medusae were measured and their gut contents identified. A subsample of the ambient zooplankton were identified and counted, as described above. Pearre's selectivity index calculations were performed for each collection period.

#### *Trophic interactions with fishes*

The hypothesis that the potential for prey competition exists between the hydrozoans and planktivorous fishes was assessed using a variety of methods, including gut-fullness calculations before, during and after the bloom period and in relation to medusa density. Comparisons of diet overlap between fishes and jellyfish were also undertaken.

Juvenile young-of-the-year striped bass and, both juvenile and mature threadfin shad were chosen for this portion of the study because both species were still relatively abundant. Up to 20 of each species captured in each of the otter and mid-water trawls were preserved in 10% formalin throughout the 2007 and 2008 sampling seasons. Beach seines were also performed at two sites to augment fish numbers. Additionally, monthly fish and plankton surveys were conducted at all four sample sites before (April and May) and after (December and January) the seasonal bloom in 2008, to investigate the possibility of changes in fish feeding during the bloom.

In the laboratory, the wet weights of the fishes and their stomach contents were measured to the nearest 0.00000 g with a Mettler Toledo balance (Columbus, Ohio, USA). All gut contents were identified to the lowest possible taxon and enumerated.

An estimate of gut fullness (Smyly 1952) was calculated for each specimen, as follows:

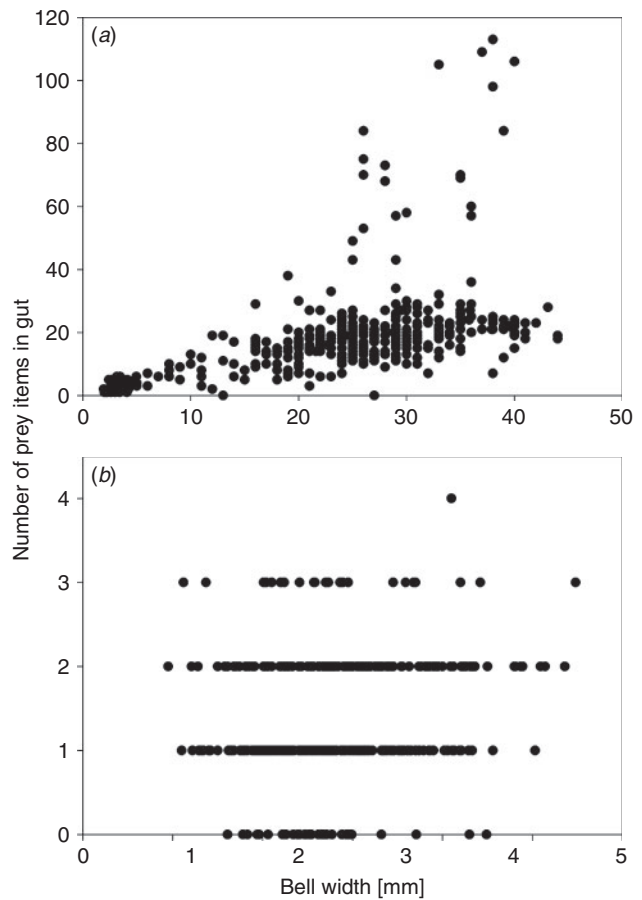
$$F = (\text{stomachcontentweight}/\text{fishweight}) \times 100.$$

Kruskal–Wallis tests were performed for each species to identify differences in gut fullness among the pre-bloom, bloom and post-bloom time periods. Additionally, during the bloom period, possible correlations between gut fullness and medusa density were examined with Spearman's  $\rho$  tests. Because large- and small-sized *Maeotias marginata* were collected with different sampling gear, only densities for the large *M. marginata* were used to test for correlations.

The level of monthly dietary overlap at the sample locations between Suisun Marsh fishes and hydromedusae was evaluated with Pianka's symmetric niche coefficient (Pianka 1974), as follows:

$$\phi_{ij} = (\sum P_{ij}P_{ik})/(\sqrt{(\sum P_{ij}^2 \sum P_{ik}^2)}),$$

where,  $P_{ij}$  is the proportion of prey type  $i$  found in the diet of species  $j$  and  $P_{ik}$  is the proportion of prey type  $i$  in the diet of species  $k$ . A resultant value of 0 indicates no overlap, whereas a value of 1 shows total dietary overlap (Huey and Pianka 1977). The impact of month and year on dietary overlap between striped bass and hydromedusa was investigated with non-parametric Kruskal–Wallis tests. Because of low numbers of threadfin shad, collections of this fish and medusae at the same



**Fig. 1.** Relationship between medusa bell diameter and number of prey items found in the guts of (a) *Maeotias marginata* and (b) *Moerisia* sp.

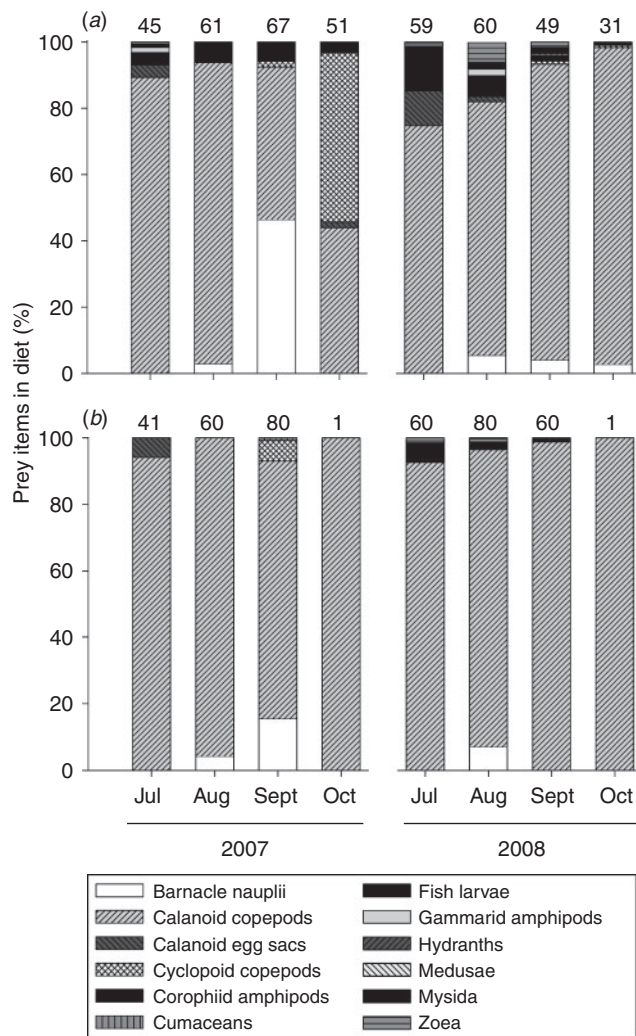
collection period were somewhat rare, making it difficult to statistically analyse these data by month and year. Instead, ranges and means of overlap values were examined for these species combinations.

## Results

### *Intra-bloom diets*

In all, 226 individuals of *Maeotias marginata* and 182 of *Moerisia* sp. from 2007 and 200 individuals of *M. marginata* and 201 of *Moerisia* sp. from 2008 were dissected for gut contents. The non-parametric Spearman's  $\rho$  correlations indicated that the number of prey items per an individual medusa had a significant positive relationship with bell width for both *M. marginata* ( $\rho = 0.620$ , d.f. = 422,  $P < 0.000$ ) and *Moerisia* sp. ( $\rho = 0.190$ , d.f. = 381,  $P < 0.000$ ) (Fig. 1).

*Maeotias marginata* was found to feed on a large number of taxa, consuming 13 different prey types over their bloom period. Their diet in 2007 consisted mainly of calanoid copepods ( $65\% \pm 8.92$ ), along with barnacle nauplii ( $14\% \pm 8.20$ ), cyclopooid copepods ( $14\% \pm 6.53$ ), corophiid amphipods ( $4\% \pm 0.60$ ) and calanoid egg sacs (no longer attached to the copepod) ( $1\% \pm 0.70$ ). Mysids, gammarid amphipods, crab zoea and cumaceans were also consumed, but contributed less than 1% to the gut contents each. In 2008, *M. marginata* fed on calanoid



**Fig. 2.** Monthly percentage of prey items found in the guts of (a) *Maeotias marginata* and (b) *Moerisia* sp. during the 2007 and 2008 sample periods. Sample size is indicated above each bar.

copepods ( $80\% \pm 3.74$ ), barnacle nauplii ( $4\% \pm 1.23$ ), corophiid amphipods ( $4\% \pm 0.88$ ), crab zoea ( $4\% \pm 1.56$ ), mysids ( $3\% \pm 1.56$ ), calanoid egg sacs ( $3\% \pm 0.74$ ) and gammarid amphipods ( $1\% \pm 0.32$ ), with lesser contributions by fish larvae, cumaceans, cyclopoid copepods, *Moerisia* sp. medusae, ostracods, and hydranths of *Cordylophora caspia*, another Ponto-Caspian hydrozoan.

A monthly assessment of gut contents over the bloom (Fig. 2a) revealed that *M. marginata* consumed mainly calanoid copepods each period. Barnacle nauplii and cyclopoid copepods comprised a large percentage of the diets during September and August, respectively, in 2007.

The percentage occurrence of prey items in *M. marginata* guts was highest for calanoid copepods (100% both years) and mysids (100% both years), followed by cyclopoid copepods (75%, 100%) and corophiid amphipods (75%, 100%). Crab zoea (75% both years), barnacle nauplii (75% both years), egg sacs (75%, 50%), gammarid amphipods (75%, 50%) and cumaceans (25%, 50%) showed moderate occurrence over the study,

whereas fish larvae (0%, 50%), hydranths (0%, 25%) and medusae (0%, 25%) were low.

Monthly selectivity calculations for *M. marginata* indicated that not all prey items in the guts were consistent with the amount available in the system, refuting Hypothesis 2. A larger proportion of corophiid amphipods was detected in the diets than in the environments, whereas the opposite was found for larval fishes, *Moerisia* sp. medusae, and ostracods. Both positive and negative values were found for the remaining prey items, except for cumaceans, harpacticoid copepods and *C. caspia* hydranths, which were never significant (Table 1).

*Moerisia* sp. also consumed a wide variety of items, feeding on eight taxa over the study period. In 2007, they consumed mostly calanoid copepods ( $87\% \pm 3.92$ ), barnacle nauplii ( $8\% \pm 3.22$ ), cyclopoid copepods ( $3\% \pm 1.42$ ) and calanoid egg sacs ( $1\% \pm 0.57$ ), whereas cumaceans were eaten in small quantities. In 2008, gut contents included calanoid copepods ( $94\% \pm 2.73$ ), mysids ( $2\% \pm 0.61$ ) and barnacle nauplii ( $2\% \pm 2.10$ ). Zoea and fish larvae each contributed less than 1%.

Gut contents of *Moerisia* sp. during each month of the bloom period predominantly comprised calanoid copepods over both study years (Fig. 2b). The percentage occurrence of calanoid copepods in the diets of *Moerisia* sp., on the basis of monthly collections, was 100% for both sample years. The remaining prey items had variable occurrence during 2007 and 2008, including barnacle nauplii (50%, 25%), mysids (0%, 75%), zoea (0%, 50%), calanoid eggs (25%, 0%), cyclopoid copepods (25%, 0%), cumaceans (25%, 0%) and fish larvae (0%, 25%).

A larger proportion of calanoid copepods was found in *Moerisia* sp. guts than in the environment. Significant and opposite trends were found for all other important taxa (Table 1). These results refute the second hypothesis.

Of the calanoid copepods consumed by both medusae species, *Acartiella sinensis* made up the greatest percentage, followed by *Pseudodiaptomus forbesi*. *Tortanus dextrilobatus* and *Eurytemora affinis* were found in smaller numbers (Fig. 3). In terms of monthly percentage occurrence of calanoid copepods, *A. sinensis* and *T. dextrilobatus* were present 100% of the time in monthly *M. marginata* gut contents for each year, whereas *P. forbesi* (100%, 75%) and *E. affinis* (75%, 75%) were more variable. *A. sinensis* had 100% occurrence in the monthly diets of *Moerisia* sp. during 2007 and 2008, with *T. dextrilobatus* (75%, 75%), *P. forbesi* (75%, 75%) and *E. affinis* (50%, 25%) present less consistently.

**Diel diets**

During a 24-h period, *Maeotias marginata* and *Moerisia* sp. consumed fewer prey taxa, six and three, respectively, than the average based on the monthly data. Pearre's selectivity index values for the diel study were less variable than those of the monthly surveys (Table 2), with the ratios of some prey items not corresponding with that seen in the water. *M. marginata* displayed a larger proportion of calanoid copepods and corophiid amphipods in their diets than the proportion in the environment. The opposite trend was found for all other prey items, except *C. caspia* hydranths, which were not significantly consumed, and gammarid amphipods and barnacle nauplii, which had both positive and negative significant index values. The gut contents of *Moerisia* sp. had a higher proportion of

**Table 1. Monthly selectivity calculations for prey by *Maeotias marginata* and *Moerisia* sp. in Suisun Marsh, using Pearre's selectivity index**  
 Bold values indicate a significant ( $\alpha = 0.05$ ) difference between relative abundance of plankton in the guts and in the water. \*, significance with Bonferroni correction ( $\alpha = 0.004$ )

n	Month	Barnacle nauplii	Calanoid copepods	Calanoid egg sacs	Cyclopoid copepods	Corophiid amphipods	Cumaceans	Fish larvae	Gammarid amphipods	Harpacticoid copepods	Hydranths	Medusae	Mysids	Ostracods	Zoea
<i>2007 Maeotias marginata</i>															
45	July	-0.01	<b>0.12*</b>	<b>0.12*</b>	0.00	<b>0.15*</b>	-	<b>-0.14*</b>	<b>-0.17*</b>	-	-	<b>-0.07*</b>	0.00	<b>-0.05</b>	0.00
61	August	<b>0.04*</b>	<b>0.05*</b>	<b>-0.05*</b>	-0.01	<b>0.12*</b>	-0.02	<b>-0.03</b>	<b>0.02</b>	-	0.00	<b>-0.09*</b>	<b>0.05*</b>	-0.02	<b>-0.03</b>
67	September	<b>-0.21*</b>	<b>0.24*</b>	-	<b>-0.06*</b>	<b>0.19*</b>	0.00	<b>-0.07*</b>	0.00	-	-	<b>-0.05*</b>	-0.02	-	-0.02
51	October	-0.01	<b>-0.05*</b>	<b>0.04*</b>	<b>0.03</b>	<b>0.16*</b>	-	-	-	-	-0.01	-	<b>-0.02</b>	-	-
<i>2007 Moerisia</i> sp.															
41	July	<b>-0.06</b>	<b>0.08</b>	<b>0.12*</b>	-0.04	-	-	-0.04	<b>-0.07</b>	-	-	-0.01	0.00	0.00	0.00
60	August	0.03	0.03	<b>-0.04</b>	-0.01	0.00	-0.03	-0.01	<b>-0.05</b>	-	<b>-0.04</b>	-0.03	-0.01	0.00	-0.01
80	September	<b>-0.21*</b>	<b>0.24*</b>	-	0.01	-0.02	0.01	<b>-0.19*</b>	-0.01	-	-	-0.01	-0.01	-	0.00
1	October	<b>-0.32*</b>	0.01	<b>-0.20*</b>	-0.03	-	-	-	-	-	-	-	<b>-0.13*</b>	-	-
<i>2008 Maeotias marginata</i>															
59	July	0.00	<b>-0.08*</b>	<b>0.18*</b>	0.00	<b>0.12*</b>	0.00	<b>-0.05*</b>	-0.01	-	-	<b>-0.04*</b>	<b>0.04*</b>	<b>-0.03</b>	<b>0.03</b>
60	August	<b>-0.05*</b>	<b>-0.10*</b>	<b>0.06*</b>	-0.01	<b>0.20*</b>	0.00	0.01	<b>0.08*</b>	0.01	0.00	<b>-0.02</b>	0.01	0.00	<b>0.05*</b>
49	September	<b>0.06*</b>	<b>-0.04*</b>	0.00	<b>0.09*</b>	<b>0.12*</b>	-0.01	-0.01	0.00	0.00	-	<b>-0.03*</b>	<b>0.03*</b>	-0.02	0.01
31	October	0.02	<b>0.03</b>	-0.02	0.00	-	-0.01	-	-0.01	-0.01	-	-	0.00	0.00	-
<i>2008 Moerisia</i> sp.															
60	July	<b>-0.11*</b>	<b>0.03</b>	-0.01	-0.01	-	-0.02	0.00	-0.01	-	-	-0.01	-0.02	0.00	-0.01
80	August	0.00	<b>0.04*</b>	0.00	<b>-0.03</b>	-	0.00	-0.01	0.00	-0.01	-0.01	-0.01	0.00	-0.01	<b>-0.04*</b>
60	September	-0.01	0.02	-0.01	-	-	0.00	-0.01	<b>-0.03</b>	-0.02	-	-0.01	0.00	0.00	0.00
1	October	-	0.06	-	<b>-0.06</b>	-	-	-	-	-	-	-	-	<b>-0.19*</b>	-

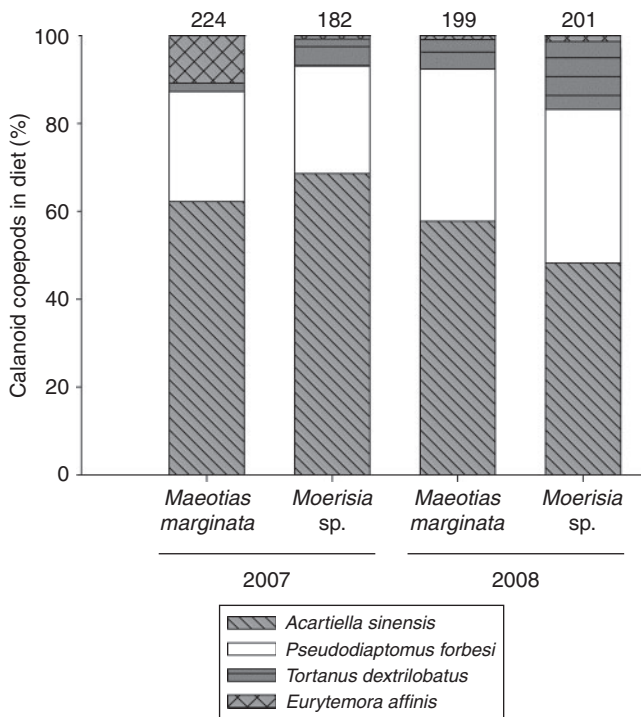


Fig. 3. Percentage calanoid copepods found in the gut contents of *Maeotias marginata* and *Moerisia* sp. during the 2007 and 2008 sample periods. Sample size is indicated above each bar.

calanoid copepods than the proportion in the environment over the entire study period. The remaining items showed an opposite trend, with the exception of *C. caspia* hydranths and fish larvae, which were not significantly consumed.

Trophic interactions with fishes

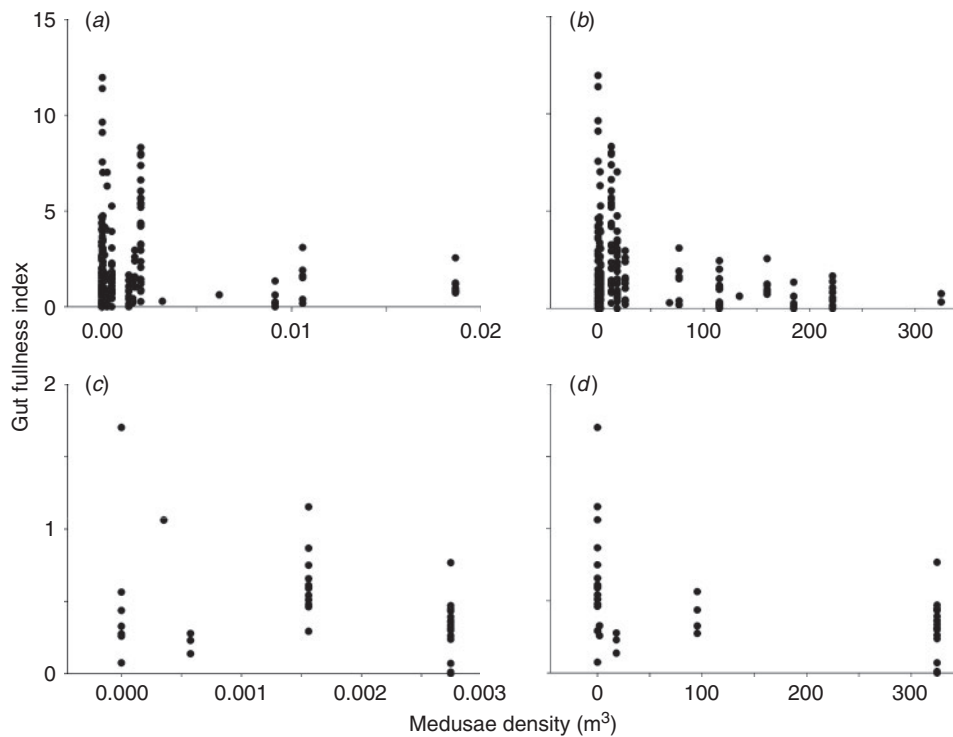
Disproving the third hypothesis, *Maeotias marginata* and *Moerisia* sp. never consumed the larvae of declining pelagic fishes. They did, however, feed on larvae of the non-native shimofuri goby, *Tridentiger bifasciatus*, at two sites during 2008. The overall contribution of fish larvae to medusa diets was low, comprising just 4% (2 fish) and 1% (2 fish) of the number of individual prey items for *M. marginata* and *Moerisia* sp., respectively, during July. August gut contents contained 1% fish larvae (5 fish) for *M. marginata*.

There was no difference in gut fullness for striped bass over pre-bloom, bloom and post-bloom periods ( $\chi^2 = 1.141$ , d.f. = 2,  $P = 0.565$ ; mean values: pre-bloom 1.293, bloom 1.320, post-bloom 1.281). Similarly, no trend was found for threadfin shad ( $\chi^2 = 0.216$ , d.f. = 2,  $P = 0.898$ ; mean values: pre-bloom 0.586, bloom 0.500, post-bloom 0.630). These results do not lend support to the idea of competition for prey between fishes and medusae during the bloom. Overall, the mean index of fullness was greater for striped bass (1.318) than for threadfin shad (0.595). Gut contents of shad, however, contained sand on several occasions during August and September, which may have compromised their fullness index values.

Within the bloom period, there was a slight positive correlation between the gut fullness of striped bass and the density of large *Maeotias marginata* ( $\rho = 0.130$ , d.f. = 230,  $P < 0.044$ ),

Table 2. Diel selectivity calculations for prey by *Maeotias marginata* and *Moerisia* sp. in Suisun Marsh using Pearre's selectivity index. 0.00 values indicate no Bold values indicate a significant ( $\alpha = 0.05$ ) difference between relative abundance of plankton in the guts and in the water. \*, significance with Bonferroni correction ( $\alpha = 0.004$ )

n	Time	Barnacle nauplii	Calanoid copepods	Calanoid egg sacs	Cyclopoid copepods	Corophiid amphipods	Cumaceans	Fish larvae	Gammarid amphipods	Harpacticoid copepods	Hydranths	Medusae	Mysids	Ostracods	Zoea
<i>Maeotias marginata</i>															
1	10:29	0.00	0.01	-	-0.03*	-	-0.01	0.00	-0.02	-0.02	-	-0.01	0.00	-0.01	-0.01
8	13:00	0.00	0.00	-	-	-	-0.03*	0.00	0.03*	-	-	-0.02*	0.00	-0.01	-0.01
3	15:22	0.03*	0.02	-0.05*	-	0.07*	-0.01	-0.01	-0.01	-	0.00	-0.03*	-0.02	-0.01	-0.02
2	17:17	-0.01	0.00	-0.14*	-0.22*	-	-0.04*	-0.02	-0.02*	-	-	-0.18*	0.00	-0.04*	0.00
18	20:30	-0.03*	0.07*	-0.03*	-0.01	0.07*	0.00	-0.01	-0.01	-0.01	-	-0.03*	-0.01	0.00	-0.04*
9	23:08	0.07*	0.01	-0.05*	-	0.20*	0.00	-0.02	-0.01	-0.01	-	-0.01	-0.01	0.00	-0.02
6	3:05	-0.01	0.01	-0.04*	-0.12*	-	-0.01	0.00	0.00	-0.12*	-	-0.06*	0.00	-0.01	-0.01
<i>Moerisia</i> sp.															
20	10:29	-0.01	0.03*	-	-0.03*	-	-0.01	0.00	-0.01	-0.01	-	0.00	0.00	-0.01	-0.02
20	13:00	0.00	0.02*	-	-	-	-0.03*	0.00	0.00	-	-	-0.02*	0.00	-0.01	-0.02
20	15:22	0.01	0.02*	-0.06*	-	-	-0.01	-0.01	-0.02	-	-0.01	-0.04*	-0.01	-0.01	-0.02
20	17:17	0.00	0.04*	-0.04*	-0.07*	-	-0.01	0.00	0.00	-	-	-0.06*	-0.03*	-0.01	-0.01
20	20:30	-0.01	0.04*	-0.08*	-0.03*	-	-0.01	0.00	0.00	-	-	-0.08*	-0.01	-0.01	-0.02
20	23:08	0.00	0.03*	-0.09*	-	-	0.00	-0.01	-0.01	-	-	-0.03*	-0.01	-0.01	-0.02
20	3:05	-0.01	0.02*	-0.02*	-0.07*	-	0.00	0.00	0.00	-0.02	-	-0.03*	0.00	0.00	-0.01
20	7:45	-0.01	0.08*	-0.02	-0.01	-	-0.01	0.00	-0.01	-0.07*	-	-0.04*	-0.03*	0.00	-0.03*



**Fig. 4.** Comparison of medusa density and the gut fullness of pelagic fishes for (a) large *Maeotias marginata* and striped bass, (b) *Moerisia* sp. and striped bass, (c) large *M. marginata* and threadfin shad, and (d) *Moerisia* sp. and threadfin shad.

and a negative trend with the density of *Moerisia* sp. ( $\rho = -0.160$ , d.f. = 230,  $P < 0.013$ ) (Fig. 4a, b). There was no relationship with the gut fullness of threadfin shad and the density of large *M. marginata* ( $\rho = -0.180$ , d.f. = 39,  $P < 0.267$ ), and a negative correlation with the density of *Moerisia* sp. ( $\rho = -0.490$ , d.f. = 39,  $P < 0.001$ ) (Fig. 4c, d). These findings do not rule out the possibility that *Moerisia* sp. may compete with pelagic fishes for prey.

The levels of diet overlap, as calculated by Pianka's symmetric niche coefficient for striped bass and *M. marginata*, were typically low (0.01–0.27, average 0.10,  $n = 16$  comparisons). However, there were some high-level overlap periods with *Moerisia* sp. (0.00–0.76, average 0.10,  $n = 14$ ). In general, the level of dietary overlap was greatest between threadfin shad and both *M. marginata* (0.06–0.99, average 0.70,  $n = 4$ ) and *Moerisia* sp. (0.67–0.92, average 0.79,  $n = 3$ ). The overlap between striped bass and *M. marginata* during blooms was not affected by month ( $\chi^2 = 6.311$ , d.f. = 7,  $P = 0.971$ ) or year ( $\chi^2 = 1.751$ , d.f. = 1,  $P = 0.186$ ). Overlap levels between striped bass and *Moerisia* sp. showed similar Kruskal–Wallis results, with no significant effect of month ( $\chi^2 = 0.815$ , d.f. = 7,  $P = 0.846$ ) or year ( $\chi^2 = 0.436$ , d.f. = 1,  $P = 0.509$ ). These results support the hypothesis for competition between both hydrozoan species and threadfin shad.

## Discussion

### *Intra-bloom and diel feeding ecology*

Over the course of the present work, *Maeotias marginata* consumed a wide variety of prey, which was consistent with the

results of smaller-scale studies. Mills and Sommer (1995) examined medusae from the Petaluma River, California, during June 1993, with copepods being the second greatest prey item in numerical abundance, behind barnacle nauplii. Interestingly, in addition to many of the prey found in the current study, the Petaluma River medusae also consumed items such as seeds, faecal pellets, terrestrial insects and filamentous algae in small amounts. Schroeter (2008) examined gut contents of *M. marginata* collected from Suisun Marsh in the summer of 2004 and fall of 2005. Calanoid copepods were numerically dominant in both samples and most of the remaining prey items were similar to those found in the present study. Some exceptions included cladocerans during the summer and copepod nauplii during the fall, both in small quantities.

The present study is the first to document the trophic ecology of *Moerisia* sp. Purcell *et al.* (1999), however, performed laboratory feeding experiments by using six prey taxa with *Moerisia lyonsi* from the Chesapeake Bay, which is considered to be a close relative of *Moerisia* sp. (Rees and Gershwin 2000). This species fed exclusively on larval and adult stages of the calanoid copepod, *Acartia tonsa*, and harpacticoids. Comparatively, the present study has shown that Suisun Marsh *Moerisia* sp. possesses a more diverse prey base than its relative. This may simply be related to fewer available prey taxa in the Chesapeake system; however, barnacle nauplii was used in the feeding study of Purcell *et al.* (1999), and although captured on tentacles, it was never consumed by *M. lyonsi* (Purcell *et al.* 1999). An additional difference is that copepod nauplii was never found in the guts of *Moerisia* sp., whereas was consumed by *M. lyonsi*.

Pearre's selectivity index indicated that both *M. marginata* and *Moerisia* sp. do not simply consume prey in relation to their proportional availability, but may be consuming specific prey types. It should be noted that this metric does not take into account important factors that influence true selectivity (e.g. capture efficiency, handling time (Eggers 1977), digestion rate of prey items) and, therefore, the results must be applied with some caution. It does, however, offer preliminary insight into the feeding strategies of these hydrozoan species.

Several morphological and behavioural mechanisms allow *M. marginata* and *Moerisia* sp. to be unique and effective predators on crustacean prey, such as calanoid copepods, in the San Francisco Estuary. First, these medusae possess numerous, closely spaced tentacles, appropriate for capturing small prey items (Purcell and Arai 2001). *M. marginata*, in particular, can have up to 600 densely packed tentacles around the bell (Mills and Sommer 1995), and the much smaller *Moerisia* sp. can possess up to 32 tentacles (Rees and Gershwin 2000).

Second, both have nematocysts used for the capture of crustacean prey. Stenoteles are found in tightly packed rings along the tentacles and clustered along the manubrial lips of *M. marginata* (Mills and Sommer 1995). This form of nematocyst is effective at penetrating hard surfaces, such as chitinous exoskeletons (Purcell and Mills 1988). *Moerisia* sp. tentacles, in addition to containing stenoteles, also have desmonemes (Rees and Gershwin 2000). Desmonemes have been found to wrap around small structures, such as copepod setae, to secure prey (Östman *et al.* 1991).

Finally, swimming behaviour and extension of the tentacles can increase the chance of prey encounter (Madin 1988). *M. marginata* appears to employ a two-stage feeding strategy. This species swims to the surface, flips over, and sinks slowly to the bottom, with its tentacles outstretched. Planktonic organisms are captured during the descent. Once it contacts the substrate, *M. marginata* remains exumbrella downward while twitching the ends of its tentacles, likely as a luring behaviour (Mills and Sommer 1995). This may allow for the capture of mostly benthic prey, such as corophiid amphipods (Schroeter 2008), and could explain the positive Pearre's selectivity index values for this diet item.

*Moerisia* sp., which possesses prominent ocelli at the base of each tentacle bulb, is strongly phototactic (Rees and Gershwin 2000). Although a weak swimmer, it can be observed pulsing towards the water's surface during calm periods. On reaching the top of the water column, *Moerisia* sp. drifts towards the bottom, without flipping over, and with its tentacles outstretched (A. P. Wintzer, pers. obs.). It is unclear how much, if any, time is spent resting on the bottom, although lack of benthic prey in its diet suggests that feeding takes place only in the water column. A similar feeding strategy description is given for *M. lyonsi*, which does not spend time on the bottom (Purcell *et al.* 1999).

Specialisations of the prey species may also play a large role in determining hydromedusa diets. Physical characteristics of prey species can also have an impact on the feeding efficiency of hydromedusae (Madin 1988). Suchman and Sullivan (1998) found that the size of the copepod *Acartia hudsonica* affected its selectivity by the scyphozoans *Aurelia aurita* and *Cyanea* sp., with small copepodites experiencing reduced predation. Small prey items may evade capture because of the smaller surface

area of their bodies (Suchman and Sullivan 1998), the ability to pass between tentacles without contact (Spadinger and Maier 1999), or by tentacle collision that is not powerful enough to cause nematocyst discharge (Larson 1987). This may explain why only one individual of *Limnoithona tetraspina*, a small cyclopoid copepod that has recently become very abundant in the upper San Francisco Estuary, was found in the gut contents of *M. marginata*, and why copepod nauplii was not consumed in the present study.

Prey behaviour can also influence capture. Predator-avoidance behaviour may include the speed that zooplankton swim (Mills 1981), their ability to detect hydrodynamic disturbances by predators (Suchman 2000), and the directionality and strength of their escape response (Suchman and Sullivan 1998). These behaviours may vary with the stage of particular taxa (Suchman 2000) and certainly differ among species.

Finally, the density of a prey species can affect its rate of capture by predators. Madin (1988) indicated that because medusae are non-visual predators, they must rely on random entanglement with their prey. At least one species, *A. aurita*, however, shows chemosensory ability and is attracted to water conditioned by its prey (Arai 1991). In both scenarios, prey capture would be increased when prey are at high densities. In the present study, both hydrozoans consumed some prey species over the bloom period that were present in high abundance.

#### Hydrozoan predation on larval fishes

Although some cnidarians are soft-prey specialists, feeding exclusively on fish larvae, these taxa constitute only a small portion of most gelatinous zooplankton diets (Purcell 1985). Medusae that prey primarily on crustaceans will commonly feed on fish eggs and larvae when their densities are high compared with other potential prey items (Purcell and Arai 2001). The youngest fish larval stages, which have limited escape responses, may be particularly vulnerable prey items for medusae (Purcell *et al.* 1987).

*Maeotias marginata* has been previously shown to consume fishes. Mills and Sommer (1995) maintained medusae in the laboratory, occasionally feeding them small fish. Additionally, Schroeter (2008) found six goby (*Tridentiger* sp.) larvae in the guts of 40 wild-caught *M. marginata* individuals. There was, however, no indication that the much smaller *Moerisia* sp. could catch and consume fish larvae. In the present study, medusae as small as those with a 3.05-mm bell width were quite capable of feeding on larvae of shimofuri goby (*T. bifasciatus*). The trend of proportionally more larvae in the environments than in the gut contents of *Moerisia* sp. may be a factor of size limitation, because many of the *T. bifasciatus* were larger than this species of medusa. Large *M. marginata* individuals, however, were able to consume the largest sizes of *T. bifasciatus* (20 mm) available.

Although both *M. marginata* and *Moerisia* sp. consumed larval fish, none of the declining pelagic fish species was found in their guts. Striped bass and the imperiled delta and longfin smelts spawn early in the year so their larval stages may have limited temporal and spatial overlap with the medusae bloom (Schroeter 2008). Larval threadfin shad co-occurred with the early portion of the bloom, typically July (Schroeter 2008), but was never consumed. These results indicate no direct predation



impact on larvae of declining pelagic fishes in Suisun Marsh by non-native hydrozoans.

#### *Prey competition between hydrozoans and pelagic fishes*

Competition is a difficult interaction to prove (Purcell and Arai 2001). However, substantial dietary overlap has been documented between scyphozoans, a ctenophore, a hydrozoan and four juvenile fishes in Alaska (Purcell and Sturdevant 2001). High levels of prey-resource competition were deemed possible in that study based on temporal and spatial co-occurrence of potential competitors (Purcell and Sturdevant 2001).

In Suisun Marsh, the plankton-feeding stages of the four declining pelagic fishes have a strong spatial and temporal overlap with *M. marginata* (Schroeter 2008) and *Moerisia* sp. (A. P. Wintzer, pers. obs.). Striped bass did not show a great degree of dietary overlap with either of the hydrozoans, whereas threadfin shad did, especially with *Moerisia* sp.

Although our study did not perform gut-content analyses on the threatened smelt species, some level of dietary overlap may still be inferred. In an analysis of dietary patterns of Suisun Marsh fishes, Feyrer *et al.* (2003), for example, found that delta smelt and threadfin shad had high levels of pelagic copepods in their diets, along with similar levels of gut fullness and diet composition. Additionally, longfin smelt and juvenile striped bass were similar because of the high mysid content of their diets. Given these results, it is likely that delta smelt and longfin smelt follow the dietary overlap trends of threadfin shad and juvenile striped bass, respectively.

The lack of high dietary overlap, in addition to similar trends in gut fullness during pre-bloom, bloom and post-bloom periods, refutes the hypothesis that juvenile striped bass is competing with non-native hydrozoans for prey at any significant level. Longfin smelt, although not directly studied here, is likely to be similar. Conversely, threadfin shad has high dietary overlap with medusae. The sand found in its stomach makes its gut-fullness data difficult to interpret; however, Ingram and Ziebell (1983) reported that shad feeds on benthic prey when its preferred planktonic prey is limited. Additionally, shad gut-fullness calculations were negatively correlated with the density of *Moerisia* sp. For these reasons, it is possible that this fish species, and perhaps the trophically similar delta smelt, will compete for prey resources with *M. marginata* and especially with *Moerisia* sp. during jellyfish blooms.

#### Conclusions

*Maeotias marginata* and *Moerisia* sp. are predators on a variety of small crustaceans in the San Francisco Estuary. Evidence suggests that they may employ some selectivity during feeding; however, this requires further study to confirm. Although their ability to consume the larvae of imperiled fishes is reduced by limited spatial and temporal overlap, the medusae and some planktivorous fishes do consume a similar prey base. Threadfin shad and delta smelt populations, in particular, may be affected by both hydrozoans because of their dietary overlap of copepods with these fish species. These findings are troubling, especially in conjunction with evidence of increasing medusa populations (Schroeter 2008), declining zooplankton populations, and the presence of additional, well established invasive zooplanktivores, such as the overbite clam (*Corbula amurensis*).

As mentioned above, true competition is a difficult phenomenon to confirm. The next step for research within the San Francisco Estuary will involve determining the cropping potential of *M. marginata* and *Moerisia* sp. in relation to the production rate of calanoid copepods. These data should provide an estimate of the potential level of prey depletion by medusae, as well as the level of prey availability for planktivorous fishes, which can inform our hypothesis of competition between hydrozoans and both threadfin shad and delta smelt for prey resources.

In a global context, there are reports of *M. marginata* in Holland (Hummelinck 1941), the Sea of Azov (Ostroumoff 1896), the Loire Estuary in France (Denayer 1973), Chesapeake Bay (Calder and Burrell 1969) and the Baltic Sea (Väänölä and Oulasvirta 2001). Similarly, *M. lyonsi* (a close relative of *Moerisia* sp.) has invaded several systems in the eastern United States (Calder and Burrell 1969; Poirrier and Mulino 1977; Purcell *et al.* 1999) and the Baltic Sea (Väänölä and Oulasvirta 2001). The findings from the present study add to the limited understanding of how jellyfish blooms may affect the trophic ecology of an invaded system and may be applicable to other locations. It is urged that studies on negative interactions between these hydrozoans and planktivorous fishes continue so as to determine any potential ecological impacts to specific systems and to establish necessary management options.

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