San Francisco Estuary mysid abundance in the fall, and the potential for competitive advantage of *Hyperacanthomysis longirostris* over *Neomysis mercedis*

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Historically, the native mysid *Neomysis mercedis* was a key source of food for fish in the San Francisco Estuary (SFE). Following the introductions of the over-bite clam and many invasive zooplankton species in the mid-1980s, populations of native zooplankton species plummeted, including *N. mercedis*. In July 1993, *Hyperacanthomysis longirostris*, an invasive mysid, was first documented in the SFE, and it quickly became the most abundant mysid in the upper estuary. Since 2011, the California Department of Fish and Wildlife has sampled mysid abundance throughout the upper SFE concurrently with their Fall Midwater Trawl, which targets juvenile Striped Bass. We analyzed data from these mysid trawls to investigate environmental correlates of *N. mercedis* and *H. longirostris* abundance. We found that *H. longirostris* was found at higher temperatures significantly more often than *N. mercedis,* and there was a trend towards greater frequency of *H. longirostris* at higher salinities. Increases in water temperature over time, coupled with *H. longirostris's* smaller size at maturity and lower food needs may partially explain its success in the SFE.

Key Words: crustaceans, Delta Smelt, fish diets, invasive species, Longfin Smelt, Mysidacea, Sacramento, San Joaquin Delta, Striped Bass, temperature tolerance, zooplankton

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Mysid shrimp (or opossum shrimp), are small aquatic crustaceans that form a critical link in the San Francisco Estuary (SFE) foodweb. There are seven species of mysids found in the upper SFE (Mecum 2007). Historically, the native mysid *Neomysis mercedis* was the dominant mysid species and served as a key source of food for fish species in the area. *N. mercedis* dominated the diets of Splittail (*Pogonichthys macrolepidotus*) (Daniels and Moyle 1983), Longfin Smelt (*Spirinchus thaleichthys*) (Feyrer et al. 2003), and young Striped Bass (*Morone saxatilis*) (Bryant and Arnold 2007). They were also once an important food item for juvenile and adult Delta Smelt (Moyle et al. 1992), though their abundance in smelt gut

contents has declined in recent years (Slater and Baxter 2014). In fall months, when overall zooplankton abundance decreases, *N. mercedis* was particularly important and comprised a significant portion of Longfin Smelt and Striped Bass diets (Feyrer et al. 2003). Following the introductions of the over-bite clam, *Potamocorbula amurensis,* and many zooplankton species in the late 1980s to early 1990s, populations of native zooplankton species plummeted, including *N. mercedis* (Winder and Jassby 2011). Competition with invasive clams and zooplankton for food, and predation by introduced fish and predatory invertebrates, created a massive shift in zooplankton species composition throughout the SFE (Kayfetz and Kimmerer 2017; Winder and Jassby, 2011). In July 1993, *Hyperacanthomysis longirostris* (formerly *Acanthomysis bowmani*) (Fukuoka and Murano 2005)*,* an invasive mysid considered semi-endemic to the Ariake Sea in Japan (Suzuki et al. 2009) was first documented in the SFE, most likely introduced through ballast water (Modlin and Orsi 1997). It quickly spread and is currently the most abundant mysid in the region (Bryant and Arnold 2007; Hennessy and Enderlein 2013).

Despite the importance of mysids to the diets of many fish species (Feyrer et al. 2003; Bryant and Arnold 2007), there are knowledge gaps concerning mysid abundance, geographic distribution, and life history in the SFE. Much of the region was not sampled for mysids until recently, and few studies have examined the causes of mysid declines (though see Winder and Jassby 2011), or the shift in dominance of the mysid community from native to nonnative species. Even basic information on environmental correlates for dominant mysid species remain unstudied (though see Kimmerer 2002 for a discussion of flow effects on *N. mercedis*). There is also little information published on the life history of *H. longirostris,* despite it being the most commonly observed mysid in the region.

The California Department of Fish and Wildlife's (CDFW) Zooplankton Study, part of the multi-agency Environmental Monitoring Program (EMP), began monthly mysid data collection in 1972, but the current sampling is limited (20 locations per month) and does not extend into habitats considered important for native fishes, such as upstream to the Cache Slough Complex, or the Sacramento River Deepwater Ship Channel (SDWSC) (Hennessy and Enderlein 2013). The Cache Slough Complex is currently the focus of large-scale restoration efforts, an attempt to improve habitat for many fish species (Department of Water Resources and Department of Fish and Wildlife 2015), so there is an interest in monitoring data on zooplankton availability.

EMP has documented peak abundances of mysids in spring and summer, with lower abundances in fall (Hennessy and Enderlein 2013), but due to the importance of food for juvenile fish in the fall for later survival (Brown et al. 2014), understanding drivers of mysid abundance during this time frame is key. The CDFW Fall Midwater Trawl survey (FMWT), added concurrent zooplankton sampling in 2008 to a subset of its long-term fish monitoring stations to address this lack of data. This paper seeks to describe the overall patterns of mysid abundance. We then answer several key questions regarding the most common taxa, *H. longirostris,* and the taxa that was historically most common, *N. mercedis*:

- What are the spatial and temporal patterns of mysid abundance in the upper SFE?
  - Was *H. longirostris* more abundant than other mysid species in the fall?
- Is *H. longirostris* out-competing the native mysid, *N. mercedis*?
  - How do water quality conditions correlate to abundance of *H. longirostris* and *N. mercedis* and are there differences between the two species?
  - How does size and fecundity differ between *H. longirostris* and *N. mercedis*?

METHODS

Sampling methods

The FMWT survey samples mysid shrimp monthly from September through December at 32 of the 122 fixed FMWT sampling stations (Figure 1). Stations were grouped into 8 geographic regions. Mysid shrimp are sampled using a 30 cm diameter, 505 µm mesh macro-zooplankton net attached to a metal frame. The net was 1.48 m long with a taper ending at the codend with a collecting jar. A flowmeter (model 2030R, General Oceanics, Miami, FL) was fitted in the mouth of the net to allow volume for the tow to be calculated. A 10-minute stepped oblique tow was conducted with the mysid net either immediately before or after the regular midwater trawl at each zooplankton sampling location. The sample was then preserved in a quart jar of 10% formaldehyde dyed with rose Bengal for later processing at the CDFW laboratory (Stockton, CA). Surface water temperature (in degrees C) and specific conductance (µS/cm) were measured using a handheld YSI meter (Yellow Springs Instruments Pro30; YSI Inc. Yellow Springs, OH). Values for specific conductance were converted to practical salinity units (psu) (Schemel 2001). Surface turbidity (in Nephelometric Turbidity Units, ntu) was measured using a portable turbidity meter (Hach 2100Q; Hach, Loveland, CO, USA).
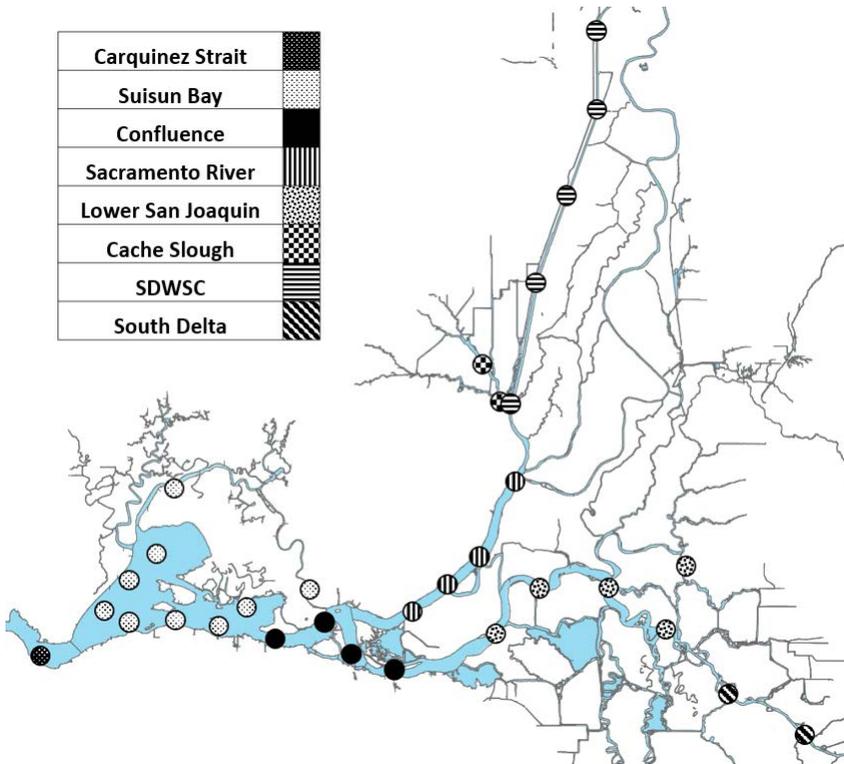
Figure 1. Map of Fall Midwater Trawl zooplankton sampling locations in the upper San Francisco Estuary, CA by region (see legend for region titles).

In the laboratory, we decanted and rinsed samples in water where mysids were removed from detritus and preserved for later processing. Processing included identification of the seven species known to occur in the SFE, measurement, and classification of individuals as juvenile, adult male, and adult female (Figures 2, 3). Species identified were: *H. longirostris, N. kadiakensis, N. mercedis, Alienacanthomysis macropsis*, *Orientomysis aspera* (formerly *A. aspera* per Fukuoka and Murano), *O. hwanhaiensis* (formerly *A. hwanhaiensis* per Fukuoka and Murano)*,* and *Deltamysis holmquistae.* Sample processing protocols did not allow staff to positively distinguish between *N. kadiakensis* and the very similar mysid *N. japonica*; for analysis, all are assumed to be *N. kadiakensis*. Sexual classification was based on elongated fourth pleopod in males and brood pouch/marsupium in females (Figures 2, 3). If these characteristics were not fully developed it was classified as juvenile. For a key to all seven taxa, see Mecum, 2007.
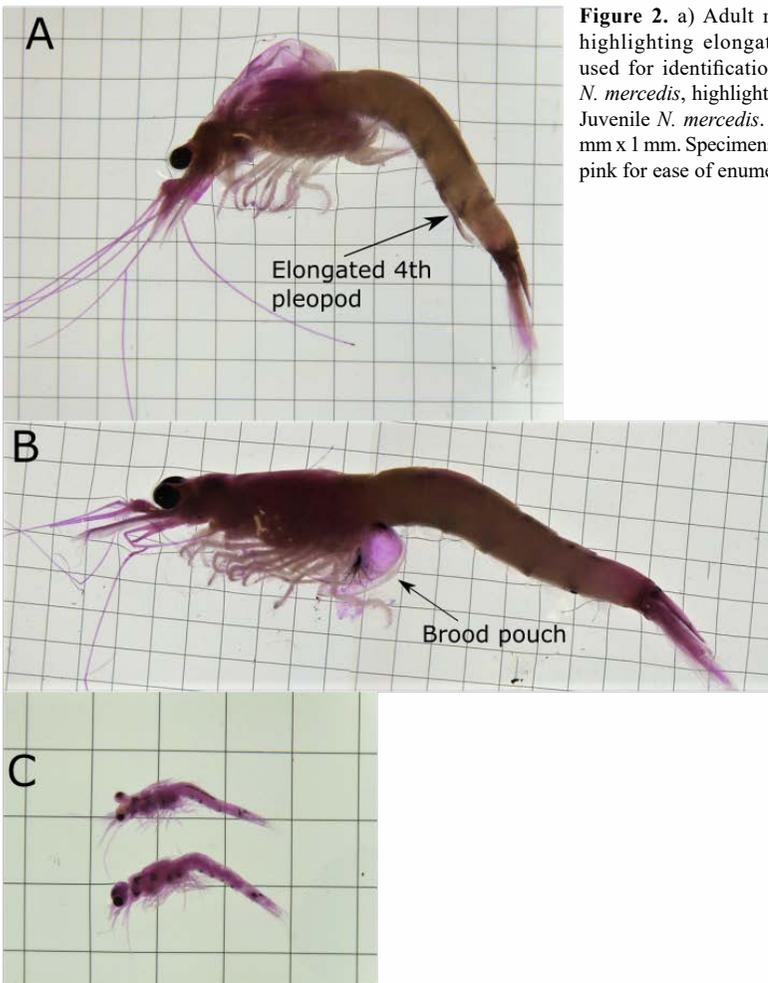
Figure 2. a) Adult male *N. mercedis*, highlighting elongated forth pleopod used for identification b) Adult female *N. mercedis*, highlighting brood pouch c) Juvenile *N. mercedis*. Grid squares are 1 mm x 1 mm. Specimens are artificially died pink for ease of enumeration.
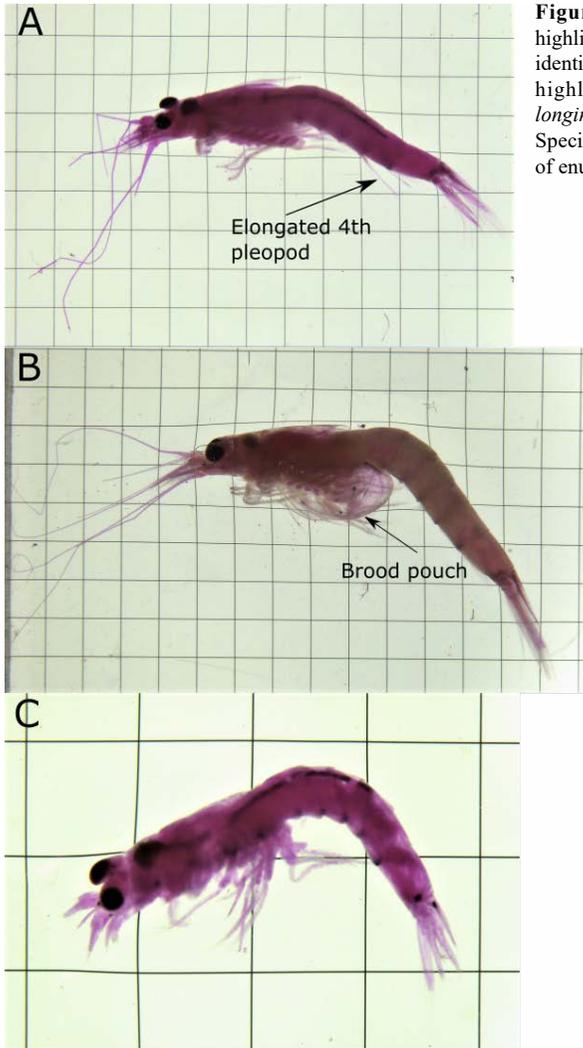
Figure 3. a) Adult male *H. longirostris*, highlighting elongated forth pleopod used for identification b) Adult female *H. longirostris*, highlighting brood pouch c) Juvenile *H. longirostris*. Grid squares are 1 mm x 1 mm. Specimens are artificially died pink for ease of enumeration.

The first 100 non-gravid (male, juvenile, or non-gravid female) mysids of each species were measured to the nearest mm (rounded up) from the tip of the eyestalk to the base of the telson; any additional mysids were identified and enumerated. The first 30 gravid females of each species were also measured, and the remainder were enumerated. Laboratory staff counted the embryos of each gravid female and classified them based on their development as: eggs were classified as stage 1, comma shaped embryos as stage 2, and embryos with visible eyes as stage 3. In samples with more than 400 non-gravid or 100 gravid mysids of a single species, laboratory staff subsampled for that species using a grid tray and recorded the fraction of the total sample processed (F_{sub}). In the case of subsampling, the total catch (N) of a species and life stage was calculated as: $N = N_{sub} / F_{sub}$.

Analysis methods

To assess our first question on spatial and temporal distribution of mysids, we used FMWT mysid shrimp catch data from 2011 to 2016 (sampling was sporadic and not standardized until 2011). Catch per unit effort (CPUE) for each species (*Sp*) at each station (*St*) was calculated as:

$$CPUE_{SpSt} = \frac{N_{SpSt}}{V_{St}}$$

Where N = Catch and V = volume sampled. From the CPUE at each station, we created an index of abundance for each species to allow us to make comparisons across years and across regions. The species-specific regional abundance index (*R*) for each month was calculated as:

$$R_{Sp} = mean(CPUE_{SpSt})$$

The overall species-specific monthly abundance index (I_{Sp}) was calculated as:

$$I_{Sp} = mean\ (R_{Sp})$$

The regional abundance indices and overall abundance were then graphed to illustrate the difference in temporal and spatial distribution for the seven species of mysid caught by the FMWT.

To explore the potential for competitive interactions between *H. longirostris* and *N. mercedis,* we examined their environmental correlates and life history patterns. To graphically display ranges of environmental parameters where these species were caught, we averaged CPUE (excluding trawls with zero catch) for surface water temperature, salinity, and turbidity. Environmental parameters were summarized for both species at intervals of 1°C for temperature, 1 psu for salinity, and 10 ntu for turbidity.

To test the statistical relationship between these environmental parameters and species' presence, two zero-inflated negative binomial models were run on the CPUE of *H. longirostris* and *N. mercedis*, using temperature, salinity, turbidity, as predictor variables. Predictor variables were centered and scaled by subtracting the mean and dividing by the variance to put all variables on a common scale. These analyses were conducted using the pscl package (Jackman et al. 2016) in R version 3.6.1 (R Project for Statistical Computing, 2019).

Mean lengths for each mysid sex and minimum and maximum size at maturity were calculated for *H. longirostris*. A binomial generalized linear model was then used to calculate the maximum likelihood estimator of the median of the distribution, using the glm function in R. A two-factor ANOVA with a Tukey post-hoc test was used to compare size of each sex classification between *H. longirostris* and *N. mercedis.*

Data on gravid *H. longirostris* were used to determine the mean number of embryos per female. Females with obviously damaged brood pouches were excluded, as well as those with less than three embryos (assumed to be damaged brood pouches). Fecundity of *N. mercedis* and other, less common, species was not examined due to an insufficient sample size of gravid females. Therefore, we compared data on *H. longirostris* fecundity to literature values of *N. mercedis* to explore whether differential fecundity might result in a competitive advantage.

RESULTS

Temporal trends

The historically common *N. mercedis* was rarely seen from 2011-2013, completely absent from catch in 2014 and through most of 2015, and much more common in 2016 (Figure 4), particularly in the Sacramento River and SDWSC (Figure 5). *H. longirostris* dominated catch numerically (Figure 4) in all but a few regions and months. *N. kadiakensis* was the second most abundant species caught. Three other species, the native *A. macropsis*, and the non-native *O. aspera* and *O. hwanhaiensis* appeared sporadically. *O. aspera* was present in 2013 through 2016 and *O. hwanhaiensis* in 2015 and 2016 (Figure 4). Only 5 specimens of *D. holmquistae* were found: 2 in 2013, 1 in 2015, and 2 in 2016. In general, overall mysid
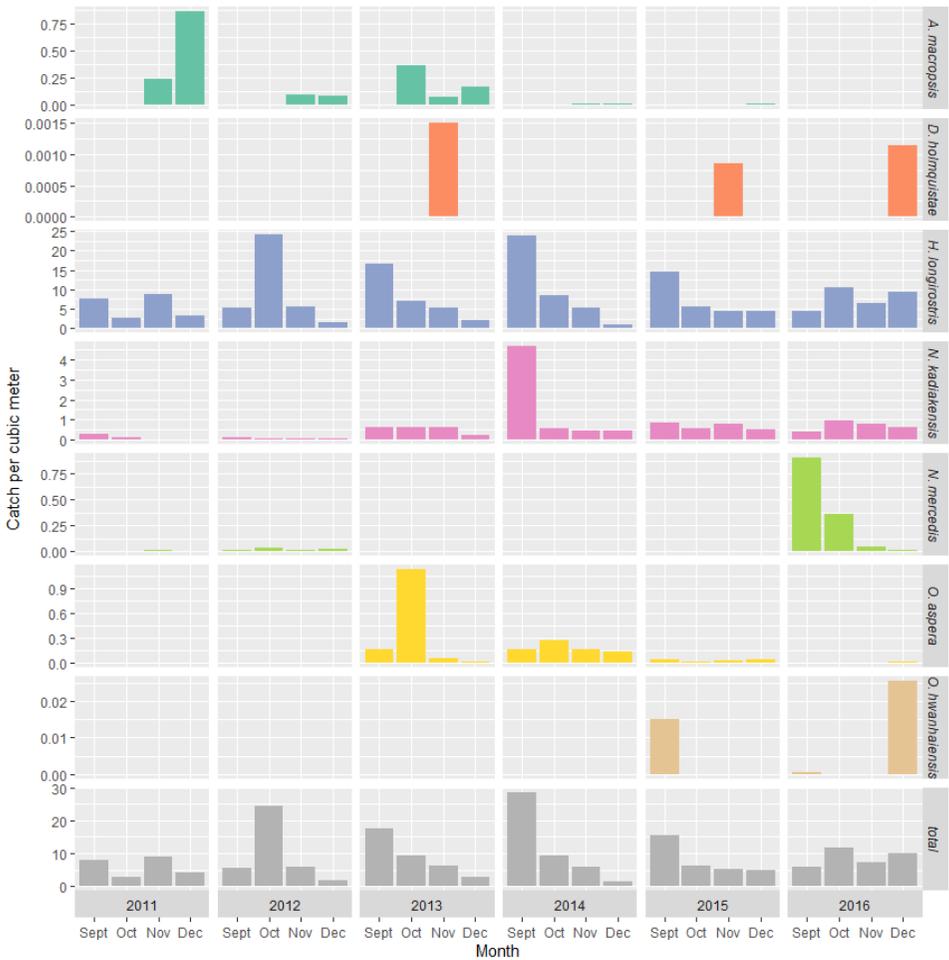
Figure 4. Monthly mean CPUE (catch per cubic meter) of the mysid species collected by Fall Midwater Trawl mysid sampling, 2011–2016, separated by species.

abundance during the FMWT survey was highest in September and lowest in December (Figure 4), though this varied by species and by year, with *O. aspera*, *O. hwanhaiensis* and *D. holmquista*e peaking later in the year.

Spatial Trends

H. longirostris was widespread in the FMWT study area across all years (Figure 5) and occurred in every region sampled. CPUE of *H. longirostris* was highest in the SDWSC, followed by the lower Sacramento River and Suisun Bay; CPUE was low in Cache Slough, the lower San Joaquin River, and the East Delta regions (Figure 5). *N. kadiakensis* occurred widely in regions of the Sacramento River downstream of the SDWSC and Cache Slough Complex and the East Delta in the San Joaquin River. *N. mercedis* occurred mainly in the SDWSC and Sacramento River. Other species were limited to downstream regions (Figure 5) generally associated with higher salinity.

Environmental correlates

FMWT mysid sampling collected *H. longirostris* across a wide range of environmental conditions, while ranges for *N. mercedis* were slightly narrower. *H. longirostris* abundance peaked at a higher temperature than *N. mercedis* (22-23 ˚C versus 20-21˚C), and although *H. longirostris* did occur at temperatures as low as 8 ˚C, both frequency of occurrence and abundance of *H. longirostris* increased with higher temperatures (Table 1, Figure 6). In contrast, *N. mercedis* rarely occurred at <17˚C or >21˚C and showed a much lower relationship between abundance and temperature than *H. longirostris* (Table 1). Abundance of *H. longirostris* was significantly higher at low salinities (Table 1, Figure 7), but they were collected at the most saline sampling location, Carquinez Strait, and frequency of occurrence of *H. longirostris* had a slight positive relationship with salinity (Table 1). *N. mercedis* CPUE was concentrated around 0-1 psu with a second, smaller peak at 15-16 psu (Figure 7), though there was no significant relationship between presence and salinity (Table 1). No *N. mercedis* were collected at >17 psu. CPUE peaked at turbidities between 31-41 ntu for *H. longirostris* and 10-20 ntu for *N. mercedis* (Figure 5) and both species were common from 10-80 ntu. This relationship between abundance and turbidity was significant for *H. longirostris*, but not for *N. mercedis* (Table 1).

Size and fecundity

Size of adult *H. longirostris* was smaller for males than females (Tukey post-hoc p < 0.001, Figure 9). A binomial model of size at maturity predicted the median size of adult males to be 6.3 mm (SE = 1.03, p < 0.001), and adult females to be 9.2 mm (SE = 1.03, p < 0.001). The mean number of embryos per gravid female declined in later embryonic developmental stages, with stages 1 through 3 averaging 18.4, 11.7, and 7.7 embryos, respectively. The average size of *H. longirostri*s was less than *N. mercedis* for adult males and females (Tukey post-hoc p < 0.0001, Figure 9). Juveniles were not significantly different in length (Tukey post-hoc p = 0.7293, Figure 9)
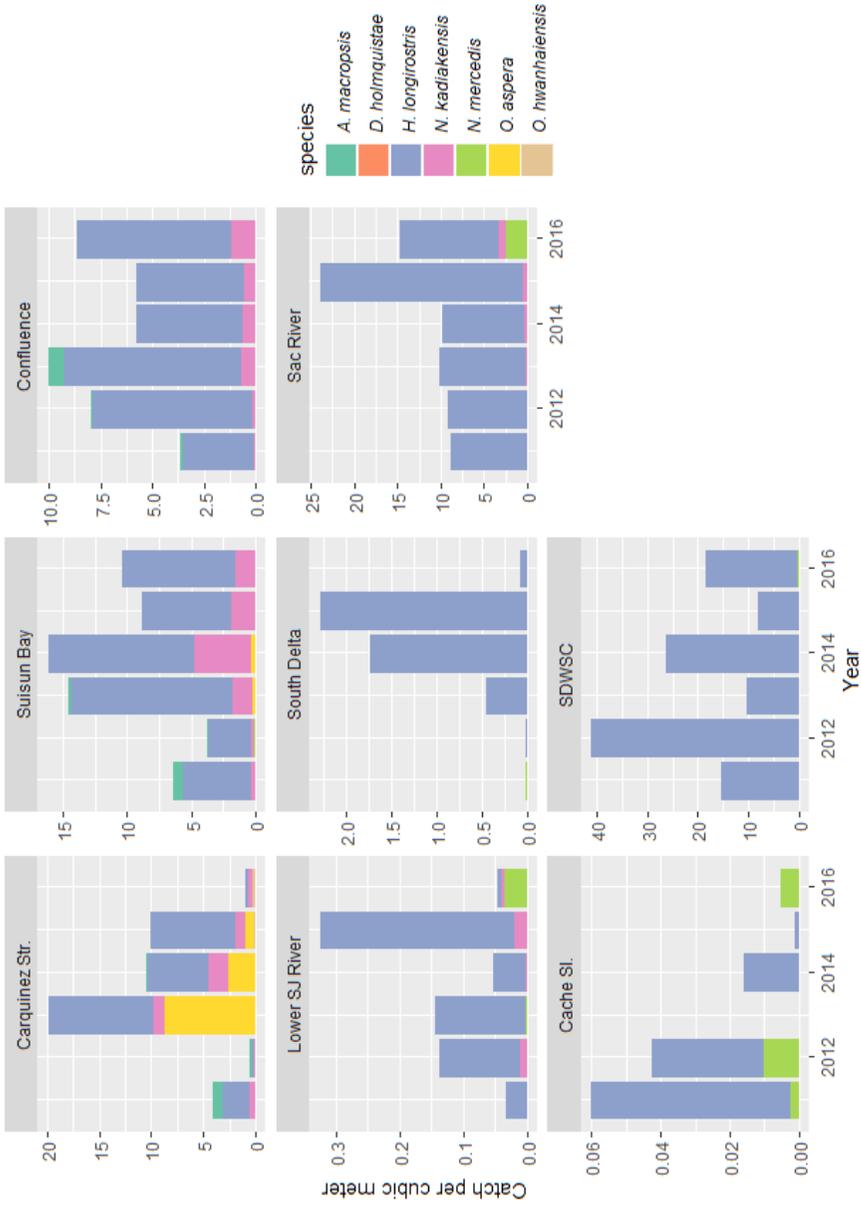
Figure 5. Regional mean CPUE (catch per cubic meter) of mysids collected by Fall Midwater Trawl mysid sampling, 2011–2016, with species differentiated by color. Note the differences in y-axes for the different regions.

Table 1. Count model coefficients (negative binomial with log link)

	N. mercedis				*H. longirostris*			
	Estimate	**SE**	**z-value**	**p-value**	**Estimate**	**SE**	**z-value**	**p-value**
(Intercept)	-2.020	0.123	-16.478	<0.0001*	2.133	0.066	32.104	<0.0001*
Temperature	-0.230	0.148	-1.551	0.121	0.386	0.065	5.963	<0.0001*
Turbidity	0.079	0.095	0.833	0.405	0.468	0.105	4.466	<0.0001*
Conductivity	-0.056	0.134	-0.419	0.675	-0.198	0.066	-2.996	0.0027*
Log(theta)	11.268	156.942	0.072	0.943	-0.776	0.059	-13.108	<0.0001*

Zero-inflation model coefficients (binomial with logit link)

	N. mercedis				*H. longirostris*			
	Estimate	**SE**	**z-value**	**p-value**	**Estimate**	**SE**	**z-value**	**p-value**
(Intercept)	-7.223	3.936	-1.835	0.067	-22.685	5.956	-3.809	0.0001*
Temperature	-4.679	2.351	-1.990	0.047*	-0.492	0.206	-2.391	0.0170*
Turbidity	0.059	0.502	0.117	0.907	-4.115	1.214	-3.390	0.0007*
Conductivity	2.336	1.487	1.571	0.116	-26.858	8.107	-3.313	0.0009*
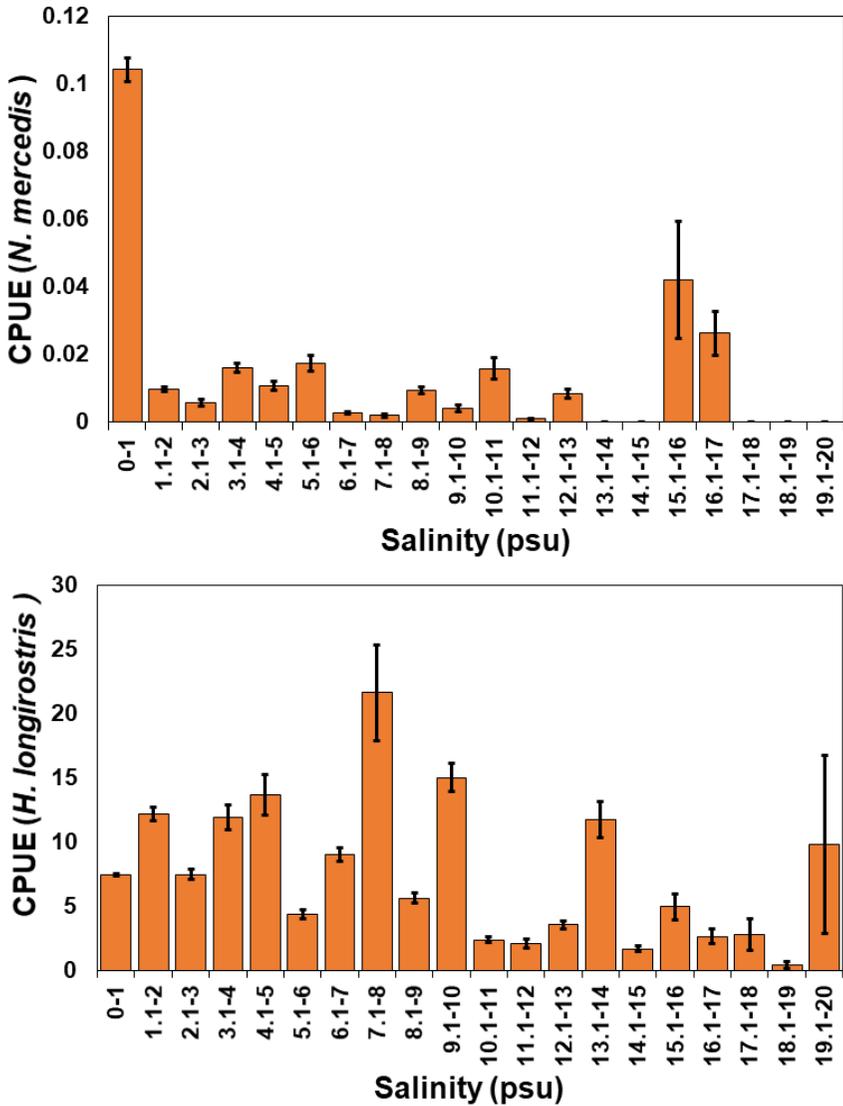
Figure 6. Mean CPUE (catch per cubic meter) (± 1 SE) for *N. mercedis* (top) and *H. longirostris* (bottom) by 1°C temperature intervals, from Fall Midwater Trawl mysid sampling, 2011–2016.

DISCUSSION

Among the mysid species, the invasive *H. longirostris* is by far the most abundant in the region of the upper estuary sampled by the FMWT. FMWT mysid data confirmed the dominance of *H. longirostris* both numerically and geographically over all other mysid species present. *H. longirostris* matured at a smaller size and possessed larger broods at size, which may result in shorter generation times and lower food requirements. *H. longirostris* was more common across a wider range of temperatures than *N. mercedis*. Some combina-
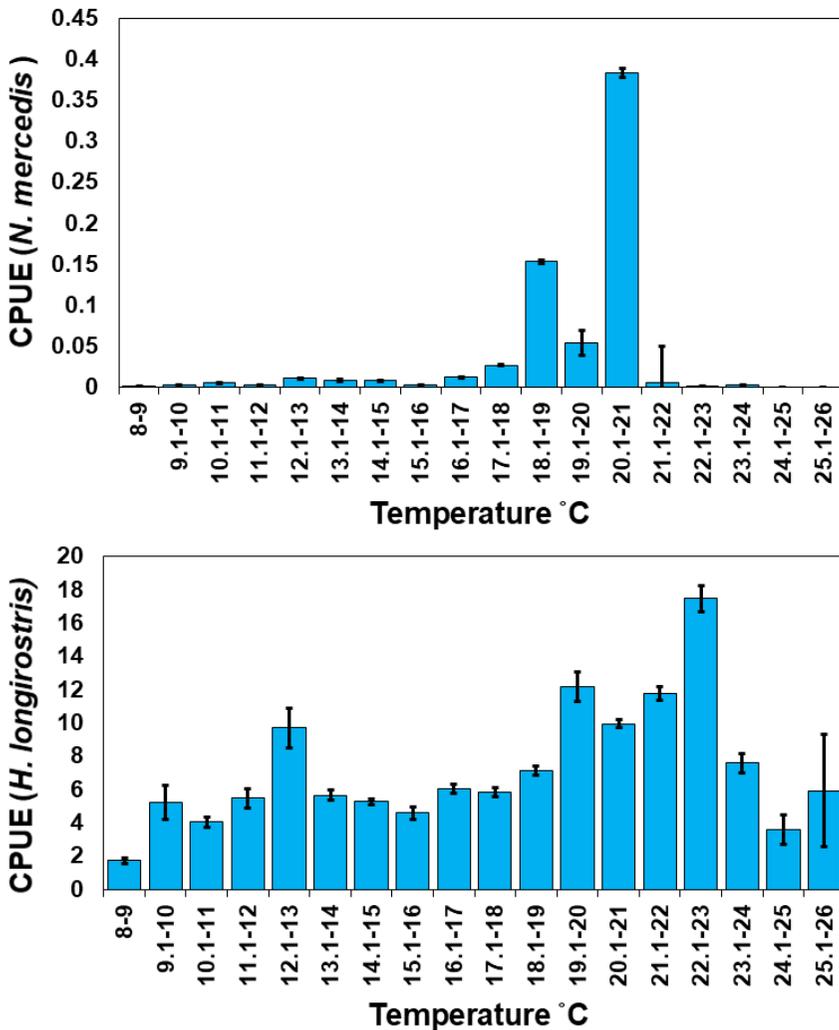
Figure 7. Mean CPUE (catch per cubic meter) (±1 SE) for *N. mercedis* (top) and *H. longirostris* (bottom) by 1 psu salinity intervals, from Fall Midwater Trawl mysid sampling, 2011–2016.

tion of these factors likely allows *H. longirostris* to out-compete *N. mercedis* in fall. The replacement of *N. mercedis* with *H. longirostris* may ultimately be detrimental to fish in the SFE, since work by Feyrer et al. (2003) suggests that *H. longirostris* may be a less favorable source of energy for fish due to its smaller size.

      Given the continued low density of mysids caught in the FMWT, availability of *N. mercedis* as a food source for fish remains limited during the fall months (Figure 4). *H. longirostris* abundance was greater than all other species by several orders of magnitude (Figure 4). *N. kadiakensis*, a mysid similar in size to *N. mercedis*, was the second most

abundant collected after *H. longirostris*. Other mysid species were either found sporadically (*D. holmquistae)* or in low numbers (*O. aspera* and *O. hwanhaiensis*) and only collected in downstream regions suggesting that FMWT mysid stations sample a very limited portion of their geographic range in the SFE.

The collapse of mysid populations as a whole in the last few decades is likely related to food limitation (Orsi and Mecum 1996, Winder and Jassby 2011), but the FMWT mysid data may provide clues as to why *H. longirostris* dominates over the previously abundant *N. mercedis.* One possible factor is temperature tolerance, since our data show abundance of *H. longirostris* peaks at a higher temperature than *N. mercedis*. Laboratory experiments from the 1950s and 1970s showed a sharp decrease in *N. mercedis* survival at 22°C (Hair 1971), with one study determining the upper lethal temperature as 24.2°C to 25.5 °C for specimens caught in the SFE (Hair 1971) and another citing 23.9°C for organisms from a British Columbia population (Wilson 1951). A laboratory rearing experiment using *N. mercedis* for toxicity testing employed an ideal temperature of 16-19°C and documented a slight increase in mortality corresponding with higher temperatures (Brandt et al 1993). Heubach (1969) noted a sharp decline in *N. mercedis* abundance in September 1965 and August 1966 when temperatures exceeded 22 °C. Knutson and Orsi (1979) reported *N. mercedis* in the estuary at daytime temperatures as high as 25.6 °C as long as dissolved oxygen levels remained saturated, but admitted that this was likely outside the ideal range for the species. In the FMWT mysid results, *N. mercedis* CPUE peaked at 20-21°C (Figure 6), although this may be driven by two specific tows in the lower Sacramento River in 2016. Without those two tows, the peak would be 18-19 °C, and *N. mercedis* was not collected in FMWT mysid sampling at temperatures above 23.7°C.

There are no known laboratory temperature experiments on *H. longirostris*, so temperature data is limited to field observations. In FMWT mysid sampling, likelihood of *H. longirostris* presence increased with temperature, and CPUE was highest at 22-23°C, at the upper end of the thermal tolerance for *N. mercedis*. Some individuals were caught at 25-26°C (highest temperature range recorded during the sample period). One study of mysids in Suisun Marsh in the spring also noted *H. longirostris* peaking at warmer temperatures and hypothesized that their smaller size may give them a competitive advantage at high temperatures (Carlson and Matern 2000). From their native range, Suzuki et al (2009) found high densities of juvenile *H. longirostris* between 15-25°C in the Chikugo River estuary, with organisms present in waters up to 30°C. Further sampling at warmer temperatures, or controlled laboratory experiments on *H. longirostris* are needed to refine our knowledge of their temperature tolerances.

Water temperature data for FMWT was limited by the seasonality of the sampling period, declining from a median around 20 °C in September to 10 °C in December (Figure 26 in Brown et al. 2011). The Environmental Monitoring Program (EMP), which samples year-round, reported that mean CPUE for both *H. longirostris* and *N. mercedis* since the introduction of *Potamocorbula* is usually higher in spring (March-May) and summer (June-August), and extremely low in fall (September-November) (Hennessy and Enderlein 2013). Suzuki et al (2009) found a seasonal variation among life stages of *H. longirostris;* small juveniles (<1 mm carapace length) were almost completely absent during July and August, except in one case of high flows resulting in lower water temperature. EMP data also indicates a consistent food limitation in late summer and fall months (Hennessy and Enderlein 2013); abundance of copepods (a major food source for mysids) drops sharply

as grazing rates of *Potamocorbula* increase in the summer. With food limitation already present during warmer months, temperature may be a secondary detrimental factor for *N. mercedis* and allow the apparently more heat tolerant *H. longirostris* to flourish in its place (Figure 6). If higher temperature tolerance is the driving factor, as hypothesized here, then the predictions of increased temperature under most climate change scenarios may further favor this invasive species (Brown et al. 2016).

The FMWT mysid data can be used to examine the salinity range of *H. longirostris*, but it is limited by the geographic range and seasonality of estuarine conditions encountered in the study (i.e., seasonal location of the mixing zone and salinity gradient). *H. longirostris* was often collected at the most saline sampling locations (Figure 7, Suisun Bay and Carquinez Strait), and likelihood of presence increased with salinity (Table 1), so it is unlikely that FMWT data captures the upper salinity maximum of the species. The highest salinity recorded during the study for *H. longirostris* was 19.2 psu, though Mecum (2007) cites a salinity range of freshwater to 28 psu for the species. CPUE was highest between 0-10 psu, which is consistent with data from the Chikugo River estuary in Japan (Suzuki et al 2009).

N. mercedis was documented across a wide range of salinities (freshwater to 17 psu), with an upper salinity limit slightly lower than *H. longirostris*. Orsi (1997) reported that *H. longirostris* was slightly more euryhaline than *N. mercedis*. Previous laboratory work using *N. mercedis* demonstrated mortality in freshwater for specimens collected in areas of higher salinity (Wilson 1951). Field studies (Heubach 1969) hypothesized that reproduction may be reduced in freshwater due to lower percentages of gravid females compared with low salinity regions. The FMWT mysid data did not show reduced abundance in freshwater, however, *N. mercedis* catch was extremely low, so salinity values may not be an accurate representation of salinity habitat distribution within the estuary, or *N. mercedis* may be excluded from higher salinity water due to food limitation or competition with the more euryhaline *H. longirostris*.

The higher CPUE of mysids at turbidity values >10 ntu is likely related to negatively phototaxic behavior. Studies have documented the vertical migration of other mysid species following changes in light intensity (Beeton and Bowers 1982), with individuals moving towards the bottom of the water column as light intensity increases. Kimmerer et al. (1998) found *N. mercedis* vertically migrates at night, however the incidence of this behavior changed with environmental conditions, including turbidity. The FMWT mysid data found low CPUE values for both *H. longirostris* and *N. mercedis* at very low turbidity levels (<10 ntu; Figure 8) where light intensity is highest. Low CPUE associated with low turbidity could be due to vertical migration to deeper waters during daytime hours. FMWT mysids were sampled using oblique tows exclusively during the day, so the net only spent a portion of each tow near the bottom.

The FMWT mysid data indicated an upper turbidity limit of between 140-160 ntu for both *H. longirostris* and *N. mercedis*, but this is likely a sample size limitation resulting from few samples taken during extremely high flows. In the Chikugo River estuary, where *H. longirostris* is overwhelmingly dominant, turbidities often exceed 200 ntu during high flows (Suzuki et al. 2009). An upper limit for *H. longirostris* and *N. mercedis* could be determined with more mysid sampling, but the FMWT mysid data indicate that both species are common across a turbidity range of 10-80 ntu.

Due to small sample size, size-at-maturity statistics were not developed for *N. mercedis* from FMWT mysid data though there is some published information. It is already known that *H. longirostris* is smaller than *N. mercedis* (Feyrer et al. 2003; Hennessy 2011), with
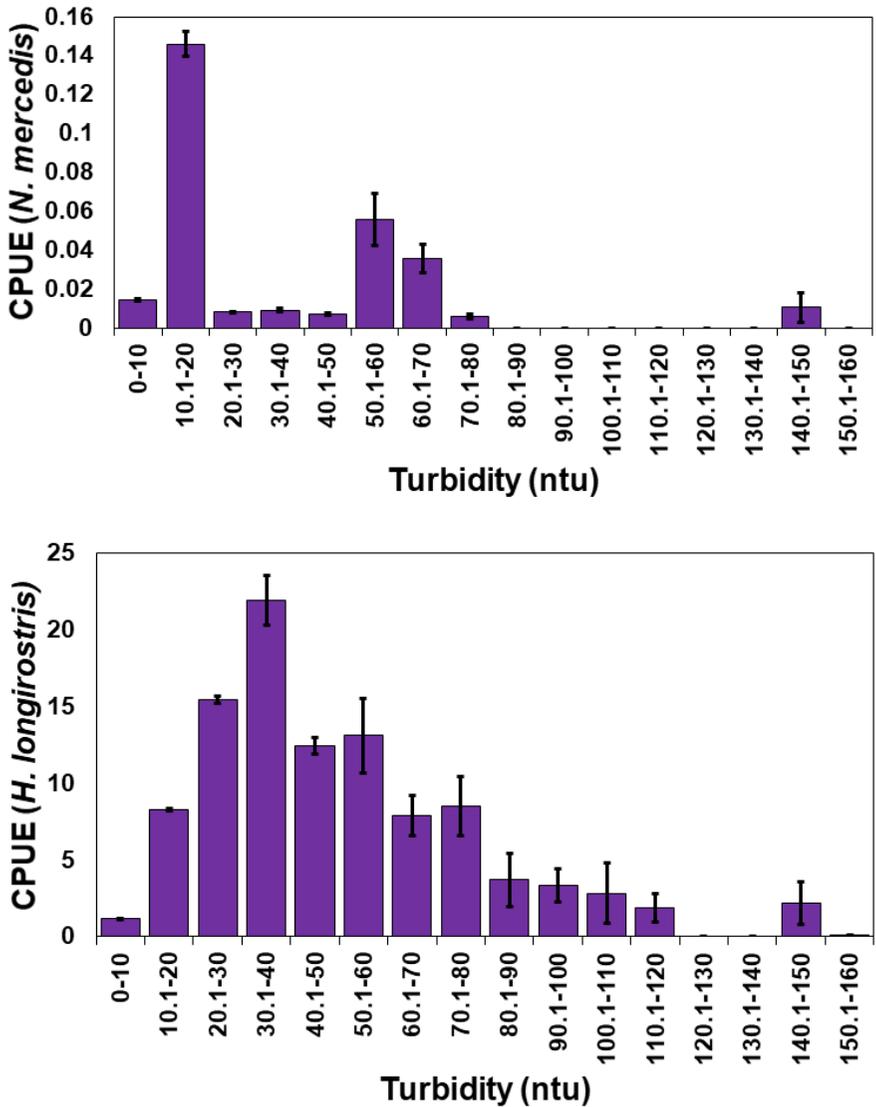
Figure 8. Mean CPUE (catch per cubic meter) (±1 SE) for *N. mercedis* (top) and *H. longirostris* (bottom) by 10 ntu intervals, from Fall Midwater Trawl mysid sampling, 2011–2016.

the latter maturing around 7 mm (Heubach 1969). In contrast, FMWT mysid data contained mature *H. longirostris* as small as 4-5 mm, and average size of adults being smaller overall (Figure 9). There is no known data on age-at-maturity for *H. longirostris.* If the smaller size at maturity of *H. longirostris* results in a younger age-at-maturity this shorter generation time may result in a competitive advantage over *N. mercedis.* Furthermore, smaller size may make *H. longirostris* less subject to food limitation, a chronic problem in the SFE (Orsi and Mecum 1996).
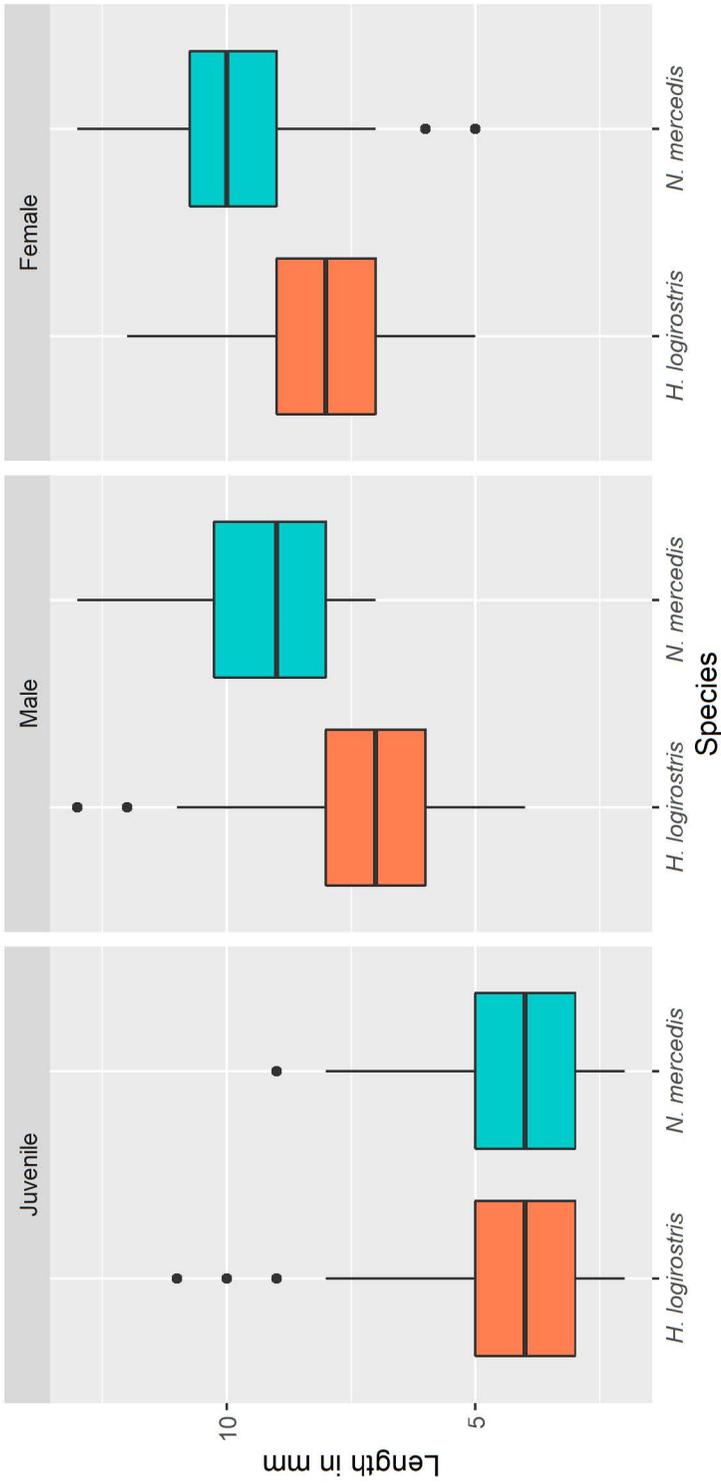
Figure 9. Length distribution of juveniles, adult males, and adult females for *N. mercedis* and *H. longirostris*.

As with size-at-maturity, sample size for gravid *N. mercedis* in FMWT was too small to directly compare fecundity with *H. longirostris.* Previously published information on *N. mercedis* (referred to as *Neomysis awatschensis* in the study) found that fecundity is based on size and time of year (Heubach 1969) with relatively high numbers of eggs produced by females of the same size during spring and summer, and lower numbers in fall and winter. Laboratory raised *N. mercedis* were found to have brood sizes ranging from 4 to 31, with an average of 15.1 (Bailey 1985) based on number of young successfully released from the brood pouch. This is higher than the mean brood size of *H. longirostris* found in the FMWT mysid data (7.7 for stage 3, the closest to being released), but the ideal laboratory conditions used in the study likely produced high values that would not be seen under normal field conditions. *H. longirostris* may follow the same trend as *N. mercedis*, with the highest reproduction in spring. If reproduction is normally reduced in fall, FMWT mysid data is inadequate for determining actual brood size ranges for either mysid species. An analysis of EMP data from 1993-1996 (Orsi 1997) found that *H. longirostris* at the same size had larger average brood sizes than *N. mercedis.* Future analysis of more recent EMP data compared with that of FMWT would improve our knowledge of mysid fecundity.

Further studies are necessary to document the overall abundance of mysid species across the full range of the SFE, characterize the life history of *H. longirostris*, and further understand why *H. longirostris* is the most abundant mysid in the upper SFE and the native *N. mercedis* is not.

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Author Contributions

Conceived and designed the study – MA
Collected the data – MA
Performed the analyses – MA & RH
Authored the MS – MA
Critical revisions - RH

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