These changes in primary productivity and the invasion of the overbite clam *P. amurensis* have also resulted in changes in the abundance and community composition of zooplankton in the San Francisco Estuary (SFE) (Winder and Jassby 2011). Declines in native zooplankton abundances coupled with increases in populations of smaller invasive species has resulted in a decline in the average size, and likely quality, of zooplankton in the estuary (Winder and Jassby 2011). As a result, pelagic fish populations that rely on zooplankton as food, including the Longfin Smelt, may have been negatively affected by changes in prey availability and quality. The diets of Longfin Smelt in the San Francisco estuary (SFE) vary temporally and spatially depending on prey seasonalities and salinity tolerances. For instance, marine calanoid copepods consumed by Longfin Smelt are only found in the upper estuary during dry years, and peak in abundance in spring(*Acartia spp.*, preferred salinities >15 ppt., present mainly in San Pablo and Central Bays, fig. 1) (Kimmerer *et al.* 2005) or summer and fall (*Pseudodiaptomus marinus*, fig. 2). The native calanoid copepod *Eurytemora affinis* is less salinity tolerant and peaks in abundance from March-May (fig. 3). Further upstream where more freshwater calanoids occur, the invasive *Pseudodiaptomus forbesi* peaks in abundance in summer at salinities less than 1 ppt (fig. 4). The invasive cyclopoid copepod, *Limnoithona* *spp.*, shows both a spring and a late fall bloom, especially in salinities greater than 1 ppt. (fig. 5). Mysids are most abundant in late spring and early summer and are almost nonexistent from October through March (fig. 6). Their highest densities occur at salinities of 1-6 ppt (fig. 6). Amphipods are available as prey throughout the estuary most of the year, but especially in dry water years (fig. 7). During wet years, consumption by bivalves in spring and summer keeps their densities low until winter (fig. 7). There is little information on the diets of Longfin Smelt in the SFE (but see Feyrer *et al*. 2003, Hobbs *et al.* 2006, Burris and Baxter in prep); most diet studies have focused on landlocked populations of adult fish in Lake Washington, Washington (Dryfoos 1965, Chigbu 1993, Sibley and Chigbu 1994, Chigbu *et al.* 1998, Chigbu and Sibley 1994, 1998a,b). Below we discuss Longfin Smelt diets, feeding success, and selection as a function of fish size, season and location in the estuary, and highlight areas needing further investigation.

Larval Longfin Smelt may begin feeding before their yolk sac is completely absorbed (Burris and Baxter in prep). For instance, in five regions of the SFE (Carquinez to the Cache-Slough) in late January 2013, up to 80% of young larvae (mean lengths: 6.4-8.2mm) still had yolk sacs present, but around 21% of those also had food in their stomachs (Burris and Baxter in prep). By February (mean length: 7.1-9.3mm), however, fewer than 40% of fish still had yolk sacs remaining, and up to 50% of those had consumed prey. For all larvae in February (with and without yolk sacs), frequencies of empty stomachs were still high in some regions: 10% in Suisun Marsh, 38% in Carquinez, 40% in Suisun Bay, and 60% in the Central Delta. In the first three of these regions, larval Longfin consumed mostly cyclopoid copepods (*Limnoithona spp.*)(66-88% of diets by weight), targeting the juvenile stage more often than the adult stage (Fig. 8). In the Central Delta, however, Longfin consumed mostly copepod nauplii (~60% by weight). By March (mean length: 10.4-17.6 mm), between 14-55% of larvae in Napa River, Suisun Bay, and the Central Delta had empty stomachs. In the Napa River, larvae consumed mostly copepod eggs (~40% W) and copepod nauplii (~30%W), while those in Suisun Bay and the Central Delta consumed mostly *Eurytemora* (>50%W) but some *Limnoithona* as well (~20%W) (Fig. 8). Since its invasion in the early 1990s, the cyclopoid *Limnoithona* is often the most abundant copepod in these regions of the SFE (Bouley and Kimmerer 2006, Winder and Jassby 2011) (Fig. 5). Delta Smelt have also been shown to consume this cyclopoid, but only when densities of *Limnoithona* are extremely high (Slater and Baxter 2014), suggesting that larval Longfin may be consuming it because of its availability rather than because it is a preferred prey. Compared with other copepods, *Limnoithona* is likely poor food for fishes because of its small size and predator avoidance behaviors (Bouley and Kimmerer 2006, Gould and Kimmerer 2010, Winder and Jassby 2011). In addition, larval Delta Smelt have been shown to grow more slowly when feeding on this prey item compared with the calanoid copepod, *Pseudodiaptomus forbesi* (Kimmerer *et al.* 2011). Thus, it is possible that *Limnoithona* may not be nutritionally sufficient for larval Longfin Smelt growth either.

As with young larvae, there is also evidence of food limitation in older larval Longfin Smelt (~8-25 mm FL; late March-May) (Burris and Baxter in prep). Large numbers of larvae have been found with either completely empty stomachs (up to 39%) or stomachs less than 10% full, regardless of the region in which they were collected (San Pablo Bay, Napa River, Suisun Bay, Suisun Marsh, and the West Delta) (Burris and Baxter in prep). This is consistent with high instances of empty stomachs found in larval fish in Lake Washington (29% had empty stomachs) (Dryfoos 1965), suggesting that this life stage may have especially poor feeding success. In addition, the dominant prey item consumed by older larvae in most regions of the SFE is the native calanoid copepod *Eurytemora affinis* (up to 90% of diets by weight) (Burris and Baxter in prep) (Fig. 9), which has been declining in abundance since the mid-1980s (Jassby *et al.* 2002, Kimmerer 2002, Kimmerer 2004, Winder and Jassby 2011). As a result, larvae likely have much lower encounter rates with this prey than historically, and this may explain the high frequencies of empty stomachs. Still, this copepod appears to be the preferred prey type of larval Longfin; fish positively select for it regardless of its abundance in the plankton (Burris and Baxter in prep). Such selection was not noted for other zooplankton prey, except when they occurred at extremely high densities. For example, during two dry years (2007 and 2008) in the Napa River, barnacle nauplii and rotifers were eight times more abundant than *E. affinis* and fish positively selected for them as a result (Burris and Baxter in prep). These prey types may be of lower quality than *E. affinis*, because of their small size (rotifers), fast swimming ability and possible structural defenses (barnacles) that may increase handling time (Greene *et al.* 1986, Barnhisel 1991, Winder and Jassby 2011). This, coupled with lower abundances of *E. affinis*, may explain the high instances of empty stomachs and low stomach fullness values observed in larvae throughout the SFE. For many fish species, successful first feeding is critical for the survival of larvae (Leggett and DeBlois 1994,Sirois and Dodson 2000). In feeding experiments with larval striped bass, copepod escape responses influenced feeding success (Meng and Orsi 1991). Not surprisingly, *E. affinis* was one of the most easily captured species, and this may explain why larval delta smelt and striped bass positively select for it (Meng and Orsi 1991, Nobriga 2002, Slater and Baxter 2014).

Similar to larval Longfin, young juveniles (~25-45 mm FL, May to July) also have high frequencies of empty stomachs (up to 70%) or stomachs that are near empty (Burris and Baxter in prep). Long-term declines in calanoid copepod populations throughout the estuary, but particularly in the Suisun Bay region (Winder and Jassby 2011), may explain why some regions of the SFE have greater feeding success than others. For instance, fish with near full stomachs were collected only in Napa River during wet years (2005/2006 vs 2007/2008), while those in Suisun Bay across all years had consistently near empty or completely empty stomachs compared with all other regions (Burris and Baxter in prep). Similarly, Hobbs *et al.* (2006) showed that young Longfin in the South Channel of Suisun Bay had poorer somatic condition than those from the North Channel, even though there were no differences in feeding success between the two regions. They suggest that fish underwent tidally oriented vertical migration in the South Channel, resulting in higher energetic costs and less overlap between fish and their prey (Bevelhimer and Adams 1993, Bennett *et al.* 2002, Kimmerer *et al.* 2002, Hobbs *et al.* 2006). Regional differences in food use also occur, but mysids are always among the top two most important diet components of young juvenile Longfin; contributing 40- 75% of diets by weight (mainly *Hyperacanthomysis longirostris* but some *Neomysis kadiakensis*) (Burris and Baxter in prep) (Fig. 10). These fish positively select for mysids in all regions of the estuary, except when their abundances are extremely low. When this occurs, fish select for the dominant calanoid copepod species as an alternative, making their diets very regionally (salinity) dependent (Burris and Baxter in prep) (Fig. 10). For instance, the marine copepod *Acartia spp.* accounts for up to 80% of diets (by weight) of fish in San Pablo Bay during dry years. In other regions, however, or during wet years when San Pablo Bay is lower in salinity, this copepodaccounts for less than 25% of juvenile diets (Burris and Baxter in prep). Similarly, the preferred prey of larval Longfin, *Eurytemora* *affinis*, is also an important part of juvenile diets when available, accounting for up to 55% of diets (by weight) in Suisun Marsh in dry years and almost 40% in Napa River in the wet year of 2006. However, because this copepod peaks in abundance by spring (Fig. 3), declining in summer when young juveniles are present, it accounts for less than 20% of diets in most regions (Fig. 10). Finally, *Pseudodiaptomus forbesi*, a calanoid abundant in low salinity waters during summer months (Fig. 4), is most important for fish further upstream in the West Delta and Suisun Bay in dry years (~50% of diets), contributing less than 20% to diets in other regions and in wet years. However, young juveniles processed a decade earlier in Suisun Bay (1996 versus the previous study 2005-2008) consumed mostly *Pseudodiaptomus forbesi* (76% by number, South Channel) or the cyclopoid *Acanthocyclops spp.* (93% by number, North Channel) (Hobbs *et al.* 2006). The reduction in importance of these two prey types in fish a decade later may be due to the documented long-term declines in their abundance (Baxter *et al.* 2008; Winder and Jassby 2011). In the late 1980s, *Pseudodiaptomus forbesi* rapidly established itself and replaced *Eurytemora affinis* as the dominant calanoid during summer months (Winder and Jassby 2011). However, since the early 1990s, it has declined in abundance particularly in Suisun Bay and Marsh (Winder and Jassby 2011). *P. forbesi* may have a competitive advantage over *E. affinis* because its selective feeding allows it to avoid toxic prey in favor of high-quality algae (Mueller-Solger *et al.* 2006, Ger *et al.* 2010). Still, its regional decline may be due to competition and predation by the clam, as well as entrainment of its source populations in the Delta (Durand 2010, Winder and Jassby 2011).

Preliminary analysis of older juvenile Longfin Smelt stomachs (August to December) during two wet years (2006 and 2011) in San Pablo and Suisun Bays also showed high instances of empty stomachs (9-47% of fish) (Burris unpublished). Similarly, fish collected in the highly marine environment of the Central Bay (during summer in 2006-2008, summer/fall in 2011, and winter in 2011) also had high frequencies of empty stomachs (13-53%) (Burris unpublished). These findings are much higher instances than those recorded for young of the year Longfin in September and November in Lake Washington, Washington (<15% empty stomachs) (Chigbu and Sibley 1998), suggesting that food limitation may be greater for Longfin in the SFE. During 2006 and 2011 in Suisun Bay, and in San Pablo in 2011, mysids were the most important prey type (27-63% by weight, 16-53% by number, in 33-71% of fish; mostly *Hyperacanthomysis longirostris*, some *H. aspera*) (Fig. 11). Fish in the Central Bay, however, consumed few mysids, instead relying heavily on marine copepods. For instance, in summers/falls of 2005-2008 and 2011, fish consumed *Acartia spp.* (up to 70% of diets by weight, up to 80% by number, up to 100% of fish) (Fig. 12, 13). In winter 2011, Longfin consumed *Calanus pacificus* (32% W, in 40% of fish) (Fig. 12). Likewise, fish in San Pablo Bay in 2011 also relied on the marine copepod *Pseudodiaptomus marinus* (24% by W, 35% by N, in 52% of fish) (Fig. 11). Epibenthic amphipods were also regionally important prey for fish (Corophium type in Suisun and San Pablo Bays from Aug-Dec. in 2006 and Central Bay summer 2006; Gammarus type in Central Bay in summer 2011), accounting for 23-59% of diets by weight (occurring in 33-82% of fish) (Burris unpublished, Slater unpublished, Figs. 11, 12, 13). The amphipods in the Northern Channel of Suisun Bay have the lowest abundances of the benthic monitoring stations although the amphipods in the water column may reflect species that are transported in from the marsh where large populations of *Corophiidae* have been reported (Jones et al 2009, Howe et al. 2013). The Western Delta and upper Sacramento River are dominated with the freshwater tolerant species *Americorophium stimpsoni, Americorophium spinicorne*, and *Gammarus daiberi* and have maintained consistent populations from 1995 to present). All three species peak in spring and in fall. The most common amphipod in San Pablo Bay (*Ampelisca abdita*, salinity tolerance of 5-35), usually peaks in summer and/or fall. *A. abdita’s* abundance negatively covaries with that of the common bivalve *Potamocorbula* which results in bivalve abundance maximums occurring during years with low amphipod abundance (Fig. 7). In San Pablo Bay in 2006, fish consumed mostly the amphipod, *Americorophium stimpsoni*, which may have been pushed further downstream than usual from the high outflows experienced that year. Similarly, *A. abdita* may have also been transported further seaward into the Central Bay during the wet years of 2006 and 2011, making them more available to fish and explaining the high instance of this prey in longfin guts. Amphipods are likely lower quality prey types than calanoid copepods and mysids, since they provide less energy per gram (Cummins and Wuychek 1971, Davis 1993), but their presence in fish diets suggests that food sources are not confined to solely pelagic pathways. Most species of amphipods are tube dwellers that live on the bottom (*Corophidae* and *Ampelisca* species) and two species (*Gammarus* *daiberi* and *Hyalella azteca*) are always free living. Tube dwelling species frequently swim into the water column so they are available to both demersal and pelagic feeders. Long-term declines and changes in the composition of the pelagic food web may be causing fish to shift their diets to benthic food sources (Slater and Baxter 2014). Juvenile Lake Washington Longfin have also been shown to consume a variety of prey items, including mysids (summer and fall, 38-77% of diet by weight, *Neomysis mercedis*), copepods (summer, ~86%, *Diaptomus* and *Epischura* spp.), and Cladocerans (Fall, ~50%, *Daphnia*) (Dryfoos 1965, Chigbu and Sibley 1998). As with young juveniles mentioned above, Cladocerans are not a primary prey of older juveniles in the SFE.

Adult Longfin Smelt have much lower frequencies of empty stomachs than larvae or juveniles, (<15% in Lake Washington, 13-21% in SFE)(Chigbu and Sibley 1998, Feyrer *et al.* 2003), likely because these larger fish are more capable foragers able to feed on a greater variety of prey types. In the Columbia River Estuary, age-1 fish had the lowest percentage of empty stomachs in marine habitats (8%) compared with increasing freshwater habitats (Brackish: 20%, bays and fresh: 28%) (Bottom et al., 1984). This suggests that prey in the coastal ocean may be more abundant or easier to capture for fish than in the estuary. However, Simenstat *et al.* (1977) investigated the diets of juveniles and adults from July to January in the Strait of Juan de Fuca and found that 58% had empty stomachs, implying that marine waters may not provide greater feeding success. For California Longfin, there is no information on the diets of fish in the coastal ocean, but it is thought that the planktonic food supply is richer in the marine waters of the Gulf of Farallones than the estuary (Federal Register 2012). In addition, since the 1990s, Longfin Smelt in the SFE have shifted their distribution to more saline waters, possibly because of limited food availability in the upper estuary (Fish *et al.* 2009). Therefore, coastal waters and marine influenced regions of the estuary are likely important food habitats for Longfin. Diets of age 1+ Longfin from the marine Central Bay region of the estuary during late winter (January and February 2012), support this claim: none of the 21 fish had empty stomachs (Burris unpublished). These fish relied most heavily on the calanoid copepod *Calanus pacificus* (60% W, 41% N, in 90% of fish), followed by mysids (25% W), and the calanoid *Acartia spp.* (26% N, 85% of fish) (Fig. 12). *C. pacificus* is among the more abundant and large body-sized copepods off the coast of California, and, while its abundance peaks in spring during the phytoplankton bloom, a portion of the population remains reproductive in surface waters throughout the year (Runge 1985, Osgood and Frost 1994). Thus, it may be a high quality and dependable food source for Longfin Smelt in marine waters. In the Strait of Juan de Fuca, mysids and calanoid copepods were also the most important prey types, in addition to epibenthic gammarid amphipods (Simenstat *et al.* 1977). Adult Longfin in the Columbia River Estuary had similar diets, consuming mostly calanoid copepods, corophium amphipods, harpacticoids, and the mysid *Neomysis mercedis* (Bottom *et al.* 1984). Additionally, fish collected in winter near the mouth of the Nooksack River in Washington were found to have consumed juvenile mud shrimps (*Upogebia spp.*) (Penttila 2007).

While adult Longfin consume a diversity of prey types, they also rely heavily on mysid shrimp in the upper SFE (Feyrer *et al.* 2003), at least in Suisun Marsh. In this region, over 70% of the adult Longfin diet by weight was mysids (Feyrer *et al.* 2003). As with juveniles, however, adult Longfin also switch to other foods when their preferred mysid prey occurs in low abundances (Chigbu 1993, Chigbu and Sibley 1998, Feyrer *et al.* 2003I). In the SFE, Feyrer *et al.* (2003) showed that adult Longfin Smelt in Suisun Marsh consumed a greater diversity of prey (more copepods) as the abundance of mysids decreased seasonally from spring to fall. In preliminary data from January and February 2007 and 2012, the importance of mysids in adult diets is highly regionally dependent: in Suisun Marsh (2007) and the Sacramento River (2012) they contributed 55-65% of diets by weight, but less than 30% of diets in San Pablo and Suisun Bays (2012) (Burris unpublished) (Fig 13). These fish are consuming mostly the small invasive mysid, *Hyperacanthomysis longirostris,* but also *H. macropsis* and *Neomysis kadiakensis*. In the Napa River (2007), less than 5% by W of diets were mysid shrimp and fish fed most on amphipods (Corophium: 25%, Gammarus: 35%) and cumaceans (~40%) (Fig. 14). In San Pablo Bay, Suisun Bay, and the Sacramento River, amphipods (especially gammarus type) were also significant in diets (30-45% by W) (Fig. 14). Interestingly, two marine copepods, *Calanus* and *Acartia,* were also important in the western region of the SFE, in Suisun and San Pablo Bays in 2012 (Fig. 14). In Lake Washington, Longfin also feed on other prey items (Daphnia and amphipods) during seasons when mysids are scarce, as a way to optimize their energy intake (Chigbu 1993, Chigbu and Sibley 1998).

The historically dominant native mysid, *Neomysis mercedis*, has declined significantly in abundance in both the SFE (Fig. 6) (Orsi and Mecum, 1996, Winder and Jassby 2011) and in Lake Washington (Moulton, 1974; Eggers *et al.* 1978; Chigbu and Sibley 1998). Declines in mysid abundance have also been linked to declines in Longfin Smelt populations in both the SFE and Lake Washington (Feyrer *et al.* 2003, Chigbu and Sibley 1994, 1998). In Lake Washington, Chigbu and Sibley (1994) suggest that Longfin population declines are due to food limitation in the juvenile life stage, while in the SFE, Feyrer *et al.* (2003) suggest food limitation in the adult stage is responsible. In the former case, a 25% reduction in fish body size after mysid populations crashed coincided with its disappearance from the diets of juvenile Longfin during summer months. Because of the lack of optimally sized prey, these fish consumed smaller copepods and Cladocerans which may have stunted their growth, leading to a reduction in survival and reproductive output (Chigbu and Sibley 1994). In the SFE, the species of fish (Longfin Smelt, splittail, and striped bass) that relied most heavily on mysids as adults before the mysid crash, later exhibited the greatest declines in population abundance (Feyrer *et al.* 2003).

As noted above, the invasion of a phytoplankton filtering clam and competition for food from other invasive zooplankton have led to changes in the quality and quantity of available Longfin Smelt prey. Several native calanoid copepods and mysid species have declined in abundance and been partially replaced by invasive species; the mean size of zooplankton in the estuary has decreased as a result (Winder and Jassby 2011). The drastic decreases in abundance of the two major prey types of Longfin Smelt (mysid shrimp and *Eurytemora affinis*) that occurredin the late 1980s (Winder and Jassby 2011) may be responsible for the fish’s population decline. These changes in planktonic food availability may have also contributed to the Longfin Smelt’s distributional shift to higher salinity (more nutritious) waters that began in the early 1990s (Fish *et al.* 2009). After the invasion of the clam, the response of both Longfin Smelt and juvenile striped bass populations to winter-spring outflows changed. The relative abundance of striped bass stopped responding to outflow (Sommer *et al.* 2007), while that of Longfin Smelt was lower per unit outflow (Kimmerer 2002), possibly because reduced prey abundance lead to less suitable habitat *(*Kimmerer *et al.* 2000, Sommer *et al.* 2007). A similar shift out of low salinity waters coincident with a reduction in food has also been documented for the Northern Anchovy (Kimmerer 2006). Finally, intra and interspecific competition for scarce food resources have been documented in both Lake Washington and the SFE for adult fish and their mysid prey (Chigbu and Sibley 1994, Chigbu and Sibley 1998, Feyrer *et al.* 2003). In Lake Washington, Chigbu and Sibley (1994, 1998) have shown that odd year classes of age 1+ fish rely more heavily on mysids than the more abundant even year classes. In the SFE, there is likely little intraspecific competition for mysid prey, because fish and mysid abundances are low. However, sockeye salmon have significant dietary overlap with adult Longfin in Lake Washington, with both selecting for the largest *Daphnia* (Chigbu and Sibley 1993). In addition, preliminary analysis of very young larval Longfin Smelt and Pacific Herring collected concurrently in the SFE in 2013, showed moderate to very high dietary overlap between these species (Fig. 8A), suggesting the potential for interspecific competition. Fish collected in February from Carquinez and in March from Napa River had moderate overlap in diets (52-62% similar), mostly because the two species consumed different life stages of copepods (Fig. 8A). In Carquinez, Longfin preyed more on juvenile cyclopoids, while Herring consumed adult cyclopoids. Similarly, in Napa River, both consumed copepod eggs, but Longfin also consumed their nauplii. In Suisun Bay in both February and March, there was high overlap in diets (69-81% similar) as the two species consumed equal proportions of copepod nauplii, and cyclopoid juveniles and adults (February), or *Eurytemora* (March). The highest dietary overlap occurred in Suisun Marsh in February (90-95% similar), when >75% (by weight) of diets consisted of juvenile cyclopoids (Fig. 8). In the same study, the diets of larval Longfin and larval Prickly Sculpin collected concurrently were also analyzed (Fig. 8B). Of the three regions studied (Suisun Bay, Central Delta, and Cache-slough), only fish in the Central Delta in March, but not February, showed significant dietary overlap. In this region, both fish consumed mostly *Eurytemora* copepods, as well as some copepod nauplii and juvenile cyclopoids (Fig.8B). Thus, Pacific Herring and Prickly Sculpin larvae (that consume *Eurytemora spp.* and Cyclopoid copepods) may be reducing the already low availability of prey and thus increasing food limitation in larval Longfin Smelt. This may also be the case for adult and juvenile Longfin Smelt, if Striped Bass (that rely on mysids) (Orsi and Mecum 1996,Feyrer *et al.* 2003) and Delta Smelt (that consume *Eurytemora spp.* and *Pseudodiaptomus spp.*) (Slater and Baxter 2014) also reduce the prey field for these older life stages.