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Status of the Siberian Prawn, *Exopalaemon modestus*, in the San Francisco Estuary

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ABSTRACT

The freshwater Siberian prawn, *Exopalaemon modestus* (Heller 1862, Crustacea: Decapoda: Palaemonidae), was likely introduced into the San Francisco Estuary in the late 1990s. Since the initial collection in 2000, *E. modestus* spread rapidly throughout the estuary and into upstream areas, and is now the most common caridean shrimp in the upper estuary, including the Sacramento–San Joaquin Delta. We summarized data collected from 2000 to 2011 by several long-term monitoring projects, special studies, and the public concerning *E. modestus* in California. Although some specific ecological effects of this introduced species have been documented, broader effects are largely unknown. *E. modestus* is likely to expand its distribution within the estuary and watershed and become established in other freshwater areas of California.

KEY WORDS

Exopalaemon modestus, San Francisco Estuary, Siberian prawn, invasive species

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INTRODUCTON

Since the Gold Rush, a variety of taxa has been introduced to the San Francisco Estuary (estuary) (Cohen and Carlton 1998). Although historically there were several pathways of introduction, including ship hulls, live oysters and their packing material, and fish stocking, the primary pathways today are via ballast water and deliberate introduction by people. Introduced species are so pervasive in the estuary that they now dominate the benthic, fouling, brackish-water zooplankton, and freshwater fish communities (Cohen and Carlton 1998). They have also had profound ecosystem effects, such as zooplankton declines in the upper estuary that have been attributed to competition and predation by the introduced clam *Potamocorbula amurensis* (Kimmerer et al. 1994; Orsi and Mecum 1996). These changes in zooplankton composition and abundance may have contributed to the decline of longfin smelt (*Spirinchus thaleichthys*) in the estuary (Kimmerer 2002) and several fish species in Suisun Marsh (Feyrer et al. 2003).

The estuary still supports several commercial fisheries, including the bay shrimp trawl fishery, which is primarily composed of the native *Crangon franciscorum* with minor contributions by *C. nigricauda* and *C. nigromaculata*. Several listed fish species and species of concern inhabit or migrate through the upper estuary, including splittail (*Pogonichthys macrolepidotus*), delta smelt (*Hypomesus transpacificus*), longfin smelt, winter and spring-run Chinook salmon (*Oncorhynchus tshawytscha*), and steelhead (*O. mykiss*). Additionally, the native freshwater shrimp, *Syncaris pacifica*, which is a state and federally endangered species, is found in tributaries to San Pablo Bay.

The Siberian prawn, *Exopalaemon modestus* (Heller 1862, Crustacea: Decapoda: Palaemonidae), is native to freshwater areas of eastern Asia, from the Amur and Ussuri basins in Siberia, through Korea, China, and Taiwan (Holthius 1980). *E. modestus* is ecologically and economically important in these regions (Oh and Park 2000; Oh et al. 2002; Guo et al. 2005). This species was first collected in California by the California Department of Fish and Wildlife's (CDFW, formerly California Department of Fish and Game) San Francisco Bay Study in the lower Sacramento River in 2000. Since that time, its abundance and distribution rapidly expanded in the San Francisco Estuary and its watershed. *E. modestus* is also established in the Columbia River, where it was first discovered in 1995 and assumed to be introduced via ballast water (Emmett et al. 2002). It later became established in the lower Snake River, a tributary of the Columbia River watershed (Haskell et al. 2006). We do not know if the California introduction was from the Columbia River or Asia, or from ballast water or otherwise human-mediated.

The purpose of this paper is to summarize

1. the taxonomy of *E. modestus* and shrimp species similar in appearance that are present in the estuary and its watershed,
2. the abundance and distribution trends of *E. modestus*, and
3. the growth and reproduction trends of *E. modestus*.

METHODS

Study Area

The San Francisco Estuary (Figure 1) is the largest estuary in the western United States, and drains 40% of California's surface area (Nichols et al. 1986). Sampling was conducted by various monitoring programs throughout the estuary and its tributaries.

Data Collection

We used data and specimens from several long-term monitoring and special studies conducted in the estuary and its watershed from 2000 to 2011. Catch, length, sex, salinity, and temperature data came from CDFW's San Francisco Bay Study (Bay Study, *http://www.dfg.ca.gov/delta/projects.asp?ProjectID=BAYSTUDY*), the only long-term monitoring program in the estuary that routinely

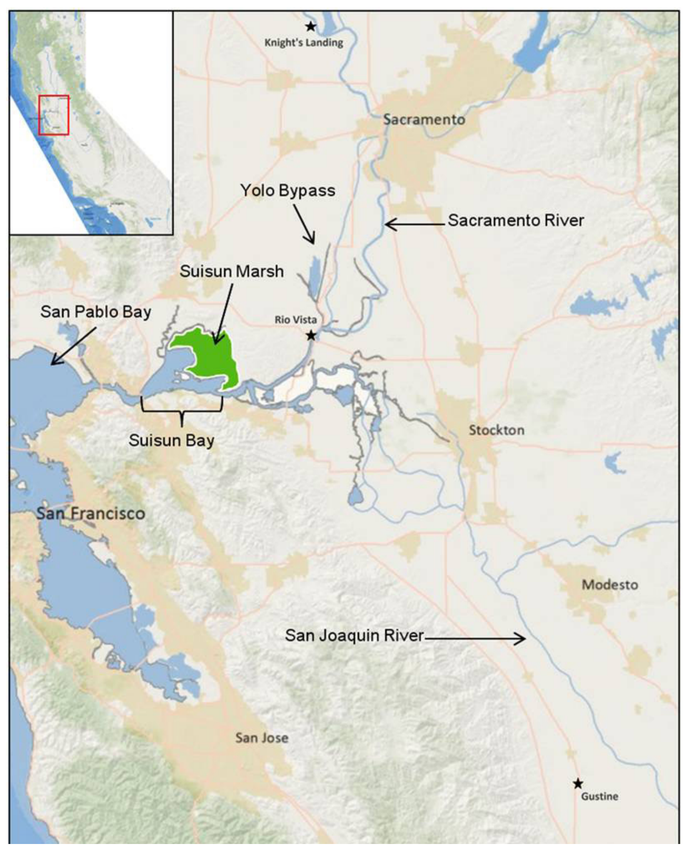

Figure 1 Map of the San Francisco Estuary. Insert shows the position of the estuary within the State of California.

Table 1 List of shrimp data sources and type of data provided

Data source	Data type	Other data	Data published in peer-reviewed format?
CDFW Bay Study	Catch, length, sex	Salinity, temperature	No
UCD Suisun Marsh	Catch	Salinity, temperature	No
DWR Yolo Bypass	Catch	None	No
USFWS Beach Seine Survey	Catch	None	No

measures and sexes shrimp (Table 1). Monthly otter trawls have been conducted at 52 stations from South San Francisco Bay to the lower Sacramento and San Joaquin rivers since 1980 (Orsi 1999). Shoals deeper than 3 m and channels were sampled with a 6-mm mesh cod-end otter trawl that was towed for 5 minutes on the bottom. Water column salinity (psu) and temperature (°C) data were recorded at each station with a Sea-Bird Electronics SEACAT 19 CTD profiler and binned by 0.5-m intervals; only the bottom readings were used for this analysis.

Catch, salinity, and temperature data from Suisun Marsh, the largest contiguous brackish marsh in California, came from the University of California at Davis' (UCD) long-term monitoring survey that began in 1979 (Table 1) (see Matern et al. 2002 for detailed methods; shrimp data from T. O'Rear, UC Davis, pers. comm., 2012). This survey sampled 21 stations monthly in the larger sloughs with an otter trawl and counted shrimp by species. *E. modestus* was grouped with *P. macrodactylus* through February 2002; the two species were counted separately beginning in March 2002, and analysis of *E. modestus* data started from this point. Surface salinity (‰) and temperature (°C) were also measured at each station.

Information on the seasonal abundance and distribution of *E. modestus* in Yolo Bypass, a floodplain that includes tidal and seasonal wetlands and perennial ponds, came from California Department of Water Resources (CDWR) beach seine and rotary screw trap samples (Table 1) (see Sommer et al. 2004 and Feyrer et al. 2004 for detailed methods; shrimp data from L. Conrad, CDWR, pers. comm., 2012 and K. Reece, CDWR, pers. comm., 2011). The Yolo Bypass seine survey estimated the total number of shrimp collected and the rotary screw trap survey enumerated *E. modestus*.

Distributional information from the Sacramento–San Joaquin Delta (Delta) and the Sacramento and San Joaquin rivers upstream of the Delta came from the U.S. Fish and Wildlife's (USFWS) beach seine survey, which sampled approximately 40 stations weekly (Table 1) (see Brandes and McLain 2001 for detailed methods; shrimp data from J. Speegle, pers. comm., 2012) and began counting *E. modestus* as of July 2002. Additional reports of *E. modestus* collections and specimens were received from several CDFW and USFWS monitoring programs that sample the Delta and rivers with a variety of gear (e.g. midwater trawl and Kodiak trawl), and from the public.

Laboratory Methods

Dorsal and ventral rostral teeth were counted for 20 *E. modestus* (10 females and 10 males) and 19 *Palaemon macrodactylus* (9 females and 10 males), a closely related introduced species. Neither the tip of the rostrum nor the gastric spine was counted as teeth. Other taxonomic information was taken from the literature cited. From the Bay Study samples, up to 100 random non-ovigerous shrimp of each species were sexed and measured (total length, tip of rostrum to tip of telson, TL) and up to 30 random ovigerous shrimp of each species were measured from each station. Larvae were collected from the CDFW Townet Survey and USFWS light traps; staging was done using the descriptions for larval *P. macrodactylus* in Little (1969).

Data Analysis

Catch per unit effort (CPUE, catch/5-min tow) from the Bay Study and Suisun Marsh data were used for abundance analyses, and total catch was used for distributional, temperature, and salinity analyses. We calculated annual CPUE for the Suisun Marsh data by averaging CPUE at all stations for each year. We calculated annual CPUE for the Bay Study data by averaging CPUE at all stations upstream of Carquinez Strait. Annual CPUE from CDFW's Bay Study data were calculated to compare upper estuary abundance trends of *E. modestus* and *P. macrodactylus* from the three stations near the confluence of the Sacramento and San Joaquin rivers, which have been consistently sampled since 1980.

We adjusted Bay Study *E. modestus* length frequencies for plus counts and subsamples, summed them by 5-mm intervals, and plotted the percentages by interval for each month. We also used the length–frequency data to calculate mean length by month and sex. We calculated monthly CPUE for each sex, and ovigerous females only by averaging CPUE for all stations upstream of Carquinez Strait.

RESULTS

Taxonomy

The first documented collection of *Exopalaemon modestus* in the estuary was a 65-mm total length (TL) female caught by an otter trawl on 19 September 2000 in the lower Sacramento River, about 8.5 km downstream of Rio Vista (water depth 11.0 m, latitude 38°06′37″N, longitude 121°43′10″W; see Figure 1), by CDFW's Bay Study. This new species was independently confirmed as *E. modestus* by Greg Jensen (University of Washington), Mary Wicksten (Texas A&M University), and Yixiong Cai (National University of Singapore). Specimens were deposited at the California Academy of Sciences in San Francisco (accession numbers CASIZ 162682 to 162684).

When taken live from the estuary, *E. modestus* is translucent white with scattered red-brown pigment cells. It has a long rostrum, about 20% of the total body length, with a strongly elevated basal crest (Figure 2A). The rostrum has 5 to 11 dorsal teeth (usually 7 to 9 here), with no teeth at the apex (Kemp 1917; Kubo 1942; CDFW Bay Study, unpublished data). All of the pereiopods are relatively slender, and the first two pairs are chelate. The chela (claw) and carpus (wrist) of pereiopod II are about equal in length while the dactyl (moveable finger) is slightly longer than the palm of the chela (Figure 2A insert; Kemp 1917; Kubo 1942). This is a medium-sized shrimp, with a maximum size of 60 to 82 mm TL.

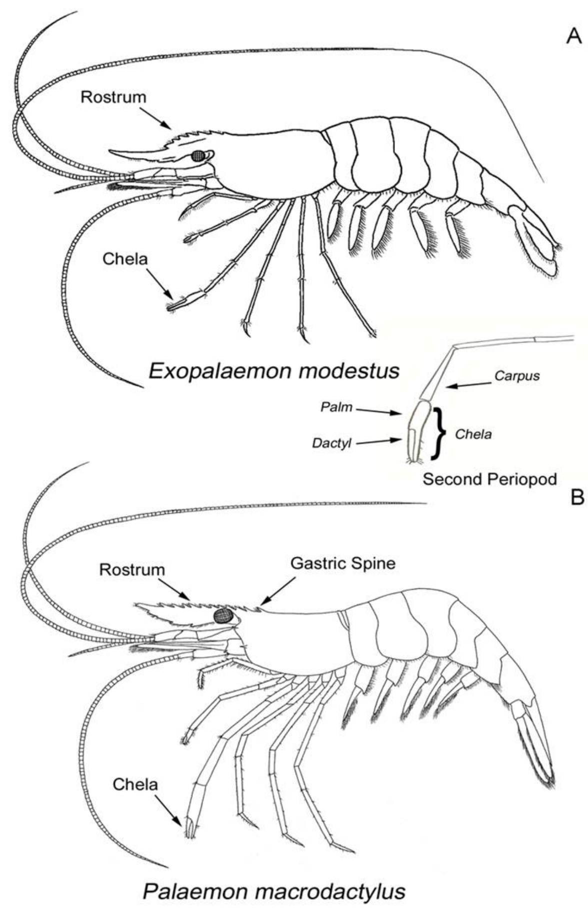

Figure 2 *Exopalaemon modestus* (A) and *Palaemon macrodactylus* (B), showing differences in the chelae of pereiopod II, and the rostrums. Insert is pereiopod II of *E. modestus*. *E. modestus* drawing by Tom Greiner, *P. macrodactylus* drawing by Eric Lazo–Wasem.

Four shrimp species from San Francisco Estuary and its watershed may be confused with *E. modestus*:

1. *Palaemon macrodactylus*, common in brackish water and occasionally in freshwater,
2. *Exopalaemon carinicauda*, found in brackish and marine waters,
3. *Palaemonetes kadiakensis*, found in freshwater, and
4. *Syncaris pacifica*, found in a limited number of freshwater streams.

Like *E. modestus*, the first three are introduced palaemonid shrimp; *S. pacifica* (Family Atyidae) is native.

Palaemon macrodactylus was introduced to the estuary in the 1950s (Newman 1963) and is common in brackish and tidal freshwater areas. Because *P. macrodactylus* and *E. modestus* are often found together, they are the two species most likely to be confused. *Palaemon macrodactylus* is readily distinguished from *E. modestus* by its straight rostrum and the number of dorsal and ventral rostral teeth (Figure 2B and Table 2). If the rostrum is broken, *P. macrodactylus* can be distinguished from *E. modestus* by the pres-

Table 2 Comparative descriptions of *Exopalaemon modestus*, *Palaemon macrodactylus*, *Exopalaemon carinicauda*, *Palaemonetes kadiakensis*, and *Syncaris pacifica*. (Sources: Eng 1981; Kemp 1917; Kubo 1942; Martin and Wicksten 2004; Newman 1963; CDFW unpublished data; USFWS unpublished data.)

Species	Family	Habitat and status in California	Rostrum	Gastric spine	Other
Exopalaemon modestus	Palaemonidae	Introduced to fresh and brackish waters of San Francisco Estuary and nontidal freshwater upstream of Estuary; established.	5–11 (usually 7–9 in CA) dorsal teeth, 2–4 ventral teeth; high basal crest.	No	Fingers of chelae about equal in length to palm; no dorsal abdominal carinae; no supraorbital spine.
Palaemon macrodactylus	Palaemonidae	Introduced to marine and brackish waters of San Francisco Estuary, occasionally in tidal freshwater; established.	9–15 (usually 10–12 in CA) dorsal teeth, 3–5 ventral teeth; no basal crest.	Yes	Fingers of chelae shorter in length than palm; no dorsal abdominal carinae; no supraorbital spine.
Exopalaemon carinicauda	Palaemonidae	Introduced to marine waters, collected only in South San Francisco Bay in 1990s; not established.	6–9 dorsal teeth, 3–8 ventral teeth; high basal crest.	No	Fingers of chelae longer in length than palm; dorsal carinae present on abdomen; no supraorbital spine.
Palaemonetes kadiakensis	Palaemonidae	Introduced to fresh water; collected only in Cosumnes River Preserve 2005–2012. Appears established, sporadic collections in the Delta.	7 dorsal teeth, 3 ventral teeth; no basal crest.	No	Fingers of chelae about equal in length to palm; no mandibular palp; no dorsal abdominal carinae; no supraorbital spine.
Syncaris pacifica	Atyidae	Native to low elevation perennial freshwater streams in Napa, Sonoma, and Marin counties. State and federal endangered species.	1–2 dorsal teeth, 5–9 ventral teeth; no basal crest.	No	Terminal tufts of setae on chelae of pereiopods I and II; no dorsal abdominal carinae; supraorbital spine present.

ence of a gastric spine and the longer, broader chelae on pereiopod II (Figure 2B).

Two specimens of *E. carinicauda* were collected on separate occasions from South San Francisco Bay in the 1990s (Wicksten 1997), but it is apparently not established in the estuary. Although the rostrums of *E. carinicauda* and *E. modestus* are very similar, *E. carinicauda* has longer chelae on pereiopod II and dorsal ridges (carinae) on the abdominal segments (Table 2), which *E. modestus* lacks. The chelae of both *E. modestus* and *E. carinicauda* are narrower than that of *P. macrodactylus*.

Palaemonetes kadiakensis, the smallest of the introduced shrimp, was first collected in the Cosumnes River Preserve in May 2005, at latitude 38°26′14″, longitude 121°44′89″ (Stover 2006). The species appears established in the Cosumnes River Preserve, based on multiple collections since 2005 and as recently as May 2012 (P. Crain, ICF International, pers. comm., 2012; C. Jeffres, UC Davis, pers. comm., 2012). A single specimen was also caught by the Bay Study otter trawl in the lower San Joaquin River in May 2012 (CDFW unpublished data) and several were collected in 2012 in Georgiana Slough near the Delta Cross Channel gates (USFWS unpublished data). *Palaemonetes kadiakensis* is common in the aquaria trade and this introduction was likely from dumped aquarium specimens rather than the bait trade (Stover 2006). *Palaemonetes kadiakensis* can be distinguished from the genera *Exopalaemon* and *Palaemon* by the lack of a mandibular palp. It also lacks the gastric spine of *P. macrodactylus* and the rostral crest of *E. modestus* and *E. carinicauda*. However, these features may be difficult to see in shrimp under 30 mm TL, in which case the absence of a mandibular palp is the only reliable way to distinguish *Palaemonetes* from the other two genera.

Syncaris pacifica is found in 17 stream reaches in Napa, Sonoma, and Marin counties (USFWS 1998), including several tributaries to San Pablo Bay. To date, *E. modestus* has not been collected with *S. pacifica*, but has been collected in San Pablo Bay. *S. pacifica* can be identified by the presence of a supra-orbital spine on the carapace, and terminal tufts of setae on the chelae of pereiopods I and II (Table 2), characteristics not found on any other extant freshwater shrimp in California.

Abundance and Distribution

The San Francisco Estuary population of *E. modestus* grew substantially during the first few years after its introduction, but numbers subsequently dropped and appeared to have stabilized in most areas. The highest numbers of *E. modestus* in CDFW Bay Study samples occurred in 2002 and 2003, with a steep decline in 2004 (Figure 3). A similar trend was reported for Suisun Marsh, where it was the most common caridean shrimp collected in 2002 and 2003 (Schroeter and Moyle 2003, 2004; T. O'Rear, UC Davis, pers. comm., 2012; Figure 4). However, unlike the Bay Study data, the decline in 2004 was followed by rebounds in 2006 and 2011. In addition, it was the dominant macroinvertebrate by late 2001 in both tidal and non-tidal habitats of the Yolo Bypass, including Liberty Island, the toe drain, and perennial ponds (Zeug et al. 2002; L. Conrad, CDWR, pers. comm.; 2012 K. Reece, CDWR, pers. comm. 2011; USFWS beach seine data).

Exopalaemon modestus spread rapidly throughout the Sacramento–San Joaquin Delta to non-tidal freshwater areas upstream of the Delta and brackish water areas outside of Suisun Marsh. By spring 2003, it ranged from Knights Landing (Yolo County) on the Sacramento River in the north to Mud Slough (Merced County), a tributary of the San Joaquin River near Gustine, in the south (Figure 1). It was also found throughout Suisun, Grizzly, and Honker bays to Carquinez Strait, and infrequently in San Pablo Bay, with the first collections there in 2004.

Because *E. modestus* was collected by different methods in each area, we cannot compare densities. However, direct observation and the use of several gear types at some locations suggest that the highest numbers were in Yolo Bypass (including Liberty Island), the lower Sacramento River, and Suisun Marsh. From USFWS beach seine data, there were

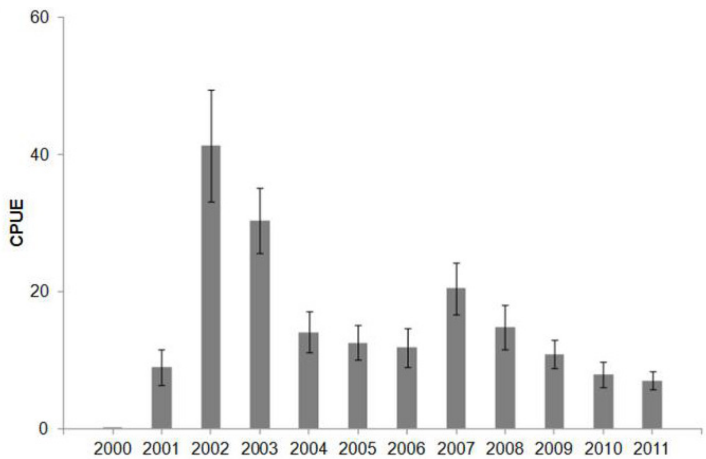

Figure 3 Average annual CPUE of *E. modestus*, from 2000 through 2011 (CDFW Bay Study)

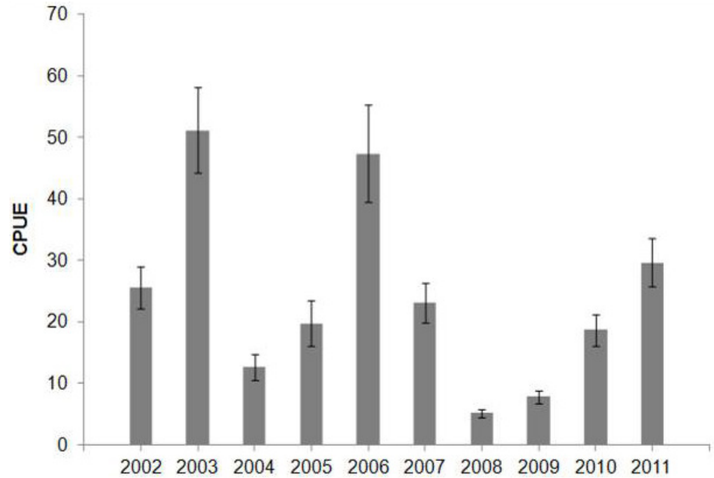

Figure 4 Average annual CPUE of *E. modestus*, from 2002 through 2011 (UCD Suisun Marsh)

also concentrations in the San Joaquin River from Stockton to the confluence of the Stanislaus River. Ovigerous females were common in the Yolo Bypass and the lower Sacramento River, from Rio Vista to Sherman Island. Since most studies neither measure shrimp nor separate ovigerous and non-ovigerous shrimp in their counts, we could not determine all the areas with high concentrations of reproductive adults.

Although the majority of the *E. modestus* were collected from freshwater, a number of shrimp were collected from brackish water in Suisun and San Pablo bays by the Bay Study and in Suisun Marsh by UCD. Ovigerous shrimp were collected as far downstream as Carquinez Strait. The mean salinity of UCD's 2002–2011 Suisun Marsh collections was slightly higher than Bay Study's 2000–2011 collections, though Bay Study collected shrimp from a wider range (Table 3). *Exopalaemon modestus* was collected over a wide range of temperatures by both studies, with similar means.

In the western Delta and lower Sacramento River, *E. modestus* has apparently displaced *P. macrodactylus*, a co-occurring shrimp species (Figure 5). Average Bay Study *P. macrodactylus* annual CPUE declined from 15 to 3 after the introduction of *E. modestus* in this region.

Growth and Reproduction

The Bay Study collected *E. modestus* from a wide range of sizes, with females generally being larger than males (Table 4). The first of the new recruits were collected in July, although collections were still dominated by the previous year class (Figure 6), with

Table 3 *E. modestus* temperature and salinity data collected by CDFW Bay Study and UC Davis Suisun Marsh Study

	Temperature (°C)		Salinity (‰)			
Study	Mean	Range	Mean	Range	SD	N
CDFW Bay Study	16.1	7.5 – 23.5	1.62	0.04 – 23.58	2.52	45,880
UCD Suisun Marsh	16.7	4.6 – 32.1	3.61	0.00 – 14.90	2.26	68,985

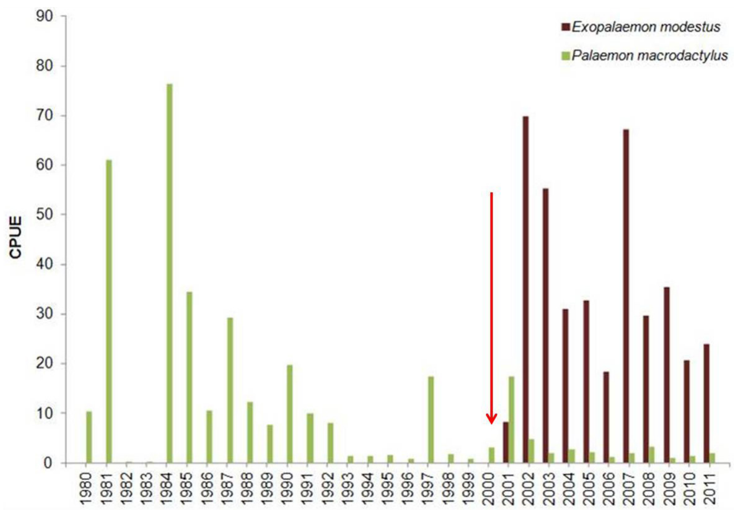

Figure 5 Average annual CPUE of *P. macrodactylus* and *E. modestus* in the western Delta and lower Sacramento River, 1980 through 2011 (CDFW Bay Study). Arrow indicates the year that *E. modestus* was first detected in the estuary.

Table 4 *E. modestus* size data collected by CDFW Bay Study

Shrimp type	Mean size (mm TL)	Size range (mm TL)	N
Non-ovigerous females	54.9	18 – 82	17,588
Ovigerous females	63.3	42 – 79	758
Males	53.0	20 – 76	27,525

most shrimp >50 m TL. By August the current year class dominated, with the peak catches in the 40 to 44 mm interval. From September through December, the peak catches were between 50 and 59 mm, with new recruits, <40 mm TL, and older shrimp (age 1) collected through the end of the year. From July through December, the mean size ranged from 49.9 to 56.8 mm TL.

Smaller shrimp continued to be collected from January through June, but in decreasing numbers. While the mean size ranged from 52.3 to 59.2 mm TL through June, the length frequency distribution became less skewed towards smaller shrimp (Figure 6). The relatively small numbers of juvenile *E. modestus* in the Bay Study data were consistent over the years; overall, less than 5% (n = 2,090) of the *E. modestus* collected were <40 mm TL. Furthermore, only 73 shrimp were <25 mm TL, with the majority of these shrimp (89%) collected from the lower Sacramento River between Sherman Island and Rio Vista.

There was a strong seasonal abundance trend in the Bay Study's *E. modestus* collections, with most collected from September to December (Figure 7A). This abundance peak was approximately 60% males and 40% females. Males were always more common than females in the Bay Study's collections, with the lowest percentage of females (21%) in summer, coinciding with the lowest abundance. This was also the period of peak reproduction; ovigerous females were collected by the Bay Study from March through December, with the majority from May to August (Figure 7B). Stage V larval *E. modestus* and small juveniles (< 10 mm) were collected from the San Joaquin River near Stockton in June 2002 (CDFW Townet Survey); Stage V larvae were also collected from flooded Liberty Island in May 2003 (USFWS light traps).

DISCUSSION

The presence of larvae and ovigerous females, a variety of size classes, and wide range indicate that *E. modestus* was well established in the estuary, including the Sacramento–San Joaquin Delta and its tributaries, by 2002. Bay Study numbers decreased and stabilized beginning in 2004, which may be because of a shift in *E. modestus* populations to areas that are under sampled, or not sampled at all, particularly upstream, where little to no monitoring for shrimp occurs. Suisun Marsh numbers, however, showed more fluctuation; the initial decline in 2004 was followed by peaks in 2006 and 2011, likely from higher freshwater outflow in these years.

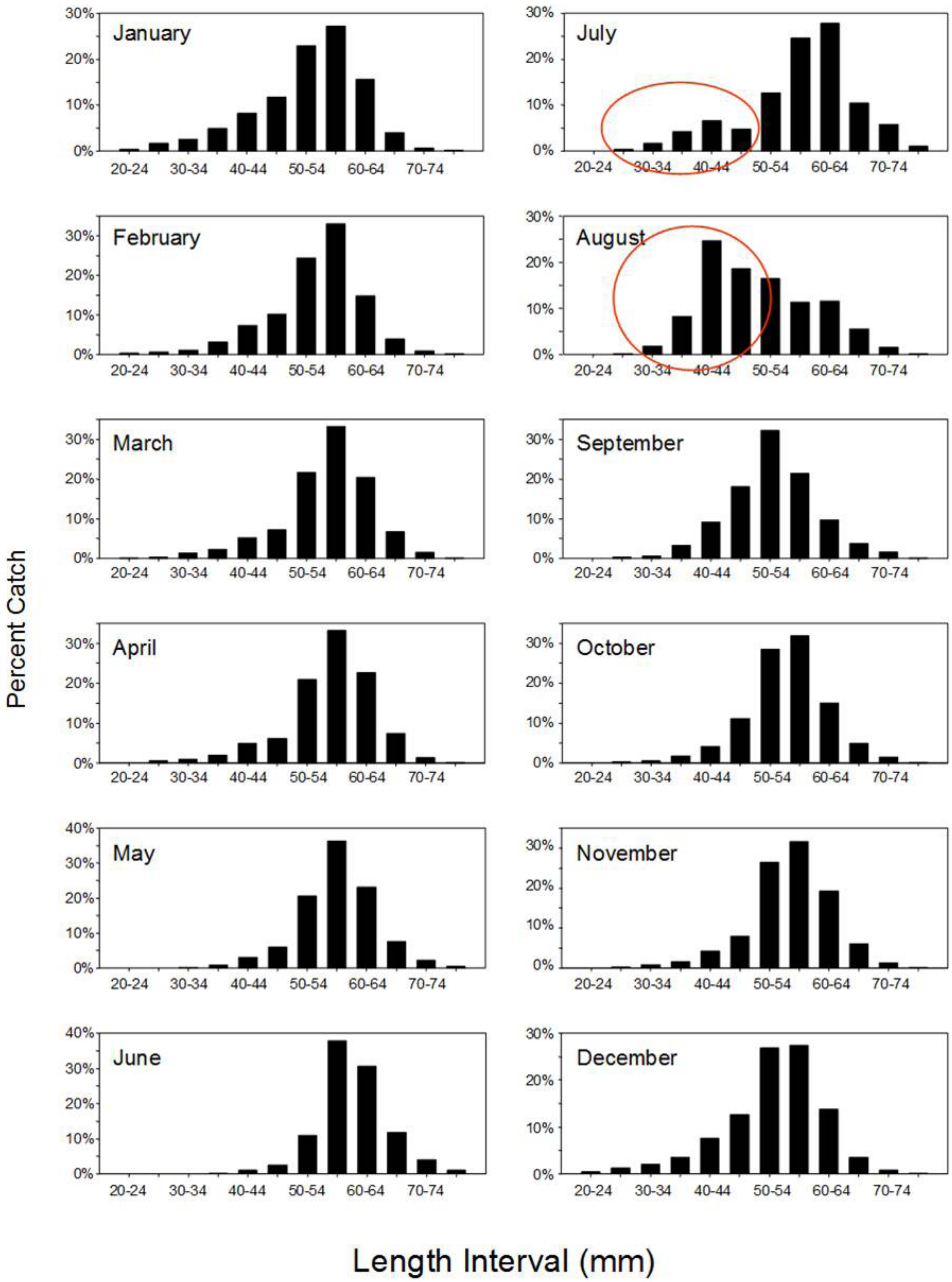

Figure 6 Length–frequency data for *E. modestus* from 2000 through 2011 (CDFW Bay Study)

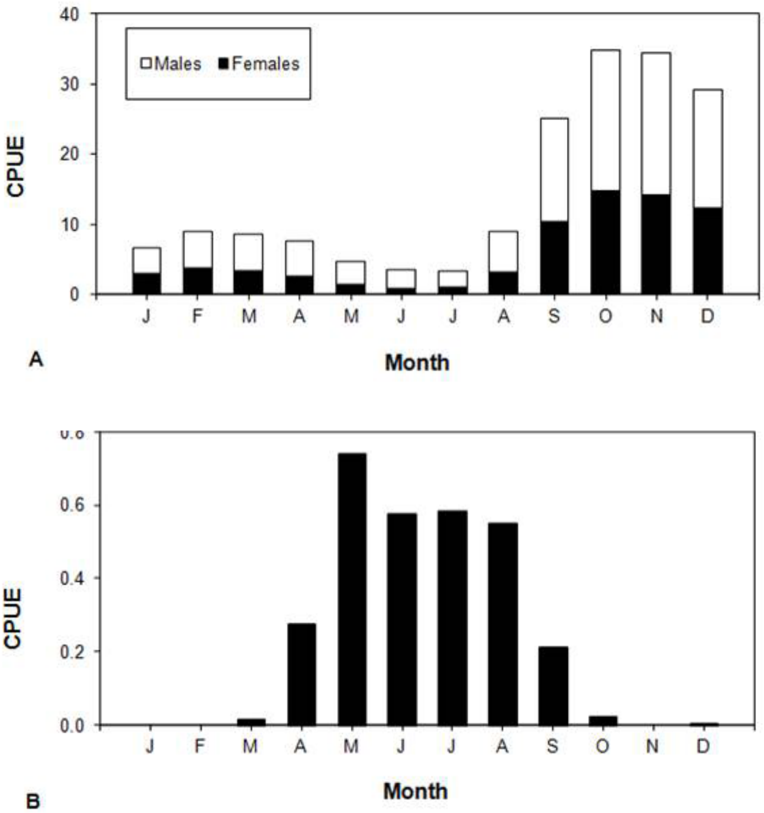

Figure 7 CDFW Bay Study average monthly CPUE of *E. modestus* for (A) males and non-ovigerous females, and (B) ovigerous females

Exopalaemon modestus can complete its life cycle in freshwater, with the main reproductive and nursery areas in freshwater, upstream of the Bay Study's sampling area. This is based on the relatively low numbers of ovigerous females and the dominance of males in the Bay Study's collections and the relatively high numbers of ovigerous females collected in upstream areas, especially Yolo Bypass and Liberty Island. Late-stage larvae and small juveniles were also collected in freshwater, with juvenile *E. modestus* most common upstream of Rio Vista on the Sacramento River and Stockton on the San Joaquin River. More targeted sampling is needed in freshwater and shallow habitats to determine the full range of where *E. modestus* reproduces and where young shrimp rear.

Less than 5% of the *E. modestus* collected by the Bay Study otter trawl were <40 mm, which was likely caused by the distributional patterns of juvenile shrimp and gear selectivity. We do not know the size of *E. modestus* that is most effectively sampled with the otter trawl; however, from *C. franciscorum* data (Hatfield 1985), it is probably larger than the 35 to 40 mm TL size range.

The reproductive season is relatively long, beginning in March and lasting until December. The peak of the season is in late spring and summer, as indicated by increased catches of ovigerous females, and the dominance of the current year class in August. In Korea, the reproductive season is shorter, with ovigerous females present from May through September, but there are multiple broods, and females are able to reproduce continually throughout the breeding season (Oh et al. 2002).

The largest specimen collected, an 82-mm female, was 22 mm larger than the maximum size given by Holthius (1980) but very close to the largest female reported by Oh et al. (2002) from its native range. (We estimated it to be 78 mm TL using the authors' measurement of 16.8 mm carapace length (CL) and our equation $TL=(CL+0.6772)/0.2225$.) This shrimp was also slightly larger than the maximum size of 76 mm TL from the Columbia River (Emmett et al. 2002). Female *E. modestus* were larger than males, consistent with the finding from Korea (Oh et al. 2002) that females grew faster and reached a larger size than males.

The causes for the apparent displacement of *P. macrodactylus* by *E. modestus* in the western Delta and lower Sacramento River are not clear; however, since *E. modestus* can complete its life cycle in freshwater, it is better adapted to conditions here. *P. macrodactylus* CPUE downstream of this area does not appear to be affected by *E. modestus*. Based on the current data, *E. modestus* is relatively rare downstream of the confluence of the Sacramento and San Joaquin rivers, possibly because of higher salinities in those areas. This displacement is also indicates potential species interactions should *E. modestus* become established in other freshwater regions outside of the estuary. More work is needed on the general life history and diet of *E. modestus* in the estuary to determine what factors affect or control *E. modestus* populations here.

E. modestus has also been documented as a prey item for several larger fishes in the estuary, particularly striped bass (Nobriga and Feyrer 2007, 2008). Palaemonid shrimp such as *E. modestus* play an important role in aquatic ecosystems, serving as both predators of meiofauna and prey for fish (Oh and Park 2000; Oh et al. 2002). In the estuary, the introduced *P. macrodactylus* preys primarily upon crustaceans, including mysid shrimp, amphipods, and copepods (Sitts and Knight 1979; Siegfried 1982). High densities of *E. modestus* could affect invertebrate prey abundance, creating competition for resources between *E. modestus* and native shrimps and fishes. If it preys upon mysid shrimp, it could be another factor that contributes to the decline of this important prey item for planktivores in the estuary.

The establishment of *E. modestus* in the estuary continues a long history of successful species introductions to the area. The range of *E. modestus* within California is likely to expand downstream to include tributaries of south and central San Francisco and San Pablo bays, as well as upstream to other non-tidal freshwater areas. Should *E. modestus* invade tributaries with *S. pacifica*, it could pose an additional threat to this endangered species. Because of its limited distribution, low fecundity, and specialized habitat needs, *S. pacifica* is particularly vulnerable to disturbances such as introduced species (Eng 1981; USFWS 1998). Because *E. modestus* is present in the south delta near the Clifton Court Forebay, it may be transported to southern California via the California Aqueduct. Several introduced freshwater fishes have been transported to southern California reservoirs in this manner and have established reproductive populations there (Matern and Fleming 1995). Deliberate human-mediated dispersal could also extend the range of *E. modestus* above physical barriers (e.g. weirs and dams) to lakes and reservoirs, and to other watersheds. In the Snake River (Columbia River Basin, WA), *E. modestus* has been caught upstream of several dams, likely transported there from human-mediated vectors such as commercial barge traffic (Haskell 2006).

Currently, *E. modestus* is not identified and enumerated by all monitoring surveys or special studies, so it may be difficult to determine areas with high abundance and, consequently, the largest effects. Many fisheries studies throughout the estuary and its watersheds are likely to collect *E. modestus*; adding it to the list of species enumerated would help track the spread and relative abundance of this potentially wide-ranging species.

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