

# Ancient fish and recent invaders: white sturgeon *Acipenser transmontanus* diet response to invasive-species-mediated changes in a benthic prey assemblage

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**ABSTRACT:** Invasive organisms can have significant impacts on native species, and the San Francisco Estuary (SFE), California, USA, is one of the world's most invaded estuaries. Decline of native white sturgeon *Acipenser transmontanus* abundance in the SFE has been acknowledged, but underlying mechanisms are poorly understood. Invasion by the overbite clam *Potamocorbula amurensis* has drastically altered the SFE benthic prey community, yet little is known about how this change has affected sturgeon diets. We investigated changes in the diet of white sturgeon following the overbite clam invasion and subsequent shift in the SFE benthic prey assemblage. Gut content analysis was used to compare white sturgeon prey composition and importance between the pre- and post-invasion periods. Additionally, stable isotope analysis was employed to estimate the assimilation of prey items to sturgeon biomass. Overbite clams dominated diets in the post-invasion period, accounting for 82 to 93% of total volume. Stable isotope analysis confirmed the importance of this prey item, although their assimilated contribution to sturgeon biomass was estimated to be less (70 to 83%) than gut contents indicated. The frequency of fish in white sturgeon guts increased in the post-invasion period, and isotope analysis indicated relatively large contributions of fish to sturgeon biomass (3.7 to 19%). The trophic adaptability of white sturgeon has allowed them to exploit this new prey source (overbite clam). Future conservation and restoration efforts must consider a potentially destabilized food web given the large importance of a single prey item.

**KEY WORDS:** Overbite clam · *Potamocorbula amurensis* · San Francisco Estuary · Stable isotope analysis · Gut content analysis · Food web · Mixing model · California

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## INTRODUCTION

The outcome of species introductions can be highly unpredictable. When alien species become established, there can be serious consequences for native organisms and ecological processes within the invaded ecosystem (Crooks 2002, Byrnes et al. 2007). Species invasions can directly affect native species through predation and competition, or indirectly

through alteration of food web structure and dynamics (Baxter et al. 2004, Kurlle et al. 2008) and evolutionary processes (Grosholz 2002). Further, species invasions often occur in ecosystems already stressed by multiple anthropogenic disturbances (MacDougall & Turkington 2005, Didham et al. 2007), making it difficult to distinguish among impacts and design effective recovery plans for native species and the ecosystems they inhabit.

The San Francisco Estuary (SFE) is the most invaded estuary on the west coast of the USA and possibly the world, averaging one new invasion every 14 wk from 1961 to 1995 (Cohen & Carlton 1998). One of the most ecologically relevant invaders, the overbite clam *Potamocorbula amurensis*, was discovered in 1986. By 1988, densities reached 10 000 m<sup>-2</sup>, and by 1990, the overbite clam was the dominant benthic species in the northern portion of the SFE, comprising up to 95% of living biomass (Carlton et al. 1990, Nichols et al. 1990, Peterson & Vayssières 2010). These bivalves are native to the western Pacific Ocean, and it is hypothesized they were introduced to the SFE via cargo ship ballast water (Carlton et al. 1990). Fish may also serve as biological mechanisms of dispersal within the SFE (Kogut 2008). Overbite clams are relatively small (<25 mm), can live and reproduce over a wide range of salinities (Nicolini & Penry 2000), and are able to filter feed on a wide range of planktonic organisms (Kimmerer et al. 1994). Since the arrival of the overbite clam, significant changes have been observed in the pre-invasion benthic macroinvertebrate and plankton assemblages (Nichols et al. 1990, Kimmerer et al. 1994). Additionally, Feyrer et al. (2003) documented direct and indirect dietary shifts in certain fish species mediated by changes in the taxonomic composition of the pelagic food web (sturgeon were not studied). Filter feeding by these clams has been linked to predation on early life stages of planktonic organisms (Kimmerer et al. 1994) and a decline in the standing stock of phytoplankton in the estuary (Alpine & Cloern 1992).

Concomitant with the establishment of the overbite clam has been an overall decline in native SFE white sturgeon *Acipenser transmontanus*; however, this decline remains unexplained (Schaffter & Kohlhorst 1999). Sturgeon (Pisces: Acipenseridae) are a long-lived, ichthyo-megafauna found throughout many rivers of the Northern Hemisphere. Sturgeon represent a unique and commercially valuable group of ancient fishes, and their populations are threatened across the globe due to a combination of harvest and habitat impacts (Rochard et al. 1990, Birnstein 1993, Boreman 1997, Pikitch et al. 2005). Similar to other sturgeon species, white sturgeon exhibit life history characteristics that make their populations especially vulnerable to overexploitation, including long life, delayed maturation, and irregular reproduction (Helfman et al. 1997). Additionally, white sturgeon are exposed to threats affecting other species in the SFE and freshwater spawning tributaries, including habitat loss, altered flow and temperature regimes, overfishing, and exposure to various potential contami-

nants. Despite serious concerns about the persistence of sturgeon populations, many aspects of their biology remain unknown, which complicates attempts to understand abundance declines (Secor et al. 2002). Understanding white sturgeon diet and how it may be impacted by invasive species like the overbite clam is essential to inform effective sturgeon management actions.

As benthic predators, white sturgeon may have experienced significant diet shifts associated with the overbite clam invasion. Indeed, overbite clams have been observed in the stomachs of white sturgeon (Kogut 2008); however, comprehensive diet information from the post-invasion period has not been reported, and recent evidence suggests that the clams may be largely unassimilated. Kogut (2008) observed overbite clams defecated undigested and even live from wild-captured SFE white sturgeon, and Richman & Lovvorn (2004) reported that the overbite clam was more resistant to crushing than native SFE clams in a foraging study of the diving duck *Aythya affinis*.

We combined white sturgeon stomach content data and stable isotope analysis of sturgeon tissue and potential prey items to quantify how SFE invasion by the overbite clam has influenced sturgeon feeding ecology. Specifically, we compared white sturgeon gut contents from the pre- and post-invasion period to determine how prey composition and importance have responded to changes in benthic assemblage structure. We then combined stable isotope ratios of white sturgeon and their prey from the post-invasion period in a mixing model to estimate the proportional contribution of overbite clams and other potential prey to sturgeon biomass to determine whether dietary proportions observed in stomachs match assimilation into tissue. Combining these techniques has been shown to provide robust estimates of prey importance (Polito et al. 2011, Spitz et al. 2013). Our results provide critical information on the trophic ecology of a vulnerable sturgeon species, supporting restoration efforts as well as furthering our understanding of how invasive species influence estuarine food webs.

## MATERIALS AND METHODS

### Study site

The SFE is the largest estuary on the Pacific coast of North America, draining over 40% of the California landscape and receiving runoff from a 163 000 km<sup>2</sup> watershed. The SFE extends from the limit of

tidal influence on the Sacramento (near the city of Sacramento) and San Joaquin Rivers (near Vernalis) to the Golden Gate Bridge (Fig. 1). Freshwater inputs are primarily from the San Joaquin and Sacramento Rivers that come together to form the Sacramento–San Joaquin Delta, covering 3000 km<sup>2</sup> of freshwater tidal habitat. From this delta, water flows into Suisun Bay, which is bordered on its north side by Suisun Marsh, the largest contiguous wetland along the Pacific coast of the western USA. Suisun Bay is shallow, turbid, and, depending on outflow, partially to well mixed with a strong horizontal salinity gradient (Cole & Cloern 1984). From Suisun Bay, water flows through Carquinez Strait, a deep and narrow channel, into San Pablo Bay. From Carquinez Strait through San Pablo Bay, salinities are variable, ranging from 15‰ during a typical summer to 30‰ during fall (Conomos et al. 1985). San Pablo Bay is a mostly shallow, circular bay with a muddy bottom and a deep channel in the south, dredged for shipping (Jaffe et al. 2007). The Central Bay has the greatest mean depth, is the most saline part of the SFE, and is the point of entry for seawater (Conomos

et al. 1985, Kimmerer 2004). The largest part of the SFE is the South Bay, which demonstrates a variety of environmental conditions. At the northern part of the bay, salinities range from 18‰ during a typical summer to 30‰ during fall, and the water column is generally well mixed (Conomos et al. 1985). The southern end of the South Bay is influenced by freshwater discharge from local creeks and year-round municipal sewage discharge (Conomos et al. 1985, Walters et al. 1985).

The SFE has been subjected to intense modification over the last 170 yr in response to growth in municipal, agricultural, and industrial practices. By 1900, the SFE had already undergone major changes, including alien species invasions, pollution from hydraulic mining debris, agricultural, industrial, and municipal runoff, marshland conversion, and overfishing (Nichols et al. 1986). A significant amount of freshwater is diverted from the SFE for agricultural, municipal, and industrial uses altering flow, depth, surface area, and water temperature, clarity, and quality. These anthropogenic modifications have been implicated in facilitating invasion of the SFE by a variety of species

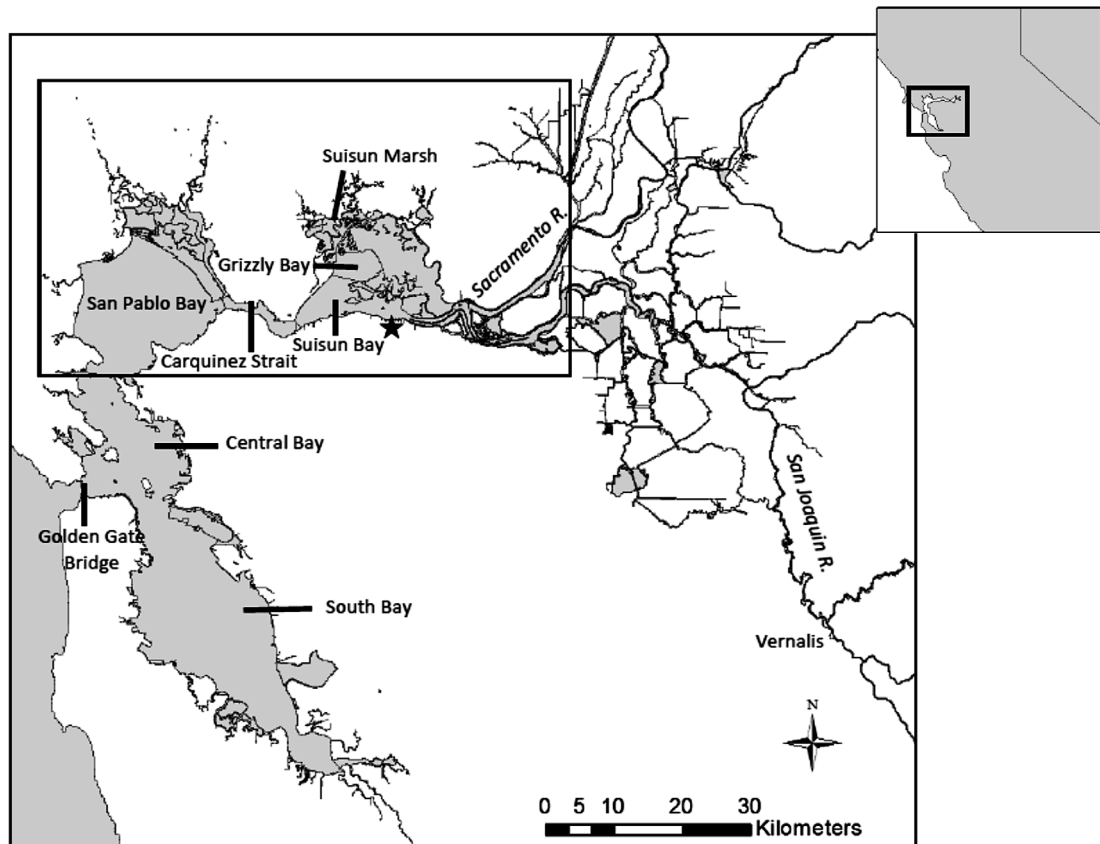


Fig. 1. San Francisco Estuary (SFE) in California (USA) and the study region within the SFE. The box indicates the general location where most white sturgeon *Acipenser transmontanus* were captured, and the star indicates the location of the sturgeon derby where collection occurred in 2012 and 2013

(Cohen & Carlton 1998) and have had a tremendous impact on valuable recreational and commercial fisheries (Nichols et al. 1986).

Prior to the *Potamocorbula amurensis* invasion, the benthic assemblage was composed of both native and invasive species, and the structure of the assemblage exhibited a shift in response to variation in freshwater outflow (Nichols et al. 1990). In the first few years following the invasion, the previous patterns of assemblage variation were disrupted and *P. amurensis* became increasingly dominant in the benthic assemblage. Peterson & Vayssières (2010) analyzed an expanded data set that included greater spatial coverage over a longer time period after the invasion. This study revealed that wet–dry patterns were present in the benthic assemblage but that assemblage composition in these periods was significantly different than it was prior to the *P. amurensis* invasion. The dominance of *P. amurensis* also varied among sampling stations along a salinity gradient (fresh to marine), with the greatest abundance at intermediate salinities (Peterson & Vayssières 2010).

### Study population

White sturgeon are native to the Pacific coast of North America and range from Alaska (USA) to northern Baja California (Mexico) (Ruiz-Campos et al. 2011), where they are popular targets of commercial and recreational fisheries. This species primarily resides in estuaries and uses freshwater rivers for reproduction and juvenile rearing. However, large-scale marine movements between estuaries have been documented (Welch et al. 2006). Commercial white sturgeon fishing in the SFE began as early as the 1860s, peaking at 1.65 million pounds and closing in 1901, when catches dropped to 0.02 million pounds (California Department of Fish and Wildlife [CDFW] 2001). The fishery reopened in 1909; however, low catch closed the fishery again in 1917, which remained closed until 1954 when it was reopened for sport fishing with a minimum size restriction and catch per year limit. During the 1980s, harvest increased 40% over the previous 2 decades, and in 1990, the CDFW implemented a maximum size limit (CDFW 2001), with size limits changing in recent years.

White sturgeon can be found year round throughout the SFE, congregating most heavily in San Pablo and Suisun Bays (Kohlhorst et al. 1991; Fig. 1). When sexually mature, white sturgeon appear to move upstream in response to freshwater flow and salinity changes to spawn, primarily in the Sacramento River

between late winter and spring. Spawning in the San Joaquin River appears to be highly correlated with river discharge during the March–May period (Jackson & Van Eenennaam 2013). It appears that white sturgeon spend most of their adult lives in the SFE: as of 1991, less than 1% of fish tagged in the SFE had been recovered in other river systems (Kohlhorst et al. 1991).

### Sturgeon stomach collection

All sturgeon stomachs were collected from angler-harvested fish during 3 different periods. From April of 1965 through November of 1967, collections were made year-round by party boat skippers in northern San Francisco Bay, including San Pablo Bay, Carquinez Strait, and Suisun Bay (Fig. 1; McKechnie & Fenner 1971). The entire alimentary tract was removed and frozen. Contents were identified from the esophagus and stomach sections by staff from the CDFW (McKechnie & Fenner 1971). A database was prepared from the original records of that study for use in the current analysis. The size limits for recreationally caught sturgeon changed multiple times between 1965 and 2013. To avoid bias from potential size-based diet variation, the gut-content analysis was limited to fish of 117 to 168 cm in total length (TL) to exclude sizes that were outside the legal limit for some of the sampling periods. From September 2001 through September 2003, party boat skippers collected stomachs year-round from angler catches in San Pablo and Suisun Bays (Fig. 1). The entire alimentary tract was collected and placed in a cooler with ice during transport to the lab. In 2001, a portion of the samples was fixed in formalin for 48 h and then preserved in 70% ethanol. Some samples were stored in formalin until 2013, when they were transferred to ethanol. Upon arrival at the lab, samples collected in 2002–2003 were kept frozen until analysis was performed in 2013. In February and October 2012 and February 2013, samples were acquired from catches at sturgeon tournaments. Most sturgeon were caught in San Pablo Bay, Carquinez Strait, Suisun Bay, and the lower Sacramento River delta. The esophagi and stomachs were collected and preserved in formalin on site and transferred to 85% ethanol in the lab; some 2013 samples were placed in 85% ethanol on site when formalin was not available.

For all samples collected from 2001 to 2013, esophagus and stomach (hereafter referred to as gut) contents were identified in the laboratory with a 10× dissecting microscope to the lowest feasible taxonomic

level, enumerated, and measured volumetrically by water displacement in a graduated cylinder to the nearest 0.1 ml.

### Isotope sample collection

Data for the isotope mixing model analysis were obtained from an earlier study by Stewart et al. (2004). White sturgeon tissue and potential prey items were collected for analysis of carbon and nitrogen stable isotope ratios during fall 1999 and early winter of 2000 and 2001 (Stewart et al. 2004). This constrained time period limited the influence of temporal and spatial variation in isotope ratios when migratory species would have been in the SFE for weeks to months. The isotope collections were part of a separate study of contaminants, and although these samples were collected over a shorter time period than stomachs, stable isotopes integrate feeding information over relatively long time periods and should provide reliable information on sturgeon feeding history in the estuary (Peterson & Fry 1987, Vander Zanden et al. 1997). Muscle tissue of individual fish and crabs was removed for stable isotope analysis. Soft tissues of *P. amurensis* were removed and separated from shell material. Shrimp and amphipods were combined into composite samples and analyzed whole. For a complete description of isotope collection and processing, see Stewart et al. (2004).

All stable isotope values (‰) are reported as deviations relative to standards (delta notation):

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 \quad (1)$$

where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ . The standards for carbon and nitrogen were Pee Dee Belemnite limestone and atmospheric nitrogen, respectively.

### Diet analysis

For each time period, gut contents were quantified by volumetric proportion and frequency of occurrence of each prey item in the combined esophagus and stomach sections. Due to incomplete metadata that prevented linking prey items to individual fish, only 1965–1967 and 2012–2013 data were quantified by frequency of occurrence. For items missing counts or volume in the 1965–1967 data, estimates were calculated by using a regression of prey number and volume that incorporated data from all years. Volume measurements were missing from 9% of observa-

tions, and counts were missing from 32% of observations. Many prey species were only observed rarely. Thus prey items were aggregated into broader taxonomic classifications for analysis (Table 1). To test for changes in white sturgeon diets between the pre- and post-invasion period, a chi-squared goodness of fit test was performed where the volumetric proportions in the pre-invasion period were used to calculate expected values. Two tests were performed where the pre-invasion diet was compared against each post-invasion sampling period.

To describe the degree of specialization in the sturgeon diets, niche breadth was calculated for each of the 3 time periods with Levins' measure (Levins 1968):

$$B_j = \frac{1}{\sum p_{ij}^2} \quad (2)$$

where  $B_j$  is the niche breadth in time period  $j$ , and  $p_{ij}$  is the volumetric proportion of prey item  $i$  in time period  $j$ . Values of  $B_j$  range from 1 (most specialized diet) to  $n$  (least specialized diet), where  $n$  is the number of prey categories in the diet during each time period. Time periods with a wide niche breadth (large Levin's measure) indicate that sturgeon employed a more generalist strategy, whereas time periods with a narrow niche breadth indicate a more specialized strategy.

### Stable isotope analysis

The contribution of major prey categories to white sturgeon biomass was estimated using stable isotope ratios and the Bayesian mixing model MixSIR (Moore & Semmens 2008). We chose this mixing model because it accounts for uncertainty in the isotope values of prey and predator as well as uncertainty in tissue–diet fractionation. Not all prey items identified in guts were included in the model because the isotope data were not collected specifically to compare with stomach contents. However, the most abundant prey categories found in the diet were represented by individual species in the mixing model. Tissue–diet fractionation values specific to white sturgeon were not available; therefore, we used mean fractionation values reported by Post (2002) that incorporated a wide range of aquatic consumers from copepods to polar bears *Ursus maritimus*. The value for carbon was 0.4 (SD = 1.3) and the value for nitrogen was 3.4 (SD = 1.0).

Prior to running the mixing model, multi-response permutation procedures (MRPPs) were employed to determine whether there were significant differences between prey taxa based on their  $\delta^{13}\text{C}$  and



Table 1. All taxa identified from each prey category during the pre- and post-invasion periods. Categories are listed in order of their rank in total volumetric proportion

Prey category	Taxa identified	Pre-invasion period	Post-invasion period
Clams	<i>Gemma gemma</i> <sup>a</sup>	X	
	<i>Macoma</i> sp. <sup>b</sup>	X	
	<i>Tapes semidecussata</i> <sup>a</sup>	X	
	<i>Potamocorbula amurensis</i> <sup>a</sup>		X
	<i>Corbicula fluminea</i> <sup>a</sup>		X
Fish eggs	<i>Clupea pallasii</i> <sup>b</sup>	X	
Fish	<i>Morone saxatilis</i> <sup>a</sup>	X	
	<i>Platichthys stellatus</i> <sup>b</sup>	X	
	<i>Clupea pallasii</i> <sup>b</sup>	X	
	<i>Engraulis mordax</i> <sup>b</sup>	X	
	<i>Porichthys notatus</i> <sup>b</sup>	X	
	<i>Leptocottus armatus</i> <sup>b</sup>	X	
	<i>Menidia beryllina</i> <sup>a</sup>		X
	Gobiidae <sup>a</sup>	X	X
	Cottidae	X	X
	Barnacles	<i>Balanus</i> spp. <sup>a</sup>	X
Crabs	<i>Rhithropanopeus harrisi</i> <sup>a</sup>	X	X
	<i>Metacarcinus magister</i> <sup>b</sup>	X	
Shrimp	<i>Palaemon macrodactylus</i> <sup>a</sup>	X	X
	<i>Crangon</i> spp. <sup>b</sup>	X	X
	<i>Neomysis</i> spp. <sup>c</sup>	X	
Crayfish	Astacidae		X
Isopods	<i>Synidotea</i> sp. <sup>a</sup>	X	X
Gastropods	Opisthobranchia		X
	Physidae		X
Polychaetes	<i>Nereis</i> sp. <sup>c</sup>	X	
Mussels	<i>Mytilus</i> sp. <sup>c</sup>	X	
Amphipods	Gammaridae		X
Nematodes	Unidentified	X	

<sup>a</sup>Introduced; <sup>b</sup>Native; <sup>c</sup>Native and introduced species within this taxonomic classification

$\delta^{15}\text{N}$  values. This technique is analogous to multivariate analysis of variance but instead uses Euclidean distance among and within pre-defined groupings in isotope-space to determine the significance of groupings. If differences between groups were not significant, they were combined in the mixing model.

## RESULTS

### Gut contents

Ten taxonomic prey categories (Table 1) were identified from 254 guts in the pre-invasion period, with 14% of guts having no identifiable contents. Several native and invasive clam species (*Bivalvia*) and Pacific herring *Clupea pallasii* eggs were the dominant prey items in sturgeon guts, comprising 30% and 27% of the total volume, respectively

(Fig. 2). Ray-finned fish (Actinopterygii) and barnacles (Cirripedia) were the only other prey items that comprised  $\geq 10\%$  of the total diet volume (Fig. 2). Other prey items comprised  $< 5\%$  of the total volume and included isopods (Isopoda), shrimp (Pleocyemata), gastropods (Gastropoda), mussels (Mytilidae), amphipods (Amphipoda), and nematodes (Fig. 2). Clams were also the most frequently encountered prey items during this period (58% of all stomachs) followed by shrimp, isopods, and crabs. No other prey item was found in more than 10% of stomachs examined (Fig. 3).

In the post-invasion period (2001–2013), 8 prey categories were identified from approximately 81 stomachs with  $\sim 10\%$  empty (Table 1). Incomplete metadata for some samples collected from party boats during 2001–2003 did not allow us to get an exact number of stomachs examined. Gut contents in the post-invasion period were dominated by clams that accounted for 93% and 82% of total prey volume during 2001–2003 and 2012–2013, respectively (Fig. 2). This represented a 310% and 270% increase in the volume of clams in sturgeon diets relative to the pre-invasion period. The vast majority of these clams were the overbite clam (96%), with the

remainder composed of the Asian clam *Corbicula fluminea*, another introduced clam primarily found in fresh water (Table 1). None of the clam species identified in the pre-invasion diets was found in post-invasion diets regardless of origin (native or introduced; Table 1). In the 2001–2003 period, no other prey item accounted for more than 3% of the total prey volume (Fig. 2). In the 2012–2013 period, crayfish (Astacidea) accounted for 11% of the diet, and no other prey item accounted for  $> 3\%$ .

Niche breadth decreased from 4.8 in the pre-invasion period to 1.2 during 2001–2003 and 1.5 during 2012–2013. A chi-squared test comparing volumetric proportions of prey categories between the pre-invasion and the first post-invasion period (2001–2003) yielded a significant difference ( $\chi^2 = 3162$ ,  $p < 0.001$ ), as did a test for differences between the pre-invasion and the second post-invasion period ( $\chi^2 = 1495$ ,  $p < 0.001$ ). The frequency of prey occurrence in white

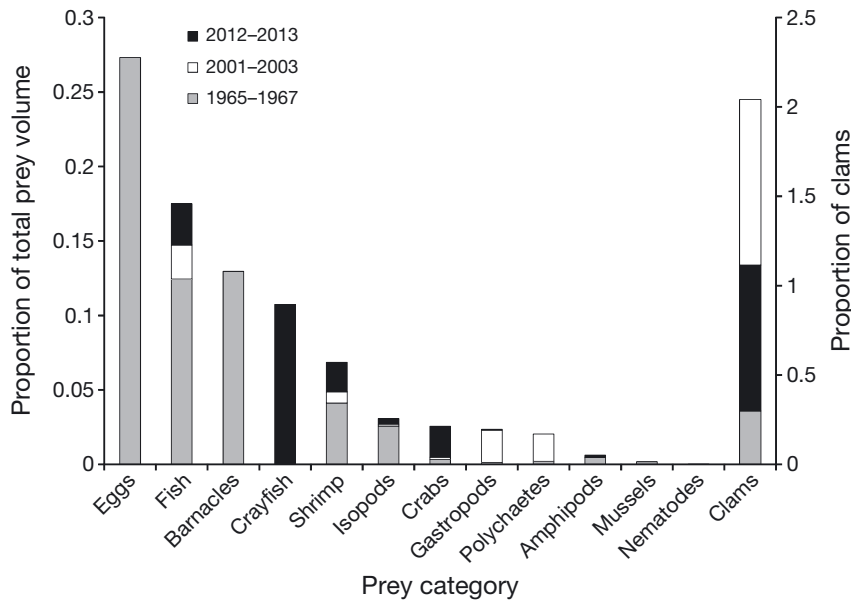


Fig. 2. Volumetric proportion of prey items identified in 254 white sturgeon *Acipenser transmontanus* guts during the pre-invasion period (1965–1967) and approximately 81 guts during the post-invasion periods (2001–2003, 2012–2013). Values for clams appear on the secondary y-axis due to differences in scale between the volumes of clams observed relative to other prey categories. The species composition of each category is listed in Table 1

frequency of occurrence. However, differences among prey categories varied widely. The largest change in frequency was the 22% increase in clams in the post-invasion period. Fish increased in frequency by 17% following the invasion. The frequency of isopods, herring eggs, and barnacles fell by 13 to 16%. All other changes in prey item frequency were  $\leq 10\%$  (Fig. 3).

### Isotope results

Stable isotope ratios were obtained for 8 taxa representing 6 of the frequently encountered prey categories in sturgeon guts (Fig. 4). Individual taxa included shrimp in the genus *Crangon*, Dungeness crab *Metacarcinus magister*, 2 amphipod crustacean genera (*Ampelisca* and *Corophium*), isopods, overbite clams, and 2 benthic fish, yellowfin goby *Acanthogobius flavimanus* and starry flounder *Platichthys stellatus*.

Statistical comparisons of isotope ratios for *Crangon* spp. and *M. magister* with MRPP indicated no significant difference ( $A < 0.001$ ,  $p = 0.406$ ; the  $A$  parameter indicates how much variance in distance between samples is explained by group identity).

Results from the mixing model based on data from 1999 through 2001 indicated a 95% probability that the overbite clam contributed more than 70.3% but less than 83% to sturgeon biomass, i.e. less than their observed proportion in sturgeon guts for the years 2001–2003 and 2012–2013 (0.82–0.93). Starry flounder consistently provided the next highest contribution (percentage), whereas only small contributions were found for all other prey taxa used in the model (Table 2).

### DISCUSSION

White sturgeon gut contents changed significantly following alteration of prey community structure by the overbite clam invasion. Overbite clams appeared to be readily consumed by sturgeon and made up a large volumetric proportion of their diet (0.82–0.93). Analysis of stable isotope ratios indicated that this prey item likely contributed slightly less to sturgeon biomass (70–83%) than suggested by gut contents determined by volumetric analysis. The difference

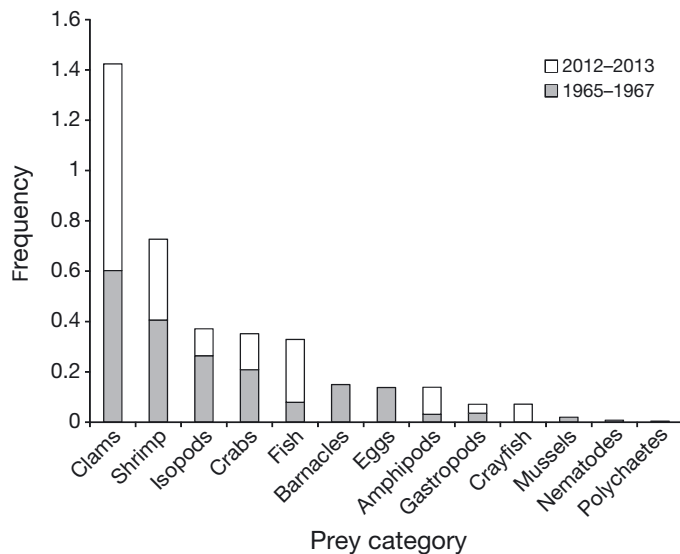


Fig. 3. Frequency of occurrence for prey categories identified in 254 white sturgeon *Acipenser transmontanus* guts during the pre-invasion period (1965–1967) and 28 guts during the post-invasion period (2012–2013). Metadata for stomachs sampled during 2001–2003 were incomplete and frequency could not be accurately calculated

sturgeon diets also differed significantly between the pre- and post-invasion period ( $\chi^2 = 38.48$ ,  $p < 0.001$ ). As described above, only the 2012–2013 data set was available to compare with the pre-invasion data for

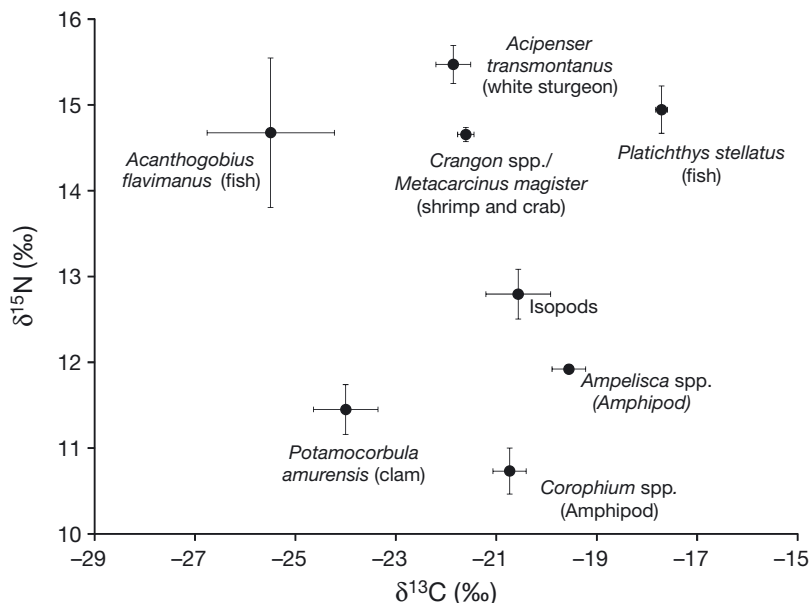


Fig. 4. Bi-plot of mean stable isotope values with standard errors for white sturgeon *Acipenser transmontanus* and all potential prey items used in the mixing model. The prey category to which each species belongs is listed in parentheses

Table 2. Proportional contribution of each prey item to white sturgeon *Acipenser transmontanus* biomass at 5 cumulative probability levels from the stable isotope mixing model

Prey item	0.05	0.25	0.50	0.75	0.95
<i>Crangon</i> spp./ <i>Metacarcinus magister</i> (shrimps/crab)	0.001	0.006	0.013	0.026	0.055
<i>Ampelisca</i> spp. (amphipods)	0.001	0.009	0.020	0.039	0.080
<i>Corophium</i> spp. (amphipods)	0.001	0.006	0.014	0.027	0.071
Isopoda (isopod)	0.001	0.007	0.016	0.033	0.076
<i>Potamocorbula amurensis</i> (clam)	0.703	0.746	0.770	0.796	0.830
<i>Acanthogobius flavimanus</i> (yellowfin goby)	0.001	0.003	0.008	0.016	0.037
<i>Platicthys stellatus</i> (starry flounder)	0.037	0.097	0.127	0.152	0.190

between gut content and biomass assimilation indicated by isotope ratios is likely explained by the percent content of clam shells or other material that is not easily digested but is included in volumetric assessment of prey contributions. Depending on species and reproductive condition, soft tissues of clams can account for anywhere from 10 to 95% of the total volume of the clam (including shells). Additionally, tissue diet fractionation values specific to sturgeon were not available, and using values for other species may have contributed to the observed variation. Mismatches between stomach contents and isotope-based estimates of assimilation have been reported for other aquatic species that consume large volumes of material that is relatively difficult to digest (Mantel

et al. 2004, Winemiller et al. 2007). Kogut (2008) performed observations on live sturgeon collected in the SFE and found that overbite clams were defecated live, supporting our finding that gut contents alone may not accurately represent the strength of trophic links between sturgeon and potential prey and should be verified by additional tools such as stable isotope analysis. Another potential explanation for the discrepancy in gut contents and stable isotope ratios is that the white sturgeon gut content study excluded analysis of the spiral valve intestine, the primary section for digestion and absorption (Buddington 1983). It is important to note that intestinal contents are often not readily identifiable. Increased availability of genetic tools may help to identify intestinal contents in future studies, further adding to our understanding of trophic linkages. Nevertheless, both methods of estimating prey importance indicate that white sturgeon are utilizing the overbite clam as a food source.

Optimal foraging theory is used to predict components of an animal's diet, most often from the viewpoint of maximizing energy intake per unit time, although nitrogen content, essential amino acids, indigestible or toxic components, ease of absorption, and degree of food crypsis are all important during diet choice (Taghon 1981). In a study of Lakes Michigan and Huron, lake whitefish *Coregonus clupeaformis*

diets shifted from non-mollusk macroinvertebrates to mollusks after lake invasion by a dreissenid mussel (Pothoven & Madenjian 2008). Even though total consumption was unchanged and the proportion of maximum consumption increased, lake whitefish weight at age was at least 38% lower during post-invasion than pre-invasion; furthermore, whitefish would have to increase consumption by up to 122% to achieve pre-invasion growth rates under their post-invasion diet regime. While our study does not demonstrate a significant response, our results suggest that a potential reduction in white sturgeon growth rates is possible due to the invasion and subsequent diet shift for the species. This potential effect on white sturgeon energy intake and growth rate should be studied further.



Changes in white sturgeon gut contents between the pre- and post-invasion period reflected changes in benthic community structure following the overbite clam invasion and its dominance in the benthic community. Sturgeon diets became more specialized following the clam invasion, whereby niche breadth decreased from 4.8 in the pre-invasion period to 1.2 during 2001–2003 and 1.5 during 2012–2013. The pre-invasion period included a greater number of stomachs examined, which may have influenced this result given the well known relationship between abundance and species richness (Preston 1962); however, similar numbers of prey categories were identified in the pre- and post-invasion period (10 vs. 8, respectively). Additionally, none of the clam species identified in the pre-invasion diets was found in post-invasion diets regardless of origin (native or introduced). However, some clams were too degraded to identify, and if other species occurred at a low frequency, they may not have been detected. *Potamocorbula amurensis* is now numerically dominant in many areas of the SFE, and it is likely that a reduction in the evenness component of benthic diversity affected the reduction in niche breadth more than species richness. Indeed, Peterson & Vayssières (2010) reported that richness either increased or stayed the same at most long-term SFE monitoring sites after the invasion.

Modeling stable isotope ratios of white sturgeon and their prey revealed that starry flounder was the second-most important contributor to sturgeon biomass (median contribution = 12.7%). This species was not observed in gut contents during the post-invasion period; however, most fish were difficult to identify to species due to extensive digestion. Additionally, species within similar trophic guilds often have indistinguishable isotopic signatures (Phillips et al. 2005). Thus, the importance of starry flounder may represent other trophically similar species. The other benthic fish in the mixing model (yellowfin goby), also a relatively recent SFE invader, only had the potential for small contributions, but this prey species had a more depleted  $\delta^{13}\text{C}$ , indicating that this species was found in habitats with a larger freshwater influence (Stewart et al. 2004). In contrast, the importance of starry flounder may reflect white sturgeon predominantly feeding in higher-salinity habitats of the SFE. Piscivory has frequently been observed in other sturgeon species, suggesting that this is not an uncommon feeding strategy (Gerrity et al. 2006, Grohs et al. 2009). White sturgeon can travel between riverine, estuarine, and marine habitats, and trophic adaptability is essential for this type of

life history. Alteration of the lower food web by the overbite clam has resulted in the decline or altered distributions of certain fish species in the SFE (Feyrer et al. 2003, Kimmerer 2006); however, it remains unknown whether shifts in fish abundance may have indirectly affected white sturgeon diets. Clearly, additional research on this topic is needed given the results presented here.

The mixing model yielded small estimates for crabs and shrimp despite being found in similar proportions to fish in white sturgeon diets. Fish comprised only a small percentage of total prey volume observed (~3%), yet the stable isotope model indicated that they made relatively large contributions to white sturgeon biomass (median = 12.7%). Fish lack significant external protection (e.g. hard bodies), which may allow them to be more easily digested and assimilated than invertebrates such as crabs, shrimp, and bivalves. Fish and other soft-bodied prey have been shown to be digested more rapidly than crustaceans in studies of fish and *in vitro* trials (Jackson et al. 1987, Hopkins & Larson 1990), and gut-content analysis may have been biased toward identification of hard-bodied prey items. Isopods and amphipods were other categories of hard-bodied prey items encountered in sturgeon guts, yet estimates of prey importance from the isotope model and volumetric proportions in guts were similarly low.

Employing a combination of gut contents and stable isotope analysis provided considerable insight into how white sturgeon diets have changed since the overbite clam invasion. However, both methods have limitations, which should be noted when interpreting these results. Stomach content analysis provides only a snapshot of white sturgeon diets, and seasonal or discrete feeding events can skew the perception of prey item importance (Bowen 1996). For example, Pacific herring eggs comprised a large volume of white sturgeon diets in the pre-invasion period, yet this item is only available to sturgeon for a brief period during the year, as reflected in the low frequency of occurrence (Haegele & Schweigert 1985). Additionally, the volume of prey in predator guts may not represent prey importance due to differential assimilation. Stable isotopes provide a good estimate of prey that is assimilated into predator tissues; however, mixing models are limited by the taxa available for analysis and estimates of tissue–diet fractionation (Vanderklift & Ponsard 2003). Overlap of isotope ratios among different prey categories can result in poor taxonomic resolution and uninformative estimates of prey contributions (Phillips et al. 2005). Bond & Diamond (2011) found that Bayesian

mixing models can also be sensitive to tissue–diet fractionation values. However, concordance between isotope-based and diet-based estimates suggests that the values we selected here were appropriate. Additionally, all fish were sampled by hook and line, which may have selected for individuals with a certain degree of specialization that may not be representative of the entire population. All of these issues were represented to different degrees in our data set, but, by using a combination of these analyses, we were able to make strong conclusions about the role of overbite clams in white sturgeon diets during the post-invasion period. Combining multiple methods of analysis is effective for elucidating trophic relationships among other species as well (Polito et al. 2011, Spitz et al. 2013).

The data presented here suggest that consequences of the invasion and establishment of the overbite clam on food availability for white sturgeon may be minimal because they readily consume and assimilate this species. However, the overbite clam invasion may have other indirect consequences for white sturgeon. Since relatively high numbers of the clams are not digested, white sturgeon may have to expend more energy on average to acquire the same caloric value as with more easily digested prey items. Furthermore, this bivalve readily accumulates the trace element selenium (Schlekat et al. 2000, Stewart et al. 2004, 2013, Lee et al. 2006) to levels that have been shown to result in reproductive toxicity in surrogate species (Stewart et al. 2013). Greater clam consumption in the post-invasion period could result in reduced juvenile growth and increased reproductive damage in sturgeon (Linville 2006) and may pose risks to their predators (humans). Stewart et al. (2004) reported greater selenium concentrations in trophic pathways leading to SFE white sturgeon relative to other top predators. Future studies of the trophic transfer of selenium and other contaminants can benefit by including the strength of trophic interactions between sturgeon and their prey presented here.

*P. amurensis* is now a major trophic pathway in the SFE, and our data confirm that it has become the dominant prey item supporting the white sturgeon population. Although there has been a large shift in the composition of the benthic prey assemblage, the trophic adaptability of white sturgeon likely allowed them to readily exploit this new prey resource. Species within food webs may be deleted and replaced at various spatiotemporal scales while the web structure remains stable (de Ruiter et al. 2005). However, theoretical work has suggested that food webs become less stable as species richness decreases

(MacArthur 1955, May 1972), and lower niche breadth following the *P. amurensis* invasion may indicate that food webs including sturgeon are now less stable. Given the large importance of one numerically dominant prey item (*P. amurensis*) to white sturgeon, its potential to transfer toxic substances, and the potentially reduced biomass contribution it provides, conservation and restoration efforts will need to recognize the potential for a destabilized and impaired food web when managing for this valuable fishery.

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