

Do sturgeon limit burrowing shrimp populations in Pacific Northwest Estuaries?

Brett R. Dumbauld · David L. Holden ·
Olaf P. Langness

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Abstract Green sturgeon, *Acipenser medirostris*, and white sturgeon, *Acipenser transmontanus*, are frequent inhabitants of coastal estuaries from northern California, USA to British Columbia, Canada. An analysis of stomach contents from 95 green sturgeon and six white sturgeon commercially landed in Willapa Bay, Grays Harbor, and the Columbia River estuary during 2000–2005 revealed that 17–97% had empty stomachs, but those fish with items in their guts fed predominantly on benthic prey items and fish. Burrowing thalassinid shrimp (mostly *Neotrypaea californiensis*) were important food items for both white and especially for green sturgeon taken in Willapa Bay, Washington during summer 2003, where they represented 51% of the biomass ingested (84.9% IRI). Small pits observed in intertidal areas dominated by these shrimp, are likely made by these sturgeon and

we present evidence from exclusion studies and field observation that the predator making the pits can have a significant cumulative negative effect on burrowing shrimp density. These burrowing shrimp present a threat to the aquaculture industry in Washington State due to their ability to de-stabilize the substrate on which shellfish are grown. Despite an active burrowing shrimp control program in these estuaries, it seems unlikely that current burrowing shrimp abundance and availability as food is a limiting factor for threatened green sturgeon stocks. However, these large predators may have performed an important top down control function on shrimp populations in the past when they were more abundant.

Keywords Endangered · Predation · Oyster · *Neotrypaea* · Willapa Bay · *Acipenser*

B. R. Dumbauld (✉)
US Department of Agriculture,
Agricultural Research Service,
2030 S.E. Marine Science Drive,
Newport, OR 97365, USA
e-mail: brett.dumbauld@oregonstate.edu

D. L. Holden
Department of Biology, University of Washington,
Seattle, WA 91985, USA

O. P. Langness
Washington Department of Fish and Wildlife,
2108 Grand Boulevard,
Vancouver, WA 98661, USA

Introduction

Two diadromous species of sturgeon, green sturgeon, *Acipenser medirostris*, and white sturgeon, *Acipenser transmontanus*, are common inhabitants of Pacific Northwest coastal estuaries from northern California, USA to British Columbia, Canada. Green sturgeon are anadromous, spending 1–3 years in their natal river and estuaries as juveniles before entering the ocean. The sub-adult phase of their life is marine-oriented and during winter and spring months they live off the coast in the shallow (<100 m) portion of

the sub-littoral zone (Erickson and Hightower 2007). In the summer and late fall, they are aggregated in coastal estuaries, particularly in the Columbia River estuary, Willapa Bay, and Grays Harbor, Washington (Moser and Lindley 2007). They do not return to their natal stream until first spawning around age 15 to 20 (Moyle 2002). Adults appear to join sub-adults when at sea and thus there is no distinct separation by life stage during estuarine residence. White sturgeon are amphidromous. While a minority might venture to sea, and to other fresh water locations, this sporadic migration behavior is not linked to breeding. Thus, white sturgeon of various sizes may be found in the coastal estuaries and rivers, at any time of the year. Stray rates vary from year-to-year but are low (ranging from 2% to 18% of tagged fish >90 cm total length; James 2001), and likely correlate to prey abundance or environmental conditions in the natal river and estuary.

Green sturgeon are known to consistently spawn in the Sacramento River (California), the Klamath River (California and Oregon), and Rogue River (Oregon). These spawning populations cluster into two distinct population segments (DPS): the Southern (Sacramento River); and Northern (principally the Klamath and Rogue rivers) DPS. Mixed stock analysis allocates approximately 80% of green sturgeon present in the Columbia River and Willapa Bay estuaries to the Southern DPS. The Grays Harbor aggregation is more evenly allocated between both DPS (Israel and May 2007). The Southern DPS was listed as threatened under the US Endangered Species Act (ESA), by the US National Marine Fisheries Service (NMFS) in 2006 (Adams et al. 2007). The Northern DPS was listed as a species of concern by NMFS, with a 5-year evaluation period stipulated.

White sturgeon found in Pacific Northwest estuaries belong to the population below Bonneville Dam (river kilometer 233) on the Columbia River (DeVore et al. 1999). White sturgeon stocks were heavily exploited in the late 1800s and have been greatly impacted by other anthropogenic activities such as hydropower dams which fragmented the population. The lower Columbia River population however is arguably one of the healthiest of any sturgeon species worldwide. Significant sport and commercial fisheries have been sustained for decades within the lower Columbia River, and neighboring estuaries (Reiman and Beamesderfer 1990; DeVore et al. 1995). White

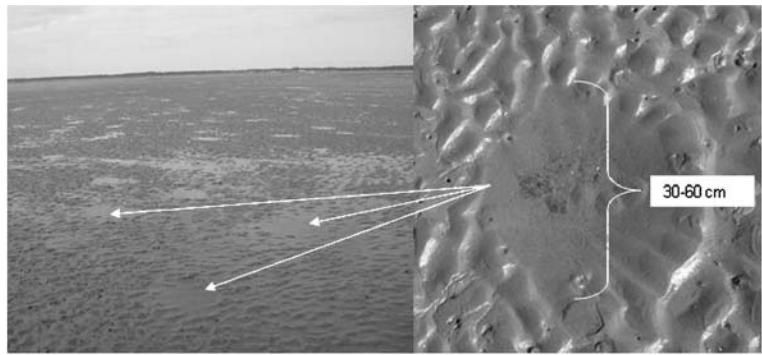
sturgeon greatly outnumber green sturgeon in the Columbia River estuary, while green sturgeon usually dominate in Willapa Bay and Grays Harbor (depending on the white sturgeon stray rate).

Anecdotal information from fishers and processors suggested that both green and white sturgeon feed when they are in coastal estuaries. While Atlantic coast anadromous sturgeon are known to forage in estuaries (Hatin et al. 2002; Taverny et al. 2002; Harris et al. 2005), most diet studies on the Pacific coast had been conducted in estuaries and large rivers where the fish spawn, so documentation of feeding behavior during estuarine residence outside these areas was limited. Juvenile and sub-adult white sturgeon feed on benthic invertebrates and fish in the Columbia River estuary (Muir et al. 1988), yet stomach contents from 46 commercially caught Columbia River green sturgeon consisted of only algae and pebbles (Farr and Kern 2005). This result supported the notion that green sturgeon do not feed while in coastal estuaries (Adams et al. 2002).

Two species of burrowing thalassinid shrimp, ghost shrimp, *Neotrypaea californiensis*, and mud shrimp, *Upogebia pugettensis*, are common and widely distributed tideflat residents in estuaries along the open Pacific coast (Swinbanks and Murray 1981; Bird 1982; Dumbauld et al. 1996). Both species of shrimp are indigenous, but considered to be pests by the oyster aquaculture industry due to their burrowing behavior that causes cultured bivalves to be smothered by sediment and die (Feldman et al. 2000; Dumbauld et al. 2004). These shrimp are also considered to be excellent sturgeon bait by recreational fishers and have been reported to occur in the stomachs of these fish, particularly those taken incidentally in summer commercial salmon fisheries. Anecdotal evidence also suggested that small pits commonly observed on broad tideflats dominated by shrimp in most coastal estuaries (Fig. 1), are made by these fish as they forage.

Declines in shrimp predator populations, including sturgeon, have been suggested as one reason for unexplained increases in shrimp populations in the 1950s in both Oregon and Washington estuaries. These expansions resulted in an ongoing burrowing shrimp control program which uses the pesticide carbaryl (brand name Sevin®) applied directly to the tideflats to kill the shrimp and protect the shellfish industry in Washington State (Feldman et al. 2000). Enhancement of sturgeon and other predator popula-

Fig. 1 View of an individual feeding pit (*right*) and multiple feeding pits (*left*) on an exposed tideflat in Willapa Bay, Washington where a dense burrowing shrimp population was present



tions has also been suggested as one potential alternative mechanism to be used in an integrated pest management plan for these shrimp, especially since an out-of-court settlement resulted in the industry agreeing to stop using carbaryl by 2012 (Dumbauld et al. 2006). We implemented the present study to: (1) document whether green and white sturgeon feed during their estuarine residence periods and if so whether their diet includes burrowing shrimp, and (2) use the feeding pits observed on shrimp dominated tideflats to document whether large predators like sturgeon feeding could affect shrimp populations.

Methods

Study area

The three estuaries along the Pacific Northwest Coast of the USA where this study took place are geologically young drowned river valleys, but vary widely in the level of freshwater inflow (Emmet et al. 2000). The Columbia River estuary is heavily influenced by dramatic freshwater inflow (average $7,500 \text{ m}^3 \text{ s}^{-1}$) from the large watershed it serves whereas the flow from relatively small rivers entering Grays Harbor, and Willapa Bay in Washington State is an order of magnitude less ($<500 \text{ m}^3 \text{ s}^{-1}$). The estuaries are located relatively close to one another, are small relative to coastline area and similar estuaries along the US east coast, but have extensive tideflats covering $>50\%$ of this area: Columbia River ($124^\circ 02' \text{ W}$, $46^\circ 15' \text{ N}$, 419 km^2), Willapa Bay ($124^\circ 06' \text{ W}$, $42^\circ 24' \text{ N}$, 260 km^2), and Grays Harbor ($124^\circ 10' \text{ W}$, $46^\circ 55' \text{ N}$, 235 km^2). Due to their proximity, Willapa

Bay and Grays Harbor are also influenced by the Columbia River plume (Hickey and Banas 2003).

Diet

We opportunistically sampled sturgeon from test fisheries and commercial sturgeon landings (either dockside or at nearby fish processing facilities). The first set of samples was taken in November 2000 during a sturgeon-directed commercial gillnet fishery in Willapa Bay. Since the fish processors reported to us that many sturgeon taken earlier that summer in the salmon fishery had full stomachs with burrowing shrimp present, our 2002–2005 sampling efforts focused on sturgeon landed as bycatch during the summer commercial salmon gillnet fisheries in Willapa Bay, the Columbia River estuary, and Grays Harbor. Although gastric lavage has been used to sample gut contents from sturgeon (Haley 1998; Brosse et al. 2002), this technique was not successful in previous studies on white sturgeon in the Columbia River (Sprague et al. 1993), due in part to the convoluted shape of their gastrointestinal tracts. Farr et al. (2001) were unsuccessful in performing gastric lavage on dead sub-adult green sturgeon using a variety of equipment choices. They were unable to get either flexible or stiffer tubing past the first bend in the digestive tract, and were unable to fill the stomach with water as it was diverted into the air bladder. What worked for the short upper digestive system of juvenile sturgeon did not work for the larger sub-adult and adult gut. Thus, we sampled fish carcasses either at the dock when they were landed, or at nearby fish processing facilities. During fish processing or dissection, entire gastrointestinal tracts were removed, cut open, and contents rinsed into jars where they

were either frozen or fixed with 10–20% buffered formaldehyde solution. Sturgeon were identified to species and measured (fork length and/or total length in cm). Gut contents were later sorted, identified to the lowest taxonomic level, and items weighed separately (wet weight, g) in the laboratory.

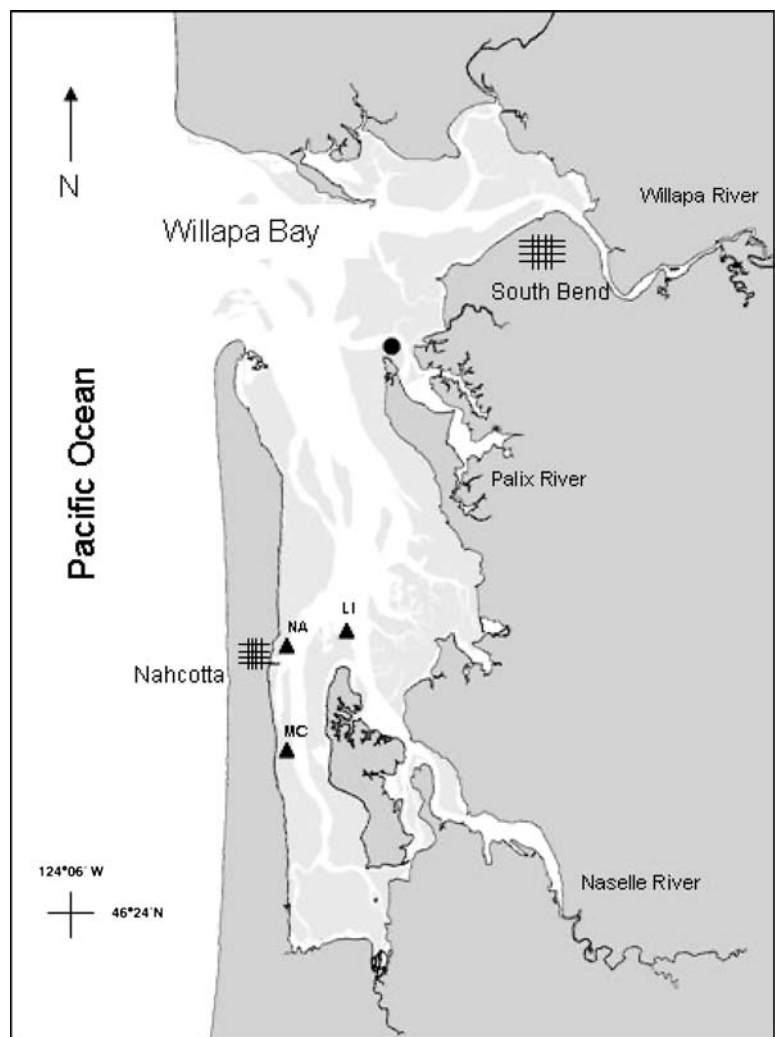
Feeding pits

Initial surveys of intertidal feeding pits were conducted in 2004 at two intertidal locations that had dense ghost shrimp colonies in the southern arm of Willapa Bay (Fig. 2). Shrimp burrow openings were counted within pits and within a similar area (0.25 m²) just outside these pits at both Long Island (seven pits) and Nahcotta (15 pits) locations. Actual shrimp densities

were later assessed using a large stainless steel core (40 cm diameter by 90 cm depth, but sampled to 60 cm) which was placed over and just outside of pits at the Long Island location (six samples each). Contents of each core were sieved through a 3 mm mesh sieve and all shrimp retained were identified, counted and measured (carapace length, CL from the tip of the rostrum to the posterior margin of the cardiac region, in mm). Sex was determined for individuals larger than 4 mm CL based on presence of anterior pleopods.

Since feeding pits are likely to persist for only short periods in the sandy and highly bioturbated environment of a shrimp colony, and shrimp were likely to reinvade these areas rapidly, a second more comprehensive effort was initiated in Willapa Bay

Fig. 2 Map of Willapa Bay, Washington showing sampling locations (*filled triangles*) for feeding pits and experimental enclosures (*LI* Long Island, *NA* Nahcotta, *MC* Mill Channel). Also shown is the location of a long-term monitoring location at Goose Point (near the Palix River, *filled circle*) where burrowing shrimp have been collected since 1989



during 2006 to assess abundance and persistence of these feeding pits. This effort included enclosure experiments designed to determine whether the predators making the feeding pits actually influenced shrimp abundance. Plots (100×40 m) were marked with PVC stakes in dense shrimp colonies at three different locations (Nahcotta, Long Island, and Mill Channel, Fig. 2). On the first day, all pits within these plots were marked and counted using strips of flagging tape attached to long wires placed in the center of the pit. On the next lower low tide, all new pits at each of the plots were marked and counted and pits which had been marked on the previous tide, but had not been washed away, were also counted and remained marked. Flagging tape from pits that had been washed away was removed. This survey process was carried out daily at low tide on successive dates through two tide series. Pits were counted at Mill Channel and Long Island on June 26, and at all three locations on June 27–30 during the first tide series. For the second tide series, pits were only counted at Nahcotta and Long Island (July 12 and 13).

To assess the effect of the predator making these feeding pits, we created enclosures to restrict access of sturgeon to certain areas of the Nahcotta and Long Island locations. These enclosures consisted of a ring of PVC stakes 5 m in diameter with 10 cm spacing between stakes along the outside. Stakes were approximately 1 m long and were driven halfway into the sediment (0.5 m exposed). One flagged stake was placed in the center encircled by eight additional stakes. Five enclosures were set up at both the Long Island and the Nahcotta locations. Enclosures remained in place for approximately 5 weeks, during which time no feeding pits were observed within them. Shrimp density was measured at the conclusion of the experiment using the large stainless steel core described above. Three cores were taken on the inside and the outside of each enclosure. Exterior cores were taken approximately 1–3 m from the edge of the enclosure. All shrimp were counted, sexed, and measured as noted above.

Data analysis

The importance of the different prey types was assessed by calculating average proportions (by occurrence, number and weight) of each taxon found in the gut. Due to the small number of sturgeon with items

present in their stomachs, we calculated a compound index of relative importance (IRI) for green and white sturgeon in 2003 Willapa Bay samples only. We calculated percent frequency of occurrence ($\%F$) = (number of stomachs containing prey i) × (total number of stomachs containing prey)⁻¹ × 100, percent abundance ($\%N$) = (number of prey i) × (total number of prey)⁻¹ × 100, and percent weight ($\%W$) = (weight of prey i) × (total weight of all prey)⁻¹ × 100. These values were then used to estimate IRI for each taxonomic category: $IRI = (\%N + \%W) \times \%F$ (Pinkas et al. 1971), expressed as a percentage (%IRI). Using %IRI provides an unbiased general index of dietary importance (Cortes 1997; Liao et al. 2001).

Parametric t tests and analysis of variance (ANOVA) were used to compare mean density of shrimp inside and outside feeding pits and between locations when the data satisfied normality and equal variance assumptions. A non-parametric Kruskal–Wallis test was used to examine feeding pit count data which did not fit a normal distribution even when transformed (ln count +1) and followed by a Bonferroni multiple comparison test on the medians. All tests were run with $\alpha=0.5$.

Results

Diet

We examined the gastrointestinal tracts from 35 green sturgeon taken in a directed sturgeon gillnet fishery in Willapa Bay during November 2000. Twenty sturgeon were sampled at the packing plant where the fish had been held on ice for a day and 95% of these fish had empty stomachs (one contained a juvenile Dungeness crab, *Cancer magister*). Fifteen sturgeon were sampled directly at the dock and 46% of these had empty stomachs (Table 1). Most of the remaining eight sturgeon had very few items in their stomachs. Individual items were not counted, but Dungeness crab, fish, and crangonid shrimp represented an average of 18%, 15% and 7% of the weight of identifiable items present (Fig. 3). No sturgeon had burrowing shrimp present in their stomachs. We sampled 33 green sturgeon from the Willapa Bay salmon fishery in August 2002. Fish were again sampled at the processing plant and most of these fish had empty stomachs with only one fish that appeared

Table 1 Description of sturgeon sampled in this study including location, sample size (*N*), proportion of fish with empty stomachs and size range of the fish

Date	Estuary	Location	Species	<i>N</i>	Proportion with empty stomachs	Size Range (FL in cm)
11/2000	Willapa Bay	Packing plant	Green	20	0.95	107–143
11/2000	Willapa Bay	Dock	Green	15	0.46	111–133
8/2002	Willapa Bay	Packing plant	Green	33	0.97	114–152
8/2003–5	Willapa Bay	Dock	Green	13	0.31	113–158
7/2003	Willapa Bay	Test Fishery	Green	1	0.0	148
8/2005	Grays Harbor	Test Fishery	Green	1	0.0	119
8/2003	Willapa Bay	Dock	White	6	0.17	113–137
9/2004–5	Columbia River	Dock	Green	12	0.50	120–148

to have fish parts present. All of these green sturgeon ranged in size from 107 to 152 cm fork length (Table 1).

A final sample of 27 green sturgeon gastrointestinal tracks (12 landed in the Columbia River, 14 in Willapa Bay, and one in Grays Harbor during 2003–2005) and six stomachs from white sturgeon (sampled in Willapa Bay) had consistently more material present than those from previous years (>50% of sturgeon stomachs from all estuaries sampled with items present, Table 1). With the exception of the green sturgeon taken in September 2005 in the Columbia River, all of these fish were sampled in late July and early August. The stomach contents of

sturgeon with items present were often difficult to identify, but both green and white sturgeon fed predominately on benthic food items in Willapa Bay (Fig. 3, Table 2). Only two of six green sturgeon landed in the Columbia River had identifiable items present and these were mostly crangonid shrimp. Burrowing thalassinid shrimp were a very important food item for green sturgeon in Willapa Bay, where they represented 51% of the biomass ingested and 83% of the index of relative importance (IRI). Burrowing shrimp were also important prey for white sturgeon representing 22% of the biomass (60% IRI), but less important for green sturgeon from the Columbia River where they represented only 2% of

Fig. 3 Prey habits (average % prey weight) of eight green sturgeon, *Acipenser medirostris*, sampled during a directed sturgeon gillnet fishery in Willapa Bay, Washington in November 2000 (*top left*) and nine green sturgeon (*top right*) and five white sturgeon, *Acipenser transmontanus* (*bottom*) sampled during summer 2003 salmon directed fisheries in Willapa Bay, Washington

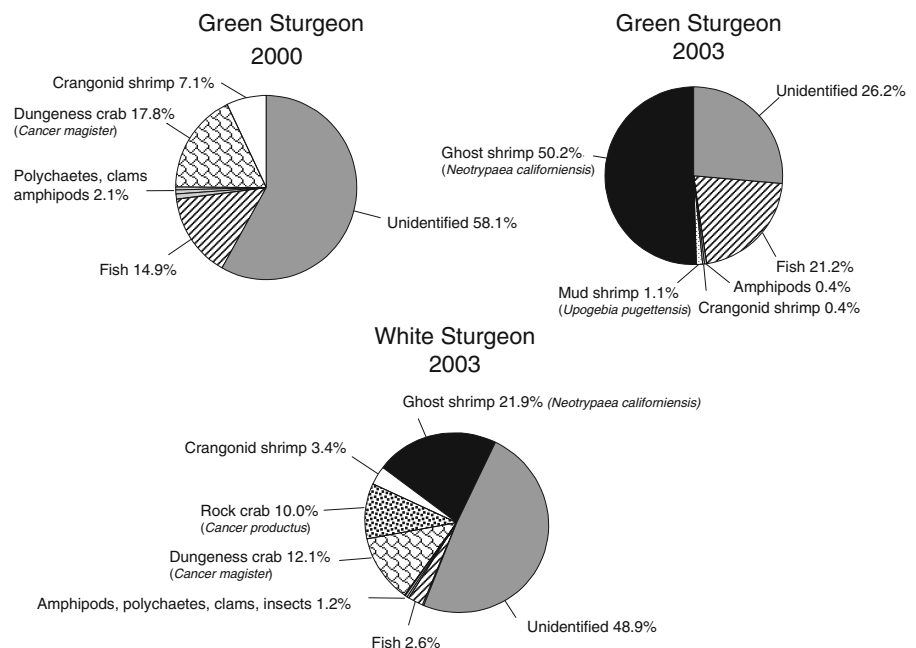


Table 2 Stomach contents of green sturgeon, *Acipenser medirostris*, and white sturgeon, *Acipenser transmontanus*, taken as bycatch in a 2003 salmon fishery in Willapa Bay, Washington

Taxon	Green sturgeon (n=9)					White sturgeon (n=5)				
	%F	%N	%W	IRI	%IRI	%F	%N	%W	IRI	%IRI
Crustacea										
<i>Neotrypaea californiensis</i>	55.5	71.8	73.2	8055	82.9	60.0	46.1	57.7	6232	60.5
<i>Neotrypaea gigas</i>	22.2	2.8	2.8	125	1.2	0.0	0.0	0.0	0	0.0
<i>Upogebia pugettensis</i>	11.1	2.8	3.2	67	0.6	0.0	0.0	0.0	0	0.0
<i>Crangon</i> spp.	33.3	7.0	0.1	237	2.4	0.0	0.0	0.0	0	0.0
<i>Crangon stylirostris</i>	0.0	0.0	0.0	0	0.0	20.0	7.7	1.4	181	1.7
<i>Cancer magister</i>	0.0	0.0	0.0	0	0.0	60.0	3.8	12.2	966	9.4
<i>Cancer productus</i>	0.0	0.0	0.0	0	0.0	20.0	1.9	11.4	266	2.5
<i>Anisogammarus pugettensis</i>	22.2	2.8	0.002	63	0.6	0.0	0.0	0.0	0	0.0
<i>Grandifoxus grandis</i> & <i>Eohaustorius washingtonianus</i>	0.0	0.0	0.0	0	0.0	20.0	30.8	0.06	617	5.9
Mollusca										
<i>Cryptomya californica</i>	11.1	1.4	0.03	16	0.2	20.0	1.0	0.1	22	0.2
Unid. clam	0.0	0.0	0.0	0	0.0	20.0	2.9	0.05	59	0.5
Polychaeta	0.0	0.0	0.0	0	0.0	20.0	1.0	0.1	22	0.2
Insects	0.0	0.0	0.0	0	0.0	20.0	1.0	0.1	22	0.2
Fish										
<i>Ophiodon elongatus</i>	11.1	2.8	3.3	68	0.7	0.0	0.0	0.0	0	0.0
Unidentified fish	22.0	2.8	0.4	72	0.7	20.0	1.0	1.0	40	0.4
Unidentified matter	44.4	5.6	17.0	1004	10.3	100.0	2.9	15.7	1861	18.1

Frequency (%F) = (number of stomachs containing prey *i*) × (total number of stomachs containing prey)⁻¹ × 100, abundance (%N) = (number of prey *i*) × (total number of prey)⁻¹ × 100, weight (%W) = (weight of prey *i*) × (total weight of all prey)⁻¹ × 100, index of relative importance (IRI) = (%N + %W) × %F, and percent index of relative importance (%IRI) = IRI × (total IRI)⁻¹ × 100.

the prey biomass (1% IRI). Crab were also important prey for the white sturgeon we sampled (11% IRI, Table 2) and crangonid shrimp for green sturgeon in the Columbia River (24% IRI). While three species of burrowing shrimp were found in at least one sturgeon from Willapa Bay (*Upogebia pugettensis*, *Neotrypaea californiensis* and *N. gigas*), *N. californiensis* were predominant and ranged in size from 11 to 22 mm CL. Both green and white sturgeon were similar in size to those sampled in 2000 and 2002 (113–158 cm FL).

Feeding pits

The density of shrimp burrows measured at Nahcotta and Long Island locations was significantly different both between locations and inside and outside of feeding pits (Fig. 4, ANOVA, location and pit factor both $p < 0.001$). However, when the large core was used to sample shrimp at the Long Island location, no significant difference in shrimp density inside and outside the pits was observed (*t* test, $n = 6$, $p = 0.33$; statistical power only 0.15 at $\alpha = 0.05$).

The number of feeding pits present within plots at each of three locations where density was tracked over time was highly variable and appeared correlated between locations (Fig. 5). The plot at Nahcotta had the highest average number of feeding pits (6.4 pits per 100 m²), followed by Long Island (5.6 pits per 100 m²), and Mill Channel (1.6 pits per 100 m²) which was significantly lower than that at Nahcotta, but could not be distinguished from that at Long Island (Kruskal–Wallis test, $H = 8.59$, $n_1 = 7$, $n_2 = 5$, $n_3 = 6$, $p = 0.0136$; Bonferroni *Z*-test $Z = 2.92$). Individual pits ranged from 30–60 cm in diameter and were very transient, persisting for <48 h in all cases.

Mean shrimp density inside predator/pit enclosures was 21.6 shrimp per core or 120 shrimp m⁻² at the end of the experiment. This was statistically higher than the shrimp density found outside the enclosures (18.3 shrimp per core or 102 shrimp m⁻², *t* test, $n = 10$, $p = 0.006$). Sex ratio and average shrimp size were not significantly different (approximately 78.2% females outside enclosures versus 77.9% females inside enclosures; *t* test, $p = 0.87$). Mean male size was

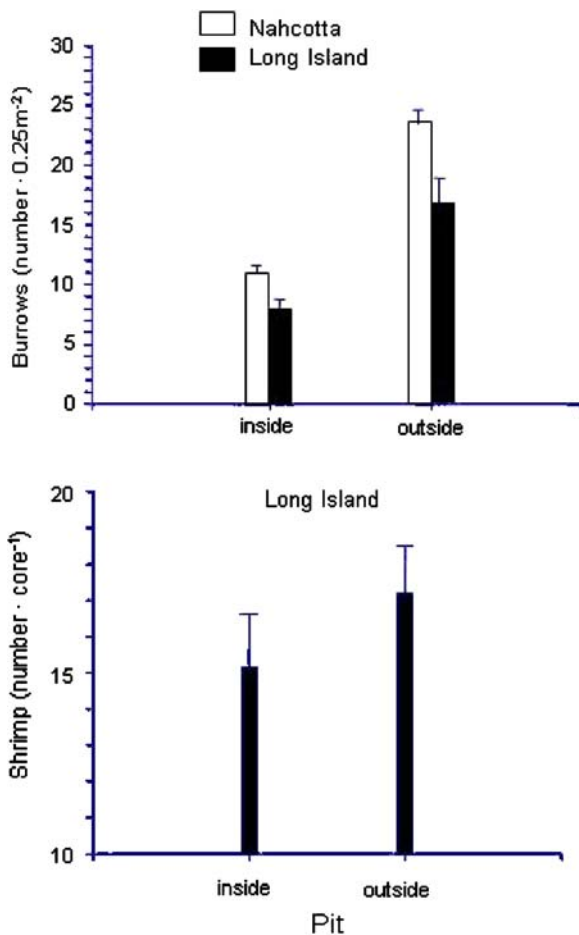


Fig. 4 Comparison of average ghost shrimp, *Neotrypa californiensis*, burrow counts made inside and outside feeding pits observed on tideflats at two locations (Nahcotta and Long Island) in Willapa Bay, Washington (*top*), and number of ghost shrimp sampled in a core (40 cm diameter by 90 cm depth, sampled to 60 cm depth) at the Long Island location only (*bottom*)

17.0 mm CL outside exclosures and 16.9 mm CL inside exclosures (t test, $p=0.77$), while mean female size was 14.1 mm CL both inside and outside exclosures.

Discussion

We found that both green sturgeon, *Acipenser medirostris*, and white sturgeon, *Acipenser transmontanus*, fed on benthic prey found on tideflats during their estuarine residence periods along the Pacific Northwest coast of the USA. The sturgeon we examined ranged from 106 to 158 cm FL (Table 1)

and thus were approximately 10 to 25 year old animals (estimated from growth curves and age determinations, Adams et al. 2007). These fish were predominately immature individuals or just becoming sexually mature (histological confirmation, Talbott and Webb, US Fish and Wildlife Bozeman Fish Technology Center, Montana). Tagged green sturgeon of similar size have recently been shown to enter these estuaries during summer when water temperatures exceed coastal marine temperatures by at least 2°C (Moser and Lindley 2007) and exhibit rapid and extensive inter- and intra-estuary movements, perhaps due to favorable conditions and the abundance of food in these systems.

A large proportion (17–97%) of the sturgeon we sampled, particularly those taken in the late fall (November 2000), had empty stomachs. A life history pattern which involves fasting during the majority of the year with brief but intensive feeding periods has been reported for other sturgeon species (Sulak and Randall 2002). We suspect however, that our results may also be an artifact of sampling and handling. Unfortunately, there is no method of sampling gut content, even sacrificing fish, that can completely capture the full array of food items in a sturgeon diet. The high number of empty gut samples in commercially landed sturgeon is likely due to a combination of post-capture digestion and regurgitation (Bowen 1983; Johnson et al. 1997; Haley 1998). Ball (1948) found that fish exposed to summer temperatures in the bottom of a boat for 30 min were so affected by increased digestive action that their stomach contents were useless for food studies. Some soft-bodied items are difficult to retain from live fish (Brosse et al. 2000) and when retained may not be identifiable

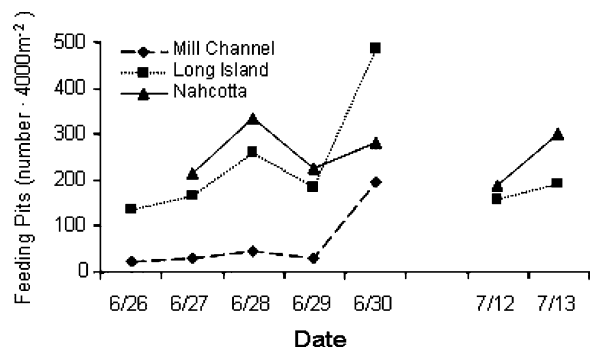


Fig. 5 Comparison of the total number of feeding pits observed within a 4,000 m² area at three locations in Willapa Bay, Washington over a 2 week period in the Summer of 2006

because of full or partial digestion before the gut contents can be examined (Haley 1998). Commercially caught sturgeon in the coastal estuaries we sampled, likely experienced such handling. Evidence that this may have occurred is the even higher proportion of empty stomachs we observed in fish sampled at the processing plant (Table 1) versus those sampled dockside and to a lesser extent the presence of items in the guts of both fish taken at the time of sample in the test fishery. Bowen (1983) also noted that diet of fish may vary over the course of a day. If the commercial fishery occurs during a time of day when little or no active feeding is taking place, then most gut samples will be empty. Gillnet fisheries could also be more selective for sturgeon moving between areas of extended localized feeding (Fox et al. 2002). Future dietary studies on green and white sturgeon sub-adults and adults, should therefore take a more systematic approach to sampling in order to identify any diel or seasonal effects. It would also be preferable to sample fish at time of capture, rather than awaiting delivery of the fish to a fish processor. At the time of this study, we were able to sample commercial landings, however the recent listing of a portion of the green sturgeon population will make this difficult in the near future. It seems imperative that effective non-lethal gut-sampling methods be developed for these threatened fish (Brosse et al. 2002). Since gastric lavage has not been shown to be very successful and emetics can be toxic or have a negative long-term effect on the digestive system, a small authorized take of green sturgeon (at all life stages), for the purpose of further defining their feeding behavior, and perhaps to allow for the development of non-lethal gut-sampling techniques that work, seems prudent.

While the majority of sturgeon we sampled had empty stomachs (Table 1), when prey items were present in the stomach, we document that both immature green and white sturgeon in estuaries fed on a diet consisting primarily of benthic prey and fish common to the estuary (Fig. 3). This is consistent with their unique jaw structure and sensory systems (Miller 2004). Sturgeon of the family Acipenseridae, have ventral, protrusible, sucker-like mouths, adapted for feeding mainly on the bottom (Wydoski and Whitney 2003), as well as other evolutionary traits adapted for benthic cruising (Findeis 1997). A benthic diet is also consistent with previously collected diet

records for these fish and other sturgeon species. White sturgeon diets are perhaps best documented for small juveniles (<80 cm FL) that feed on amphipods (primarily *Corophium* spp.), eulachon (*Thaleichthys pacificus*) eggs, clams (*Corbicula fluminea*), and mysids (*Neomysis* sp.) in the Columbia River and Sacramento–San Joaquin (Radtke 1966; McCabe et al. 1993). Amphipods and mysids are also the only previously reported items in the diet of green sturgeon (small juveniles <57 cm FL in the Sacramento–San Joaquin, Radtke 1966). Diets of larger white sturgeon (>80 cm TL) are also documented with these fish feeding on other fish including northern anchovy, *Engraulis mordax*, in the Columbia River (Muir et al. 1988) and sculpins, sticklebacks, *Gasterosteus aculeatus*, and seasonally important items like eulachon in the Fraser River (Semakula and Larkin 1968). Brackish and freshwater prey items such as chironomid larvae, crayfish, and stonefly larvae have also been recorded as sturgeon prey in these systems and in the Sacramento–San Joaquin River estuary in California (McKechnie and Fenner 1971). These observations have all been made either in natal rivers or estuaries. We provide the first documentation of the diet of both large immature green and white sturgeon in non-natal estuaries. Although only five of six white sturgeon we sampled had prey present and most items were unidentifiable, results confirm the importance of large crustaceans and fish (ghost shrimp, crab, and crangonid shrimp, Fig. 3, Table 2). Sturgeon appear to be opportunists, since we also found Dungeness crab and crangonid shrimp to be important prey items for green sturgeon. Green sturgeon catch per unit effort in the Columbia River estuary was highest in the area of the turbidity maximum during 2004 (Langness 2005) where Simenstad et al. (1994) have shown increased food is often present.

Both green sturgeon and white sturgeon we examined fed on burrowing thalassinid shrimp. These crustaceans represented a significant proportion of the sturgeon diet, particularly for green sturgeon sampled in 2003 (58 and 51% by number and weight respectively, Fig. 3, and 83% IRI, Table 2). Gulf sturgeon *Acipenser oxyrinchus desotoi* have also been reported to feed on burrowing shrimp, *Lepidophthalmus lousianensis*, in the Suwanee River estuary (Mason and Clugston 1993) and Choctawhatchee Bay, Florida (Fox et al. 2002). While only a few fish had burrowing shrimp present in their stomachs in

those studies, extensive sturgeon movements over shallow burrowing shrimp habitat were noted.

We are reasonably confident that the small (30–60 cm diameter) feeding pits that we observed in intertidal areas dominated by thalassinid shrimp (Fig. 1) were made by sturgeon, but we suggest and are hoping to conduct underwater video observations to obtain direct confirmation of this feeding behavior (K. Patten, Washington State University, personal communication). Sturgeon distribution is closely associated with the areas where we observed these pits. Green sturgeon catch per unit effort was greatest in the catch area encompassing Long Island and Nahcotta during test fisheries conducted by the Washington Department of Fish and Wildlife (WDFW). Similar feeding pits and effects have been documented for other thalassinid shrimp predators including gray whales, *Eschrichtius robustus*, in Puget Sound, Washington (Weitkamp et al. 1992), bat rays, *Myliobatis californica*, and gray smoothhound sharks, *Mustelis californicus*, in California (Talent 1982; Gray et al. 1997) and sting-rays, *Dasyatis akajei*, in Ariake Sound, Japan (Harada and Tamaki 2004). Bat rays and smoothhound sharks are relatively common in California estuaries, but rarely found north of central Oregon. Although burrowing shrimp are reported in the diet of bat rays, they feed chiefly on clams (Gray et al. 1997), and create larger pits (1 m in diameter or even trenches up to 1 m wide by 4 m long, Karl and Obrebski 1976) than those we observed in Willapa Bay. Gray whales make much larger (up to 2–3 m in diameter) feeding pits that can even be observed from the air in both Willapa Bay and Puget Sound (Weitkamp et al. 1992). Stingray pits in Japan were also slightly larger (up to 150 cm in diameter) and persisted slightly longer (2–5 days).

While we were unable to confirm that sturgeon make the feeding pits, we present evidence that the predators that do can have a significant cumulative affect on shrimp density. The 47% reduction in shrimp burrow density we observed within pits (Fig. 4) was lower than that observed for stingrays in Japan (62–78% reduction, Harada and Tamaki 2004) and gray whales (79% reduction in shrimp density, Weitkamp et al. 1992). It should be noted that we found no difference in shrimp density or size when pits were sampled with a core, whereas these researchers did. We suggest that this was in part due to the smaller size of the feeding pits we observed

relative to the surrounding environment, making it easy for shrimp to rapidly re-colonize the small disturbed areas. The 0.25 m² sampling core we used was also slightly larger than some of the pits and shrimp clearly have convoluted burrows that make shrimp counts variable.

We detected a significant difference in burrowing shrimp density in slightly larger areas where predators were excluded for over a month. The experimental exclosures we used were designed with 10 cm of spacing between the stakes and the stakes only rose 0.5 m above the surface such that predators approaching from above such as diving ducks or other waterfowl would not be excluded, and fish that swam near the surface could descend into the exclosure. It is possible that the exclosures themselves deterred these large predators from foraging on shrimp in the vicinity. However, pits were observed immediately adjacent to the exclosures during the experiment. Thus the exclosures had the desired effect of keeping the pit-creating predators out of the area inside the exclosures, while not scaring predators away. We documented a 15% reduction in shrimp density in the area outside exclosures and an 18% increase in shrimp density inside the exclosures. Extrapolating these numbers to a larger scale involves a number of assumptions, but indicates that sturgeon and other benthic predators may be able to exert top-down control on burrowing shrimp populations. We speculate that sturgeon and other predators like staghorn sculpin, *Leptocottus armatus* (Posey 1986) may at least be partially responsible for slow declines that we have documented in shrimp density at a long-term monitoring location in Willapa Bay (Palix River location, Fig. 6, see Dumbauld et al. 2006 for further description). Shrimp recruitment however, has also been very low during the study period, so a different predator/prey interaction might be expected in estuaries where recruitment is still taking place or during periods when recruitment is more frequent in Willapa Bay (e.g. the early 1990s, Fig. 6).

Since burrowing shrimp are considered a pest by the shellfish aquaculture industry and the pesticide carbaryl has been used to control them on intertidal aquaculture beds in Willapa Bay and Grays Harbor since the early 1960s (Feldman et al. 2000), we attempt to answer two management questions: (1) What does this imply for sturgeon conservation? and (2) Could sturgeon enhancement be an alternate

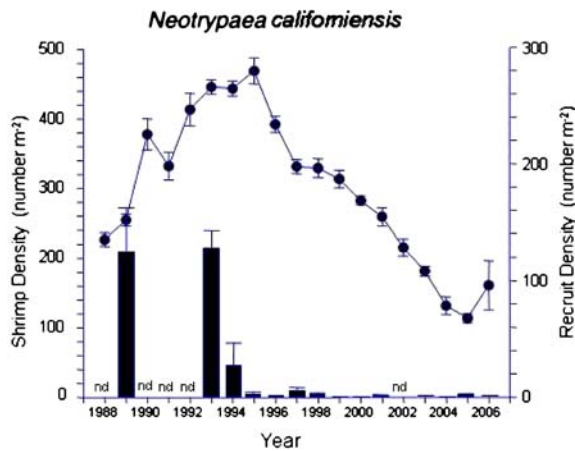


Fig. 6 Comparison of the average density of ghost shrimp, *Neotrypaea californiensis*, (represented as a line with SE brackets) sampled at a long-term monitoring location (filled circle, Fig. 2) near Goose Point in Willapa Bay, Washington, with average ghost shrimp recruitment (as small postlarvae or juveniles represented as bars with SE brackets) at the same location from 1988–2006 (nd no data collected)

method for controlling burrowing shrimp on oyster beds, or perhaps limit burrowing shrimp populations to acceptable levels in some estuaries? Sturgeon stocks (particularly green sturgeon) that utilize Willapa Bay and most other estuaries along the Pacific Northwest coast are from mixed origin and thus include individuals from ESA listed stocks in California (Israel et al. 2004; Welch et al. 2006; Adams et al. 2007; Israel and May 2007). Given the above evidence, protecting burrowing shrimp as a potential food resource for sturgeon has been suggested by others (Moser and Lindley 2007) and it has been suggested that applying the pesticide to oyster aquaculture areas may threaten sturgeon. Oyster aquaculture is actively practiced on roughly 3,642 ha or 21% of the intertidal area in Willapa Bay, of which up to 324 ha are treated with carbaryl annually. While there is some debate about historical shrimp populations (i.e. pre 1930s aquaculture), current shrimp populations in Willapa Bay are extensive. A conservative estimate suggests there are at least 2,379 ha of dense shrimp colonies present outside the oyster growing areas (Dumbauld unpublished data), and these areas are not currently treated with pesticide nor threatened by the burrowing shrimp control program. Oyster growers report significant areas of intertidal flats, used for oyster culture in the 1940s and 50s, that have since been invaded by shrimp and are therefore no longer used. Burrowing shrimp

colonies also cover even larger proportions of the intertidal area in other Pacific Northwest estuaries where oyster aquaculture is either a minor component or not present at all (e.g. over 600 ha representing 80% of the tideflat area in Oregon's Yaquina estuary, Dewitt et al. 2004). It thus seems unlikely that burrowing shrimp abundance as food for sturgeon is currently a significant limiting factor for these threatened fish populations, especially relative to other population threats such as predation on eggs, larvae and juveniles in natal streams, direct and indirect harvest of sub-adults and adults, and direct anthropogenic impacts to spawning and rearing habitat.

Our results suggest that even at current population levels, sturgeon and/or other predators may be having top down control effects on shrimp populations outside aquaculture areas. We suspect that the lack of similar feeding pits in oyster aquaculture beds is related to the presence of oysters themselves and perhaps the low density of other prey including burrowing shrimp in these areas. Some growers however, reported to us that in the past, they observed sturgeon much more frequently over these areas and have even seen sturgeon stranded on intertidal aquaculture beds at low tide. Unless these large fish could be penned or enclosed in areas where shrimp biocontrol is needed, direct shrimp control by sturgeon on aquaculture beds seems unlikely. Both white and green sturgeon have been successfully raised in captivity (Deng et al 2002; Van Eenennaam et al 2004) and hatchery produced sturgeons can contribute to wild populations (Secor et al. 2000; Smith et al 2002). Aquaculture or hatchery supplementation of wild stocks however, raises issues such as depleting wild broodstock, genetic inbreeding, and selection for maladaptive traits (Secor et al 2002). Nonetheless, some form of supplementation integrated with habitat protection and harvest restrictions is likely to be the only choice for fishery managers faced with ESA threatened fish stocks (Beamesderfer and Farr 1997). Since these animals are long-lived, slow growing, have delayed maturity, and only spawn intermittently in distant natal streams, hatchery supplementation is not a clear alternative for current chemical shrimp control measures. Humans have clearly altered the system however, and though difficult to implement, a management strategy that restores benthic predator populations like sturgeon, could have long-term ecosystem benefit.

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