

ARTICLE

Electronic Tagging of Green Sturgeon Reveals Population Structure and Movement among Estuaries

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Abstract

Green sturgeon *Acipenser medirostris* spend much of their lives outside of their natal rivers, but the details of their migrations and habitat use are poorly known, which limits our understanding of how this species might be affected by human activities and habitat degradation. We tagged 355 green sturgeon with acoustic transmitters on their spawning grounds and in known nonspawning aggregation sites and examined their movement among these sites and other

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potentially important locations using automated data-logging hydrophones. We found that green sturgeon inhabit a number of estuarine and coastal sites over the summer, including the Columbia River estuary, Willapa Bay, Grays Harbor, and the estuaries of certain smaller rivers in Oregon, especially the Umpqua River estuary. Green sturgeon from different natal rivers exhibited different patterns of habitat use; most notably, San Francisco Bay was used only by Sacramento River fish, while the Umpqua River estuary was used mostly by fish from the Klamath and Rogue rivers. Earlier work, based on analysis of microsatellite markers, suggested that the Columbia River mixed stock was mainly composed of fish from the Sacramento River, but our results indicate that fish from the Rogue and Klamath River populations frequently use the Columbia River as well. We also found evidence for the existence of migratory contingents within spawning populations. Our findings have significant implications for the management of the threatened Sacramento River population of green sturgeon, which migrates to inland waters outside of California where anthropogenic impacts, including fisheries bycatch and water pollution, may be a concern. Our results also illustrate the utility of acoustic tracking to elucidate the migratory behavior of animals that are otherwise difficult to observe.

The southern distinct population segment (DPS) of green sturgeon *Acipenser medirostris* is listed as a threatened species under the U.S. Endangered Species Act, and the northern DPS is of conservation concern. Much of the concern about the status of southern DPS green sturgeon stems from the extensive modification and degradation of habitats within their natal river basin, the Sacramento River in northern California (Adams et al. 2007). Because green sturgeon are highly migratory they may also be affected by activities far outside of their natal river basin. After one to a few years of rearing in freshwater, juvenile green sturgeon move into the estuary of their natal river and then to the ocean, where they spend 10–15 years before maturing (Moyle 2002; Allen and Cech 2007; Allen et al. 2009). Mature green sturgeon spawn every 2 to 4 years, at least in the northern DPS (Erickson and Webb 2007). In summer months, subadult and adult green sturgeon that are not spawning may remain in the ocean or aggregate in the estuaries of certain nonnatal rivers between central California and the Fraser River, British Columbia, as well as in the larger bays on the West Coast, including Grays Harbor, Willapa Bay, Humboldt Bay, and San Francisco–San Pablo Bay (Adams et al. 2007; Moser and Lindley 2007; Lindley et al. 2008; Heublein et al. 2009).

Estuaries and bays are frequently sites of intense human activity and have the potential to detrimentally affect green sturgeon populations. In the past and present these activities have included commercial and recreational fisheries (ODFW and WDFW 2002), wetland filling, shellfish aquaculture and its attendant use of pesticides (Simenstad and Fresh 1995; Dumbauld et al. 2008), dredging of shipping lanes and anchorages, dredge spoil disposal, and municipal and industrial effluent discharge. In the future, tidal energy facilities may add to the impacts on green sturgeon and their estuarine habitats.

The population structure of green sturgeon has been described primarily on the basis of genetic data. These data show that spawning groups in the Sacramento River are differentiated from those in the Rogue and Klamath rivers (Israel et al. 2004) and that the proportions of southern DPS and northern DPS green sturgeon vary considerably among nonnatal river estuaries and coastal embayments (Israel et al. 2009), which suggests

that fish from different distinct population segments may use nonnatal habitats differently. Fish may also exhibit intrapopulation variability in migratory behavior and habitat use, as exemplified by migratory contingents in populations of striped bass *Morone saxatilis* (Clark 1968) and Japanese eel *Anguilla japonica* (Tzeng et al. 2003). Such structuring within populations would not be easily revealed by genetic data, yet variation in migratory behavior can have important consequences for management because migration determines a population's accessibility to human impacts (Secor 1999; Cadrin and Secor 2009). It is therefore crucial to understand how green sturgeon use different habitats and whether there is variation in migratory behavior within and between populations.

Recently, electronic tagging has been applied to questions of population structure and migratory behavior with notable success (e.g., Lutcavage et al. 1999; Hunter et al. 2004; Block et al. 2005; Lindley et al. 2008). For species such as green sturgeon that frequently aggregate at different times and places over the course of their life history, acoustic tags are an attractive technology. Fish can be captured at locations where they are locally abundant, and their subsequent movements can be followed by means of automated data-logging hydrophones. Acoustic tags obviate the need to physically recapture the fish, overcoming the problem of low recapture rates that have limited the utility of conventional sturgeon tagging programs. Also, acoustic tags are less expensive than pop-up satellite archival tags, and because they can be implanted internally, multiyear deployments are feasible, potentially allowing investigators to directly observe the full cycle of migratory behaviors of individual fish.

In this paper, we report the results of a large-scale tagging and tracking experiment in which green sturgeon were tagged with long-lived acoustic transmitters in spawning rivers and summer aggregation sites and their subsequent movements monitored with automated hydrophones deployed in various rivers, estuaries, and bays between San Francisco and the Fraser River. In some cases, these hydrophones had been deployed for studies of other organisms or for local studies, but they proved useful for our purpose because a common technology was used and data were shared effectively. We used these tagging results to

test the hypotheses that green sturgeon populations correspond to individual spawning rivers and that green sturgeon exhibit variability in their migratory behavior among and within populations.

METHODS

Study area.—The physical and hydrological characteristics of the study estuaries are summarized in Table 1 (data from Monaco et al. 1992). Green sturgeon spawn in the Sacramento, Klamath and Rogue rivers (Figure 1). The Sacramento River has an extensive estuary that includes San Francisco, San Pablo, and Suisun bays. In contrast, the Klamath and Rogue rivers have very small estuaries. Nonnatal estuaries monitored for tagged green sturgeon included river estuaries along the Oregon coast (Yaquina, Alsea, Coos, Siuslaw, Umpqua, and Coquille rivers), a medium-sized embayment in northern California (Humboldt Bay), the large embayments in coastal Washington (Willapa Bay and Grays Harbor), the Columbia River estuary, and the extensive fjord system of Puget Sound.

Fish capture and tagging.—Details of the fish capture, handling, and surgical procedures are given by Erickson and Webb (2007), Kelly et al. (2007), and Moser and Lindley (2007) and are only briefly reviewed here. Green sturgeon were captured primarily with gill nets, although some were caught by angling using ghost shrimp (Callinassidae) as bait. In rivers where green sturgeon spawn, small, sinking, monofilament gill nets (~33 m long) were deployed from jet boats in suspected holding areas, typically deep pools (>5 m depth). Nets were fished for 30–60 min during daylight. In bays and estuaries, larger sinking gill nets (~100 m long) were deployed by means of commercial gill-net boats, with sets lasting 20–45 min. Total length (TL) and fork length (FL) of each captured fish was measured, and green sturgeon at least 1.1 m TL were retained for tagging.

Over the 2002–2005 period, green sturgeon were tagged in the Columbia River estuary, the Klamath River, the Rogue River, San Pablo Bay, the Sacramento River, Willapa Bay, and Grays Harbor (Table 2; Figure 1). Uniquely coded ultrasonic pinger tags (Vemco V16–6H and V16–5H) were implanted surgically into the abdominal cavity of the sturgeon. The V16 tag is 90 mm long, 16 mm in diameter, and weighs 14 g in water. This is less than 0.2% of the weight of the smallest green sturgeon tagged and well within the recommended maximum tag size to body size ratio suggested by Chittenden et al. (2009). Tag life ranged from 3 to 5 years, depending on pulse transmission configuration. A variety of pulse transmission rates that ranged from 90 to 120 s nominal delay were used. Tags were sterilized with benzalkonium chloride and inserted through a 2.5-cm incision that was made 2 cm from the ventral midline, midway between the pectoral and pelvic fins. Incisions were closed with sutures, and the fish were released immediately.

Receiver deployments.—Tagged green sturgeon were detected with passive hydrophones (Vemco; Model VR2) that log the identity and time of tags within their range (up to 1 km under favorable conditions for V16 tags) during 2005 and 2006. Receivers were deployed in natal rivers and estuaries—the es-

tuaries of select nonnatal rivers known to be used by green sturgeon—and large bays (Table 1; Figure 1). Coverage of estuaries during our study period included all estuaries where Emmett et al. (1991) indicated that green sturgeon are common, except for the Eel River estuary (which was covered in 2007; a single green sturgeon was detected at this site that year). Emmett et al. (1991) reported that green sturgeon are rare in Puget Sound and the Siuslaw River (both covered) and not present in other West Coast estuaries.

Arrays were deployed in three different spatial arrangements. In Willapa Bay, Humboldt Bay, and Puget Sound, receivers were deployed over a broad area within the estuary to detect movement of tagged green sturgeon within these estuaries (see Andrews et al. 2007 for an example). In the lower Columbia River, Grays Harbor in 2006, and at the Golden Gate, receivers were arranged in lines across the estuary to detect movement of tagged fish (including salmonids carrying relatively low-power tags) in and out of the estuary. Spacing between receivers was approximately 700 m and thus allowed substantial overlap of detection coverage. In 2005, Grays Harbor had only two receivers that were deployed near the mouth of the Chehalis River. In that year, green sturgeon could enter and exit Grays Harbor without being detected if they did not approach the Chehalis River (at the eastern end of the estuary). In the remaining small river estuaries, one or more receivers were placed in the channel in tidal waters such that tagged fish would be well within detection range of the receivers as they passed. We therefore expected that green sturgeon entering the study estuaries would generally be detected by one or more receivers, although under some unusual conditions detection ranges could be suppressed to such an extent that tagged sturgeon could pass undetected.

Deployment methods differed by location and included the use of submerged moorings with acoustic releases (InterOceans; Model 111) in deep areas (e.g., at the entrance to San Francisco Bay), submerged moorings tethered to shore by steel cables (e.g., the entrance to Humboldt Bay), surface moorings, and attachment to structures such as navigation buoys, pilings, and bridge abutments (Grays Harbor, Willapa Bay, and Oregon bays and rivers).

Data analysis.—In the analysis of detection data, we examined detections of fish that had been at large for at least one winter before detection. This delay allowed the green sturgeon to move away from the area where they were tagged, undertake their winter migration, and then potentially distribute themselves among various estuarine habitats.

We used logistic regression to examine whether fish length and release location influenced whether a fish was detected at one of the monitoring sites. Logistic regression models have the form

$$\log[\pi_i/(1 - \pi_i)] = x_i^T \cdot \beta, \quad (1)$$

where π_i is the probability of detection at the i th site, x_i^T is a vector of covariables that includes both continuous variables (fish length and the site characteristics total surface area,

TABLE 1. Physical and hydrological characteristics of the estuaries monitored for green sturgeon (Monaco et al. 1992; NOAA 1990, 1999).

Estuary	Stratification ^a			Tidal range (m)	Marine area (km ²)	Mixing area (km ²)	Freshwater area (km ²)	Tidal prism (million m ³)	Mean inflow (m ³ /s)	July inflow (m ³ /s)	Number of receivers	
	Mean depth (m)	At high flows	At low flows								2005	2006
Puget Sound	61.3	HS	HS	3.2	1,020	60		2,274	162	116	23	26
Grays Harbor	3.96	MS	MS	2.9	124	110	1	538	255	49	2	8
Willapa Bay	4.88	VH	VH	3.0	270	83	2	799	84	12	12	12
Columbia River	4.88	HS	HS	1.7		175	440	786	6,881	8,394	17	18
Yaquina Bay	3.05	MS	VH	2.5	8	6		27	8	1	0	5
Alesea Bay	2.1	MS	MS	1.8	5	4		9	45	6	0	7
Siuslaw River	2.74	HS	VH	2.1	6	3	1	9	65	9	0	1
Umpqua River	3.96	MS	VH	2.1	6	16	2	34	230	50	10	10
Coos Bay	4.27	MS	VH	2.2	16	24	4	66	7	0	4	2
Coquille River	3.35	HS	HS	2.1	2	5	3	10	70	6	1	0
Rogue River	1.52	HS	MS	2.0	0	2		3	280	69	10	4
Klamath River	7.01	HS	HS			2	4	5	494	146	4	4
Humboldt Bay	3.35	MS	VH	2.1	64			97	3	0	4	5
San Francisco Bay ^b	6.4	MS	VH	1.5	571	600	144	1,837	844	429	9	9

^aHS = highly stratified; MS = moderately stratified; VH = vertically homogeneous.^bIncludes San Pablo and Suisun bays.

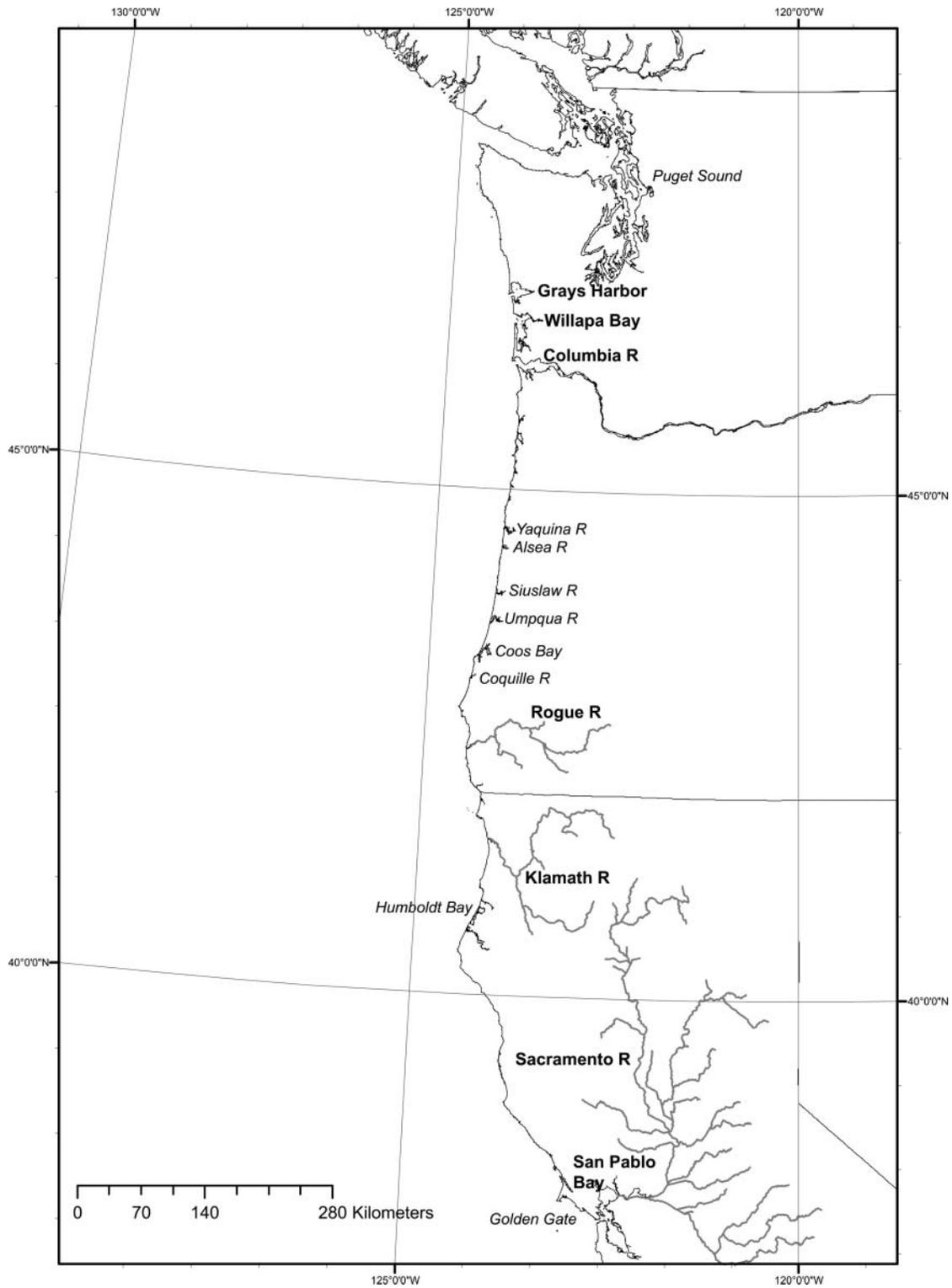


FIGURE 1. Map of the study region. The rivers and estuaries where green sturgeon were tagged and released are in bold type. Receivers were placed in those locations as well as in the other estuaries and bays shown on the map.

TABLE 2. Summary of green sturgeon release groups. Abbreviations are as follows: N = number tagged and released; min, max = minimum and maximum lengths.

Location	Release year	N	Mean TL (cm)	SD	Min	Max
Columbia River	2004	12	171	21	139	210
Grays Harbor	2005	39	173	23	124	240
Klamath River	2002	12	188	13	164	207
	2003	24	185	15	155	220
	2004	8	191	12	175	213
Rogue River	2005	8	186	13	173	203
	2002	10	171	11	153	196
	2003	44	180	17	145	216
Sacramento River	2004	4	177	10	168	189
	2005	54	188	14	161	213
San Pablo Bay	2004	54	135	20	110	203
	2005	39	151	23	115	204
Willapa Bay	2003	30	153	19	120	195
	2004	17	149	21	122	198

surface area of the mixing zone, and average annual inflow) and dummy variables that correspond to factors (detection and release sites and their interaction, and site characteristics such as the degree of stratification during high- and low-flow periods), and β is a vector of parameters. The main effects of release site and detection site are not of particular interest, as we expect the detection locations to have different detection rates due to differences in receiver coverage. Similarly, release groups may differ in their overall detection probabilities due to differential survival or other vagaries of the sampling. It is the interaction between release and detection sites that is of particular interest, as this is what indicates whether different release groups have different distributions among estuaries. The relative effect of release location, fish length, and physical attributes of the estuaries on detection probabilities was determined by comparing the fit of models with and without these terms using Akaike's information criterion (AIC; Akaike 1974). Models with lower AIC scores are preferred, and a difference of more than 2 is considered to indicate a substantially better fit (Burnham and Anderson 1998).

To gain some insight into potential differences in migratory behavior among individual green sturgeon, we characterized each individual in terms of whether it was detected at different nonnatal estuaries and bays and in quarters of the years 2005 and 2006. Further analysis was conducted on 121 green sturgeon that were detected at three or more time-place combinations. Detection or nondetection at the set of time and place combinations was represented by a vector of ones and zeros. Dissimilarity of the migration history vectors of any two individuals was quantified by Jaccard's distance, J_d , (Legendre and Legendre 1998), determined as

$$J_d = 1 - \frac{a}{a + b + c} = \frac{b + c}{a + b + c}, \quad (2)$$

where a is the number of locations where both individuals were present, and b and c are the numbers of locations where one of the individuals was present but not the other. Note that joint absences do not effect J_d . We then created a binary cluster tree from the matrix of J_d values using the unweighted pair-group method with arithmetic mean algorithm. The binary cluster tree was used to order individual presence-absence plots such that similar histories were plotted near each other. To identify which, if any, of the clusters identified by the clustering analysis were statistically significant, we used the similarity profile method of Clarke et al. (2008) as implemented in PRIMER version 6 with 1,000 permutations and a significance level of 0.01. Potential differences in the length of fish in putative clusters were investigated with analysis of variance (ANOVA).

The probability that a green sturgeon entering an estuary would be detected by receivers in that estuary was evaluated with capture-recapture models for closed populations (Borchers et al. 2002). The population in this context is assumed to consist of those green sturgeon making use of the estuary during some or all of a season, and individual receivers are viewed as capture "occasions." The simplest model assumes that all receivers have the same detection probability. A more realistic model allows detection probabilities to vary among receivers. Finally, we considered the heterogeneity models of Pledger (2000), which allow for the population to consist of two or more groups of animals with different detection probabilities. Heterogeneity in detection probabilities could arise if, for example, some green sturgeon reside in an estuary for much of the season while others are transients. Accounting for heterogeneous detection probabilities can reduce the bias that arises from violating the assumption that all animals have equal detection probabilities. These different capture-recapture models were fit to the green sturgeon detection data with Program MARK (White 2008).

TABLE 3. Models of the distribution of tagged green sturgeon among detection sites. Abbreviations are as follows: R = release site; D = detection site; E_a = total estuary area; S_h , S_l = stratification during high and low flows; M_a = mixing zone area; F = average inflow; null = common mean; and AIC = Akaike information criterion.

Detection year	Model	AIC
2005	$R + D + R \times D$	803.8
	$R + D$	885.2
	D	916.8
	$R + E_a + S_h + S_l + M_a + F$	1,009
	$E_a + S_h + S_l + M_a + F$	1,036
	R	1,107
	Null	1,133
	2006	$R + D + R \times D$
$R + D$		1,386
D		1,523
R		1,558
$R + E_a + S_h + S_l + M_a + F$		1,529
$E_a + S_h + S_l + M_a + F$		1,662
Null		1,690

RESULTS

Detection probabilities for receiver arrays were estimated to be quite high, with maximum likelihood estimates ranging from 98% to 100% depending on the estuary and model. Given the high detection rates and similarity of estimates among models, we did not attempt to expand observations for detection efficiency.

In both 2005 and 2006, fish from different release sites were distributed differently among detection sites, as indicated by the much lower AIC value for the model that included the interaction between release and detection site effects (Table 3). The significant effect of release site indicates that overall detection rates were not the same for all groups, and the significant effect of detection site indicates that rates of detection varied among detection sites for all release groups. Models with effects due only to physical characteristics of the estuary fit the data poorly compared with the best model, but they did have better fit than the null model and the model that allowed for differences due only to release group, which suggests that some variation in the use of estuaries is related to physical differences among the estuaries.

2005 Detections

Willapa Bay, the lower Columbia River, the Umpqua River estuary, and the Golden Gate area of San Francisco Bay were used by many tagged green sturgeon in 2005 (Figure 2). The temporal pattern of detections in the nonnatal estuaries was similar, with peak numbers of individuals observed in summer

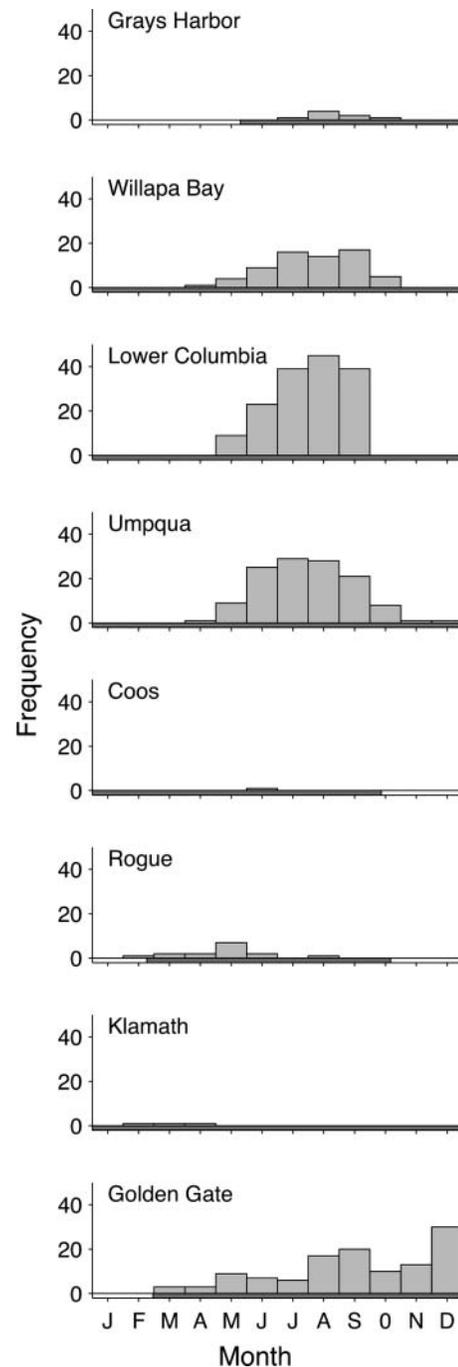


FIGURE 2. Numbers of individual green sturgeon tagged in 2004 or earlier and detected at detection sites in 2005, by month. The gray bars along the x-axes indicate the periods of receiver deployment. The plots are arranged from north to south.

months. Natal estuaries were used less frequently, and detections began earlier in the year (February–March). No tagged green sturgeon were detected in the Coquille River estuary.

Green sturgeon exhibited fidelity to natal rivers: fish tagged in the Sacramento River or San Pablo Bay were frequently

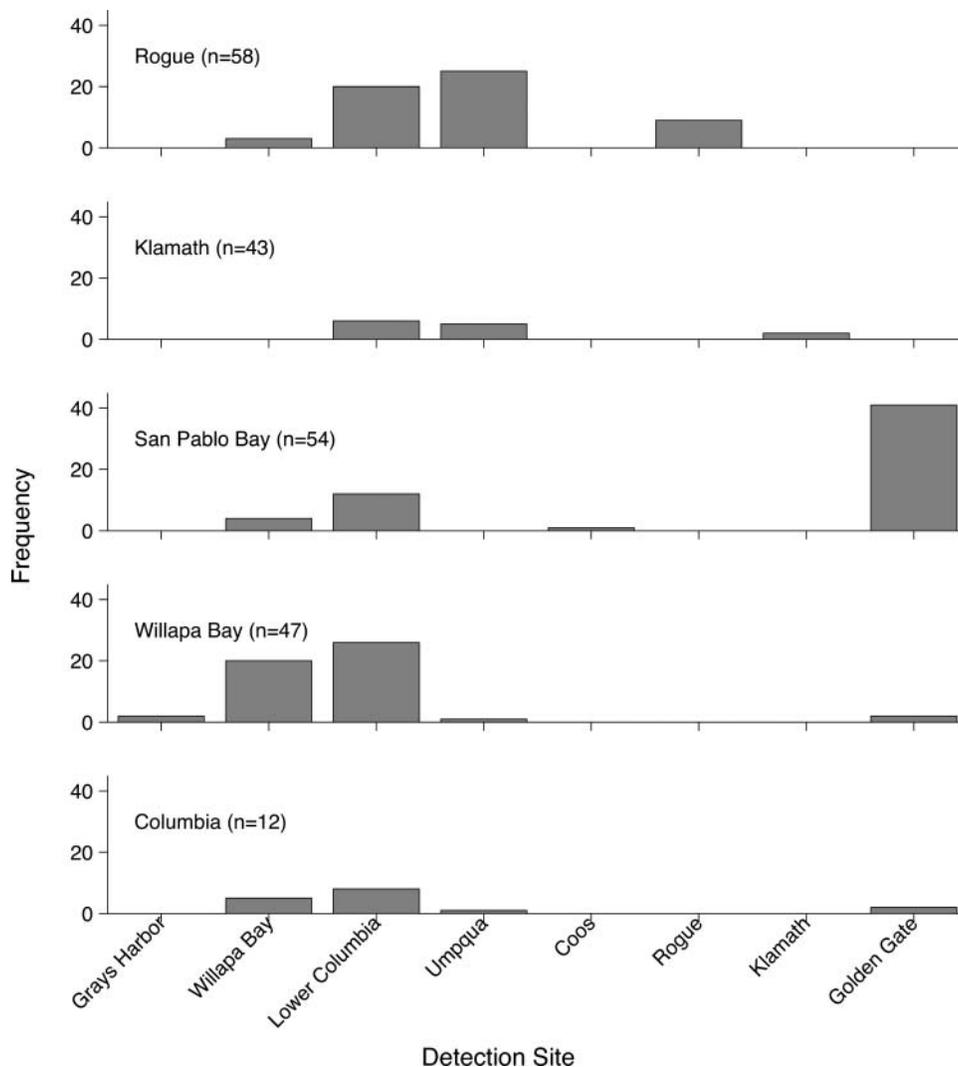


FIGURE 3. Detections of green sturgeon tagged at five tagging locations in 2004 or earlier at detection locations in 2005. The panel for the tagging locations are arranged from north to south; n = the size of the release group.

detected in San Pablo Bay but were never detected in the Klamath or Rogue river estuaries, while green sturgeon tagged in those rivers were detected as they returned to those river estuaries but were not detected in San Francisco Bay (Figure 3). Green sturgeon tagged in the Rogue and Klamath rivers also made extensive use of the lower Columbia River and the Umpqua River estuary and lesser use of Willapa Bay. Those green sturgeon tagged in San Pablo Bay, and presumably of southern DPS origin, were also detected at a high rate in the lower Columbia River and in San Francisco Bay; four fish were detected in Willapa Bay, and a single fish entered Coos Bay for a brief period.

Green sturgeon tagged in Willapa Bay or the lower Columbia River, which were potentially of Klamath, Rogue, or Sacramento river origin, moved freely between the lower Columbia River and Willapa Bay (Figure 3). In both cases, two fish from these release groups were detected at the Golden Gate and one was de-

tected in the Umpqua River. None were detected in the Klamath or Rogue rivers in 2005.

2006 Detections

In 2006, the Siuslaw river estuary, Humboldt Bay, Yaquina Bay, and Alsea Bay were monitored in addition to the sites monitored in 2005 (except the Coquille River estuary, which was not monitored in 2006). Grays Harbor and the Sacramento River were added as release sites in 2005, contributing to detections in 2006. Patterns observed in 2006 were broadly similar to those in 2005 (Figure 4), with high rates of usage apparent in Willapa Bay, the lower Columbia River, and the Umpqua River estuary. Many more green sturgeon were detected in Grays Harbor in 2006 than in 2005, most likely because of improved receiver coverage in 2006. Fewer tagged green sturgeon were detected in Humboldt Bay, but the temporal distribution of these

detections was similar to that of larger nonnatal river estuaries. Very few tagged green sturgeon were detected in the Siuslaw River estuary or Coos Bay. Detections of green sturgeon at the Golden Gate occurred in all months of the year except December 2006 (although many were detected in December 2005). Puget Sound was used at a low rate, but green sturgeon were detected there in winter as well as summer months. A single green sturgeon entered Alsea Bay for 1 d in June, and another was detected near the mouth of Yaquina Bay over the course of 3 h but not on receivers inside the bay (not shown in Figure 4).

As indicated by the logistic regression analysis, green sturgeon tagged at different locations had distinct patterns of distribution among the estuaries (Figure 5). Green sturgeon from Sacramento River and San Pablo Bay had similar patterns of detection in 2006, with high detection rates in Grays Harbor, Willapa Bay, and the lower Columbia River. Sacramento River green sturgeon were detected at higher rates than San Pablo Bay green sturgeon at these sites but were not detected in Humboldt Bay where four San Pablo Bay green sturgeon were detected. Conversely, two green sturgeon from the Sacramento River were detected in the Umpqua River estuary and another in Yaquina Bay in 2006, where no San Pablo Bay green sturgeon were detected. For green sturgeon from the Rogue and Klamath rivers, seven and four fish, respectively, were detected in Grays Harbor in 2006 (Figure 5), where none had been detected in 2005. Two Klamath fish entered Puget Sound and one entered the Rogue River in 2006, but no tagged green sturgeon were detected in the Klamath River that year. Two Rogue River fish entered the Siuslaw River estuary and Humboldt Bay. No Klamath or Rogue river fish were detected at the Golden Gate. Green sturgeon tagged in Grays Harbor, Willapa Bay, and the lower Columbia River were subsequently detected as they returned to the estuary where they were originally tagged and to the other large estuaries, indicating frequent movement among systems.

Movement of Individuals

Of the 355 green sturgeon tagged in this study, 121 were subsequently detected at three or more season–location combinations. Many of these individuals exhibited extensive movements among estuaries over the course of the study (Figure 6). Similarity profile analysis indicated eight statistically significant clusters within the migration histories. One cluster of green sturgeon (group 3) made heavy use of the Umpqua River estuary in the spring and summer of both 2005 and 2006. Green sturgeon in this group were predominately tagged and released in the Rogue and Klamath rivers, although two Sacramento River fish exhibited this behavior. Most individuals in this group were not detected in other estuaries, although a few were also detected in Humboldt Bay, the Siuslaw River estuary, Willapa Bay, and Grays Harbor.

Another distinct group (group 4) made heavy use of San Francisco Bay throughout the year but was not detected frequently at other locations. Fish in this group were tagged and released

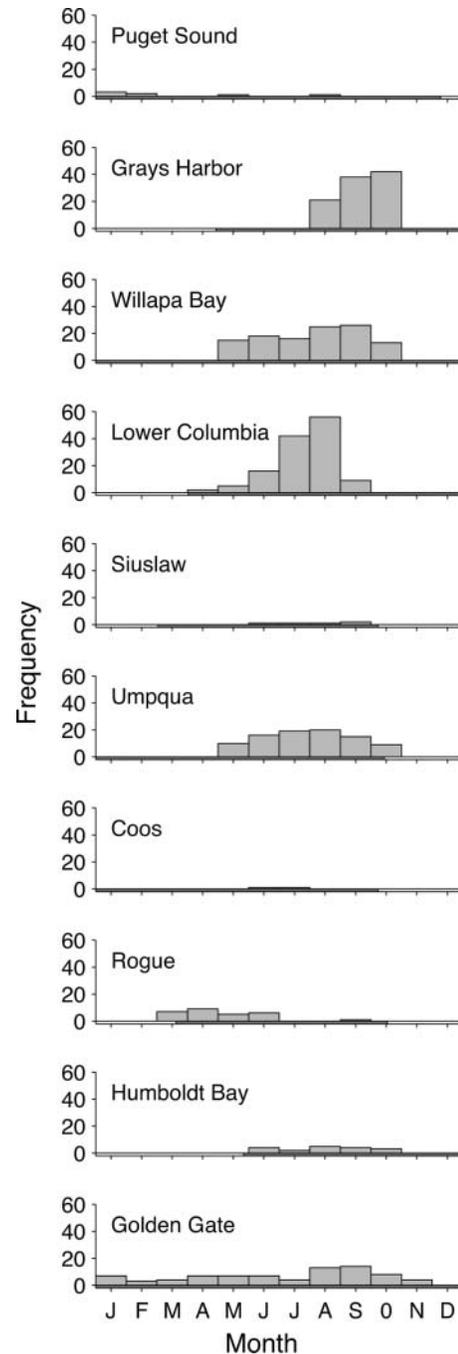


FIGURE 4. Numbers of individual green sturgeon tagged in 2005 or earlier and detected at detection sites in 2006, by month. See Figure 2 for additional details.

predominately in San Pablo Bay and Grays Harbor. Some fish in this group did exhibit movements among San Francisco Bay and Humboldt Bay, the lower Columbia River, Willapa Bay, and Grays Harbor.

Two other groups of fish (groups 7 and 8) made use of San Francisco Bay but were also detected frequently in Grays Harbor, the lower Columbia River, and Willapa Bay. They differed

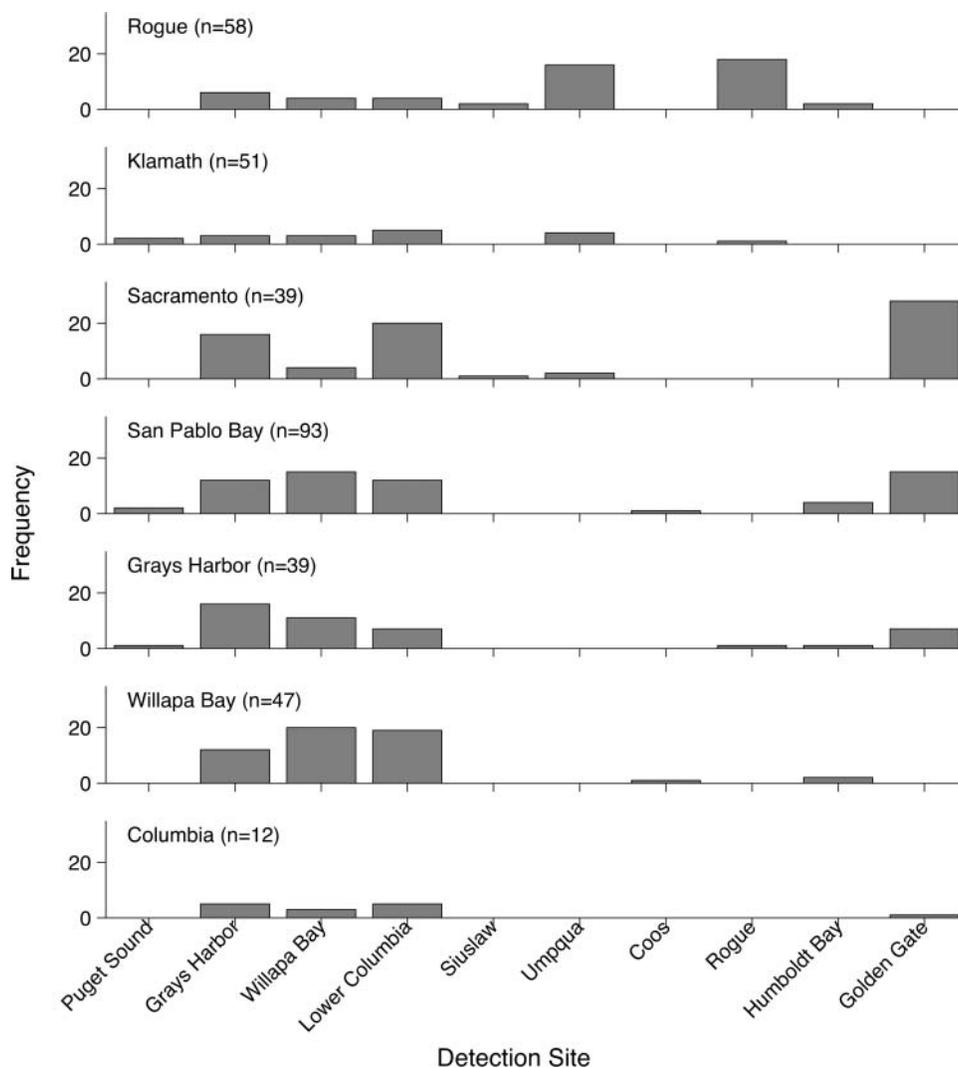


FIGURE 5. Detections of green sturgeon tagged at seven tagging locations in 2005 or earlier at detection locations in 2006. See Figure 3 for additional details.

in the timing of their detections at the Golden Gate. Group 7, detected at the Golden Gate in the fall of 2005, consisted predominantly of fish tagged that year in the Sacramento River that were presumably emigrating from the river after spawning. Green sturgeon in group 8 were detected at the Golden Gate in the summer of 2005 but not detected at the Golden Gate in 2006; these fish were tagged and released in the Sacramento River, San Pablo Bay, Grays Harbor, and Willapa Bay.

The final major group of fish (group 6) was rarely detected outside of Grays Harbor, the lower Columbia River, and Willapa Bay. This group is represented by fish tagged and released in all of the release locations. Many individuals in this group moved among all three estuaries during the course of the study.

The remaining clusters identified by similarity profile analysis contained only one to five individuals. One of these small groups of fish (group 5, five fish) was characterized by its use of

Humboldt Bay; individuals in this group typically were detected in some other estuary as well. A single fish tagged in San Pablo Bay fell into a group (group 1) by itself due to its use of Puget Sound and Coos Bay. Finally, two green sturgeon tagged in the Sacramento River were detected at the Golden Gate in the fall of 2005 and in the Umpqua estuary in 2006 (group 2).

The mean size of green sturgeon differed among the eight groups identified by the clustering procedure (ANOVA: $F_{5,115} = 5.61$, $P < 0.001$, $n = 121$). The group making extensive use of the lower Columbia River, Willapa Bay, and Grays Harbor but not San Francisco Bay (group 6 in Figure 6; mean TL = 137 cm) was made up of fish significantly smaller than those in the group that used these areas but were also detected at the Golden Gate (group 7; mean TL = 175 cm) or the group making extensive use of the Umpqua River estuary (group 3; mean TL = 181 cm). These latter two groups were not significantly different in length (Bonferroni post hoc comparison, $\alpha = 0.05$).

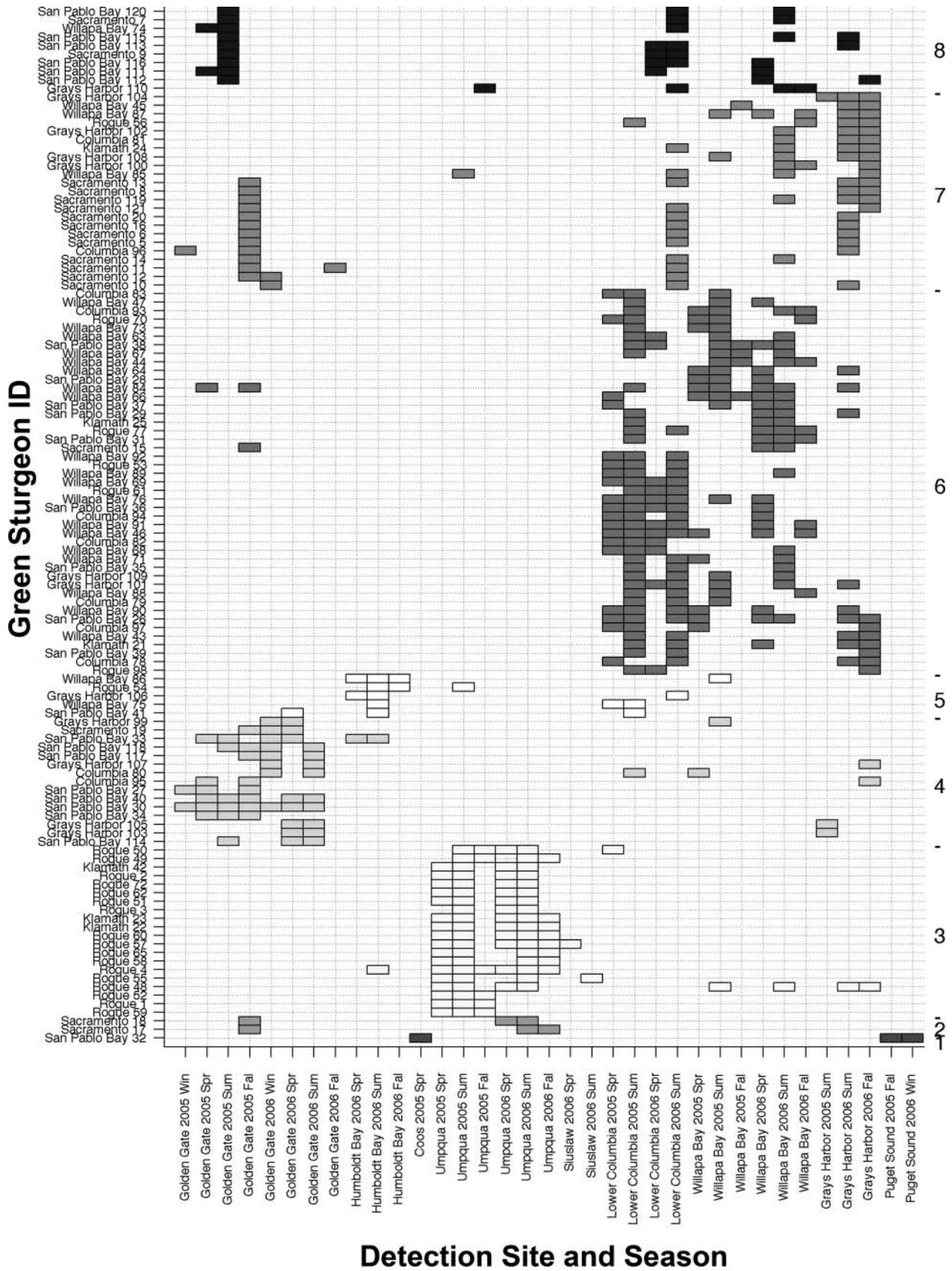


FIGURE 6. Movements of individual green sturgeon among estuaries in 2005 and 2006. The 121 individuals detected at three or more season–location combinations were clustered using the UPGMA linkage algorithm based on the Jaccard distances between their patterns of presence–absence; the clusters (shaded differently and labeled on the right side of the y-axis) were identified by similarity profile analysis based on 1,000 permutations and a significance level of 0.01.

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DISCUSSION

The results presented confirm the population structure of the species, show that green sturgeon migrate seasonally among a variety of estuarine, riverine, and marine habitats and reveal important intrapopulation diversity in migratory behavior. In the following discussion of these findings, one should bear in mind two limitations of our study. First, while the number of electronic tags deployed was relatively large for a study of this type, larger sample sizes would probably reveal more patterns of habitat use and movement that are too uncommon to be detected reliably in the present study. Additionally, we monitored a subset of West Coast estuaries for up to 2 years. We are unable to say how green sturgeon may or may not use estuaries that were not monitored. Finally, we should expect that habitat use patterns will vary among years at the population level (because of the ways in which green sturgeon may respond to changing environmental conditions) as well as at the individual level (owing to ontogenetic shifts).

Population Structure

Acoustic tagging results support the delineation of green sturgeon into southern and northern DPSs (Adams et al. 2007), as no fish tagged in the Klamath or Rogue rivers were detected at the Golden Gate and no fish tagged in San Pablo Bay or the Sacramento River were detected in the Rogue or Klamath rivers. The detection of a fish in the Rogue River that had been tagged and released in the Klamath River is consistent with these two spawning areas comprising a single DPS, as was the Klamath River recovery (at river kilometer 45) of a green sturgeon that had been tagged in the Rogue River (B. McCovey, Jr., personal observation), the detection in the lower Klamath River of a radio-tagged green sturgeon from the Rogue River (Erickson et al. 2002), and the lack of genetic differentiation of fish captured in these rivers (Israel et al. 2004). A low level of exchange of individuals between the Rogue and Klamath rivers explains the observed lack of genetic differentiation between these sites (Israel et al. 2004, 2009). Low levels of migration among populations (such as a few migrants per generation) are sufficient to erase differences in the frequencies of neutral markers (Felsenstein 1976). From a demographic perspective, however, movement between these populations does not appear to be common, thereby making it appropriate to manage the Klamath and Rogue River populations separately for many purposes.

Our results also provide further insight into the population structure of green sturgeon in nonnatal estuaries. Green sturgeon made significant use of these estuaries in the summer, and some moved among different estuaries during the summer, which confirms the findings of Moser and Lindley (2007). Non-natal estuaries support aggregations of green sturgeon from both DPSs, although certain estuaries seem to be used preferentially by green sturgeon from certain rivers (the most notable case is the high affinity of northern DPS green sturgeon for the Umpqua River estuary).

Electronic tags, which can determine the probability of individuals using certain habitats, and population genetics methods, which can determine the proportional composition of a sample from a habitat, offer complementary information about stock composition and habitat selection differences. Israel et al. (2004, 2009) used population genetics data to show that green sturgeon collected in the Columbia River were predominately southern DPS fish. Based on the presumption that southern DPS green sturgeon are less numerous than northern DPS green sturgeon (Adams et al. 2007), Israel et al. (2009) concluded that southern DPS green sturgeon make preferential use of the Columbia River estuary. We found that in 2005 northern DPS green sturgeon used the Columbia River estuary at a high frequency relative to green sturgeon tagged in San Pablo Bay, and that in 2006 northern DPS green sturgeon used the Columbia River at a lower but not insignificant rate compared with that of southern DPS green sturgeon. There are two potential implications of these results. First, there may be substantial interannual variation in the use of some habitats among populations of green sturgeon. Second, southern DPS green sturgeon may be more abundant or the northern DPS green sturgeon may be less abundant than supposed by Adams et al. (2007). Another explanation of the apparent discrepancy between the population genetics and tagging data are the relatively small sample sizes and potentially unrepresentative sampling of either or both of the studies. Estimates of population size associated with each spawning river are urgently needed to resolve this question, as the status of northern DPS green sturgeon may be less secure than presently thought.

Patterns of Estuary Use

Green sturgeon from both the southern and northern DPSs make frequent use of Willapa Bay, Grays Harbor, and the Columbia River estuary during summer and early autumn months, which confirms the importance of these areas as aggregation sites where green sturgeon may be vulnerable to exploitation or being bycaught in fisheries (Moser and Lindley 2007). The retention of green sturgeon in various fisheries in these estuaries was banned by the states of Washington and Oregon in 2006 and 2007, which greatly reduced the threat posed by fisheries in these waters, although discard mortality may be a concern. These large estuaries are clearly important habitats for green sturgeon, which emphasizes the need to better understand how green sturgeon use them so that habitat features and functions can be best conserved. Moser and Lindley (2007) suggested that growth opportunities for green sturgeon are higher in estuaries because estuaries are warmer than shelf waters and food is abundant.

The Umpqua River estuary was also used heavily for summer and autumn holding. No tagged sturgeon were detected before May, so entry into the Umpqua River was probably not related to spawning migrations. Adams et al. (2007) reported that two juvenile green sturgeon have been captured roughly 150 km up the Umpqua River, but intensive sampling by Oregon Department

of Fish and Wildlife captured no green sturgeon above the tidal influence in 2002–2004. Our observations support the assertion of Adams et al. (2007) that spawning by green sturgeon in the Umpqua River is rare, given that many especially large green sturgeon were detected in the estuary, but none were detected by a hydrophone upstream from tidal influence.

The temporal pattern of detections in San Francisco Bay is different from that observed in large, more northerly estuaries. This probably reflects the use of San Francisco Bay and the Sacramento–San Joaquin River estuary as a migration corridor by green sturgeon en route to spawning grounds, while others use the estuary for feeding or other nonreproductive purposes. Heublein et al. (2009) found that of 90 green sturgeon tagged in San Francisco Bay, only 11 moved up into the Sacramento River, which suggests that many green sturgeon enter the bay for purposes other than spawning.

The pattern of detections in the Klamath and Rogue rivers is consistent with spawning migrations, with entry beginning in February or March. The onset of spawning migrations is similar to that reported by Erickson and Webb (2007) for the Rogue River but somewhat earlier than reported by Benson et al. (2007) for the Klamath River, although Benson et al. (2007) apparently did not sample in late winter or early spring. Both the Klamath River and the Rogue River have very small estuaries (Table 1), and the paucity of detections in summer months is consistent with the idea that green sturgeon are using these estuaries as migration corridors on their way to spawning grounds.

In summary, the large estuaries along the West Coast of southern Washington, Oregon, and northern California appear to be important habitats for both northern and southern DPS green sturgeon, while the much smaller Umpqua River estuary appears to be especially important to northern DPS green sturgeon. Green sturgeon move among these estuaries and natal rivers as part of their migration to spawning rivers, overwintering habitat in the coastal ocean (Lindley et al. 2009), and summer–fall holding or feeding habitat.

Intrapopulation Diversity in Migratory Behavior

Our results show that there is significant variation in migratory behavior and habitat use within green sturgeon populations. Some of this variation is related to the size of the green sturgeon. Smaller fish make extensive use of the large estuaries in Washington in summer. Many large fish also exhibit this behavior, but some spend the summer in the Umpqua River estuary and do not use the large estuaries. The differences observed in migratory behavior do not correspond perfectly with natal origin. Rather, there is diversity in migratory behaviors within populations.

A number of hypotheses have been put forward to explain intrapopulation variation in migratory behavior, including genetic polymorphisms, state-dependent migration (e.g., Forseth et al. 1999; Nøttestad et al. 1999; Brodersen et al. 2008; Jørgensen et al. 2008), density-dependent habitat selection, and entrainment (whereby fish learn migration routes from other fish [Dodson 1988; Rose 1993; McQuinn 1997; Corten 2002; ICES

2007]). These hypotheses are not generally mutually exclusive and none can be rejected by our data. Assuming that green sturgeon spawning in the same river are part of a panmictic population, genetic polymorphism seems an unlikely explanation for differential patterns of estuary use within populations but could be responsible for differences between populations. In the absence of abundance estimates for green sturgeon we can say nothing about density-dependent habitat selection.

State-dependent migration is consistent with our observation of significant size differences among migratory contingents and the differences in distribution of fish tagged in San Pablo Bay (a mixture of small and large fish, perhaps not all of which are mature) and in the Sacramento River (generally large, mature individuals). If migration is an adaptation that allows exploitation of resources that fluctuate in time and space (Dingle and Drake 2007), green sturgeon should change their pattern of migration as they grow and mature to meet their changing resource requirements.

Several lines of evidence also support the entrainment hypothesis. Sturgeon exhibit cohesive social behavior (Sulak et al. 2002; Allen et al. 2009), are long-lived, have overlapping age cohorts, and in the case of green sturgeon, migrate along predictable routes (Erickson and Hightower 2007; Lindley et al. 2008), all of which are factors that enhance opportunities for social learning (Dodson 1988). Small and apparently immature green sturgeon have been observed migrating to spawning areas (Heublein et al. 2009), a behavior shared with other sturgeon species (Sulak and Randall 2002). Social learning of migration behaviors has been documented for coral reef fishes (Helfman and Schultz 1984; Warner 1988) and explains patterns of habitat use by fish species as diverse as Pacific herring *Clupea pallasii*, Pacific sardine *Sardinops sagax*, striped bass, bluefin tuna *Thunnus thynnus*, northern anchovy *Engraulis mordax*, and Pacific whiting *Merluccius productus* (ICES 2007).

If the existence of migratory contingents within populations of green sturgeon is due to entrainment, there are important management implications (ICES 2007). Entrainment creates a spatial memory for the population, which can be maladaptive under some circumstances. For example, a contingent may continue to use a habitat for several generations after the habitat has become suboptimal. Overexploitation in one habitat could have a “vacuuming” effect on contingents, which could cause a decline in abundance in other areas (Secor et al. 2009; Kerr et al. 2010). In the extreme case, overexploitation can extirpate a subpopulation, and habitats used by that subpopulation may remain unused even if the overall population recovers rapidly. One implication of these possibilities for long-lived fish, like green sturgeon, is that current patterns of habitat use and levels of abundance might reflect the impacts of habitat degradation or fishing activities that occurred in previous decades. Spatial memory within populations, caused by delaying population responses to environmental changes, would make it difficult to discover the cause-and-effect relationships that drive the dynamics of green sturgeon populations. Given that green sturgeon may

live for 40–60 years (Emmett et al. 1991; Moyle 2002), the delay between habitat degradation and population response could be quite long.

Conversely, if green sturgeon contingents reflect state-dependent migration or density-dependent habitat selection, habitat degradation would have a different but subtle effect (Sutherland 1996). As the quality of one habitat declines, contingents using that habitat would move to other areas and increase competition in those habitats. In this way, contingents never exposed to the degraded habitat might still suffer lower growth and survival. A corollary of the state-dependent migration hypothesis is that the Umpqua River estuary differs in some important ways from the other study estuaries. Sulak and Randall (2002) hypothesized that many sturgeon species fast for several months to control their growth. Given that members of the contingent making use of the Umpqua River estuary were relatively large, perhaps that estuary is a favorable area for holding and fasting. Regardless of how green sturgeon contingents arise, the existence of such natural variation in behavior warrants conservation, as it is a source of resilience for the population (Secor and Rooker 2005). The persistence of a diversity of high-quality estuarine habitats is fundamental to the maintenance of this behavioral diversity.

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