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[Article]

Marine Migration of North American Green Sturgeon

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Abstract.—An understanding of the distribution of North American green sturgeon *Acipenser medirostris* in coastal waters is crucial to minimize impacts on this vulnerable species from various fisheries. To determine migratory patterns, we tagged 213 subadult and adult green sturgeon in spawning rivers and summer aggregation areas with uniquely coded ultrasonic pingers and observed their coastal movements with arrays of automated hydrophones deployed along the West Coast of North America from southeast Alaska to Monterey Bay, California. Green sturgeon exhibited an annual migration along the continental shelf from U.S. to Canadian waters in the fall and an apparent return migration in the spring. Peak migration rates exceeded 50 km/d during the springtime southward migration. Large numbers of green sturgeon were detected near Brooks Peninsula on northwest Vancouver Island, British Columbia, during May–June and October–November. A single fish was detected in southeast Alaska in December. This pattern of detections suggests that important overwintering grounds may be north of Vancouver Island and south of Cape Spencer, Alaska. A high frequency of detection allowed us to estimate that annual survival of tagged green sturgeon was 0.83 in 2004. The rapid, frequent long-distance migrations by these fish may make them vulnerable to bycatch in bottom trawl fisheries on the shelf waters of western North America.

The green sturgeon *Acipenser medirostris* is a species of rising conservation concern in North America. The green sturgeon is classified as a species of special concern under the Canadian Species at Risk Act. In the United States, the distinct population segment that spawns in the Sacramento River basin, California, is listed as threatened under the federal Endangered Species Act (ESA). The other distinct population segment, which spawns in rivers in northern California and southern Oregon, is listed as a species of concern. Green sturgeon are known to spawn at present in only three rivers: the Sacramento and Klamath rivers in northern California and the Rogue River in southern Oregon. Green sturgeon are anadromous and use a wide variety of habitats over their lifetime. Juveniles spend perhaps 2 years rearing in their natal river and then leave for other, presumably marine, habitats

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before returning to spawn at about age 15 and every 2–4 years thereafter (Moyle 2002; Erickson and Webb 2007). Green sturgeon enter their natal river and spawn in the spring and typically leave the river during the subsequent autumn (Erickson et al. 2002; Benson et al. 2007; Erickson and Webb 2007). Thus, while green sturgeon are dependent upon freshwater habitats in their natal rivers for critical portions of their life cycle, they spend most of their lives elsewhere and activities far removed from the natal river may affect them.

Migrations of green sturgeon outside of their natal rivers are poorly understood. They have been encountered in marine waters between Baja, California, and the Bering Sea (Erickson et al. 2002; Moyle 2002), and they typically remain in waters less than 100 m deep (Erickson and Hightower 2007). Green sturgeon also frequent certain bays and estuaries of nonnatal rivers during summer and early fall (Moser and Lindley 2007). The timing and frequency of movements among these different habitats is poorly understood, because conventional external marking programs have resulted in only a handful of recaptures (Adams et al. 2002). If individual green sturgeon are highly migratory, they may be exposed to numerous coastal and estuarine fisheries.

Like other sturgeon species, green sturgeon populations are vulnerable to overfishing due to their late age at maturation (Boreman 1997; Pikitch et al. 2005; Heppell 2007). Green sturgeon are taken as bycatch in coastal trawl fisheries from Monterey Bay to the Bering Sea (Glavin 1996; Moyle 2002; Erickson and Hightower 2007), but the extent to which fish from the three spawning rivers interact with these fisheries is unknown. Genetic evidence suggests that green sturgeon from different populations may use some nonnatal habitats differentially (Israel et al. 2004). This has important implications for management and conservation. More generally, our poor understanding of the basic biology and demography of green sturgeon impedes effective management, which adds to the concern for their conservation (Rochard et al. 1990; Bemis and Kynard 1997; Musick et al. 2000; Adams et al. 2007).

Recently, significant insights into the migratory habits of marine fishes have been gained from electronic tagging, especially with archival geolocation tags (e.g., Lutcavage et al. 1999; Boustany et al. 2002; Stokesbury et al. 2004; Block et al. 2005). Archival geolocation tags have had limited success in deployments on green sturgeon (Erickson and Hightower 2007), perhaps because of day length estimation errors caused by topographic interference or residence in relatively deep, turbid waters (as compared with pelagic species in the open ocean). Coded ultrasonic pinger tags coupled with stationary data-logging hydrophones, however, are well suited to green sturgeon and have been used successfully in studies of their freshwater (Benson et al. 2007; Erickson and Webb 2007) and estuarine (Kelly et al. 2007; Moser and Lindley 2007) habitat use. This method has been used to document migration of a white sturgeon *A. transmontanus* from the Klamath River to the Fraser River (Welch et al. 2006) and migrations of Atlantic cod *Gadus morhua* off the eastern coast of Canada (Comeau et al. 2002).

In the past few years, large numbers of hydrophones capable of detecting ultrasonic tags have been deployed on the continental shelf of western North America to monitor populations of tagged Pacific salmon (Welch et al. 2003) and other species, providing an opportunity to elucidate the migratory behavior of green sturgeon. The long life (3–5 years) of ultrasonic tags offers the additional prospect of generating information on demographic rates, such as reproductive periodicity (Erickson and Webb 2007) and survival. We captured 213 green sturgeon in known spawning rivers and in estuaries of nonnatal rivers and tagged the fish with coded ultrasonic pingers. We report herein the detection of these tagged fish on hydrophones deployed between Monterey Bay, California, and Cape Spencer, Alaska; describe migratory patterns during 2004–2005; and provide an estimate of annual survival for 2004.

Methods

Hydrophone arrays.—The movement of tagged green sturgeon through coastal waters was detected by arrays of stationary data-logging hydrophones (Vemco, Shad Bay, Nova Scotia; Model VR2). These hydrophones detect and decode the ultrasonic pulses from pinger tags within 500–1,000 m, logging the tag code and time of detection to internal storage. Arrays were moored on the continental shelf between Monterey Bay and Cape Spencer (Figure 1). Hydrophones were deployed either in a curtain formation across the shelf, typically spaced 800–850 m apart, or in a more limited spatial arrangement (e.g., in a grid near Seal Rock, Oregon). Hydrophones were generally on or near the seafloor as part of a subsurface mooring. Details of the moorings deployed off of British Columbia and Washington can be found in Welch et al. (2003, 2004). Deployment periods varied according to designs and logistical constraints of the individual studies. In this paper, we report detection data for 2004 and 2005.

All hydrophone arrays were operated as part of studies of species other than green sturgeon: the Alaska, British Columbia, and Washington arrays were

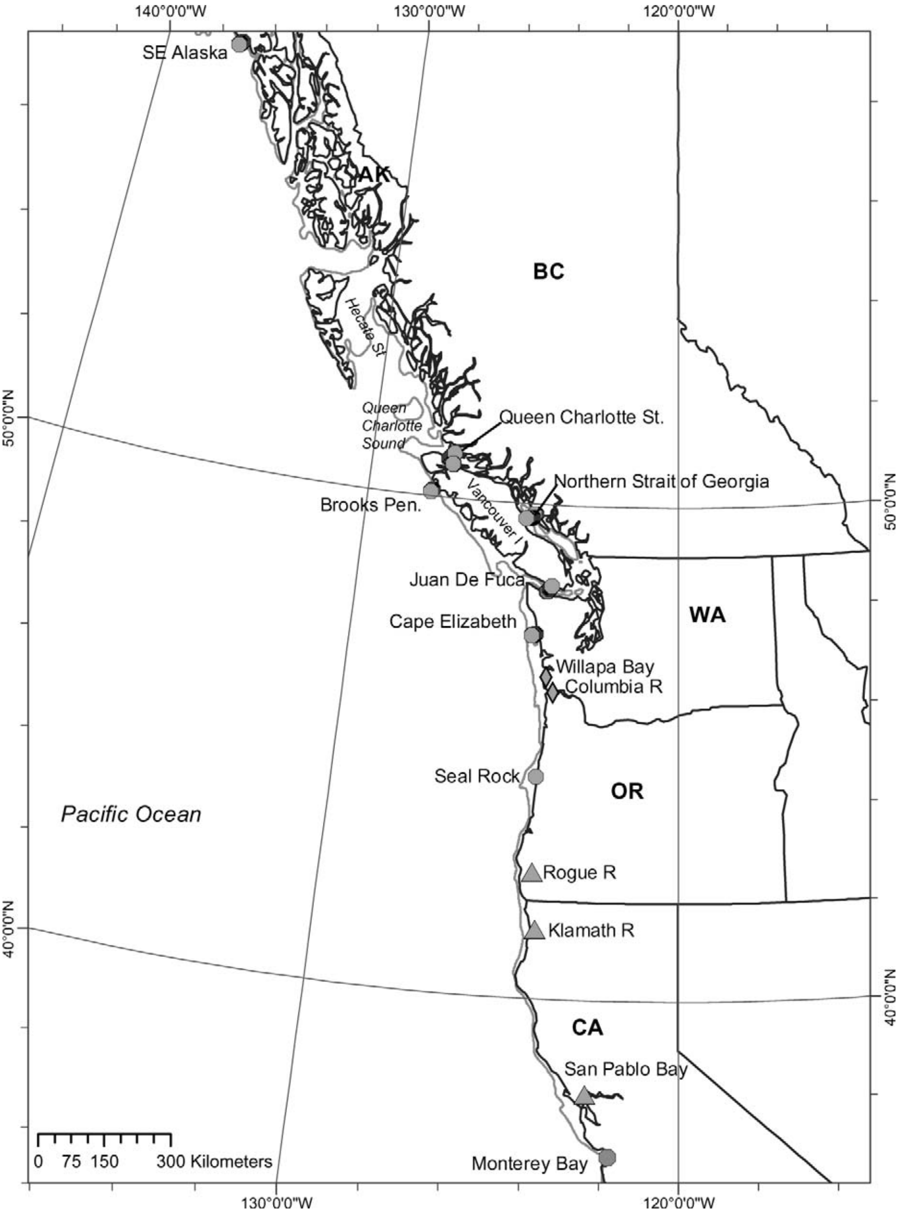

FIGURE 1.—Map of the study area from southeast Alaska to central California, where movements of pinger-tagged green sturgeon were monitored by hydrophone arrays (gray octagons). Locations of spawning population tagging (gray triangles) and nonspawning aggregations (gray diamonds) are indicated. The light gray line along the coast shows the 100-m isobath.

operated for salmonids as part of the Pacific Ocean Shelf Tracking (POST) program, the Oregon array was operated for rockfishes *Sebastes* spp., and the Monterey Bay array was operated for several species of shark. Because green sturgeon rarely inhabit depths greater than 100 m and because of the high power output of the pingers used, we expected that tagged green sturgeon would be readily detected as they passed hydrophone arrays. In particular, operating POST arrays should provide very high detection rates for tagged green sturgeon due to the tight spacing of hydrophones from the shoreline to the edge of the continental shelf. Taken together, the ensemble of receiver arrays was well situated to detect movements in the coastal ocean between Monterey Bay and southeast Alaska, extending much farther north and south than the green

TABLE 1.—The number (n) and mean, minimum (min) and maximum (max) fork length (cm) of green sturgeon that were pinger tagged at various West Coast locations in 2002–2004.

Location	Number and FL (cm)	2002	2003	2004
Columbia River, Washington	n			12
	Mean			155
	Min			125
	Max			186
Klamath River, California	n	12	23	8
	Mean	173	171	175
	Min	150	140	160
	Max	191	203	196
Rogue River, Oregon	n	10	43	4
	Mean	156	166	168
	Min	138	136	158
	Max	174	197	179
San Pablo Bay, California	n			54
	Mean			122
	Min			99
	Max			187
Willapa Bay, Washington	n		30	17
	Mean		139	136
	Min		109	112
	Max		177	180

sturgeon active migration area suggested by limited tagging data (Erickson and Hightower 2007).

Fish capture and tagging.—Details of 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 (Callianassidae) as bait. In spawning rivers, small, sinking monofilament gill nets (~33 m long) were deployed from jet boats in suspected holding areas, typically deep pools. Nets were fished for 30–60 min. In bays and estuaries, larger sinking gill nets (~100 m long) were deployed using commercial gill-net boats and sets lasted 20–45 min. Total length (TL) and fork length (FL) of each captured fish were measured; fish greater than 1.1 m TL were retained for tagging. During 2002–2004, green sturgeon were tagged in the Columbia River estuary, Klamath River, Rogue River, San Pablo Bay (California), and Willapa Bay (Washington; Table 1). Uniquely coded ultrasonic pinger tags (Vemco V16-6H) were implanted surgically into the abdominal cavity. The V16-6H tag has a 16-mm diameter and a length of 90 mm and weighs 14 g in water. Tag life ranges from 3 to 5 years depending on pulse transmission configuration. Tags were sterilized with benzalkonium chloride and inserted through a 2.5-cm incision that was 2 cm from the midline, midway between the insertion points of the pectoral and pelvic fins. Incisions were closed with sutures and the fish were released immediately.

Data analysis.—To answer the question of whether green sturgeon tagged and released in different geographic locations (Rogue, Klamath, and Columbia rivers; San Pablo and Willapa bays; and Grays Harbor) are subsequently distributed differently, we used a generalized linear model with binomial error structure and logistic link (Lindsey 1997) in R software to analyze the frequency of detection on hydrophone lines for fish released at these locations. Release site and receiving line locations were treated as factors. The response variable was the fraction of green sturgeon tagged in 2004 or earlier that were detected in 2005 on a marine hydrophone line; the number known to be alive in 2005 was used as a weight in the model. The number alive was determined from acoustic detections of fish on the hydrophone arrays described previously and on any other hydrophones (S.T.L., unpublished data); in other words, if a fish was detected anywhere during 2005, it was assumed to be alive during that year.

The survival rate of the 96 green sturgeon tagged in 2003 was estimated for 2004 from detections in 2004 and 2005 using the Cormack–Jolly–Seber (CJS) model for live recaptures (Burnham et al. 1987) as implemented in Program MARK (White and Burnham 1999). We formed capture histories for each fish by defining three capture sessions corresponding to tagging in 2003 and acoustic detection during 2004 and 2005. We note that while acoustic detection data violate the assumption that the recapture period is of negligible duration compared with the period between capture sessions, this assumption is commonly violated in mark–recapture studies based on live resightings, such as cetacean studies (e.g., Caswell et al. 1999; Fujiwara and Caswell 2002).

To estimate migration speed, we divided the distance between the lines by the time elapsed between the last detection on one hydrophone line and the first detection on another hydrophone line. The distance between hydrophone arrays was estimated using a geographic information system assuming that the fish followed the shortest possible path between arrays while remaining between the shore and the 100-m isobath.

Results

We tagged 213 green sturgeon between 2002 and 2004 (summarized in Table 1). Of these, 115 were subsequently detected on one or more hydrophone arrays in the ocean, and an additional 46 fish were detected by hydrophones in rivers, bays, or estuaries. The size of tagged green sturgeon varied by capture site (analysis of variance: $F_{4,208} = 78.68$, $P < 0.001$, $n = 213$). Fish captured in the Klamath and Rogue rivers,

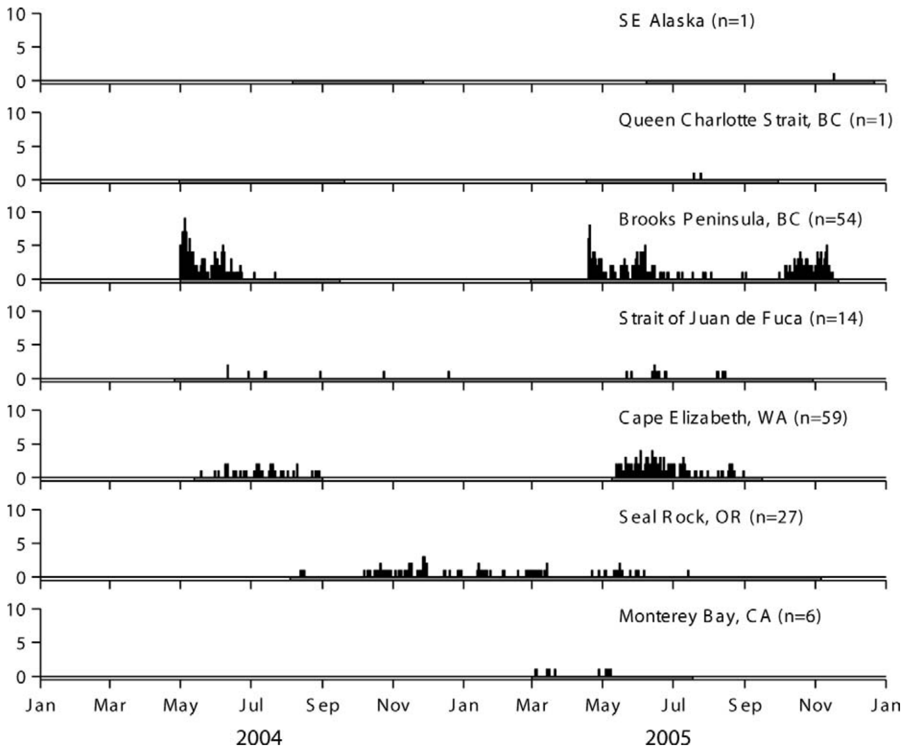

FIGURE 2.—Detections of pinger-tagged green sturgeon by hydrophone arrays along the West Coast of North America ($n =$ total number of unique fish observed at each location). Bar height indicates the number of unique fish observed per day. Gray horizontal boxes along the *x*-axes indicate deployment periods for hydrophone arrays.

both of which are spawning areas, were the largest, averaging 156–175 cm FL. The other tagging areas were used by a mixture of mature and immature fish; thus, mean sizes were smaller, but maximum sizes were similar.

At least one tagged green sturgeon was detected at all marine hydrophone arrays except the northern Strait of Georgia array in 2004–2005 (Figure 2). A single green sturgeon was detected on the southeast Alaska line in the winter of 2005, and another individual was detected on the Queen Charlotte Strait line in the summer of 2005. Numerous green sturgeon were detected on the Brooks Peninsula line; up to nine unique individuals were detected on a single day in 2004. Tagged green sturgeon were continuously present in the vicinity of the Brooks Peninsula line during May–June 2004 and 2005 and October–December 2005. These periods correspond fairly closely to the operation times of the Brooks Peninsula line. A few green sturgeon were detected on the Strait of Juan de Fuca line, but there was little apparent temporal pattern to the detections. A pattern of detections similar to that observed on the Brooks Peninsula line was observed on the Cape Elizabeth line during periods when both lines were in operation, although there were relatively more detections in summer months on the Cape Elizabeth line than on the Brooks Peninsula line. Green sturgeon were frequently detected on the Seal Rock line and were also detected on the Monterey Bay line during its brief period of operation.

Seventy-seven individual fish were observed at more than one hydrophone array, providing direct evidence of migration by individuals. The maximum migration rate observed was 58 km/d (Table 2), and 12 of the movements were made at rates greater than 40 km/d. These rapid movements were observed for fish moving from the north to the south between Brooks Peninsula or the Strait of Juan de Fuca and Cape Elizabeth in June (Figure 3). Northerly movements were generally less rapid (<39 km/d), although estimated northward velocities may be biased because the Cape Elizabeth and Brooks Peninsula lines were not operating during the fall and winter of 2004. Speeds of 40 km/d correspond to roughly 0.25 body lengths per second (BL/s) for fish with a TL of 2 m. In spring 2004 and 2005, green sturgeon were detected first on the Brooks Peninsula line and on the Cape Elizabeth line. In fall

TABLE 2.—Mean migration rate of pinger-tagged green sturgeon as determined by movement between hydrophone arrays along the West Coast of North America. Values in parentheses are observed minimum and maximum rates.

Movement trajectory[a]	Mean migration rate (km/d)	*n*
Brooks to Cape Elizabeth	32.44 (1.09, 58.40)	24
Brooks to Juan de Fuca	32.63 (25.79, 39.53)	6
Brooks to QCS	6.10	1
Brooks to Seal Rock	4.47	1
Cape Elizabeth to Brooks	7.63 (1.04, 38.42)	17
Cape Elizabeth to Juan de Fuca	19.73 (0.58, 31.49)	3
Cape Elizabeth to Seal Rock	2.79 (1.90, 4.04)	3
Juan de Fuca to Brooks	1.99 (1.50, 2.49)	2
Juan de Fuca to Cape Elizabeth	35.29 (0.73, 53.52)	8
Juan de Fuca to Seal Rock	19.32	1
QCS to Brooks	35.26	1
Seal Rock to Brooks	4.21	1
Seal Rock to Cape Elizabeth	10.38 (1.18, 28.70)	7
Seal Rock to Juan de Fuca	23.70	1
Seal Rock to Monterey Bay	2.03	1

[a] Hydrophone locations are Brooks Peninsula (Brooks), British Columbia (BC); Cape Elizabeth, Washington; Strait of Juan de Fuca (Juan de Fuca); Queen Charlotte Strait (QCS), BC; Seal Rock, Oregon; and Monterey Bay, California.

2005, green sturgeon were detected at the Brooks Peninsula line after being detected at the Cape Elizabeth line in the previous spring. These detection patterns indicate that many (but not all) green sturgeon make annual migrations along the coast in the spring and fall; spend winters in marine waters north of Vancouver Island and south of southeast Alaska; and spend summers in the coastal waters, bays, and estuaries of Washington, Oregon, and California.

Further insight into green sturgeon behavior was obtained by examining detection patterns of seven fish that were observed moving among hydrophone lines three or more times (Figure 4). Three of the seven fish (Figure 4B, C, and E) exhibited a rapid southward movement from the Brooks Peninsula line to the Cape Elizabeth line during the late spring or early summer of 2004. These fish were detected during the next spring or summer on the Brooks Peninsula line, which indicates that they migrated north along the coast between these detection periods probably during non-operation periods for the Brooks Peninsula and Cape Elizabeth lines. Five of the seven fish passed the Strait of Juan de Fuca line in summer on a southward migration (the exception is shown in Figure 4G; this fish came north from Seal Rock and migrated through Cape Elizabeth to the Strait of Juan de Fuca before returning south). The relatively brief periods between the first and last detections on the Strait of Juan de Fuca line are consistent with a migration pathway that hugs the coastline along the southern tip of Vancouver Island and extends through the Strait of Juan de Fuca somewhere east of the Strait of Juan de Fuca line, where the water is relatively shallow. Presumably, most green sturgeon migrating between Canadian and U.S. waters cross the Strait of Juan de Fuca over deep water to the west of the Strait of Juan de Fuca line.

Green sturgeon tagged in different locations were not distributed identically in the ocean (Figure 5). Fish from all tagging locations were detected on the Brooks Peninsula and Cape Elizabeth lines, but the Strait of Juan de Fuca and Monterey Bay lines detected fish tagged in Willapa Bay, San Pablo Bay, and the Rogue River. Tagging location, line location, and their interaction each lead to significant reductions in model

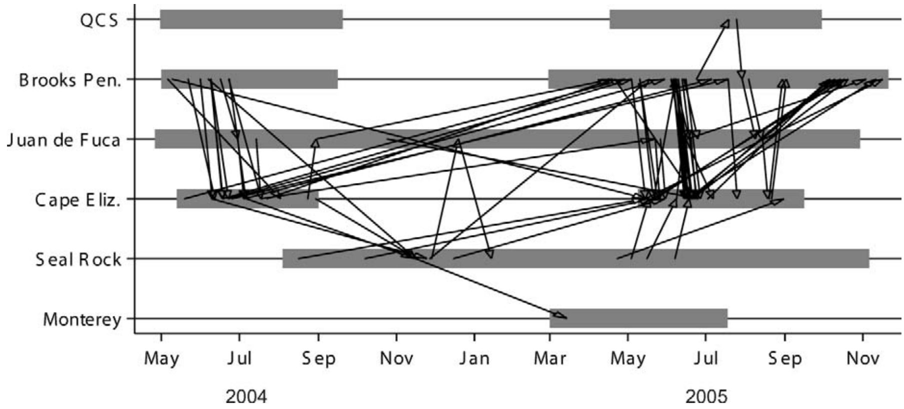

FIGURE 3.—Movements of pinger-tagged green sturgeon between hydrophone arrays along the West Coast of North America (Queen Charlotte Strait [QCS], British Columbia [BC]; Brooks Peninsula [Brooks Pen.], BC; Strait of Juan de Fuca; Cape Elizabeth [Cape Eliz.], Washington; Seal Rock, Oregon; and Monterey Bay [Monterey], California). Horizontal gray bars indicate deployment periods for hydrophone arrays. Arrow tails indicate the final date of detection on the corresponding line; arrowheads indicate the first date of subsequent detection on another hydrophone array. Arrow lines that cross time lines indicate nondetection at those arrays.

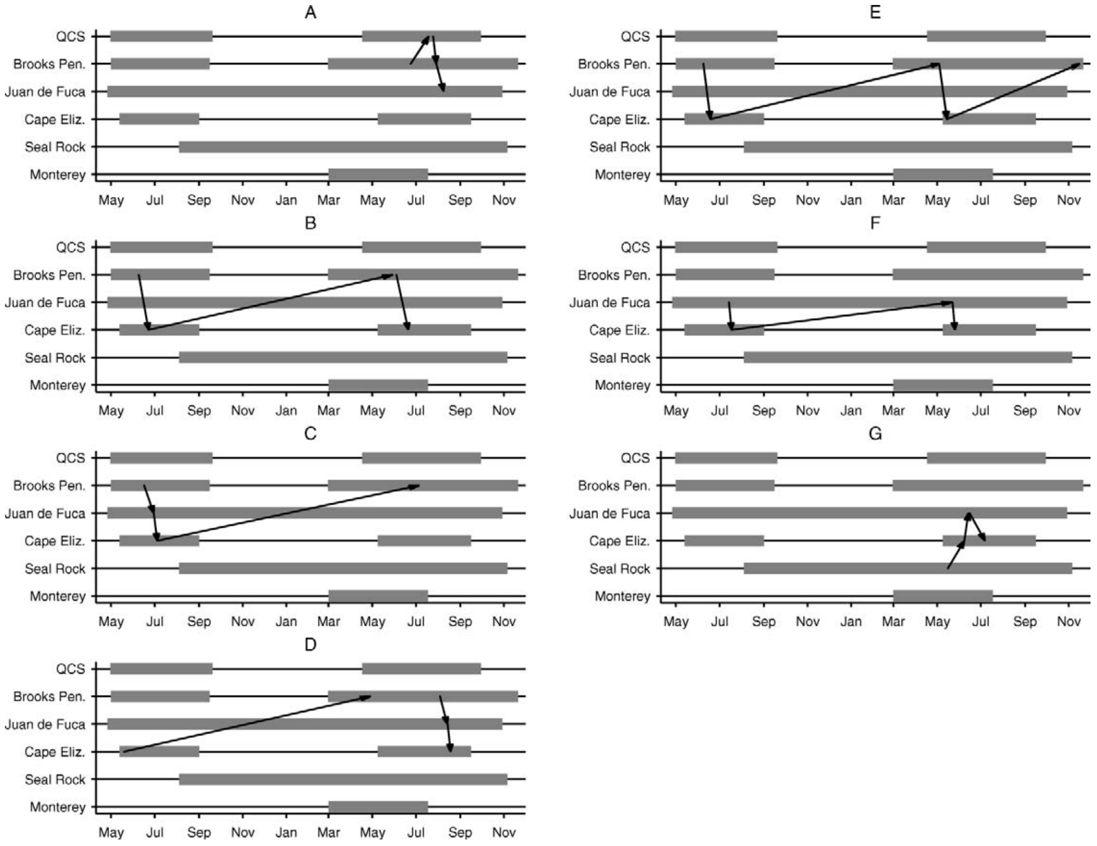

FIGURE 4.—Movements among hydrophone lines along the West Coast of North America by pinger-tagged green sturgeon individuals that were detected on three or more lines. Hydrophone sites and symbols are defined in Figure 3.

deviance (Table 3). The significant line location effect means that detection rates differed among lines for all fish, and the significant tagging location effect means that the overall rate of detection differed among fish for all lines. The highly significant interaction term indicates that the pattern of detections among lines differed depending on the tagging location. This implies that fish from different groups have different patterns of migration.

Fish tagged in 2003 had an apparent annual survival rate in 2004 of 0.83 (95% confidence interval [CI] = 0.72–0.90). This should be viewed as a minimum survival estimate, because it includes tag loss, tagging-induced mortality, and emigration from the study area. The hydrophones on the continental shelf detected 75% (95% CI = 64–84%) of the tag group estimated to be alive in 2004.

Discussion

Our tagging results broadly corroborate and add substantial detail to the general distributional information for green sturgeon reported by Moyle (2002) and Erickson and Hightower (2007). Only one green sturgeon was detected on the southeast Alaska line, suggesting that use of the Bering Sea and Aleutian archipelago is uncommon for North American green sturgeon. Green sturgeon have been captured in fisheries in the these waters but could possibly be Sakhalin sturgeon *A. mikadoi*, a morphologically similar (North et al. 2002) but genetically distinct species (Birstein et al. 1993) that is endangered (Birstein et al. 1997). The Bering Sea and Aleutian Islands are subject to intensive trawl fisheries (Rose and Jorgensen 2005), and it would be beneficial for fisheries observers to gather additional data and samples that would allow sturgeon taken in these areas to be identified to species. Due to the limited deployment of the Monterey Bay array and the lack of arrays south of that point, our study does not provide much new insight into the degree to which green sturgeon use coastal waters in central or southern California.

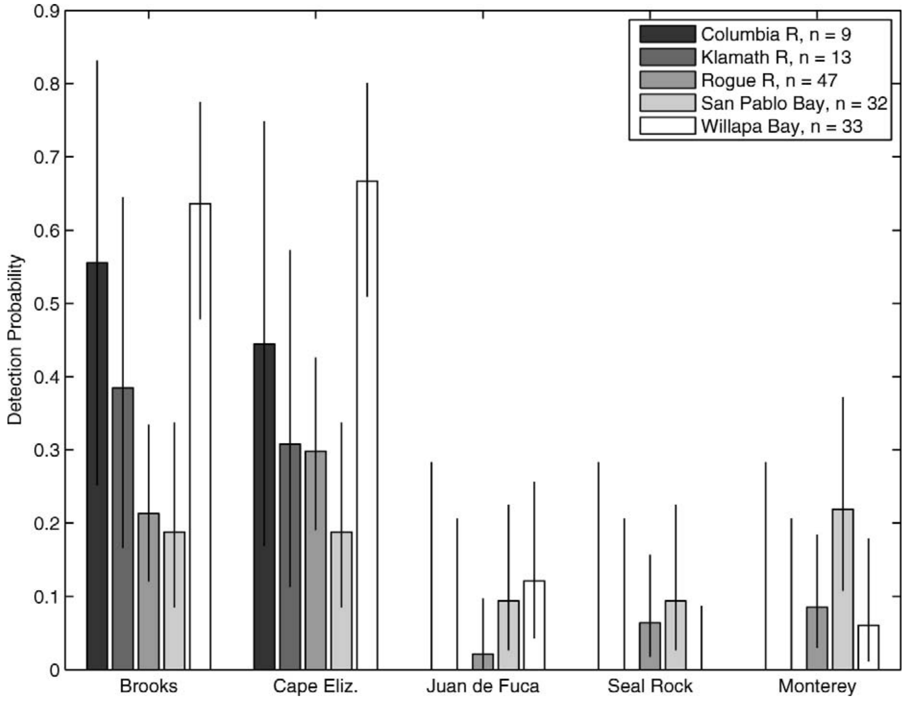

FIGURE 5.—Probability (±90% CIs) of detection on marine hydrophone arrays (Brooks Peninsula [Brooks], British Columbia; Cape Elizabeth [Cape Eliz.], Washington; Strait of Juan de Fuca; Seal Rock, Oregon; and Monterey Bay [Monterey], California)for green sturgeon that were pinger tagged in five locations along the West Coast of North America (Willapa Bay and Columbia River, Washington; Rogue River, Oregon; and Klamath River and San Pablo Bay, California).

Our study revealed that green sturgeon make rapid, long-distance seasonal migrations along the continental shelf of North America, at least between central California and central British Columbia. Quinn and Brodeur (1991) defined migration as "movements of individuals coordinated in space and time ... accompanied by return movements," and they distinguished migratory movements from dispersal and movements within a home range. Movements of green sturgeon observed in this study are clearly coordinated in space and time; in the fall, many tagged green sturgeon move northward along the continental shelf to or past northern Vancouver Island, where they appear to spend the winter. Many of these fish migrate southward again in the spring and are known to spend summers in bays and estuaries (Moser and Lindley 2007) or rivers (Erickson et al. 2002). Furthermore, green sturgeon exhibited rates of travel consistent with directed movements; peak velocities during the northern migration approached 0.25 BL/s, which is about one-third of the critical swimming velocity of age-0 and older green sturgeon (Lankford et al. 2005) but near the sustained swimming speed of lake sturgeon *A. fulvescens* (Peake et al. 1997). Peak velocities were quite similar to the mean velocities of green sturgeon making directed movements within San Francisco Bay (Kelly et al. 2007) and down the Klamath River (Benson et al. 2007). Northward movements were somewhat slower: the maximum observed velocity was 38 km/d. The difference between northward and southward migration velocities may be partly due to currents, since the nearshore core of the California Current has a southward velocity of 1–3 cm/s (0.9–2.6 km/d: Marchesiello et al. 2003) over the shelf in waters 25–75 m deep (where green sturgeon are common). Similar, although less-extensive, coastal migrations have been documented for Atlantic sturgeon *A.*

TABLE 3.—Analysis of deviance in models of pinger-tagged green sturgeon detection frequency on West Coast marine hydrophone lines. Factors were tagging site (tag) and hydrophone site (line).

Model	Deviance reduction	Residual df	Residual deviance	$P\ (>\chi^2)$
Null		24	158.6	
Tag	18.1	20	140.5	0.001
Tag + line	99.58	16	40.88	<0.001
Tag + line + tag × line	40.88	0	0.00	0.001

oxyrinchus (Laney et al. 2007) and Gulf sturgeon *A. oxyrinchus desotoi* (Edwards et al. 2007).

While a significant fraction of the tagged green sturgeon exhibited migratory behavior, it appears that some tagged fish did not make large-scale migrations. Differential migration is a common phenomenon in birds (Berthold 1993) and has been observed in Atlantic cod (Comeau et al. 2002). The most direct evidence for differential migration was the observation of nine green sturgeon on the Seal Rock line in winter 2004–2005 (Figure 2), during which many fish were inferred to be north of Vancouver Island. Moreover, a slight majority of tagged fish was not detected on ocean hydrophones or was detected on only one hydrophone. Perhaps these fish did not migrate within range of hydrophones or only migrated when the hydrophone lines were inactive. They may also have migrated south, where hydrophone deployments were spatially and temporally limited. These alternatives could be resolved in future studies by expanding the arrays and operating them year-round.

According to the model of Northcote (1978), fish migrate among three basic types of habitat (spawning, feeding, and wintering) to optimize feeding and reproduction, avoid unfavorable conditions, and enhance colonization. Presumably, the choice of wintering habitat balances the need to avoid unfavorable conditions, the need to feed, and the energetic cost of migrating from spawning or feeding habitats. In temperate regions, migratory fishes (Harden Jones 1968; Leggett 1977; Quinn and Brodeur 1991), birds (Berthold 1993) and cetaceans (Lockyer and Brown 1981) frequently move poleward for feeding in the summer and then move toward the equator to overwinter at lower latitudes. In contrast with most other temperate animals, green sturgeon in our study were observed to overwinter at high latitudes, which agrees with the pop-off satellite tag data of Erickson and Hightower (2007).

At present, we can only speculate on the advantages of this behavior, noting that there are broad areas of relatively shallow water north of Vancouver Island, in Queen Charlotte Sound, and in Hecate Strait (Figure 1). These waters are warmer in winter than might be expected from their latitude due to frequent, storm-driven advection of surface waters from the southeast and are somewhat protected from wave action by the Queen Charlotte Islands (Crawford and Thomson 1991). Coastal waters off the western coast of Vancouver Island are highly productive and are characterized by some of the highest fishery yields of resident fish (e.g., herrings and groundfish) along the West Coast of North America; this is partially attributable to high rates and efficient retention of primary production in this area (Ware and Thomson 2005). Benthic invertebrates are abundant throughout the year on the western Canadian continental shelf (Brinkhurst 1991). Before spawning in late winter or early spring (Hay and McCarter 1997), Pacific herring *Clupea pallasii* overwinter in these areas in dense schools near the bottom (Outram 1965), where they may be vulnerable to predation by green sturgeon. Some gray whales *Eschrichtius robustus* migrate to these waters to feed benthically in spring and summer on dense populations of ampeliscid amphipods, ghost shrimp, and herring eggs (Oliver et al. 1984; Darling et al. 1998). The feeding habits of green sturgeon are poorly known, but according to Moyle (2002), green sturgeon prey upon benthic invertebrates and occasionally fishes, such as sand lances *Ammodytes* spp. and anchovies (Engraulidae). Examination of the stomach contents, energetic condition, and lipid biomarker profile of green sturgeon captured on their summer and winter grounds would clarify the roles of migration and overwintering in the species' life history.

Green sturgeon are highly migratory and prone to aggregating in restricted areas; this behavior has important implications for their conservation. The western coast of Vancouver Island, Queen Charlotte Sound, and Hecate Strait are subject to an intensive bottom trawl fishery (Kulka and Pitcher 2001), and catches of green sturgeon have been observed in these fisheries (Figure 6). Our tagging results indicate that green sturgeon populations that spawn in the USA, including one under ESA protection, could be affected by Canadian bottom trawl fisheries in addition to the U.S. bottom trawl fisheries identified by Erickson and Hightower (2007). More generally, green sturgeon move frequently among waters under the jurisdiction of a variety of state, provincial, and national entities, which will make coordinating conservation actions a challenge.

The 2004 survival estimate of 0.83 is similar to the estimate of 0.87 produced by Beamesderfer et al. (2007) from a catch curve analysis that indicated a natural mortality rate of 0.08 and a harvest mortality rate of 0.05. Pine et al. (2001) found that a Gulf sturgeon population with an annual adult survival rate of 0.84 was increasing in abundance but that a slight increase in mortality would cause the population to decline. Gulf sturgeon mature around age 10 (Huff 1975), while green sturgeon mature at age 15 (Moyle 2002), suggesting that Gulf sturgeon can sustain higher natural and fishing mortality than green sturgeon can. Given the general similarities between green sturgeon and Gulf sturgeon life histories, it is reasonable to suspect that green sturgeon populations may also be highly sensitive to small changes in adult mortality

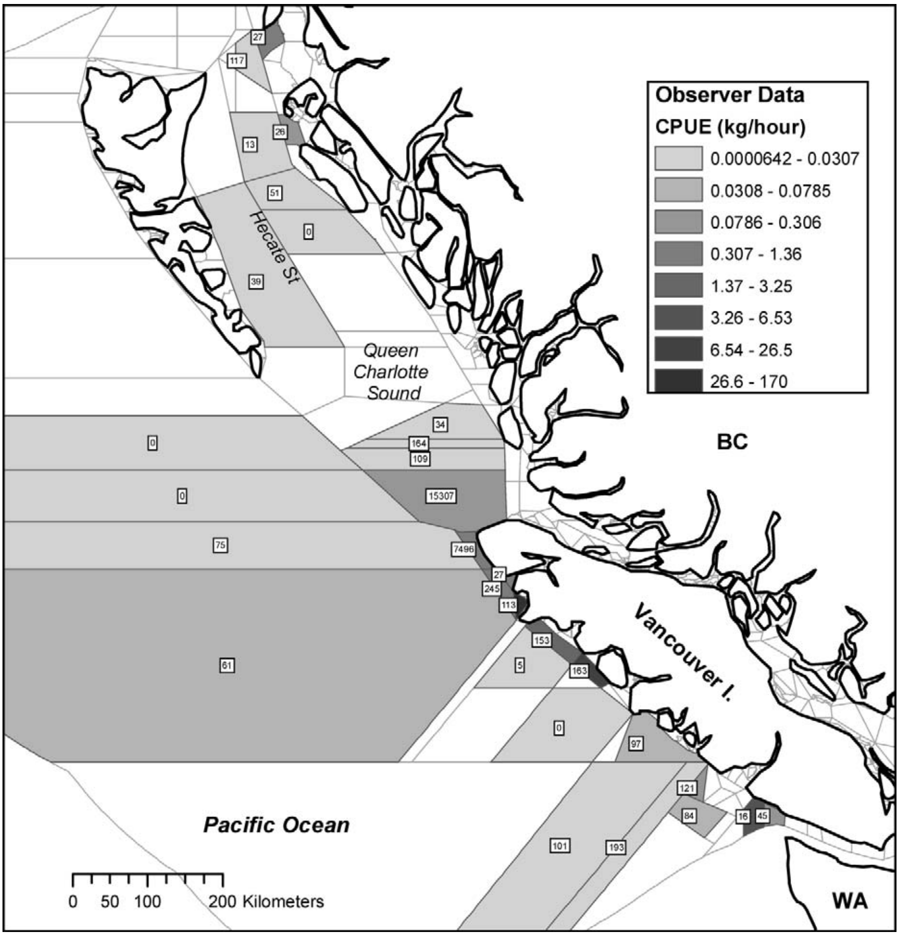

FIGURE 6.—Observed catch of green sturgeon by the Canadian bottom trawl fishery during 1996–2006. Polygons delimit Canada Department of Fisheries and Oceans (CDFO) statistical areas, which are gray-scale coded to indicate bycatch (catch per unit effort [CPUE], kg/h); total catch (kg) is denoted by numbers in small boxes. Data are from the PacHarvTrawl database of Canadian trawl landings during 1996–2007 (CDFO Pacific Biological Station, Nanaimo, British Columbia, unpublished data).

(Boreman 1997; Heppell 2007). We note, however, that application of the CJS model to acoustic tag detections violates the assumption that the tag recovery period is instantaneous. Although Burnham et al. (1987) suggested that violation of this assumption was the least serious of six assumptions related to study design, survival estimates from the CJS model based on tag detections are expected to be biased. Preliminary simulations suggest that if detections and mortality occur at random within the observation interval, survival will tend to be overestimated because some fish will be seen alive during the interval but will not survive to the end of the interval. Barker (1997) proposed a model that accommodates live resightings and dead recoveries between live recapture periods as well as several forms of temporary emigration. Barker's (1997) model has many more parameters than the CJS model, and it is sensible to place various constraints on some or all of the parameters. In a model comparison setting (Anderson and Burnham 1999), we found that the most parsimonious version of Barker's (1997) model was one that was equivalent to the CJS model; therefore, our data set was too small to support a more complex model that would allow for differences between live resighting rates and live recapture rates. While the data reported here are barely adequate to estimate survival for a single year, long-lived acoustic tags and mark–recapture models offer the potential to estimate and monitor total mortality of green sturgeon and other large fish that are likely to be detected by hydrophones.

Our findings further illustrate the potential that large-scale, coordinated tagging and hydrophone arrays have for advancing our knowledge of marine fish migrations, as noted by Welch et al. (2003). The hydrophones deployed in marine waters used in this study were not primarily operated for detection of green sturgeon but rather were aimed at smaller-scale questions, such as regional migration and early life survival of juvenile salmonids (Welch et al. 2004) and the home ranges of rockfishes and sharks. Consequently, there were gaps in the temporal coverage, a rather coarse spatial coverage outside of the Vancouver Island area, and insufficient coverage in California. The gaps in temporal coverage are particularly problematic because they may bias our view of migratory behaviors, since certain behaviors would not be observable (for example, the timing of the northward migration). Despite these shortcomings, acoustic telemetry has allowed us to greatly expand our knowledge of the migratory behavior of green sturgeon. With continuous temporal coverage over more years and larger tag–release groups, it will be possible to learn much more by applying advanced mark–recapture models capable of estimating survival, migration, and recruitment rates (e.g., Kendall and Nichols 2002; Buckland et al. 2004).

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