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Marine migration of North American green sturgeon

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Abstract

Understanding the distribution of North American green sturgeon (*Acipenser medirostris*) in coastal waters is crucial to minimize impacts on this vulnerable species by various fisheries. To determine their migratory patterns, we tagged 213 sub-adult 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 US to Canadian waters in the fall, with an apparent return migration in the spring. Peak migration rates exceeded 50 km/day during the springtime southward migration. Large numbers of green sturgeon were detected near Brooks Peninsula on northwest Vancouver Island during May-June and Oct-Nov. A single fish was detected in southeast Alaska in December. This pattern of detections suggests that important over-wintering grounds may be north of Vancouver Island and south of Cape Spencer, AK. The high frequency that tagged sturgeon were detected allowed us to estimate that annual survival of tagged fish was 0.83 in 2004. The green sturgeon's rapid, frequent, long distance migrations may make them vulnerable to bycatch in bottom trawl fisheries on the shelf waters of western north America.

Introduction

The green sturgeon (*Acipenser medirostris*, Ayers) is a species of rising conservation concern in North America. Green sturgeon are classified as Special Concern under the Canadian Species at Risk Act. In the United States, the distinct population segment that spawns in the Sacramento River basin, CA, is listed as Threatened under the Endangered Species Act. The other distinct population segment, which spawns in rivers in northern CA and southern OR, is on a list of 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 two years rearing in their natal river and then leave for other, presumably marine, habitats before returning to spawn at about age 15 years and every two to four years thereafter (Moyle, 2002, Erickson and Webb, 2007). Green sturgeon enter their natal river and spawn in the spring, and typically leave the river the following 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 impact them.

Where green sturgeon go when they are not in their natal rivers is poorly understood. They have been encountered in marine waters between Baja, CA and the Bering Sea (Moyle, 2002; Erikson et al., 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 non-natal rivers during summer and early fall months (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).

49 Green sturgeon are taken as bycatch in coastal trawl fisheries from Monterey Bay to the
50 Bering Sea (Erickson and Hightower, 2007; Glavin, 1996; Moyle, 2002), but it is
51 unknown to what extent fish from the three spawning rivers might interact with these
52 fisheries. Genetic evidence suggests that green sturgeon from different populations may
53 use some non-natal habitats differentially (Israel et al., 2004). This has important
54 implications for management and conservation. More generally, our poor understanding
55 of the basic biology and demography of green sturgeon impedes effective management,
56 adding to the conservation concern (Rochard et al., 1990; Bemis and Kynard, 1997;
57 Musick et al., 2000; Adams et al., 2007).

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

71 In the past few years, large numbers of hydrophones capable of detecting ultrasonic
72 tags have been deployed on the continental shelf of North America to monitor
73 populations of tagged salmon (Welch et al., 2003) and other species, providing an
74 opportunity to elucidate the migratory behavior of green sturgeon. The long life (3-5
75 years) of ultrasonic tags offers the additional prospect of generating information on
76 demographic rates such as reproductive periodicity (Erickson and Webb, 2007) and
77 survival. We captured a total of 213 green sturgeon in known spawning rivers and in
78 estuaries of non-natal rivers, and tagged them with coded ultrasonic pingers. In this

paper, we report the detection of these tagged fish on hydrophones deployed between Monterey Bay, CA and Cape Spencer, AK, describe migratory patterns during 2004-05, and provide an estimate of annual survival for 2004.

Materials and methods

Hydrophone arrays

The movement of tagged green sturgeon through coastal waters was detected by arrays of stationary data-logging hydrophones (Vemco model VR2, Shad Bay, Nova Scotia). These hydrophones detect and decode the ultrasonic pulses from pinger tags within 500-1000 m, logging the tag code and time of detection to internal storage. Arrays were moored on the continental shelf between Monterey Bay, CA and southeast AK (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, OR). Hydrophones were generally on or near the seafloor as part of a subsurface mooring. Details of the moorings deployed off of BC and WA can be found in Welch et al. (2003) and Welch et al. (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 of these hydrophone arrays were operated as part of studies of species other than green sturgeon: the AK, BC and WA arrays were operated for salmonids as part of the Pacific Ocean Shelf Tracking (POST) program, the OR array for *Sebastes* spp., and the Monterey Bay array for several species of shark. Because green sturgeon rarely exceed depths of 100 m, and the high power output of the pingers used, we expect that tagged green sturgeon would be readily detected as they pass hydrophone arrays. In particular, the POST arrays should provide very high detection rates for tagged green sturgeon when they are in operation, 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, CA and southeast Alaska, extending much further north and south than the area in

which limited tagging data suggests green sturgeon actively migrate (Erickson and Hightower, 2007).

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 (Callianassidae) as bait. In spawning rivers, small sinking monofilament gillnets (≈ 33 m long) were deployed from jet boats in suspected holding areas, typically deep pools. Nets were fished for 30 to 60 minutes. In bays and estuaries, larger sinking gillnets (≈ 100 m long) were deployed using commercial gillnet boats, with sets lasting 20-45 minutes. Total and fork length of each captured fish was measured, and sturgeon greater than 1.1 m total length were retained for tagging. Over the 2002-2004 period, green sturgeon were tagged in the Columbia River estuary, the Klamath River, CA, the Rogue River, OR, San Pablo Bay, CA, and Willapa Bay, WA (Table 1). Uniquely-coded ultrasonic pinger tags (Vemco V16-6H) were implanted surgically into the abdominal cavity of the sturgeon. The V16-6H tag has a 16 mm diameter and length of 90 mm, and weighs 14 g in water. Tag life ranges from three to five years, depending on pulse transmission configuration. Tags were sterilized with benzalkonium chloride and inserted through a 2.5 cm incision that was 2 cm off of 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, Columbia rivers, San Pablo and Willapa bays, and Grays Harbor) are subsequently distributed differently, we analyzed the frequency of detection on hydrophone lines of sturgeon released at these different locations using a generalized linear model (GLM) with binomial error structure and logistic link (Lindsey, 1997), using the GLM function of R. Release site location and receiving line

location 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, with the number known alive used as weights in the model. The number known to be alive in 2005 was determined from acoustic detections of fish on the hydrophone arrays described in this report and on any other hydrophones (Lindley et al., in prep), i.e., if a sturgeon was detected anywhere in 2005, it was assumed to be alive in 2005.

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 to the period between capture sessions, this assumption is commonly violated in mark-recapture studies based on live resightings, as is common in 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 sturgeon follow the shortest possible path between arrays while remaining between the shore and the 100 m isobath.

Results

A total of 213 green sturgeon were tagged 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 sturgeon were detected by hydrophones in rivers, bays or estuaries. The size of tagged green sturgeon varied by where they were captured (ANOVA, $F_{4,208} = 78.68$, $P < 0.001$, $n = 213$). Fish captured in the Klamath and Rogue rivers, both spawning areas used by mature fish, were the largest, averaging 156-175 cm

fork length. The other tagging areas were used by a mixture of mature and immature fish, and 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 single sturgeon was detected on the Queen Charlotte Strait line in the summer of 2005. Numerous green sturgeon were detected on the Brooks Peninsula line, with up to nine unique individuals 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 during Oct-Dec 2005. These periods correspond fairly closely to the times that the Brooks Peninsula line was in operation. A few green sturgeon were detected on the Strait of Juan de Fuca line, with 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 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/day (Table 2), and 12 of the movements were made at rates > 40 km/day. These rapid movements were observed for fish moving from the north to the south between Brooks Peninsula and Cape Elizabeth and Strait of Juan de Fuca and Cape Elizabeth in June (Figure 3). Northerly movements were generally less rapid (< 39 km/day), although estimated northward velocities may be biased because the Cape Elizabeth and Brooks Peninsula lines were not in operation in the fall and winter of 2004. Speeds of 40 km/day correspond to roughly 0.25 body-lengths second^{-1} for fish with a total length of 2 m. In the spring of 2004 and 2005, green sturgeon were detected first on the Brooks Peninsula line and on the Cape Elizabeth line. In the fall of 2005, green sturgeon were detected at the Brooks Peninsula line after being detected at the Cape Elizabeth line in the previous spring. These patterns of detections indicate that many (but

192 not all) green sturgeon make annual migrations along the coast in the spring and fall,
193 spending winters in marine waters north of Vancouver Island and south of southeast
194 Alaska, and summers in the coastal waters, bays and estuaries of Washington, Oregon
195 and California.

196 Further insight into green sturgeon behavior was obtained by examining detection
197 patterns of seven fish that were observed moving among hydrophone lines three or more
198 times (Figure 4). Three of the seven fish (B, C, E in Figure 4) exhibited a rapid southward
199 movement from the Brooks Peninsula line to the Cape Elizabeth line during the late
200 spring or early summer of 2004. These fish were detected the following spring or summer
201 on the Brooks Peninsula line, suggesting that they migrated north along the coast between
202 these detection periods, probably at a time when the Brooks Peninsula and Cape
203 Elizabeth lines were not operating. Five of the seven sturgeon passed the Strait of Juan de
204 Fuca line in summer, on a southward migration (except for G, which came north from
205 Seal Rock, through Cape Elizabeth to Strait of Juan de Fuca, before returning south). The
206 relatively brief periods between the first and last detections on the Strait of Juan de Fuca
207 line are consistent with a migration pathway for these fish that hugs the coastline along
208 the southern tip of Vancouver Island, with a migration route over the Strait of Juan de
209 Fuca somewhere east of the Strait of Juan de Fuca line, where the water is relatively
210 shallow. Presumably, most green sturgeon migrating between Canadian and US waters
211 cross the Strait of Juan de Fuca over deep water to the west of the Strait of Juan de Fuca
212 line.

213 Green sturgeon tagged in different locations were not distributed identically in the
214 ocean (Figure 5). Fish from all tagging locations were detected on the Brooks Peninsula
215 and Cape Elizabeth lines, but the Strait of Juan de Fuca and Monterey Bay lines detected
216 fish tagged in Willapa Bay, San Pablo Bay, and the Rogue River. Tagging location, line
217 location, and their interaction each lead to significant reductions in model deviance
218 (Table 3). The significant line location effect means that detection rates differed among
219 lines for all fish, and the significant tagging location effect means that the overall rate of
220 detection differed among fish for all of the lines. The highly significant interaction term
221 means that that pattern of detections among lines differed depending on the location

where fish were tagged. 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 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% (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 may not be common for North American green sturgeon. Green sturgeon have been captured in fisheries in the these waters, but could possibly be Asian green 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 Aleutians are subject to intensive trawl fisheries (Rose and Jorgensen, 2005), and it would be beneficial for fisheries observers to gather further 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 CA.

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) define migration as “movements of individuals coordinated in space and time ... accompanied by return movements”, and distinguish 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, where they 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 BLs^{-1}, about 1/3 the critical swimming velocity of age 0+ green sturgeon (Lankford et al., 2005), but near the sustained swimming speed of lake sturgeon *A. fulvescens* (Peake et al., 1997), and 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, with a maximum observed velocity of 38 km/day. The difference between northward and southward migration velocity may be in part due to currents, since the near-shore core of the California Current has a southward velocity of 1-3 cm s^{-1} (0.9-2.6 km/day; 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. oxyrinchus*) and Gulf sturgeon (*A. oxyrinchus desotoi*) by Laney et al. (2007) and Edwards et al. (2007), respectively.

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 is the observation of nine green sturgeon on the Seal Rock line in the winter of 2004-05 (Figure 2), a period when we infer that many green sturgeon were north of Vancouver Island. Moreover, a slight majority of tagged sturgeon were detected on one or no hydrophones in the ocean. Perhaps these fish did not migrate within range of hydrophones or did so 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.

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

291 At present, we can only speculate on the advantages of this behavior, noting that there
292 are broad areas of relatively shallow water north of Vancouver Island, in Queen Charlotte
293 Sound, and in Hecate Strait (Figure 1). These waters are warmer in winter than might be
294 expected from their latitude due to frequent, storm-driven advection of surface waters
295 from the southeast, and are somewhat protected from wave action by the Queen Charlotte
296 Islands (Crawford and Thomson, 1991). Coastal waters off of the west coast of
297 Vancouver Island are highly productive, with some of the highest fishery yields of
298 resident fish (e.g., herring and groundfish) along the west coast of North America, due in
299 part to high rates and efficient retention of primary production in this area (Ware and
300 Thomson, 2005). Benthic invertebrates are abundant year-round on the western
301 Canadian continental shelf (Brinkhurst, 1991). Prior to spawning in late winter or early
302 spring (Hay and McCarter, 1997), Pacific herring overwinter in these areas in dense
303 schools near the bottom (Outram, 1965), where they may be vulnerable predation by
304 green sturgeon. Some gray whales (*Eschrichtius robustus*) migrate to these waters to feed
305 benthically in spring and summer on dense populations of ampeliscid amphipods, ghost
306 shrimp, and herring eggs (Oliver et al., 1984; Darling et al., 1998). The feeding habits of
307 green sturgeon are poorly known, but according to Moyle (2002), green sturgeon prey
308 upon benthic invertebrates and occasionally fishes such as sand lance and anchovy.
309 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 that migration and over-wintering play in green sturgeon life history.

That green sturgeon are highly migratory and prone to aggregating in restricted areas has important implications for their conservation. The west 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 impacted by Canadian bottom trawl fisheries as well as the USA 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.

Our estimate of survival for 2004 of 0.83 is similar to the estimate of 0.87 that Beamesderfer et al. (2007) produced from a catch-curve analysis which indicated a natural mortality rate of 0.08 and a harvest mortality rate of 0.05. Pine et al. (2001) found that a Gulf of Mexico sturgeon (*A. oxyrinchus desotoi*) 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 15 years (Moyle, 2002), suggesting that Gulf sturgeon can sustain higher natural and fishing mortality than green sturgeon. Given the general similarities between green 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 (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. While 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 animals will be seen alive in the interval, but will not survive until 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 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 model was one that is equivalent to the CJS model, i.e., our data set is 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 with behaviors that make them 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 home ranges of rockfish 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, in particular, are 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). In spite of 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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Table 1: The number *n* and size (mean, min, max fork length (cm)) of green sturgeon tagged at various locations in 2002-2004.

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

Table 2: Mean migration speed of green sturgeon as determined by movement between hydrophone arrays. Values in parentheses are observed minimum and maximum velocities.

Move	Mean Velocity (km/day)	*n*
Brooks to Cape Eliz.	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 Eliz. to Brooks	7.63 (1.04, 38.42)	17
Cape Eliz. to Juan de Fuca	19.73 (0.58, 31.49)	3
Cape Eliz. 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 Eliz.	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 Eliz.	10.38 (1.18, 28.70)	7
Seal Rock to Juan De Fuca	23.70	1
Seal Rock to Monterey Bay	2.03	1

552

Table 3: Analysis of deviance.

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	40.881	0	0.00	0.001

553

554

Figure captions

Figure 1. Map of study area, from southeast Alaska to central California. Triangles denote location of tagging in spawning populations, diamonds denote non-spawning aggregations, and octagons the location of hydrophone arrays. The light grey line shows the 100-m isobath.

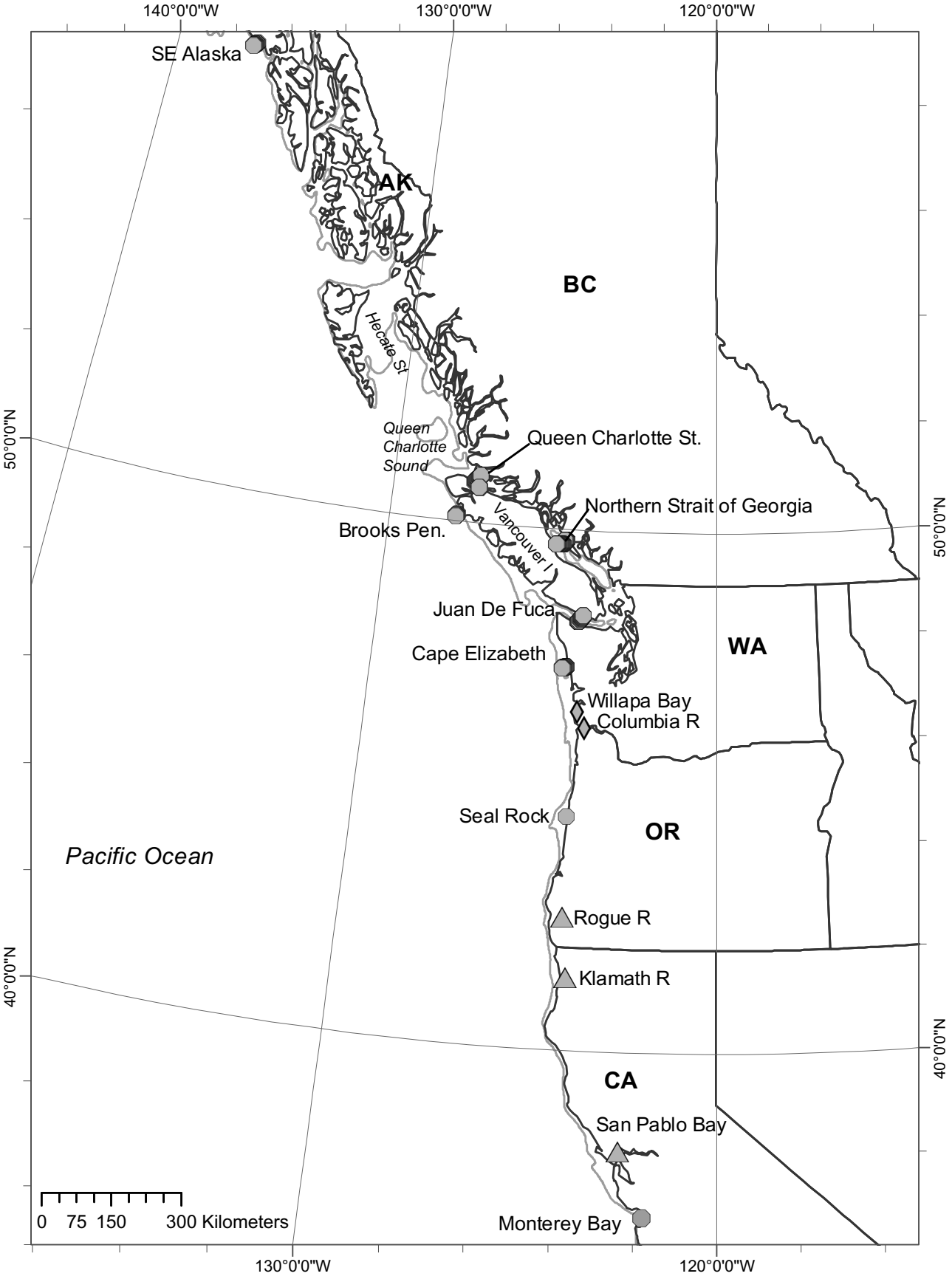
Figure 2. Detections of tagged green sturgeon by hydrophone arrays. Height of bar indicates the number of unique fish observed per day. Grey boxes along *x*-axis indicate deployment periods for hydrophone arrays. Numbers in parentheses following location labels indicate the total number of unique fish observed at that location.

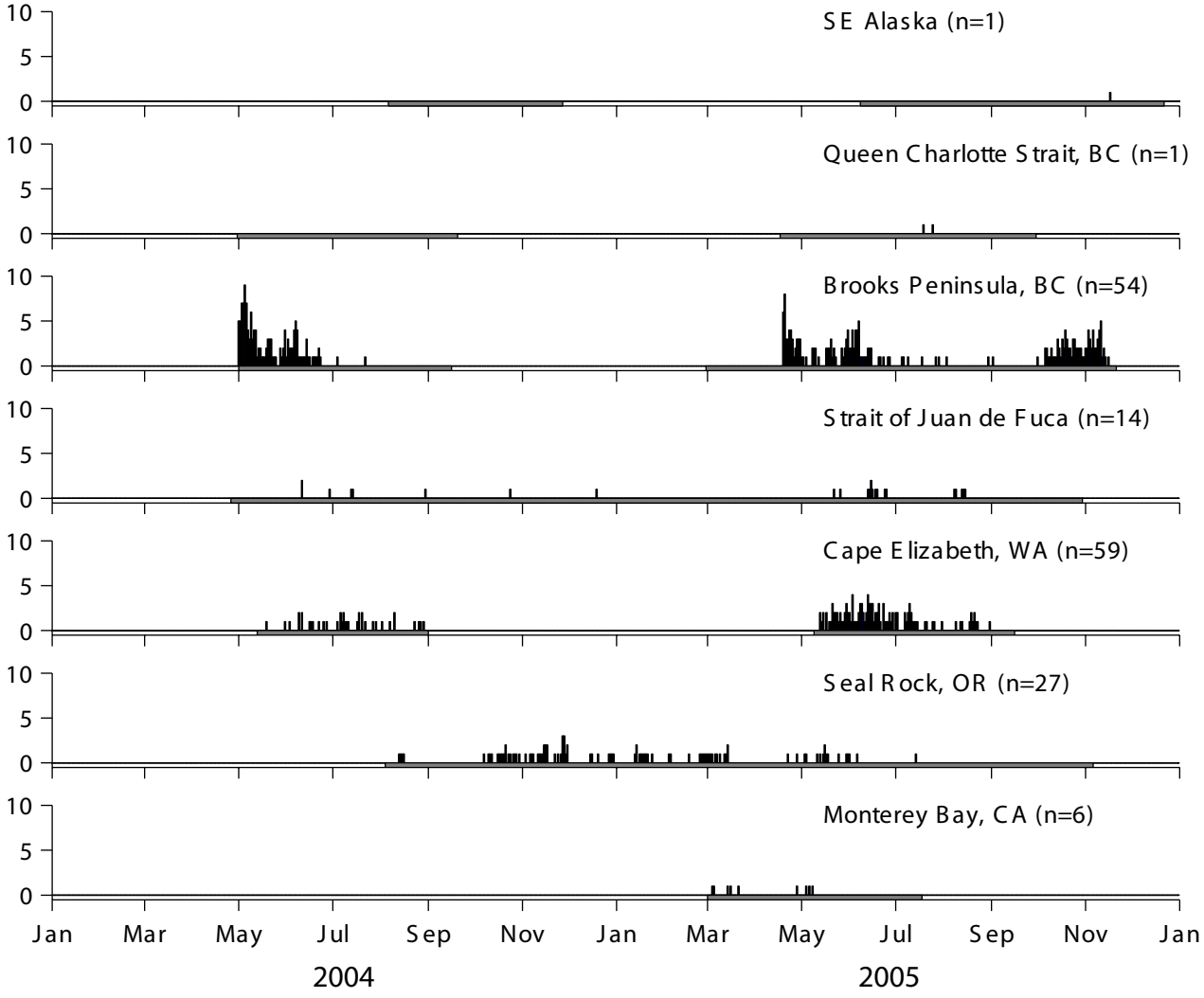
Figure 3. Movements of green sturgeon between hydrophone arrays. Grey lines indicate deployment periods of the hydrophone arrays. Tails for arrows indicate the last time that the sturgeon was detected on the corresponding line, and arrow heads indicate the first time that the sturgeon was subsequently detected on another hydrophone array. Arrow lines crossing time lines for hydrophone arrays indicate that the sturgeon was not detected on that hydrophone array.

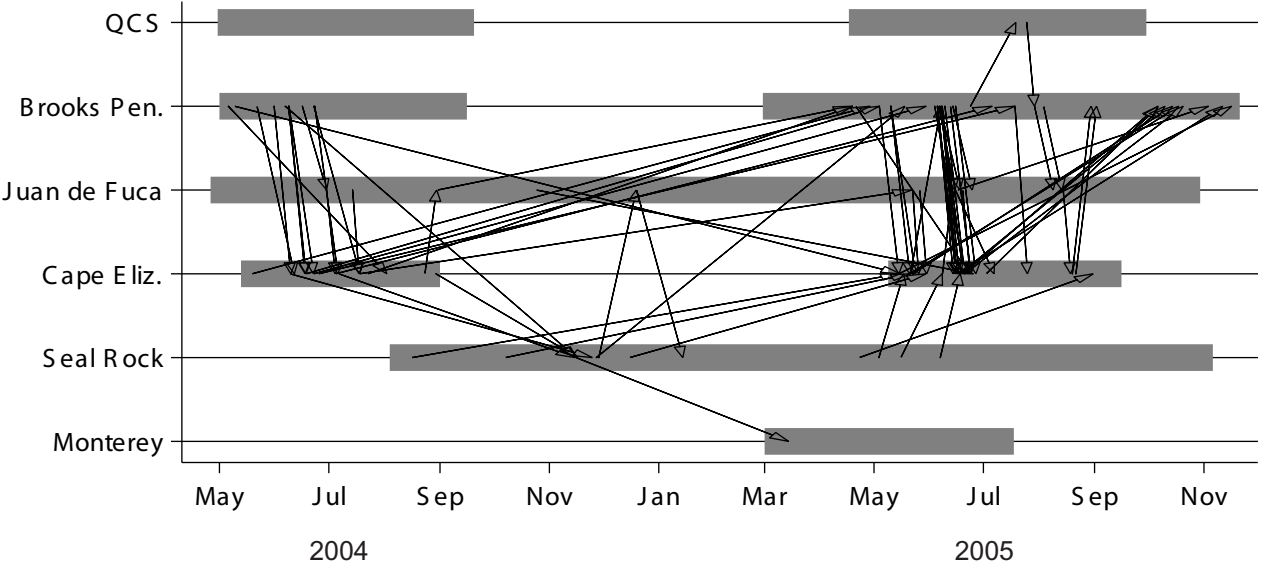
Figure 4. Movements of individual green sturgeon among hydrophone lines for individuals that were detected on three or more hydrophone lines. Symbols as in Figure 3.

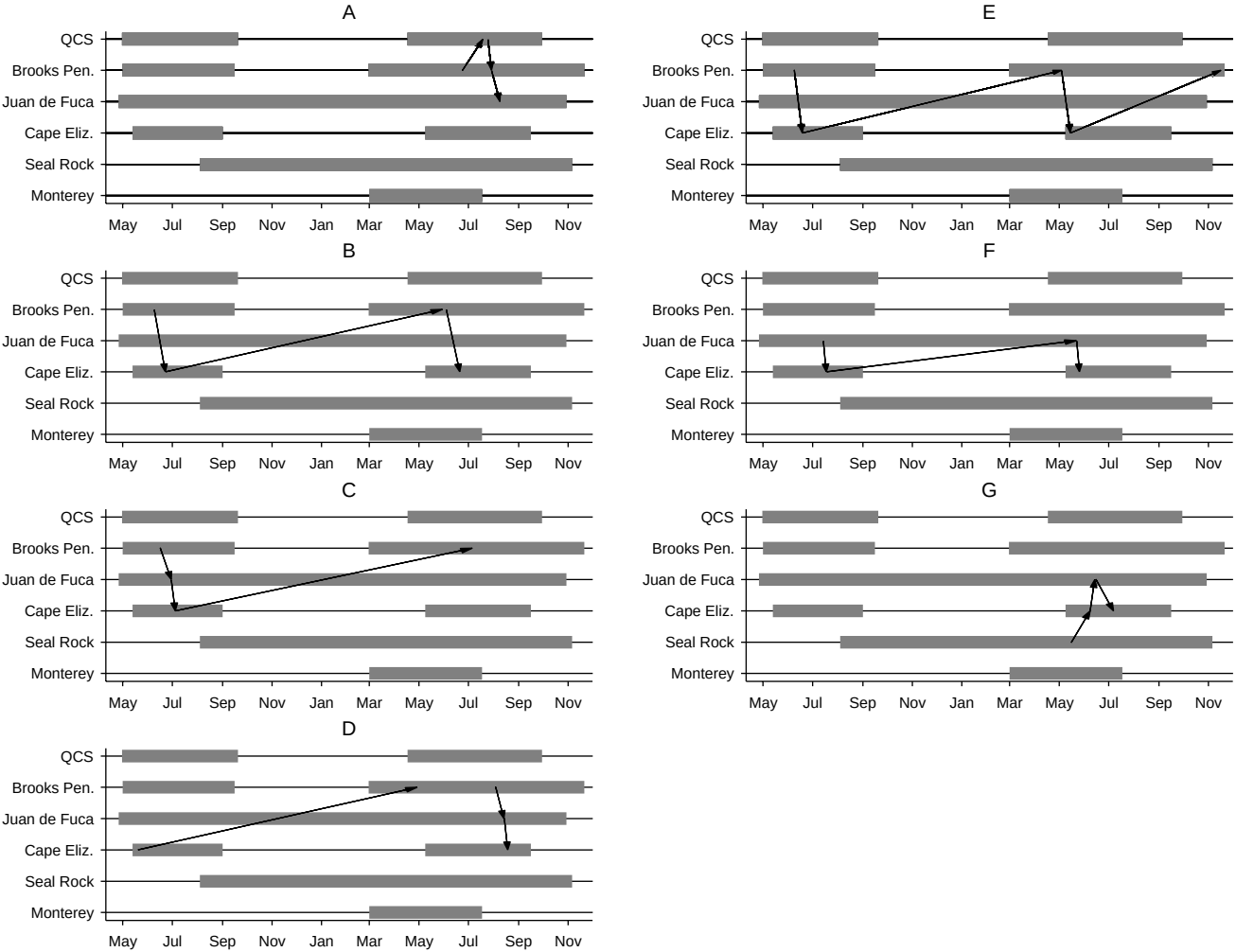
Figure 5. Detection probability on marine hydrophone arrays of green sturgeon tagged in five locations. Vertical lines represent 90% confidence intervals.

Figure 6. Observed catch of green sturgeon by the Canadian bottom trawl fishery, 1996-2006. Polygons delimit Department of Fisheries and Oceans statistical areas, which are grey-scale coded by catch per unit effort (kg/hour); total catch (kg) is denoted by numbers in small boxes. Data from PacHarvTrawl. Canadian trawl landings, 1996-2007. SQL Server database, Groundfish Section, Marine Ecosystems and Aquaculture Division, Science Branch, Fisheries and Oceans, Canada. Pacific Biological Station.


140°0'0"W
130°0'0"W
120°0'0"W
50°0'0"N
40°0'0"N
SE Alaska
AK
BC
Hecate St
Queen Charlotte Sound
Queen Charlotte St.
Northern Strait of Georgia
Brooks Pen.
Vancouver I
Juan De Fuca
Cape Elizabeth
WA
Willapa Bay
Columbia R
Seal Rock
OR
Pacific Ocean
Rogue R
Klamath R
CA
San Pablo Bay
Monterey Bay
0 75 150 300 Kilometers


SE Alaska (n=1)
Queen Charlotte Strait, BC (n=1)
Brooks Peninsula, BC (n=54)
Strait of Juan de Fuca (n=14)
Cape Elizabeth, WA (n=59)
Seal Rock, OR (n=27)
Monterey Bay, CA (n=6)
10
5
0
Jan
Mar
May
Jul
Sep
Nov
Jan
Mar
May
Jul
Sep
Nov
Jan
2004
2005


QCS
Brooks Pen.
Juan de Fuca
Cape Eliz.
Seal Rock
Monterey
May
Jul
Sep
Nov
Jan
Mar
May
Jul
Sep
Nov
2004
2005


A
B
C
D
E
F
G
QCS
Brooks Pen.
Juan de Fuca
Cape Eliz.
Seal Rock
Monterey
May
Jul
Sep
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Jul
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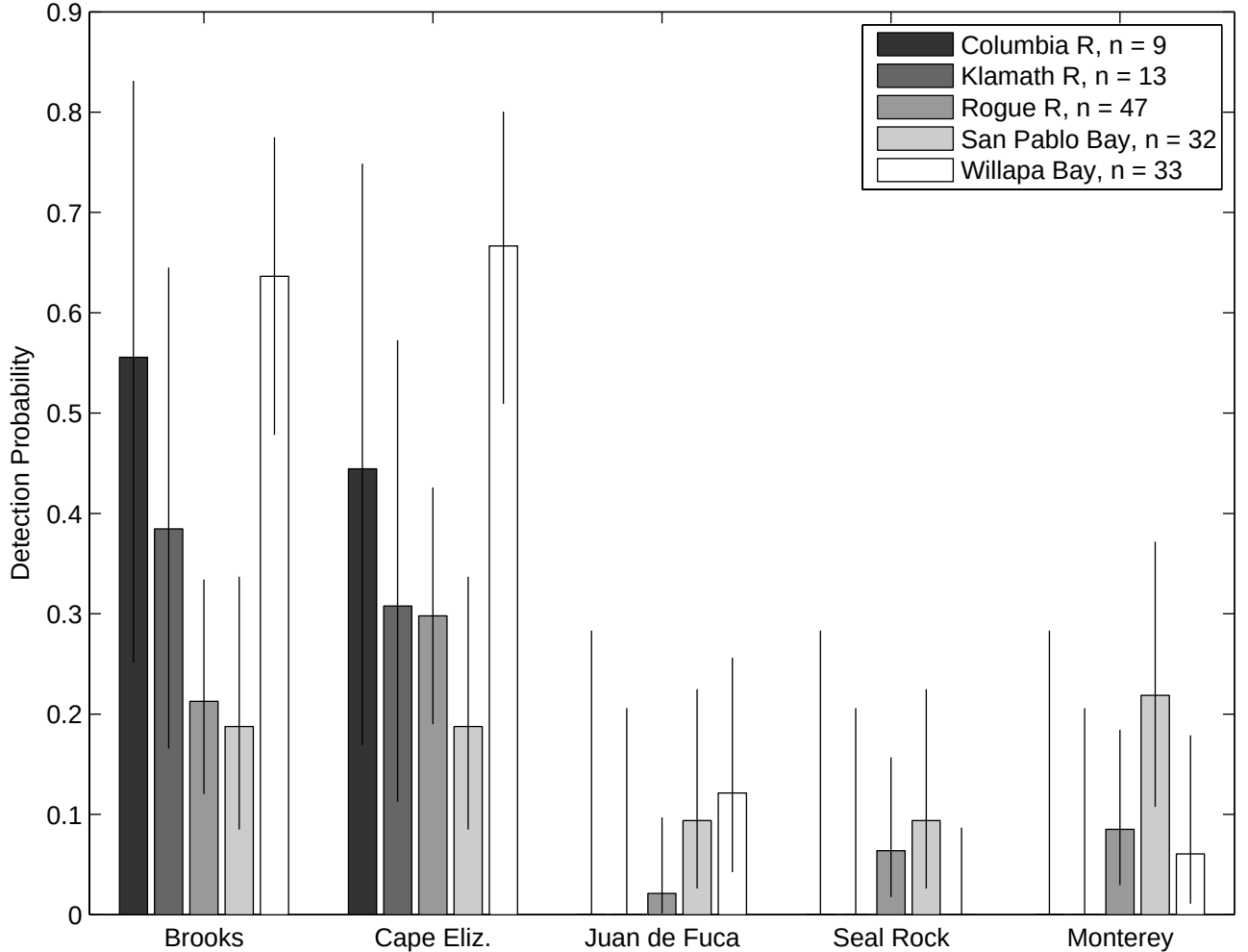
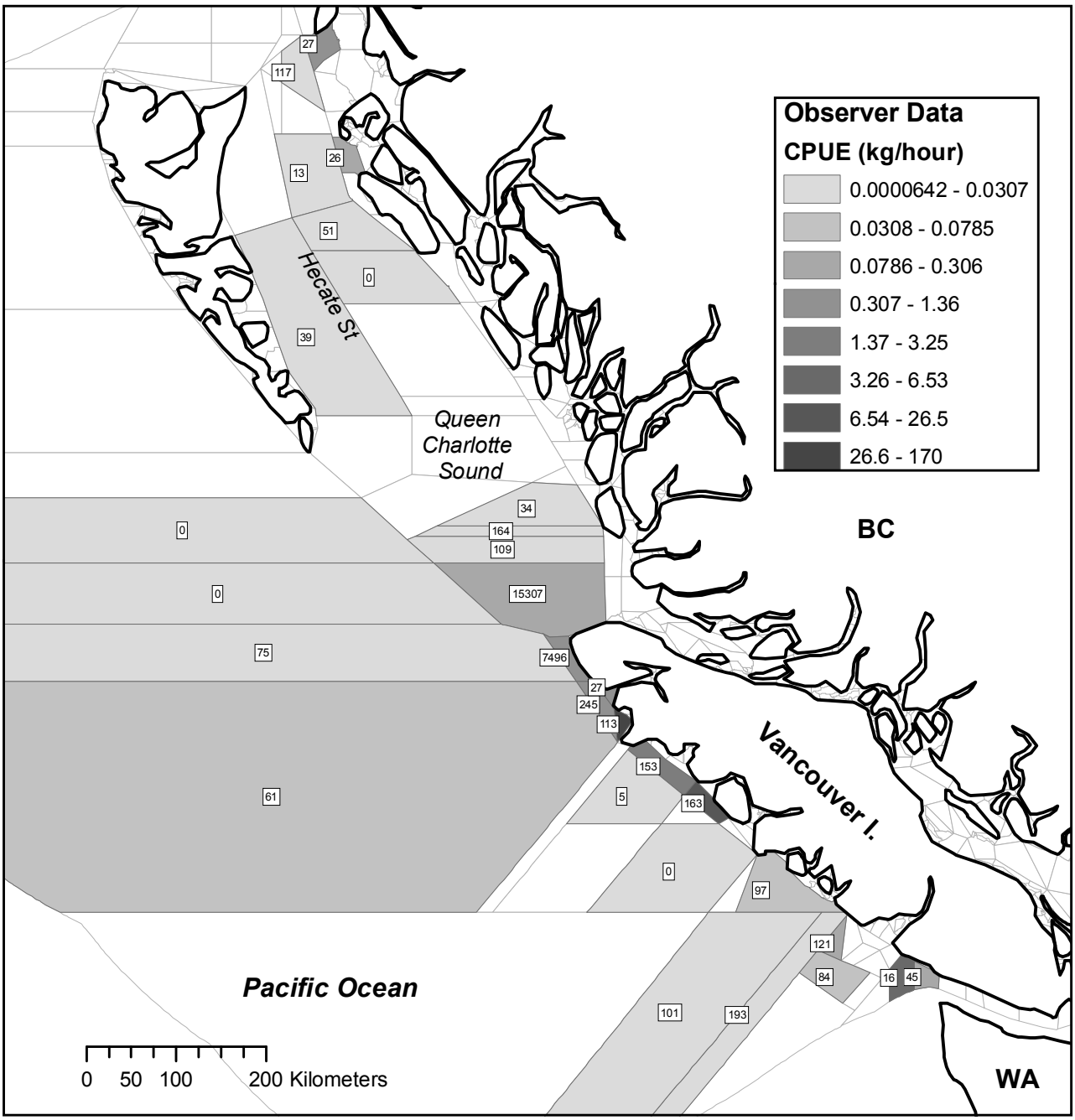
Nov


Columbia R, n = 9
Klamath R, n = 13
Rogue R, n = 47
San Pablo Bay, n = 32
Willapa Bay, n = 33
Detection Probability
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Brooks
Cape Eliz.
Juan de Fuca
Seal Rock
Monterey


Observer Data
CPUE (kg/hour)
0.0000642 - 0.0307
0.0308 - 0.0785
0.0786 - 0.306
0.307 - 1.36
1.37 - 3.25
3.26 - 6.53
6.54 - 26.5
26.6 - 170
Hecate St
Queen Charlotte Sound
Vancouver I.
BC
WA
Pacific Ocean
0 50 100 200 Kilometers
27
117
26
13
51
0
39
34
164
109
15307
7496
27
245
113
153
163
5
61
0
97
121
84
16
45
101
193