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Predator–prey interactions between harbor seals and migrating steelhead trout smolts revealed by acoustic telemetry

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ABSTRACT: Changes in the Puget Sound ecosystem over the past 3 decades include increases in harbor seal (*Phoca vitulina*) abundance and declines in many of their preferred prey species. Harbor seals were outfitted with acoustic telemetry receivers and GPS tags to investigate spatial and temporal interactions with steelhead trout *Oncorhynchus mykiss* smolts implanted with acoustic transmitters. A total of 6846 tag detections from 44 different steelhead trout smolts (from an initial group of 246 smolts released into 2 rivers) were recorded by the 11 recovered seal-mounted receivers. Central Puget Sound seal receivers detected a greater proportion of smolts surviving to the vicinity of the haul-out locations (29 of 51; 58%) than Admiralty Inlet seal receivers (7 of 50; 14%; $p < 0.001$). Detection data suggest that none of the tagged smolts were consumed by the 11 monitored seals. Nine smolts were likely consumed by non-tagged harbor seals based partly on detections of stationary tags at the seal capture haul-outs, although tag deposition by other predators cannot be ruled out. Smolts implanted with continuously pinging tags and smolts implanted with tags that were silent for the first 10 d after release were detected in similar proportions leaving Puget Sound (95% CI for the difference between proportions: −0.105 to 0.077) and stationary at harbor seal haul-outs (95% CI: −0.073 to 0.080). This study suggests that harbor seals contribute to mortality of migrating steelhead smolts, and we hypothesize that documented changes in the Puget Sound ecosystem may currently put steelhead smolts at greater risk of predation by harbor seals and possibly other predators.

KEY WORDS: Top-down · Ecosystem shift · Salmonid survival · Pinniped · Migration behavior

INTRODUCTION

Shifts in marine ecosystems occur on varying scales and time periods and can be triggered by climatic fluctuations and a combination of human activities such as urbanization, fishing, and species protection (Rocha et al. 2015). The high degree of complexity in large estuarine systems combined with abrupt shifts in species composition and food web dynamics make it challenging to identify the current factors influencing depleted populations of conservation concern. Inland waters of the Salish Sea (Puget Sound, Strait of Juan de Fuca, and Strait of Georgia) have undergone an ecosystem shift over the past several decades (Harvey et al. 2012, Preikshot et al. 2013). Numerous demersal fish species experienced steep declines in the late 1980s and have remained at low levels of abundance (Gustafson et al. 2000, Drake et al. 2010), despite fishing closures (Essington et al. 2013). During a similar timeframe, Salish Sea seabirds were more likely to exhibit population declines if they depended on forage fish as their primary food source (Vilchis et al. 2015). However, some higher-trophic-level predators, such as harbor seal *Phoca*

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vitulina (Jeffries et al. 2003) and harbor porpoise *Phocoena phocoena*, have increased substantially following implementation of the US Marine Mammal Protection Act of 1972. Higher-trophic-level predators have been shown to switch to less-preferred prey after depleting preferred prey resources (Tinker et al. 2008), and in particular, when protections effectively lead to increases in the abundance of top predators (e.g. in marine protected areas; Berriman et al. 2015).

Seven species of anadromous salmonids (*Oncorhynchus* spp.) migrate through Puget Sound en route to the Pacific Ocean as smolts and return as adults to spawn in their natal streams. Salmonid species that enter Puget Sound at a small size (pink salmon *O. gorbuscha* and chum salmon *O. keta*) have exhibited stable or increasing abundance trends in recent decades, possibly related to reductions in certain piscivorous bird and fish populations (discussed in Ruggerone & Goetz 2004), whereas the abundance and survival of species that migrate to the Pacific Ocean at older ages and larger body sizes (coho salmon *O. kisutch* and steelhead trout *O. mykiss*) have declined (Scott & Gill 2008, Zimmerman et al. 2015). Steelhead trout suffer high mortality rates during their rapid migration through Puget Sound (Moore et al. 2015), consistent with high overall marine mortality in recent decades. Similar patterns of declining abundance and lower early marine survival of steelhead are consistent with patterns in the northern regions of the Salish Sea (i.e. the Strait of Georgia; Melnychuk et al. 2007).

Steelhead trout undergo osmoregulatory changes necessary for marine life and enter Puget Sound during the spring at larger body sizes (approximately 175 ± 40 mm) than any other species of Pacific salmon. The large body size of migrating steelhead smolts limits the diversity of potential predators capable of consuming large percentages of the steelhead smolt populations to a few birds (e.g. Caspian terns *Hydroprogne caspia*, Evans et al. 2012; Western gulls *Larus occidentalis*, Osterback et al. 2014; and cormorants *Phalacrocorax auritus*, Hostetter et al. 2012) and marine mammals. Some work in both large and small estuaries infers predation by harbor seals based on the 'behavior' of tags from active telemetry tracking (Melnychuk et al. 2013) and associations between mortality hotspots and harbor seal haul-outs (Romer et al. 2013). The abundance of harbor seals in greater Puget Sound increased significantly between the 1970s (2000–3000 seals) and 1999 (nearly 14 000 animals; Jeffries et al. 2003), and appears to have remained stable since that time (S. J. Jeffries unpubl. data). Similar trends in harbor seal populations occurred in the Strait of Georgia during the same period (DFO 2010). Harbor seals feed predominantly on Clupeidae (herring) and Gadidae (cod and hake), but also feed opportunistically (Thomas et al. 2011) from just a few to over 100 km from their (capture) haul-outs (Peterson et al. 2012). Steelhead trout were not identified as prey in a fairly extensive year-round analysis of harbor seal diet around the San Juan Archipelago (Lance et al. 2012, Bromaghin et al. 2013). However, steelhead presence in seal diets may have been overlooked due to the lack of detectability of steelhead hard parts in diet composition analyses and because the relative number of steelhead available as prey compared to other prey types is inherently small.

Conventional approaches to quantifying predator–prey interactions between pinnipeds and fish prey include a combination of spatio-temporal foraging behavior (with the use of satellite tags) and data on diet composition (Thomas et al. 2011, Ward et al. 2012). Small acoustic telemetry receivers (Vemco mobile transceiver; hereinafter 'VMT') capable of detecting 69 kHz transmitters (hereinafter 'tags') implanted in fish in a variety of marine species have recently been deployed on pinnipeds to test the feasibility of using pinnipeds as mobile receiver platforms (Hayes et al. 2013), spatio-temporal precision, and error associated with the technique (Lidgard et al. 2012), and to quantify overlap between pinnipeds and prey species (e.g. Atlantic cod *Gadus morhua*, Lidgard et al. 2014). Thus far, 'association studies' have not revealed evidence of predation by pinnipeds on any fish species and detection rates have generally been quite low. Recent work has shown that harbor seals in particular can hear the sound generated by Vemco 69 kHz tags (Cunningham et al. 2014), and they can learn to associate the sound from the tags with food in a laboratory setting. This raises the question of whether the sound of the tag rings a 'dinner bell' that puts tagged fish at greater risk of predation (Stansbury et al. 2015).

To investigate predator–prey interactions between harbor seals and steelhead trout smolts and simultaneously test the potential effect of an audible tag on survival, we investigated (1) the degree of association between harbor seals and migrating steelhead smolts, (2) evidence for predation by harbor seals on steelhead smolts in Puget Sound, and (3) the effect of sound produced by acoustic telemetry tags on detection rates by seal-mounted VMTs and survival of steelhead smolts.

MATERIALS AND METHODS

Steelhead smolt tagging

Steelhead smolts were captured at rotary screw trap locations in the Nisqually River and Green River, which enter the east side of Puget Sound (Fig. 1). Captured smolts were held for 1 to 2 d before being anesthetized with tricaine methanesulfonate, weighed, measured, and implanted with a Vemco V7 2L acoustic tag (7 mm diameter × 20 mm long; 1.6 g). Tagged smolts ranged from 34 to 237 g and 155 to 251 mm (fork length); thus the tag mass to smolt body mass ratio never exceeded 5%. Surgical implantation procedures are described in Moore et al. (2015). A total of 103 Green River and 143 Nisqually River smolts were tagged between April 28 and May 20, 2014 (Fig. 1). Tags implanted into all of the smolts, with the exception of 43 of the Nisqually River smolts (see next subsection), were configured to emit an acoustic signal (136 dB) every 30 to 90 s on a random delay cycle. All smolts were held for approximately 24 h before being transported and released at river-kilometer 19 in either the Green River or Nisqually River. The smolts monitored in this study were part of a larger reciprocal transplant experiment designed to identify population and location factors influencing steelhead survival in Puget Sound (Moore & Berejikian unpubl.). Therefore, 50 of the 103 Green River smolts were released into the Nisqually River, and 50 of the 143 Nisqually River smolts were released into the Green River. Hereinafter, we refer to smolts released into their home river as 'home' and those released into the other river as 'away'. For example, Nisqually-away refers to fish captured in the Nisqually River but released into the Green River.

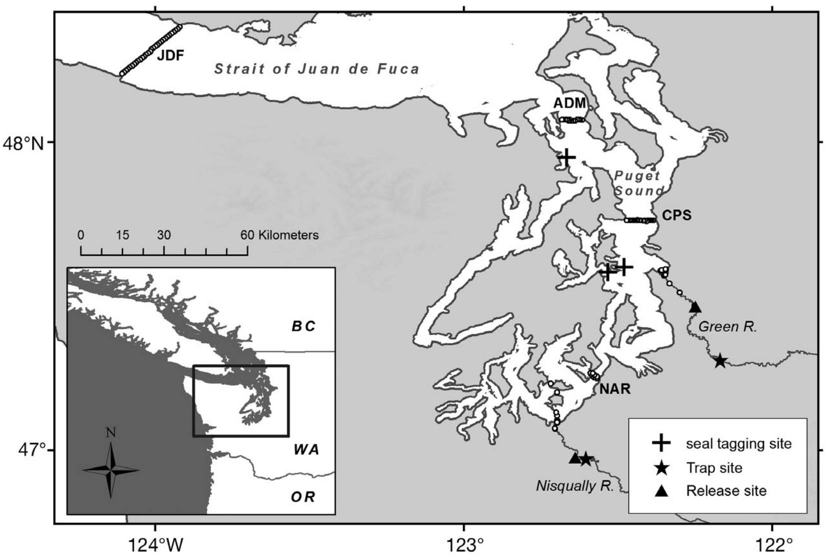

Fig. 1. Study area, including stationary acoustic receiver arrays in the Strait of Juan de Fuca (JDF), Admiralty Inlet (ADM), Central Puget Sound (CPS), and the Tacoma Narrows (NAR). Each circle represents an individual receiver. The haul-out locations where seals *Phoca vitulina* were collected and outfitted with instrument packs are also shown. Seals collected south of the CPS line are referred to as CPS seals and those collected north of the CPS line are referred to as ADM seals. Inset: location in western North America

Stationary receiver locations

Six stationary Vemco VR2W receivers were deployed in each river mouth. Arrays of Vemco VR3 receivers were also deployed approximately 20 km north of the Nisqually River near the Tacoma Narrows (8 receivers), 20 km north of the Green River in Central Puget Sound (19 receivers), in Admiralty Inlet (13 receivers), and at the western end of the Strait of Juan de Fuca (30 receivers; maintained by the Ocean Tracking Network; Fig. 1).

To determine whether the sound from the V7 tags caused increased mortality, 43 of the 93 Nisqually-home smolts were implanted with tags programmed to be silent for the first 240 h after release (hereinafter 'delay' tags), then to turn on and subsequently function exactly as all of the other tags (hereinafter 'continuous'). The delay and continuous tags were implanted into a common group of fish on each of the 4 Nisqually River tagging days, transported in the same vessel, and released at the same location (river km 19) at the same time. On 2 of the tagging days, delay tags were implanted first, and on 2 days, continuous tags were implanted first. The 10 d delay was determined based on average travel time from Nisqually River to Admiralty Inlet (Fig. 1) determined from previous studies (Moore et al. 2015). The goal was to have smolts implanted with delay tags to remain silent as they complete the majority of their migration through the main basin of Puget Sound, and to have the tags switch on and become audible prior to reaching the outer receiver arrays located in Admiralty Inlet and the Strait of Juan de Fuca where surviving smolts could be detected (Fig. 1). To test the assumption that delay tags were silent during most of the smolt migration through the main basin of Puget Sound before the tags turned on, 2 × 2 contingency table analyses (Sokal & Rohlf 2013) were performed to determine whether tag type was independent of detection history (detected or not) at each stationary receiver line (Estuary, Tacoma Narrows, Central Puget Sound). We tested the null hypothesis that tag type (delay or continuous) was independent of detection history (detected or not detected) at the last 2 fixed arrays (Admiralty Inlet and Strait of Juan de Fuca). Rejecting the null hypothesis would indicate tag noise (the only difference between the 2 treatments) affected survival through the study area. We also calculated 95% confidence intervals (CIs) for the difference between the 2 proportions using the following formula:

$$(p1-p2)\pm 1.96\sqrt{\left(\frac{p1(1-p1)}{n1}\right)+\left(\frac{p2(1-p2)}{n2}\right)} \quad (1)$$

where $p1$ is the proportion of surviving smolts with continuous tags, $p2$ is the proportion of surviving smolts with delay tags, and $n1$ and $n2$ are the sample sizes for continuous and delay tags, respectively.

Harbor seal tagging and monitoring

Harbor seal research activities were conducted under Marine Mammal Protection Act Research Permit 13430 issued by the National Marine Fisheries Service (Office of Protected Resources, Silver Spring, MD 20910). Twelve adult harbor seals (5 females and 7 males) were captured between April 3 and 28, 2014 (see Table 1). All capture and handling of the research animals in this study were reviewed and approved by the Alaska and Northwest Fisheries Science Centers' Institutional Animal Care and Use Committees (IACUC) in approved protocol A/NW 2013-1. Each seal was weighed, measured, and fitted with an instrument pack that was glued to the pelage with quick-set Epoxy. Each pack contained: (1) a VMT receiver capable of detecting both the V7 tags (69 kHz) and transmissions from the VMTs, (2) a satellite-linked time depth recorder (TDR) and Fastloc GPS tag (model MK10AF, Wildlife Computers, www.wildlifecomputers.com), and (3) a VHF tag (164–165 MHz, Advanced Telemetry Systems; www.atstrack.com) used for locating the instrument packs after they had been shed by the harbor seals. All 3 instruments were consolidated in a single floatation pack, which was attached to the seals along the dorsal mid-line, on the anterior portion of the back. The GPS receivers were programmed to transmit ARGOS and GPS data and to store Fastloc GPS locations in the tag. The Fastloc sampling interval was 30 min, so there were a maximum number of 48 possible locations per day, although the actual number was much lower because the tags were programmed to a maximum of 4 failed transmissions, which occurs when the tag is underwater or there is insufficient satellite coverage. Transmissions were also suppressed during haul-outs (i.e. when the pack was dry). Stored data were downloaded from recovered tags. GPS data was only recorded once per week beginning on July 1, 2014 to conserve battery life and ensure that transmissions would continue after the packs had separated from the seals. Previous studies indicated that steelhead smolts complete their migration through Puget Sound sometime in June (Moore et al. 2015). We used only Fastloc GPS positions that incorporated data from 5 or more satellites to minimize error (Hazel 2009). We determined GPS locations by analyzing archival GPS data from each tag using proprietary software from the manufacturer.

The VMTs mounted on the seals were continuously 'listening' for steelhead tags from the time of deployment until recovery, but could only detect tags when fully submerged. To estimate the success rate at which VMTs were capable of detecting a V7 transmitter at different distances from the tag, we conducted a 'range test' with the VMT receivers that were recovered from the harbor seals. The 11 VMTs were simultaneously deployed in the vicinity of the Orchard Rocks haul-out, and a V7 tag was immersed for 3 min, 10 m from the receiver. The tag was removed and redeployed repeatedly at 10 m increments from the location of the receivers. The seal-mounted VMTs were also programmed to transmit an acoustic transmission at the same frequency as the V7 tags (69 kHz) every 15 min. The data from the VMT transmissions provided little information concerning the interactions between harbor seals and steelhead, so data are not presented here.

Data analysis

We used the accurate timestamps provided by the GPS units and VMT receivers to associate VMT detections of tagged steelhead with the detecting seal location, and thereby estimate the location of the steelhead tag. We merged the Fastloc GPS timestamp data for a particular seal with the VMT timestamp data for steelhead tags detected by the same seal VMT, and calculated the minimum time differences (lag) between each VMT detection of a steelhead tag and the detecting seal's GPS location. Because of the infrequency of the GPS locations, many VMT detections were not closely time-associated with a GPS location. Determining the appropriate association time between a VMT detection and a GPS location represents a trade-off between position accuracy and the number of positions for determining the location of individual steelhead tags. To empirically determine VMT–GPS time associations that provide reasonably precise tag location information for the monitored seals in this study, we deployed stationary sentinel tags near the Orchard Rocks, Blakely Rocks, and Colvos Rocks haul-out locations. The known position of the fixed sentinel tag and the distance between a seal GPS location and the detected sentinel tag allowed us to estimate the spatial error associated with each VMT detection for a specified lag time (i.e. time between VMT detection and GPS location). We did not attempt to interpolate locations when VMT detections occurred between 2 GPS locations, as has been done in other studies (e.g. Lidgard et al. 2014), because the Fastloc GPS location frequency was insufficient.

To determine whether spatio-temporal overlap between harbor seals and steelhead trout differed between Central Puget Sound versus Admiralty Inlet, we tested whether detection history (detected or not) on harbor seal VMTs was independent of haul-out location. To do this, we first estimated how many smolts released into each river survived to the vicinity of each of the tagging haul-outs, by multiplying instantaneous survival estimates from Moore & Berejikian (unpubl.) by the distances from river mouths to each haul-out location. We report 95 % CIs for survival estimates (obtained from the program MARK; White & Burnham 1999) at the stationary array nearest the respective haul-out location (Moore & Berejikian unpubl.). Because steelhead smolts migrating through Puget Sound exhibit a rapid, directional, northern migration (Moore et al. 2015), we could not reliably estimate the number of smolts from the Green River that may have wandered westward across Puget Sound to be detected by Central Puget Sound seal VMTs (Fig. 1). Therefore, we compared just the proportions of smolts entering via the Nisqually available to Central Puget Sound seals that were detected to the total number of smolts entering Puget Sound available to and detected by Admiralty Inlet seal VMTs.

RESULTS

Associations between harbor seals and migrating steelhead smolts

Steelhead smolts were detected on the Admiralty Inlet fixed receiver array from May 4 through June 6, and slightly later on the Strait of Juan de Fuca array (May 11 through June 10; Fig. 2). No steelhead smolts were detected on either of these arrays after June 10, indicating that any surviving smolts migrating to the ocean had likely passed the area inhabited by monitored harbor seals by June 10 (Fig. 2).

Instrument packs were recovered from 11 of the 12 harbor seals between 66 and 156 d (average: 141 d) after deployment (Table 1). Four of the 5 packs were recovered from seals outfitted in Central Puget Sound and from all 7 seals outfitted in Admi-

Table 1. Harbor seal *Phoca vitulina* capture location, sex, length, weight, and deployment and recovery dates of instrument packs consisting of GPS tags and acoustic receivers. Orchard and Blakely Rocks are located in Central Puget Sound and Colvos and Snake Rocks are adjacent haul-outs in Admiralty Inlet (separated by 1.5 km). nr: not recovered

Pack #	Deployment date (mo/d/yr)	Capture location	Sex	Length (cm)	Weight (kg)	Date recovered (mo/d/yr)	Days deployed
1	4/3/14	Orchard Rocks	M	148	102	9/5/14	155
2	4/4/14	Orchard Rocks	M	145	55	9/4/14	153
3	4/4/14	Orchard Rocks	M	153	79	nr	nr
4	4/15/14	Blakely Rocks	M	152	70	9/13/14	151
5	4/18/14	Colvos Rocks	M	154	76.5	6/23/14	66
6	4/21/14	Snake Rocks	F	141	77.5	9/18/14	150
7	4/21/14	Snake Rocks	F	142	93	9/2/14	134
8	4/21/14	Colvos Rocks	F	144	87	9/18/14	150
9	4/21/14	Colvos Rocks	F	134	79	9/18/14	150
10	4/21/14	Colvos Rocks	F	150	90	9/18/14	150
11	4/28/14	Colvos Rocks	M	148	78	9/12/14	137
12	4/28/14	Orchard Rocks	M	169	101	10/1/14	156

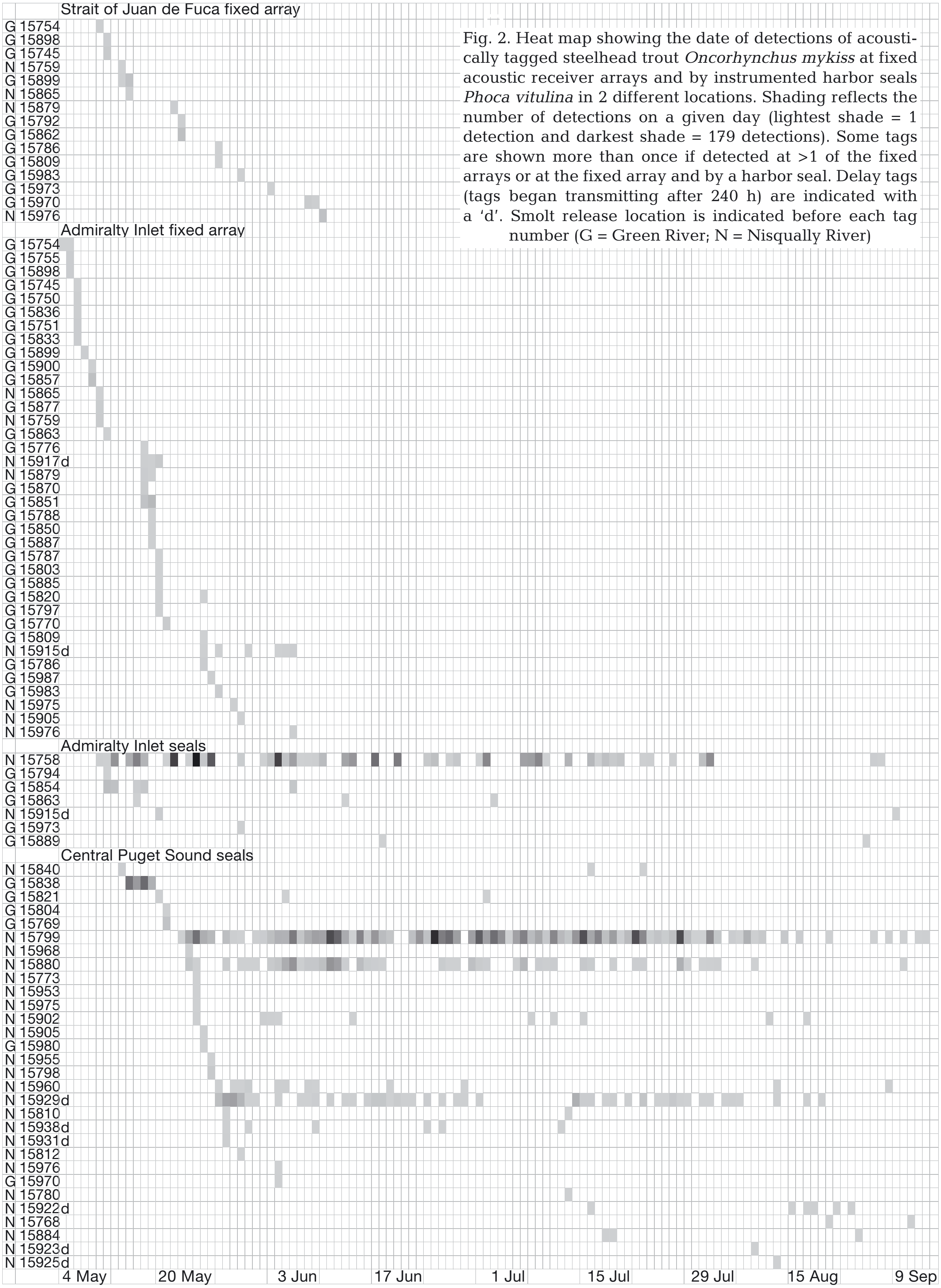

Fig. 2. Heat map showing the date of detections of acoustically tagged steelhead trout *Oncorhynchus mykiss* at fixed acoustic receiver arrays and by instrumented harbor seals *Phoca vitulina* in 2 different locations. Shading reflects the number of detections on a given day (lightest shade = 1 detection and darkest shade = 179 detections). Some tags are shown more than once if detected at >1 of the fixed arrays or at the fixed array and by a harbor seal. Delay tags (tags began transmitting after 240 h) are indicated with a 'd'. Smolt release location is indicated before each tag number (G = Green River; N = Nisqually River)

ralty Inlet. The 11 GPS tags yielded 2761 Fastloc locations (Fig. 3). The 3 sentinel tags were detected by seal-mounted VMTs a total of 830 times over the course of the study, and 329 of those detections were associated with a seal GPS location that occurred within 30 min of a sentinel tag detection. The percentage of GPS locations that fell within 250, 500, and 750 m radii from the known tag locations ranged from 87% to 98% (Table 2), and all of the 30 min associations were within 1.25 km of the known tag location. Thus, a 30 min association threshold provided a fairly high degree of accuracy in determining the location of a detected tag on these spatial scales.

The range testing that was conducted near Orchard Rocks with the recovered VMTs demonstrated that all of the 11 recovered VMT receivers detected 100% of transmissions from the test tag up to 30 m away, and mean percent detections decreased to 30% at 100 m, which was the furthest distance tested. This indicates that when seals swam within 30 m of a tag, the VMTs were very likely to detect the tag, and likelihood of detection declined at distances greater than 30 m.

Table 2. Percentage of sentinel tag associations that yielded GPS locations within 250, 500, and 750 m of known locations of the 3 sentinel tags. Data include associations of < 30 min between the Vemco mobile transceiver (VMT) detection and the GPS location by an individual seal (*Phoca vitulina*)-mounted instrument pack

Location	n	Tag associations (%) 750 m	500 m	250 m
Blakely Rocks	194	97.4	95.4	87.1
Orchard Rocks	32	93.7	90.6	90.6
Colvos Rocks	102	98.0	98.0	96.1

An estimated 226 of the 243 tagged smolts survived their downstream migrations to the river mouths (Moore & Berejikian unpubl.). A total of 6846 V7 detections from 44 different steelhead trout smolts were recorded by the 11 seal VMTs. Steelhead tags were detected by Admiralty Inlet seal VMTs from May 11 through September 9, and by Central Sound VMTs from May 11 through September 26. Thus, detections of steelhead tags by seal VMTs occurred both during and after the smolt outmigration period (Fig. 2). The 4 VMTs mounted on seals captured at Orchard and Blakely Rocks in Central Puget Sound detected 37 of the 44 smolts (84%), and the 7 seal VMTs in Admiralty Inlet detected 7 (16%) tagged smolts (Table 3). No steelhead smolts were detected by both a Central Puget Sound and an Admiralty Inlet seal VMT. An estimated 51 steelhead smolts (95% CI: 46–56) entering through the Nisqually River survived to the vicinity of the Central Puget Sound haul-outs, and an estimated 50 steelhead smolts (95% CI: 42–58) survived to the Admiralty Inlet haul-outs, which included 33 from the Green River and 17 from the Nisqually River. Central Puget Sound seals detected a significantly greater proportion of smolts migrating from the Nisqually River (29 of 51; 58%) than Admiralty Inlet seals detected migrating from both the Nisqually and Green Rivers (7 of 50; 14%; $p < 0.001$).

Most steelhead tags (29 of 44) were detected by not more than 1 seal VMT, and the total number of VMT detections of these 29 tags ranged from 1 to 35 (median: 2). The 15 steelhead tags detected by 2 (n = 7), 3 (n = 7), or 4 (n = 1) seal VMTs were detected more frequently (range: 2–3266 detections; median: 55), and were never detected at fixed receiver arrays further along their migration path to the ocean (Table 4). Fourteen of the tags detected by no more than 1 seal VMT (48.3%) were detected by a fixed

Table 3. Detections of steelhead trout *Oncorhynchus mykiss* smolts by Central Puget Sound (Orchard and Blakely Rocks) and Admiralty Inlet (Snake and Colvos Rocks) harbor seals *Phoca vitulina* by river of release and population. The number of tagged seals and smolts released is shown next to each group. Forty-three of the 93 Nisqually population released into the Nisqually river were delay tags that were silent for 10 d (240 h) after release. The 7 of 43 Nisqually smolts with delay tags that were detected by harbor seal Vemco mobile transceivers (VMTs) are shown in parentheses

Seal tagging location	Nisqually River release Nisqually population (n = 93)	Nisqually River release Green population (n = 50)	Green River release Nisqually population (n = 50)	Green River release Green population (n = 53)	Total
Central Puget Sound (n = 4)	16 (6)	13	5	3	37
Admiralty Inlet (n = 7)	2 (1)	0	3	2	7

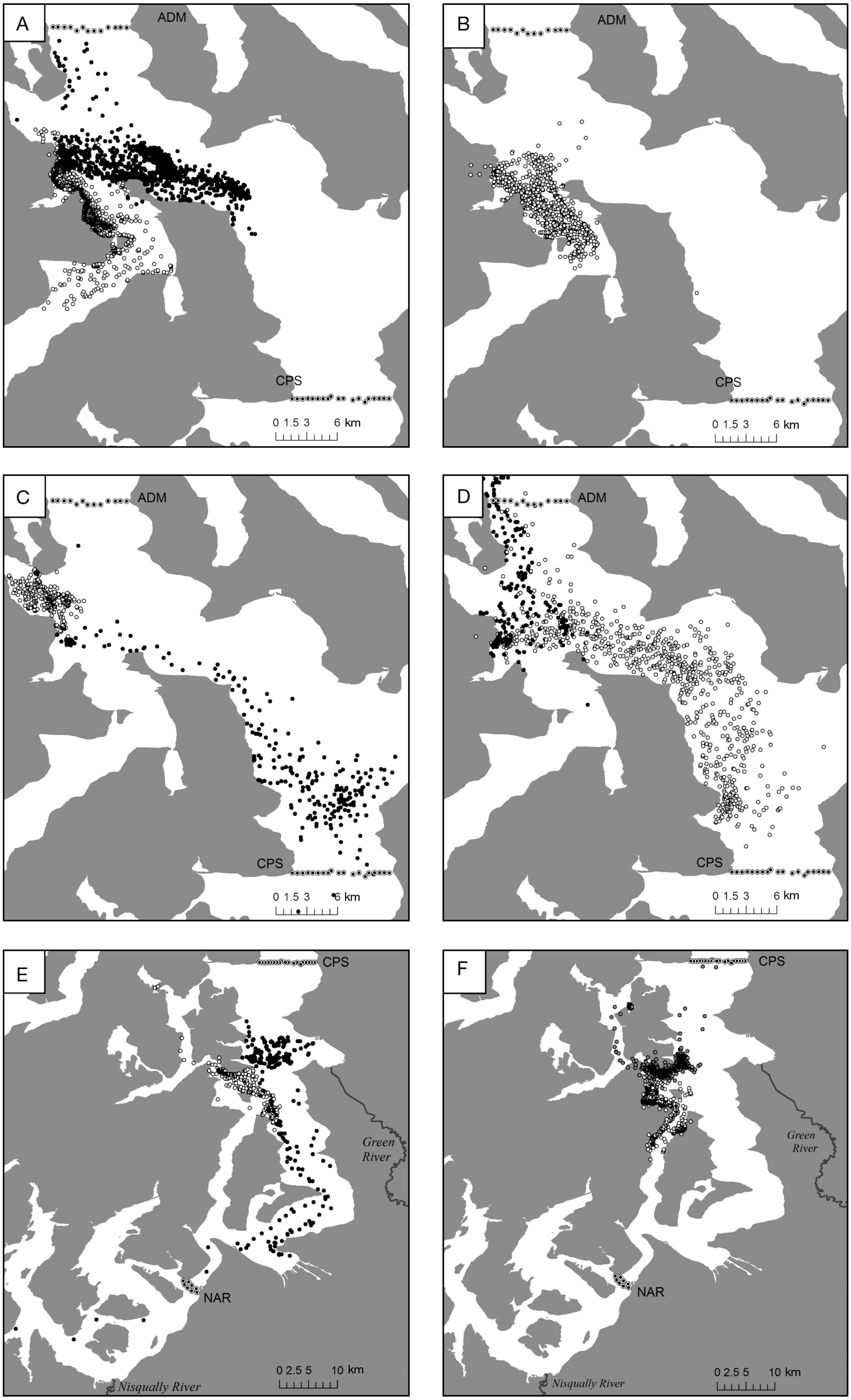
A
ADM
CPS
0 1.5 3 6 km
B
ADM
CPS
0 1.5 3 6 km
C
ADM
CPS
0 1.5 3 6 km
D
ADM
CPS
0 1.5 3 6 km
E
CPS
Green River
NAR
Nisqually River
0 2.5 5 10 km
F
CPS
Green River
NAR
Nisqually River
0 2.5 5 10 km

Table 4. Determinations of the final locations of 29 of the 44 steelhead trout *Oncorhynchus mykiss* smolts detected by harbor seals *Phoca vitulina*, including the number of seals detecting each smolt, total number of detections, whether the last detection occurred before or after the smolt migration window (June 10), the shortest duration between a Vemco mobile transceiver (VMT) detection of a steelhead tag and a GPS location, and the number of associations that were less than 30 min. The 9 tags assigned to haul-outs are inferred to have been consumed by harbor seals. The 'stationary' tags were detected multiple times and after the smolt outmigration period. The fixed VR3 array location is also provided for smolts that migrated past the location of their detection by a harbor seal, and therefore were known to have survived the encounter. The final location of the remaining 15 seal-detected smolts was unknown because there were no close (i.e. less than 30 min) associations, and they were not later detected at any of the fixed arrays. ADM: Admiralty Inlet, CPS: Central Puget Sound, JDF: Strait of Juan de Fuca

Tag	No. of seals	Total detections	Last detect before or after Jun 10	Last location (mo/d/yr)	Closest association (min)	Associations less than 30 min	Final location
Haul-out							
15902	1	17	After	7/15/14	6	4	Blakely
15915[a]	3	66	Before	6/6/14	0	18	Colvos
15929[a,b]	2	314	After	8/1/14	0	36	Orchard
15838[b]	2	295	Before	5/18/14	0	159	Orchard
15864[b]	3	411	After	7/15/14	0	196	Orchard
15880	3	504	After	8/8/14	0	208	Orchard
15799	2	3266	After	8/22/14	1	276	Orchard
15894	3	55	After	7/8/14	0	45	Orchard
15854	4	1750	After	8/1/14	0	415	Colvos
Stationary							
15960	2	24	After	6/29/14	22	2	See Fig. 4
15758	1	5	After	6/13/14	20	1	See Fig. 4
15794	2	2	After	6/16/14	9	1	See Fig. 4
15923	1	2	After	8/8/14	9	2	See Fig. 4
15768	2	2	After	8/22/14	20	2	See Fig. 4
15883	1	35	After	6/19/14	4	10	See Fig. 4
Survivors							
15769	1	15	Before	None	171	0	CPS
15812	1	1	Before	None	176	0	CPS
15855	1	1	Before	None	122	0	CPS
15980	1	1	Before	None	151	0	CPS
15968	1	3	Before	None	351	0	CPS
15852	1	2	Before	5/11/14	32	0	CPS
15862	1	5	Before	None	39	0	JDF
15970	1	2	Before	None	270	0	JDF
15976	1	1	Before	6/4/14	21	1	JDF
15973	1	2	Before	5/30/14	7	2	JDF
15770	1	2	Before	None	114	0	ADM
15905	1	2	Before	None	1437	0	ADM
15975	1	1	Before	None	478	0	ADM
15863	1	1	Before	5/12/14	30	1	ADM

[a]Delay tags
[b]Tags showing patterns consistent with harbor seal movements (see text)

VR3 receiver array at a later time and further along their migration path to the Pacific Ocean, indicating that the tags were probably still inside live steelhead smolts; these were categorized as 'survivors' (Table 4).

Evidence of predation by harbor seals

Nine of the steelhead smolt tags were likely consumed by harbor seals based on tag detection patterns including: (1) repeated associations placed the

Fig. 3. Fastloc GPS locations for the 11 harbor seals *Phoca vitulina* monitored in Puget Sound. Within each panel, the white or black represent 1 of 2 different seals corresponding to Table 1: (A) white = Seal 10, black = Seal 9; (B) white = 8; (C) white = 6, black = 11; (D) white = 5, black = 7; (E) white = 1, black = 4; (F) white = 2, black = 12. Maps A–D show Admiralty Inlet (ADM) seals, and Maps E and F show Central Puget Sound (CPS) seals. Black areas reflect a high density of overlapping locations. Some locations for seal 9 (Panel A) and seal 7 (Panel D) were outside the study area but are not shown. NAR: Tacoma Narrows

tag at a seal capture haul-out site, (2) the total number of detections was significantly greater than for 'survivors', (3) tags were never later detected at any stationary array, (4) the final detection came after the smolt outmigration period (7 of 9), and (5) detections occurred on more than 1 seal-mounted VMT (8 of 9; Table 4). Although outfitted harbor seals provided spatio-temporal information to identify likely predation by harbor seals on steelhead based on the above criteria, the data did not indicate that any of the tagged steelhead were consumed by any of the outfitted harbor seals.

Six of the 9 inferred seal-caused mortalities were associated with repeated seal locations near the Orchard Rocks haul-out site (n = 3), Blakely Rocks haul-out site (n = 1), and Colvos Rocks haul-out sites (n = 2; Fig. 4). In all cases, the 30 min (or less in most cases, Table 4) associations placed the tags within 700 m of the haul-outs. All were stationary, and all were still being detected after the smolt outmigration period. Three additional tags repeatedly associated with the Orchard Rocks haul-out exhibited behavior consistent with being carried by a non-instrumented harbor seal. One tag was detected by 3 harbor seals (often synchronously) over a period of 3 d at Orchard Rocks on consecutive incoming tides (Fig. 5A). After 3 d, the tag was never detected again by a harbor seal or at any fixed receiver. The other 2 tags exhibited similar patterns of detection by the same 3 harbor seals (Fig. 5B,C). Repeated detections by multiple harbor seals at the haul-out site on multiple days during similar stages of the tide is consistent with harbor seal movements. These 2 tags (15864 and 15929) were detected for 3 to 4 d at Orchard Rocks and were later detected repeatedly at nearby locations (within 4 km of the Orchard Rocks haul-out site) and were not detected elsewhere at any later time (Fig. 4). Such patterns of temporally or tidally repeatable detections on successive days were never observed at any of the 70 fixed VR3 arrays (either nearshore or offshore) in Puget Sound, and these patterns were never observed for any steelhead tags that survived to a stationary receiver further along the migration route. Thus, we interpret these data as suggesting these 3 tags were in the guts of non-instrumented harbor seals, and 2 of the 3 tags were apparently defecated by harbor seals at a nearby location.

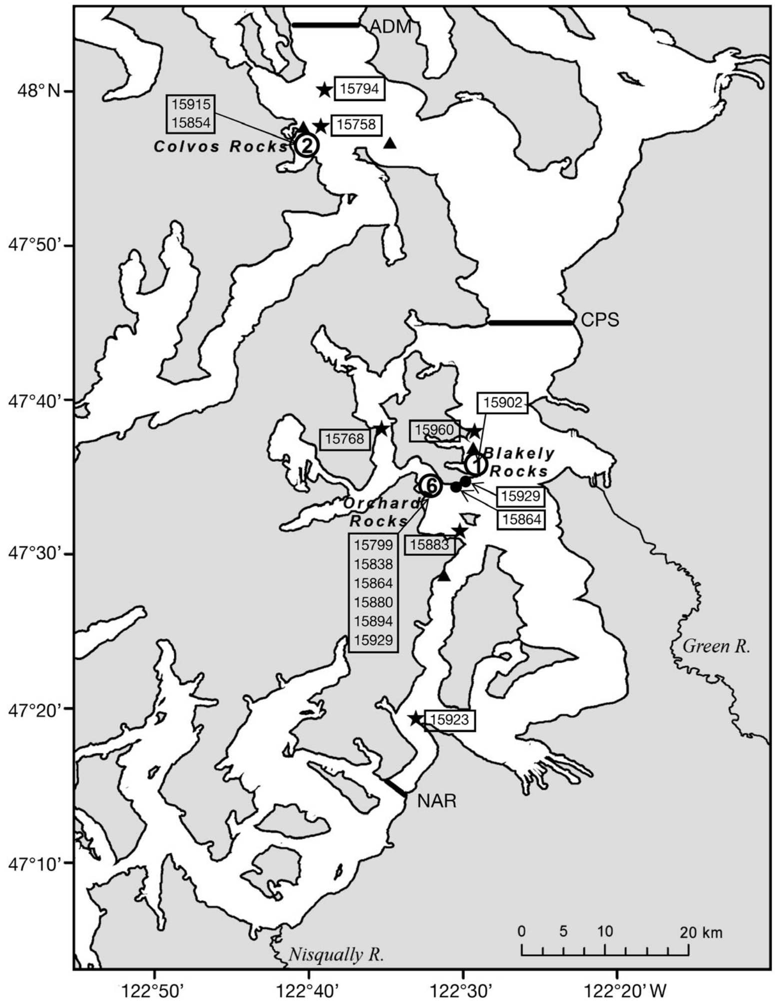

Fig. 4. Locations of steelhead trout *Oncorhynchus mykiss* smolts detected by harbor seals *Phoca vitulina* based on associations between a Vemco mobile transceiver (VMT) detection and GPS location(s) ocurring <30 min apart (see Table 3 for details). Numbers of inferred seal depredations at each haul-out are circled, and the corresponding tag numbers are shown (see Table 4 for additional information). Also shown are smolts detected by seal receivers and surviving to a stationary array further along the migration route to the Pacific Ocean (▲, no tag numbers shown), or detected after the smolt outmigration season and not later detected at a stationary array (★). The (●) correspond to 2 of the 6 smolts described in Fig. 5 that were detected at Orchard Rocks for several days and showed movement patterns indicative of harbor seals and were later found stationary at the indicated locations. ADM: Admiralty Inlet, CPS: Central Puget Sound, NAR: Tacoma Narrows

Six of the 44 tags detected by seal VMTs were likely 'stationary', but were

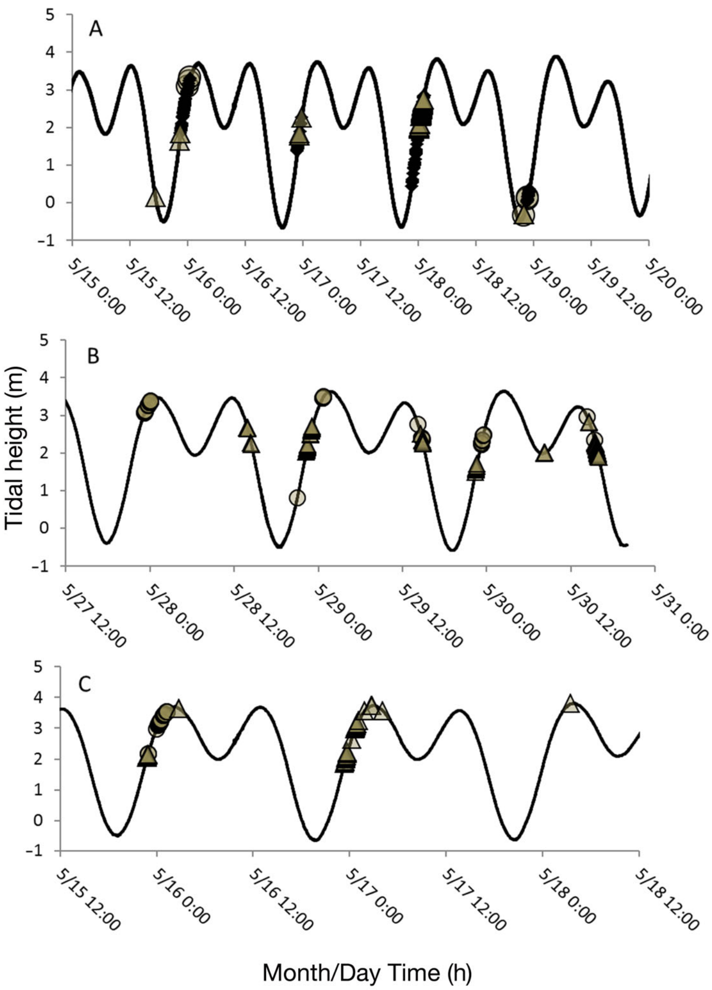

Fig. 5. Tidal height (m; black line), date (mo/d) and local time (h:min, PST), and detections of 3 different steelhead trout *Oncorhynchus mykiss* smolts (A = tag 15838, B = 15864, C =15929) at the Orchard Rocks haul-out. Each of the 3 unique symbols represents a different receiver-outfitted harbor seal *Phoca vitulina*

not included in the group of inferred seal depredations. These 6 tags were either detected at least twice by the same VMT, and in 1 case detected by 2 different seal VMTs, and the last detection(s) always occurred after the smolt outmigration period (Table 4). Locations for these tags were known from associations less than 30 min (in fact all had associations of 22 min or less; Table 4), and the locations are provided in Fig. 4.

The fate of 15 additional tags could not be categorized as either (1) surviving to a later fixed receiver line, (2) an inferred seal-caused mortality, or (3) otherwise stationary. These 15 tags were detected by either 1 (n = 9) or 2 (n = 6) seals and did not have time associations close enough to accurately determine their location. Six of the 15 non-categorized tags were last detected during the smolt outmigration period and 9 were last detected afterwards.

Tag noise effects on survival and distribution of stationary tags

There were no statistical differences between the proportion of Nisqually home-released smolts carrying delay tags (2 of 43; 0.046) and the proportion of continuous tags (2 of 50; 0.040) detected at the Admiralty Inlet and Strait of Juan de Fuca arrays (p = 0.877). The 95% CI for the difference in the 2 proportions ranged from –0.089 to 0.077. Travel time data from continuously pinging tags indicated that 14% passed the Admiralty Inlet and Juan de Fuca Strait arrays before 10 d (Table 5). Thus, as another basis for comparison, we reduced the sample size for the delay tags by 14% to n = 37 and re-calculated the proportion with this correction. Under this assumption, the proportion of delay tags detected would be 0.054 (p =

Table 5. Detections of continuously pinging tags (N = 50) and delay tags (N = 43) that began pinging 10 d after the Nisqually ‘home’ steelhead trout *Oncorhynchus mykiss* smolts (Nisqually population) were released from the Nisqually River at each of the stationary receiver arrays. The estimated percent still silent represents the percent of continuous tags arriving at each line within 10 d of release, assuming migration speeds equal to continuous tags. Based on travel times of continuously pinging tags, an estimated 86% of the delay tags would have turned on and been detectable by the Admiralty Inlet and Strait of Juan de Fuca arrays (see Fig. 3)

	Continuous		Delayed		Estimated %
	Smolts	Detections	Smolts	Detections	still silent
Estuary	47	5243	1	140	98
Narrows	23	300[a]	3	68	87
Central Puget Sound	11	316	0	0	73
Admiralty Inlet and Juan de Fuca Strait	2	12	2	25	14

[a]One tag was detected 4266 times on the Narrows fixed array and appeared to be stationary. This data point was not included in the total number of continuous tags detected on the Narrows array

0.757), and the 95% CI for the difference between the 2 proportions ranged from −0.105 to 0.077.

The low number of detected smolts on the Admiralty Inlet and Strait of Juan de Fuca arrays reflected low survival of both delay and continuous tagged smolts released into the Nisqually River. The number of continuous tags detected at previous arrays (estuary, Narrows, Central Puget Sound) was substantially and significantly greater than for delay tags as the smolts migrated through the main basin of Puget Sound ($p < 0.01$ at each fixed array; Table 5). Thus, assuming similar travel rates for steelhead smolts tagged with continuous and delay tags, 73% of the delay-tagged smolts would have been silent until sometime after they passed the Central Puget Sound array (Fig. 1, Table 5).

We failed to reject the null hypothesis that tag type (delay or continuous) was independent of detection as a stationary tag at one of the haul-out locations. Two of the 43 delay tags (0.046) were associated with haul-outs, compared to 5 of the 100 (0.050; 3 Nisqually home and 2 Green away) continuous tags implanted into smolts released into the Nisqually River ($p = 0.92$; 95% CI: −0.073 to 0.080).

DISCUSSION

Acoustic tags implanted into steelhead trout smolts were detected by harbor seal-mounted VMTs much more frequently than previous studies that deployed VMTs on pinnipeds to detect fish or other marine life. For example, Lidgard et al. (2014) recovered 64 VMTs deployed on grey seals over a 4 yr period in the Eastern Scotian Shelf (108 000 km^2) and the southern Gulf of St. Lawrence (80 000 km^2). Nine of the VMTs detected a total of 32 encounters with Atlantic cod (n = 623 tagged), Atlantic salmon (n = 298 tagged) and American eels (n = 17 tagged). Hayes et al. (2013) recovered VMTs from 21 elephant seals *Mirounga angustirostris*, which combined to detect 9 tags (great white sharks *Carcharodon carcharias*; salmon sharks *Lamna ditropis*; Chinook salmon *Oncorhynchus tshawytscha*; steelhead; and lingcod *Ophiodon elongatus*) in the Pacific Ocean. Steelhead smolts migrated very quickly through Puget Sound, which limited the temporal opportunity for encounters with harbor seals more so than for other fish species (e.g. Atlantic cod; Lidgard et al. 2014). The narrow geography of Puget Sound (approximately 3 to 10 km wide through most of the study section), on the other hand, probably facilitated detections because all of the Nisqually River smolts and some unknown proportion of Green River smolts had passed the Central Puget Sound haul-out locations, and all of the steelhead smolts had to pass the Admiralty Inlet haul-outs to migrate to the Pacific Ocean. Evidence of brief, potentially random, encounters comes from the 14 smolts that were detected infrequently by harbor seals and later passed a stationary array further along their migration path. However, half of the seal-detected tags (n = 22) were detected after the smolt outmigration period, many of which were stationary. The location of 10 tags detected after the smolt outmigration was unknown because there were no GPS associations close enough in time to determine location. These tags were also likely stationary because there is very little evidence of steelhead smolts residing within Puget Sound (Moore et al. 2015).

We inferred that at least 9 steelhead smolts were consumed by harbor seals based on the signaling pattern of tags and their final locations. It is possible that the inferred predation events attributed to harbor seals reflect predation by other species (e.g. cormorants) defecating the tags in very close proximity to the seal haul-out locations. However, given the large study area (approximately 900 km^2 of available habitat from Nisqually estuary to Admiralty Inlet array), there is approximately a 0.11% chance that any single tag not migrating through the study area would be deposited within 1 km of a random location. This percentage would be even smaller if we consider tags that may have been consumed by a predator and defecated on land (see Osterback et al. 2014) and therefore not detectable by acoustic receivers. Additional indications that the tags located at haul-outs were consumed by harbor seals comes from repeatable detection patterns of 3 tags over a 3 to 4 d period, consistent with an ingested tag present in the gut of a non-outfitted seal. Gut passage time for Passive Integrative Transponder tags (23 mm × 4 mm, 0.6 g) by harbor seals ranged between 3.0 and 7.5 d post-consumption (Chad Nordstrom, Vancouver Aquarium Marine Mammal Research Program, PO Box 3232, Vancouver, BC V6B 3X8, Canada; pers. comm.), which is very consistent with the patterns of the 3 tags we presume were consumed by non-outfitted harbor seals.

The present study provides the clearest evidence that harbor seals consume steelhead smolts in Puget Sound, which may contribute to the low marine survival rates experienced in recent decades. Harbor seal predation on steelhead smolts has been implicated as a potentially important source of steelhead smolt mortality in small coastal estuaries based on the presence of harbor seals in areas of high steelhead mortality (Johnson et al. 2010, Romer et al. 2013). Melnychuk et al. (2013) inferred that tagged steelhead smolts had been consumed by harbor seals in other regions of the Salish Sea based on spatial and temporal overlap of seals and steelhead smolts and tag movement patterns more indicative of harbor seal behavior than steelhead behavior. In the Strait of Georgia, although juvenile salmonids generally comprise a minor component of harbor seal diets, the impact on smolt populations may be substantial. Thomas (2015) discussed the possibility that even a 5% harbor seal diet composition of coho salmon smolts in the Strait of Georgia could account for millions of smolts being consumed in a single month. A rigorous estimation of a predation rate (percentage of smolts consumed by harbor seals) was beyond the scope of that study and this one, and will be informed by future work with broader spatial coverage and additional data analysis.

Predation events inferred from the type of data used in this study would need to be expanded to avoid underestimating the actual predation rate. For example, harbor seals are likely to defecate tags at locations other than monitored haul-outs, and any stationary tags defecated away from the harbor seal tagging locations were not included in our inferred predation events. Additionally, the outfitted harbor seals in this study effectively monitored the Orchard Rocks, Blakely Rocks, and Colvos Rocks haul-outs, but these represent only a small portion of the harbor seal population in Puget Sound. Different legal mandates provide protections for Puget Sound steelhead (Endangered Species Act, ESA 1973) and harbor seals (Marine Mammal Protection Act, MMPA 1972). Depending on the rate of harbor seal predation on steelhead smolts to be estimated from future studies, managers may face trade-offs associated with conservation of both predator and prey species (Marshall et al. in press). Conflicts arising from such trade-off scenarios emphasize the need for accurate assessments of predator–prey interactions.

We hypothesize that harbor seal predation on steelhead smolts under current conditions may be partly caused by increases in the Puget Sound harbor seal population, declines in other prey resources, and density-dependent predation (see Holling 1959) associated with spring pulse abundances of steelhead smolts exceeding predation thresholds (e.g. Piatt & Methven 1992). Upper-trophic-level predators can exert a strong influence on marine food webs, switching to less-preferred prey as preferred prey are depleted (Berriman et al. 2015 and see papers cited within). Juvenile salmonids typically comprise a small component of diets of harbor seals, which feed most frequently on gadoids and clupeids in the Salish Sea (Thomas et al. 2011). A major shift in the Puget Sound food web occurred in the early 1990s (Harvey et al. 2012). Although the specific causes are unknown, several previously abundant demersal species (Pacific cod *Gadus macrocephalus*, hake *Merluccius productus*, rockfishes *Sebastes* spp.) and some pelagic (Pacific herring *Clupea pallasi*) stocks suffered steep declines (Gustafson et al. 2000, Drake et al. 2010, Landis & Bryant 2010). Concurrently, marine survival rates of larger-bodied salmonid smolts (steelhead and coho salmon) also declined (Scott & Gill 2008, Zimmerman et al. 2015). These changes occurred at the same time that harbor seal numbers increased following implementation of the federal protections for marine mammals (Jeffries et al. 2003). Harbor seals are generalist foragers, but with clear species preferences that can reflect ecosystem shifts over decadal time scales (Thomas 2015). Harbor seal diets also shift seasonally in response to fish migrations, spawning aggregations, and other factors (Olesiuk 1993, Thomas et al. 2011, Lance et al. 2012). Steelhead smolts migrate rapidly to the Pacific Ocean and are only present in appreciable numbers in Puget Sound for about 2 mo (mid-April to mid-June), with a strong peak in abundance from early to mid-May. Smolts migrating both before and after the peak in abundance tend to exhibit greater survival through Puget Sound than during periods of relatively greater abundance (Moore et al. 2015), suggesting that under current conditions, steelhead smolt abundance may exceed threshold exposures, triggering higher rates of predation during periods of peak abundance.

There was no statistical evidence to support a 'dinner-bell effect' or any differential detection of delay and continuous tags in this study. A more robust test would include larger numbers of tagged fish and would provide greater confidence that tag noise has no effect on steelhead smolt survival in Puget Sound. Delay (silent for 10 d) and continuous tags were detected at similar low rates leaving the main basin of Puget Sound, stationary at haul-out locations, and at other locations after the smolt outmigration period. Continuously pinging tags released from the Green River were detected at a significantly higher rate at the Admiralty Inlet and Strait of Juan de Fuca arrays than continuous and delay tags from the Nisqually River (Moore & Berejikian unpubl.), demonstrating that a greater detection of smolts with delay tags could have been detected, had they actually survived at a higher rate. The worldwide use of acoustic telemetry tags in the marine environment and recent efforts to use pinnipeds as 'mobile receivers' (Hayes et al. 2013) has led to concerns that the 69 kHz frequency can be heard by pinnipeds and could increase vulnerability of tagged prey to predation by predators that can hear the tags. In a laboratory raceway, Stansbury et al. (2015) tested whether grey seals visited feeding boxes more frequently if associated with sound from a 69 kHz tag. Seals learned to locate food faster and visit feeding boxes more frequently if there was a pinging tag present. The ping rate (every 13 ± 8 s) was much shorter than in our study (30–90 s uniformly distributed random delay with a mean transmission interval of 60 s), and it is important to note that it took about 6 trials to generate a differential response to boxes with and without tags (Stansbury et al. 2015, their Figs. 3–5). The sound of the tags in Puget Sound may not have influenced survival or the fate of tags remaining in Puget Sound for several reasons: (1) brief encounters between tagged steelhead and harbor seals were insufficient for the harbor seals to learn to associate the sound of the tag with food, (2) the payoff (eating a single steelhead smolt) was insufficient to alter seal feeding behavior, (3) the random ping delay was too infrequent for harbor seals to locate tagged steelhead they could not see, or (4) the acoustic environment in Puget Sound may have rendered tag noise less detectable to harbor seals than in controlled laboratory environments.

In summary, the present study detected a far greater spatio-temporal overlap in harbor seals and steelhead trout smolts than has been documented in other studies outfitting pinnipeds with acoustic receivers and GPS tags. Greater overlap and evidence for inferred predation were detected in Central Puget Sound where mortality appears most acute for migrating steelhead smolts (Moore et al. 2015). A number of concurrent factors, including stationary tags near monitored harbor seal haul-outs, provided evidence of harbor seal consumption of steelhead smolts. We hypothesize that harbor seal predation on steelhead smolts during their early marine phase could be a significant source of mortality and that the underlying causes may include increases in predator populations concomitant with decreases in the availability of historically more available alternative prey. Additional research is needed to estimate the level of harbor seal predation of steelhead smolts and to evaluate potential population effects of such predation.

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