

TELEMETRY CASE REPORT

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Performance of a high-frequency (180 kHz) acoustic array for tracking juvenile Pacific salmon in the coastal ocean

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Abstract

Background: Acoustic telemetry is now a key research tool used to quantify juvenile salmon survival, but transmitter size has limited past studies to larger smolts (> 130 mm fork length). New, smaller, higher-frequency transmitters (“tags”) allow studies on a larger fraction of the smolt size spectrum (> 95 mm); however, detection range and study duration are also reduced, introducing new challenges. The potential cost implications are not trivial. With these new transmitters in mind, we designed, deployed, and tested the performance of a dual-frequency receiver array design in the Discovery Islands region of British Columbia, Canada. We double-tagged 50 juvenile steelhead (*Oncorhynchus mykiss*) with large 69-kHz tags (VEMCO model V9-1H) and small 180-kHz tags (model V4-1H). The more powerful 69-kHz tags were used to determine fish presence in order to estimate the detection efficiency (DE) of the 180-kHz tags. We then compared the standard error of the survival estimate produced from the tracking data using the two tag types which has important implications for array performance and hypothesis testing in the sea.

Results: Perfect detection of the 69-kHz tags allowed us to determine the DE of the 180-kHz tags. Although the 180-kHz tags began to expire during the study, the estimated DE was acceptable at 76% (SE = 9%) when we include single detections. However, 95% confidence intervals on steelhead survival (64%) were 1.5 × larger for the 180-kHz tags (47–85% vs. 51–77% for 69 kHz) because of the reduced DE.

Conclusions: The array design performed well; however, single detections of the 180-kHz tags indicates that under slightly different circumstances the DE could have been compromised, emphasizing the need to carefully consider the interaction of animal migration characteristics, study design, and tag programming when designing telemetry arrays. To increase DE and improve the precision of 180 kHz-based survival estimates presented here requires either an increase in receiver density, an increase in tag sample size (and modified transmitter programming), or both. The optimal solution depends on transmitter costs, array infrastructure costs, annual maintenance costs, and array use (i.e., contributors). Importantly, the use of smaller tags reduces potential tag burden effects and allows early marine migration studies to be extended to Pacific salmon populations that have been previously impossible to study.

Keywords: Pacific salmon, Array design, Acoustic telemetry, Detection efficiency, Tagging, Survival, Precision, Optimization

Background

Acoustic telemetry is now a key research tool used to study where, and in some cases how, juvenile salmon die during the early phases of their migration and to estimate survival, but transmitter size has limited past studies to larger smolts [1]. Smaller transmitters have been

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recently developed (Fig. 1a), but their size results in both more limited battery payloads and higher transmission frequencies. The smaller battery constrains how often and how “loud” (i.e., how much acoustic power) the tag can transmit, reducing the chance of detecting the emitted signals. Perhaps of greatest consequence, the natural resonant frequency at which a transducer most efficiently converts an electric field into a pressure wave (sound) shifts to higher frequencies as transducer size shrinks, due to the material properties of the piezoelectric ceramic used to form the transducer [2, 3]. Adopting the use of higher frequencies that is implicit in choosing the smallest available tags has important practical implications. The rate of sound absorption in water increases by almost an order of magnitude between 69 and 300 kHz [4]; as a result, the transmitted sound from even very loud high-frequency tags rapidly becomes attenuated with distance from the source. As a consequence of the use of smaller tags, transmitter life, signal detection range, and (often) acoustic power output are reduced, limiting study duration and reducing the probability that a tag will be detected in the vicinity of a receiver. This trade-off has

major cost implications for research programs that target juvenile salmon or other small, highly migratory fishes.

An acoustic telemetry array known as the POST array (Pacific Ocean Shelf Tracking array; [5]) has been in place since 2004 to monitor the movements of tagged animals in and out of the Salish Sea, the marine waters lying between Vancouver Island and mainland British Columbia, Canada, and within the US state of Washington [6, 7]. This array was designed using VEMCO (Bedford, Nova Scotia, Canada) acoustic receivers capable of detecting 69-kHz VEMCO transmitters. Knowledge of the early marine life history of salmonids has been greatly enhanced by the continuous successful operation of this array (e.g., [8–16]).

The POST array design was originally developed for use with low-powered V9 acoustic transmitters (69 kHz, 145 dB re 1 μ Pa @ 1 m), which were the only salmon-smolt-sized tag that was available at the time the original array design was developed [5]. This tag had a roughly 400 m detection range in the ocean ([17]; see Additional file 1: Figure S1) and approximately four month life span after activation, and in practice was detected with ~85–90% efficiency on the individual receiver arrays forming the overall POST array (also variously referred to as curtains, lines, or gates elsewhere in the literature) when the average tag transmission interval was approximately every 60 s [14]. Multiple surgical trials indicated that this tag could be reasonably implanted in large smolts \geq 140 mm in fork length (FL) [18–20].

In 2007, VEMCO introduced the V7 acoustic tag (69 kHz; 136 dB re 1 μ Pa @ 1 m) which are physically smaller than V9s and can be implanted into smolts \geq 125–130 mm fork length [19, 21–23]. The trade-off is that this smaller tag has a weaker acoustic signal at source resulting in both a reduced range (reduced from ~400 to ~300 m in our experiments; see Additional file 1: Figure S1) relative to the low-powered V9 tags and a shorter lifespan when using the same programming. With all other factors remaining equal, this drop in range means that only about three-quarters as many tagged fish will be detected on a given telemetry array and only for a reduced maximum time period, restricting the detection efficiency (DE, the proportion of tagged fish present that are detected), and the maximum potential tracking distances and study duration. Despite this loss of information, the accuracy of the results using V7 tags has generally been deemed satisfactory when using release groups of a few hundred smolts per year to achieve baseline survival estimates in British Columbia [9, 10, 14] and in other salmon-bearing rivers systems [24–26]. Nevertheless, the minimum smolt size limits of approximately 130 mm (V7) or 140 mm FL (V9) excludes a substantial proportion of the overall size spectrum of migrating

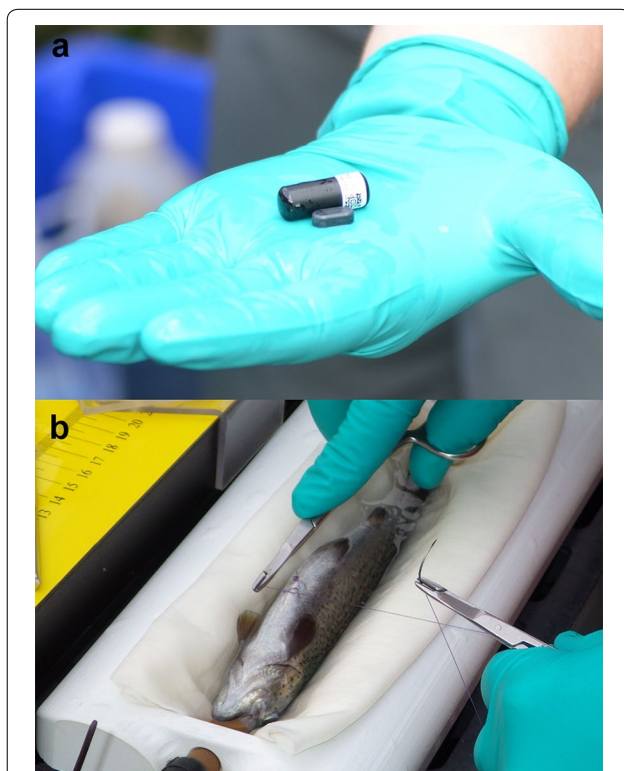


Fig. 1 Double tagging steelhead. **a** VEMCO V9-1H (69 kHz; larger tag) and V4-1H (180 kHz) acoustic transmitters being **b** implanted interperitoneally into a summer steelhead (*Oncorhynchus mykiss*) smolt. One of each tag type was surgically implanted into each of 50 smolts

Pacific salmon smolts. This raises important questions concerning the applicability of past results, given the lack of data from the population demographic that is contained within the lower end of its size spectrum.

Over the past decade, smaller tags operating at correspondingly higher frequencies have been developed, e.g., the Juvenile Salmon Acoustic Telemetry System (JSATS) tags, which transmit at 416.7 kHz [27, 28] and have been used primarily in fresh water, and VEMCO's family of 180-kHz [29] tags which are used in fresh water and marine environments. The first of the 180-kHz tags to be marketed was the V6 (V6-4H, 6 mm diameter, 16.5 mm length, 1.0 g in air, 143 dB re 1 μ Pa @1 m) followed by the V5 (e.g., V5-1H: 4.3 mm diameter, 12.7 mm length, 0.65 g in air, 143 dB) and more recently, the V4 (V4-1H: 3.6 mm diameter, 11 mm length, 0.42 g in air, 134 dB), with the latter capable of being implanted into salmon smolts smaller than 100 mm FL [30]. Despite their small size, these high-frequency VEMCO tags have roughly the same acoustic power output as some of the 69-kHz tags; however, the achieved detection range is much reduced because the higher-frequency signals attenuate more quickly in water. We found that the now-discontinued V6 tag had a detection range of ~80–100 m in the marine waters of the Strait of Georgia (see Additional file 1: Figure S1). We have not formally range tested the smaller V5 and V4 tags, but given their acoustic power relative to the V6, we expect ranges to be of roughly similar magnitude.

Use of a smaller tag has the biologically desirable feature of allowing a greater fraction of the migrating smolts to be included in a study; however, the trade-off is that with equivalent programming these smaller tags are more infrequently detected and for shorter maximum time periods. To improve performance, it is necessary to increase receiver density, tag numbers, and/or the transmission rate of the tag, which have profound implications for developing cost-effective, efficient arrays. For example, in the simplest possible case, the area monitored around a receiver is πr^2 , where r is the detection range, so using a V4 instead of a V9 tag means that an array of receivers would theoretically need 16–25 times as many receivers to achieve the same areal coverage (and detections per tag) given the expectation that the tag-detection range will be reduced to 80–100 m from 400 m. Increasing the tag sample size can also compensate for the lower DE; however, if the DE is low (or survival is low), the sample size becomes cost prohibitive to achieve the same confidence intervals as for V9 tags, and when DE is very low, survival is often not estimable in practice in mark–recapture models. Increasing the transmission rate of the tag allows more opportunities for detection, but also decreases transmitter battery life which will in turn, limit study duration. Thus, finding the right balance is

important for successfully estimating fish survival using 180 kHz tags.

To facilitate the transition to studies using smaller tags and smaller smolts, we tested the performance a new array design at detecting 180 kHz V4 tags. We deployed dual-frequency receiver arrays (VEMCO model VR4) in the Discovery Islands and Johnstone Strait region of British Columbia, a region bounded by the British Columbia mainland and Vancouver Island, and lying within the original POST array (Fig. 2). These two arrays were deployed as paired lines of receivers (each line is referred to as a subarray), with the subarrays separated by a reasonable distance that is large relative to the internode (receiver) spacing but sufficiently short so that few tagged animals were expected to die during the migration between the first and second subarrays. This resulted in a doubling of the number of receivers forming each of the new arrays, but with internode spacing close to that of the original POST array design so that an objective comparison of performance would be possible. Although we only doubled the number of receivers (rather than increasing it by 16–25 fold), we also decreased the tags' mean transmission intervals (from 60 to 20 s) to increase the probability that tags would be detected when within range of a receiver. We then double-tagged large, hatchery-reared steelhead (*Oncorhynchus mykiss*) smolts with high-power V9 (69 kHz; 151 dB re 1 μ Pa @ 1 m) and V4 (180 kHz; 134 dB re 1 μ Pa @ 1 m) tags (Fig. 1), tracked them through the array, and calculated the DE of both tag types (see "Methods"). Based on past performance, the high acoustic power V9 tags were expected to have near-perfect detection, which could then be used as a baseline to calculate the detection efficiency of the smaller 180-kHz tags as well as estimate smolt survival. That is, if the 69-kHz tag was detected and the 180-kHz tag was not, then we knew that the fish was near the receiver but not close enough for the 180 kHz receiver to detect the 180 kHz transmission. We then used a Cormack–Jolly–Seber (CJS) model to explore how the confidence intervals on estimated survival increase with decreased DE and how this may affect future 180 kHz-tag-based studies, where the actual detection probability is uncertain.

Results

Of the 50 double-tagged steelhead smolts released, 42 were detected on the Northern Strait of Georgia (NSOG) acoustic array 19 km north of the release site; eight were never detected (Table 1). One of the 42 detected fish turned south after being detected on NSOG and exited the Strait of Georgia via the Strait of Juan de Fuca. Thirty-two fish were subsequently detected on the Discovery Islands array (DI). Of those, four fish milled back and forth between NSOG and DI, with two of these four

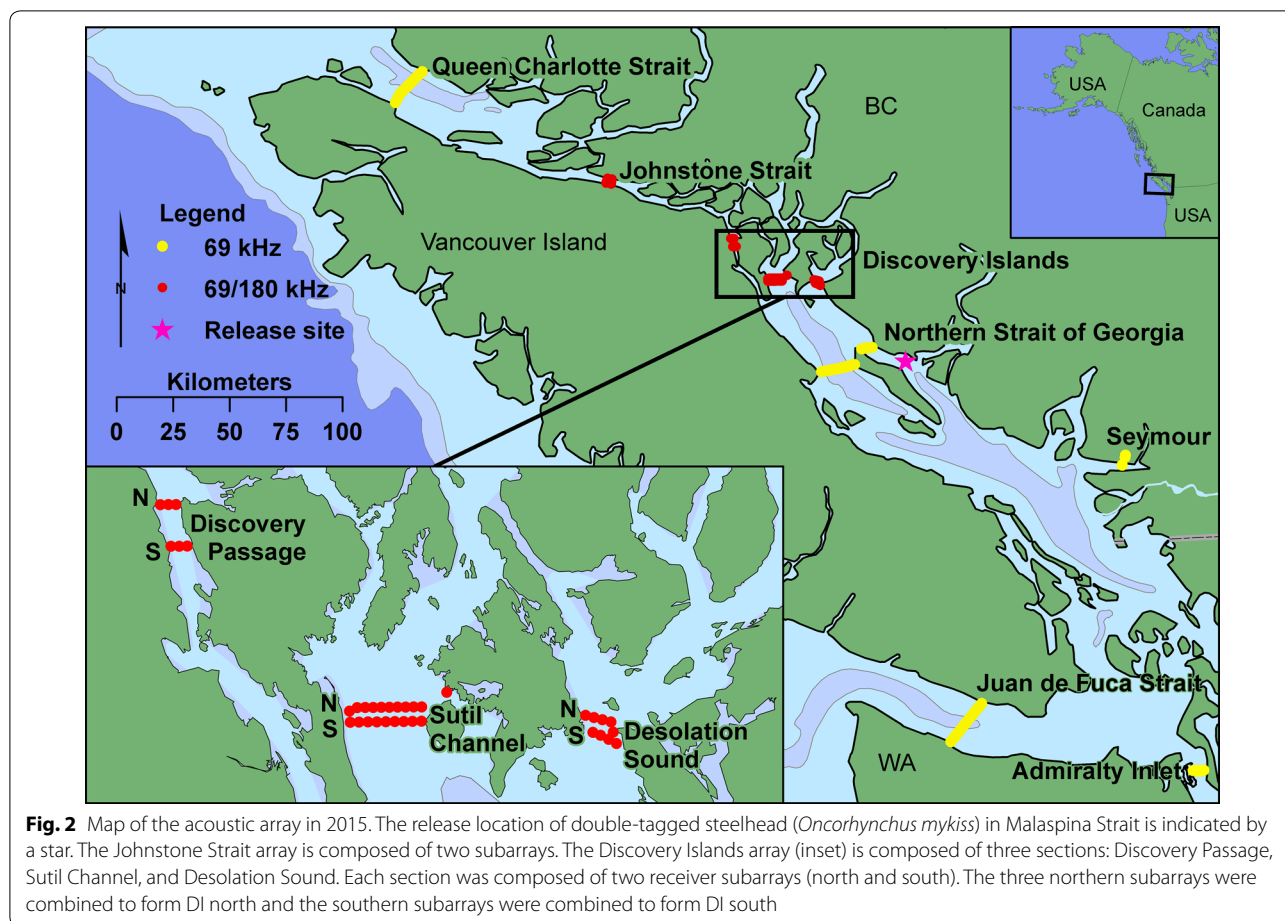


Table 1 Count of steelhead (*Oncorhynchus mykiss*) smolts by tag type detected migrating over the acoustic array

Array	69 kHz	180 kHz
Northern Strait of Georgia (NSOG) ^a	42	7
Discovery Islands (DI)	32 ^b	20 ^b
Desolation Sound (DS)	3	2
Sutil Channel (SC)	16	12
Discovery Passage (DP)	20	9
Johnstone Strait (JS)	23	4
Queen Charlotte Strait (QCS) ^c	14	NA
Strait of Juan de Fuca (JDF) ^c	1	NA

Fifty double-tagged fish were released

^a Limited capability of detecting 180-kHz tags. (Few receivers were dual-frequency.)

^b Several of the fish detected on DI were detected on more than one section

^c Receivers incapable of detecting 180-kHz tags

last detected at NSOG (i.e., travelling south). There was also milling across the three waterways spanned by the DI array (see “Methods”) with seven fish detected at more than one waterway.

A dynamic animation of the movements of the double-tagged Seymour River steelhead smolts is available [31] which can be panned and zoomed and used to obtain summary statistics as well as full detection histories. Movie versions of the animations are available on request.

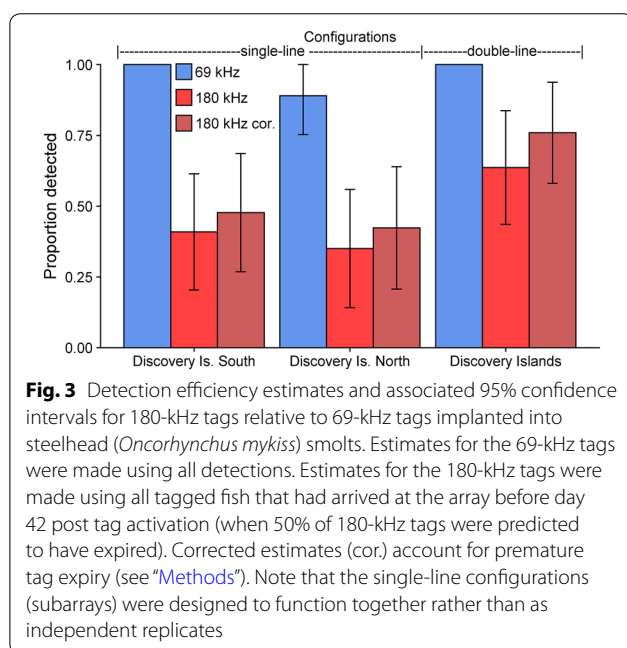
Detection efficiency (DE)

The 69-kHz transmitters had 100% DE on the NSOG, DI, and Johnstone Strait (JS) arrays (i.e., all fish detected at subsequent locations on the migration path were first detected on the prior arrays (Table 2; Fig. 3). Detection efficiency of 69-kHz tags was also high (91–100%) for each of the individual subarrays forming the DI (south and north) and JS (east and west) arrays.

The DE of the 180-kHz transmitters on DI was 61%. This, however, was a lower bound on the estimate because the tags began to expire before all fish had passed DI (Fig. 4) because we postponed the fish release date (see “Methods”). Most tagged fish (79%) arrived at DI before the median projected day of battery expiry, 42 days post activation, suggesting that some 180-kHz

Table 2 Detection efficiency (DE) of 69-kHz (V9-1H) tags implanted in steelhead (*Oncorhynchus mykiss*) smolts

Array	N present	N detected	69 kHz DE (SE)
Northern Strait of Georgia	42	42	1.00 (0)
Discovery Islands	32	32	1.00 (0)
Discovery Islands south	32	31	0.97 (0.03)
Discovery Islands north	32	32	1.00 (0)
Johnstone Strait	23	23	1.00 (0)
Johnstone Strait east	23	23	1.00 (0)
Johnstone Strait west	23	21	0.91 (0.06)

**Fig. 3** Detection efficiency estimates and associated 95% confidence intervals for 180-kHz tags relative to 69-kHz tags implanted into steelhead (*Oncorhynchus mykiss*) smolts. Estimates for the 69-kHz tags were made using all detections. Estimates for the 180-kHz tags were made using all tagged fish that had arrived at the array before day 42 post tag activation (when 50% of 180-kHz tags were predicted to have expired). Corrected estimates (cor.) account for premature tag expiry (see “Methods”). Note that the single-line configurations (subarrays) were designed to function together rather than as independent replicates

tags likely stopped transmitting before being detected. If we limit the time period under consideration to 42 days, the calculated DE was slightly higher: 64%. If we assume that all tag batteries had been actively transmitting up to day 42, the DE of the 180-kHz transmitters on DI increases to 76% (referred to as “corrected”; Table 3; Fig. 3).

The DE of the 180-kHz tags on the individual DI lines was 41% on DI south and 39% on DI north using the full dataset, and 41% and 35%, respectively, when limiting the time period to the median date of projected 180-kHz tag expiry, and 48% and 42%, respectively, when corrected for expected tag expiry (Table 3).

Detections per tag

Although the resulting DE values suggest promising performance of the modified array design at detecting higher-frequency tags, a median of only four detections

per 180-kHz tag was obtained compared to 73 detections for 69 kHz tags (Fig. 5a). Of the 22 double-tagged fish detected on DI up to day 42 using the 69-kHz tag, five 180-kHz tags were never detected (23%) and four (18%) were detected only once (Fig. 5b). Single detections are often questionable in telemetry studies, but in this case fish presence was confirmed by the paired 69-kHz tag.

Precision of survival estimates

Survival from release in Malaspina Strait to DI based on the 69-kHz data was 64% (32/50) with an SE of 7% and 95% confidence interval of 51–77%. The SE on the survival estimate for the simulated 180-kHz dataset with the same survival (see “Methods”) was 9% and the 95% CI was 47 to 85%. Thus, the CIs widen for the 180-kHz tags because of the reduced DE (Fig. 6). See Healy et al. [8] for complete early-marine survival estimates of 69-kHz tagged steelhead from the Seymour River released in or near the Seymour River and tracked to Queen Charlotte Strait (QCS) in the same year as this study.

Discussion

Array performance

High acoustic power 69-kHz transmitters had excellent (100%) DE on the Discovery Islands array, allowing us to evaluate the performance of the new array at detecting harder-to-detect 180-kHz transmitters. The estimated DE was 76% (SE = 9%) for 180-kHz tags (Fig. 3; Table 3). This is comparable to the DE of VEMCO model V7 69-kHz tags that have been used to estimate early marine survival of sockeye (*Oncorhynchus nerka*), steelhead, and Chinook (*Oncorhynchus tsawytscha*) salmon migrating through the original POST array configuration [9, 10, 14]. In a separate concurrent steelhead tracking study, we found that the new array also greatly improved the DE of V7 transmitters (94%, SE = 3.5%, 95% CI 82–98%; [8]). Our results suggest that with appropriately redesigned array geometry it is now possible to track smolts ≥ 95 mm FL in the Salish Sea and other coastal marine ecosystems with acceptable statistical precision, and to track larger fish with lower tag burden with exceptional precision, at approximately a doubling of capital costs over the original POST array design.

Two important additional considerations for future survival studies, however, are that the number of detections recorded per fish was substantially reduced with the 180-kHz tag, as was the operational lifespan of the tags. Eighteen percent of the count of 180-kHz tags deemed present were based on a single recorded detection, despite the more frequent transmission interval (20 s on average vs. 60 s for the 69-kHz tags). Because some tags had expired or were nearing expiry, the frequency of single and zero detections may be biased high in this study

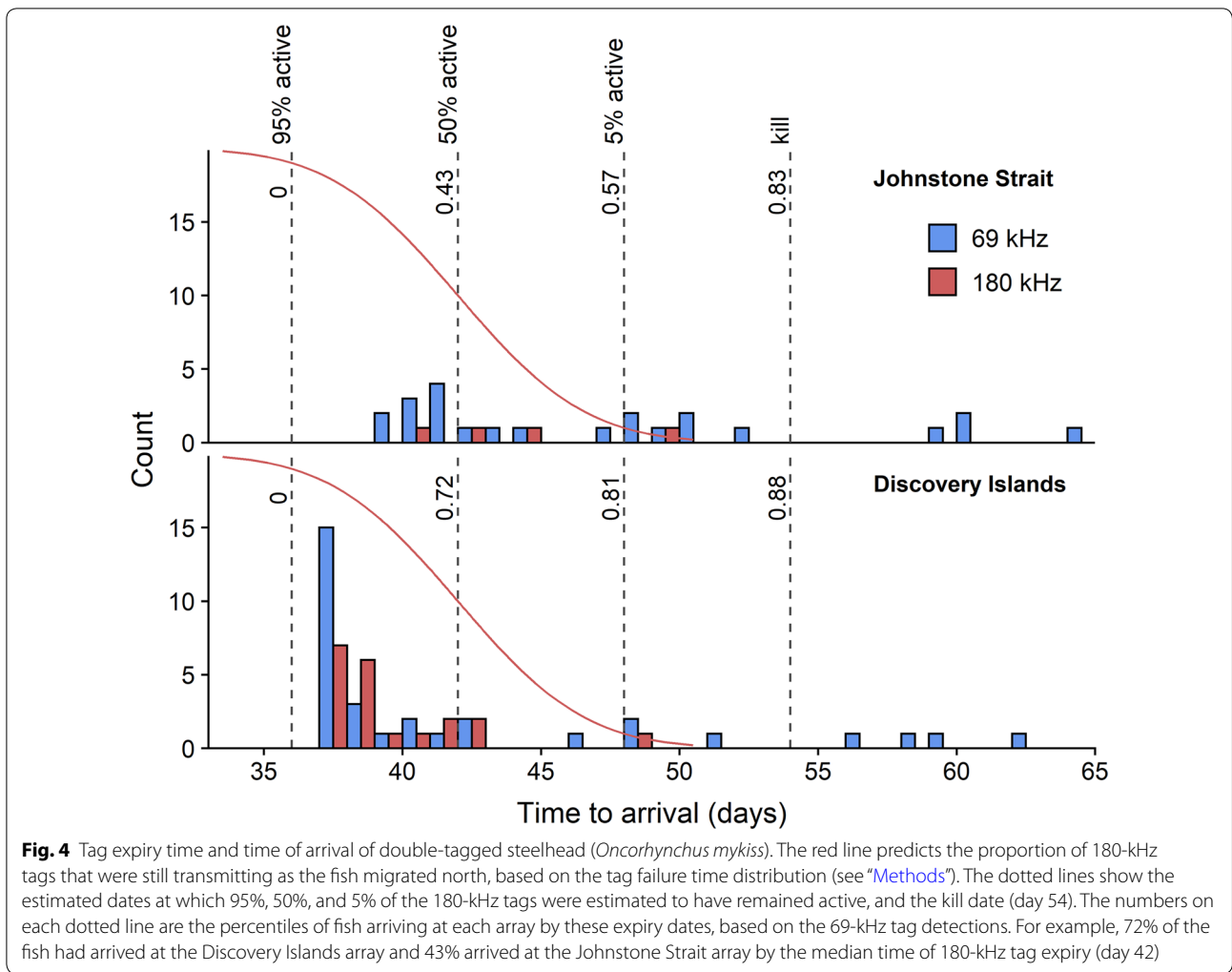


Fig. 4 Tag expiry time and time of arrival of double-tagged steelhead (*Oncorhynchus mykiss*). The red line predicts the proportion of 180-kHz tags that were still transmitting as the fish migrated north, based on the tag failure time distribution (see “Methods”). The dotted lines show the estimated dates at which 95%, 50%, and 5% of the 180-kHz tags were estimated to have remained active, and the kill date (day 54). The numbers on each dotted line are the percentiles of fish arriving at each array by these expiry dates, based on the 69-kHz tag detections. For example, 72% of the fish had arrived at the Discovery Islands array and 43% arrived at the Johnstone Strait array by the median time of 180-kHz tag expiry (day 42)

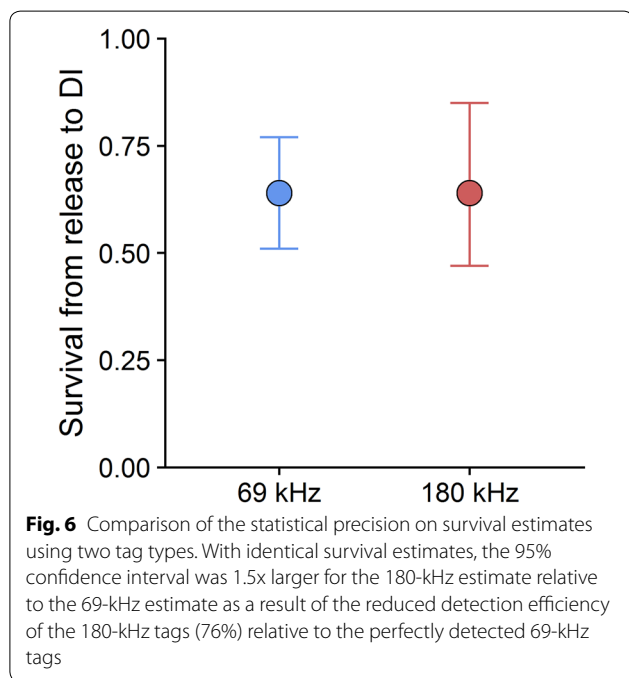
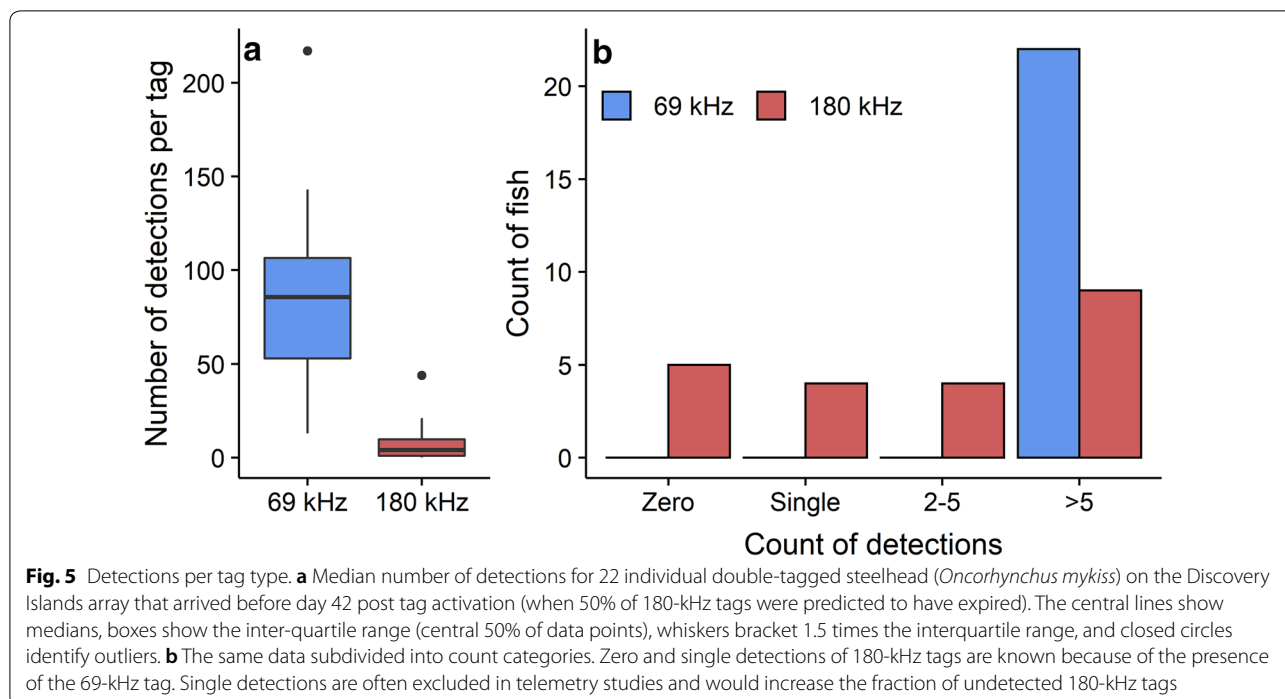
Table 3 Estimated detection efficiency (DE) of the 180-kHz (V4-1H) tags implanted in steelhead (*Oncorhynchus mykiss*) smolts

Array	Time period	N present	N detected	N corrected	DE (SE)	Corrected DE (SE)
Discovery Islands	< 50% expired	22	14	16.7	0.64 (0.10)	0.76 (0.09)
	100% off	28	17		0.61 (0.09)	
Discovery Is. south	< 50% expired	22	9	10.5	0.41 (0.10)	0.48 (0.11)
	100% off	27	11		0.41 (0.09)	
Discovery Is. north	< 50% expired	20	7	8.5	0.35 (0.11)	0.42 (0.11)
	100% off	28	11		0.39 (0.09)	

DE estimates are for two time periods: for detections recorded before day 42 following tag activation when 50% of 180-kHz tags were predicted to have expired; and for all detections until the tags were programmed to turn off (day 54). Numbers detected in both time periods exclude counts of 180-kHz tags only detected > 24 h after their paired 69-kHz tag (N = 3 at Discovery Islands, N = 5 at Discovery Islands south, and N = 3 at Discovery Islands north). N Present is known from the detection of the 69-kHz tag. The corrected DE is up to day 42

if the weakening battery reduces the acoustic power output (and thus range) near the time of battery expiry. In telemetry studies, single detections are often treated as potentially false and simply discarded, but they can be accepted as real if they meet other screening criteria

[32]. In our experience, VEMCO technology as applied in past POST array studies has been very robust to false detections so the presence of a tagged fish can be reasonably inferred from a single detection, particularly when coupled with additional evidence such as travel time



and migration sequence over preceding and subsequent arrays. It is, however, preferable to have a few detections closely spaced in time to rule out the possibility of false positive detections bearing in mind that a very high number of recorded detections may not be cost-effective [33]. In this study, which was optimized for the 180-kHz tags,

we were confident of fish presence or absence because multiple detections were recorded with the paired 69 kHz tag. If we had not had the benefit of the 69-kHz data and single 180 kHz detections had been excluded from the dataset, the efficiency of the Discovery Islands array at detecting 180 kHz tags would have dropped from 76% to ~55%. Likewise, if the array performance were to decrease due to stochastic variation, e.g., due to environmental conditions such as increased wind [34] causing potential single detections to be missed, the DE would decrease further.

Whether this further degradation in array performance is acceptable depends on the study design and objectives. A decrease in DE occurred in a subsequent study that was conducted using this array, in which tags were programmed to transmit at a slower rate. Stevenson et al. [30] tracked juvenile sockeye through this array in 2016 using 180-kHz tags transmitting every 45 s on average (to prolong transmitter life) and the resulting detection probability was 50%. It is still possible to estimate survival using CJS models with this reduced DE; however, the uncertainty in the survival estimate becomes larger as a result.

In general, the optimal design of telemetry arrays and the tagging studies that use those arrays involves complex trade-offs that must balance economic constraints (costs) and physical constraints (detection range, tag life) on scientific results. The probability of detection relies not only on the array design and tag programming, but also on

the physical environment and the behavior of the tagged animal (e.g., migration speed). For example, performance might be reduced for a species that migrates along outer-coastal routes that could be subjected to higher and more-variable wind and wave states. In our study, the Discovery Islands array was deployed in an area of strong tidal currents (daily maxima > 5 knots) which can potentially degrade detection both because of higher background noise levels (reducing the range that signals can be detected) and the time that tags remain within that detection range; however, alternating tidal currents may also sweep fish back and forth past the receivers with the cycling of the tides, increasing the possibility of repeat opportunities for detection. Some steelhead used in this study also exhibited milling behavior in the area of the Discovery Islands, with individuals moving between Sutil Channel and Discovery Passage, and others moving back south to the NSOG array after being detected on the DI array. The interplay between array geometry, oceanographic features, and animal behavior will all play a role in the achieved performance of future studies.

Precision of survival estimates and trade-offs

To explore how precise CJS survival estimates were for 50 double-tagged fish using only the 180-kHz tag data, we compared the 180-kHz result to the exactly known survival calculated using the 69 kHz tag data, where precision (uncertainty) in the proportion surviving follows a simple binomial probability density function. The 95% confidence interval associated with the 180-kHz survival estimates was nearly 1.5 times larger (Fig. 6) because of the lower detection probability of the 180-kHz tags (76% compared to 100% for 69 kHz tags), increasing the uncertainty in the survival estimate. Whether the resulting confidence intervals are acceptable depends on the study goals. In our study, the 95% confidence interval on estimated survival was 47–85%. This level of precision is likely acceptable for exploratory (or “curiosity driven”) research but may well be insufficient for hypothesis testing where smaller survival differences between two experimental groups need to be resolved to address management questions.

Trade-offs are necessary in telemetry studies. To reduce the 180-kHz tag SE on survival, either the number of receivers would have to be increased so that detection rates improve, the number of tags increased, the transmission rate of the tag increased, or some combination of all approaches. For example, a further 50% increase in receivers (and operational costs over time, which scale with array size) may increase the 180-kHz tag detection rate to that of the current 69 kHz rate; however, tighter confidence intervals on the survival estimates can always be obtained for a given array design because the

statistical precision on the survival estimates scales proportionally to tag sample size, N , following an inverse square-root law, $SE(S) \propto \sqrt{1/N}$ (unpublished analysis).

Given the same array geometry and fish survival as this study, increasing the tag sample size to $N=75$ would decrease the SE on the survival estimate to 7.2%, similar to the 69-kHz tag data. Further increasing the sample size to $N=100$, the SE on survival would decrease to 6%. If confidence intervals half the reported width are desired, then tag sample size must be increased fourfold when using the same array; reducing confidence intervals to one-third the current level requires a nine-fold increase in tagging, etc. Diminishing returns rapidly set in from attempts to increase tag numbers and therefore augmenting the array design with additional receivers may thus prove more effective. High-performing, well-maintained, and geographically extensive arrays may provide better results than a simple array with much higher levels of tagging. For very-high-performing array designs where detection efficiency is essentially perfect, precision will then be determined primarily by tag sample size as the SE approaches that of a binomial proportion (e.g., [35]).

Conclusions

Our study demonstrates that 180-kHz tags can be used in the coastal ocean with reasonable increases in array cost relative to 69-kHz tags, given careful attention to array design and tag programming. The array performed well, detecting 76% of 180-kHz tags but with an approximate doubling in the capital costs of the array relative to the earlier POST array that was designed to detect 69-kHz tags. We found that the confidence limits on estimated survival were approximately 1.5 times larger for the 180-kHz data relative to the 69-kHz data because of reduced detection efficiency (DE). Whether the resulting confidence limits on survival estimates are acceptably small depends on both the scientific questions being posed and the potential economic value of the results. To increase the level of precision, one must consider for a given tag programming the economic trade-off between receiver density (cost to increase DE), and transmitters deployed (cost to increase sample size). Importantly, the use of smaller tags reduces potential tag burden effects which reduces biological effects, and allows acoustic telemetry studies to be extended to smaller fish including some populations where individuals were previously too small to tag.

Methods

Acoustic array

The original POST arrays were deployed along the juvenile salmon migration route in the greater Salish Sea area (Northern Strait of Georgia (NSOG), Queen Charlotte

Strait (QCS), Juan de Fuca Strait (JDF); Fig. 2). These arrays have been operating continuously since their deployment in 2004 and are currently maintained by the Ocean Tracking Network (OTN), Dalhousie University, Halifax, Canada. These arrays have been mostly equipped with VEMCO VR3 receivers that can detect 69-kHz tags only and can remain deployed for multiple years with data accessed remotely via an acoustic modem. They are configured as single lines with receiver spacing averaging 750–790 m. This spacing was suitable for low-power 69-kHz VEMCO V9 acoustic tags, the only salmon-smolt-appropriate tag type available at the time [5]. The use of smaller 180 kHz tags is of interest for research on juvenile Pacific salmon, particularly in the ocean, but these tags are incompatible with 69 kHz receivers.

In 2015, we deployed two additional arrays (43 receivers total) in the Discovery Islands (DI) and Johnstone Strait (JS) using VEMCO VR4 dual-frequency receivers capable of detecting both 180 kHz and 69 kHz tags (Fig. 2). Like the VR3 receivers, VR4s can remain continuously deployed for multiple years with data remotely accessed via a modem. The DI array is composed of three separate sections spanning the possible entry routes into the Discovery Islands: Discovery Passage (DP, to the west), Sutil Channel (SC, central), and Desolation Sound (DS, to the east). DP was located farther north than SC and DS to avoid an area of extreme tidal currents present at the mouth of DP. These routes converge to the north such that only one section was required for the JS array.

Although many array geometries are possible in principle, we deployed DI and JS as paired lines (termed subarrays) separated by 1.2–3.5 kms and with ~740 m spacing between individual receivers. The use of paired lines can improve detection efficiency (e.g., [36]) and provide some information on the direction of travel [37]. The subarrays were spaced far enough apart that a single detection was unlikely to be recorded on both simultaneously, but close enough that the sampling event can be considered instantaneous (an assumption required in using CJS models) such that tagged animals were unlikely to die between them. Because they are spaced close together, the subarrays are exposed to similar environmental factors that may affect detection probability (e.g., rainstorms) and are thus not independent replicates. However, the subarray spacing can still improve detection by reducing the probability that transient factors (e.g., a boat passing) may interfere with signal reception. Our achieved subarray distances varied because of geographic and oceanographic differences between sites (DP = 3.5 km, SC = 1.2 km, DS = 1.2 km, and JS = 2.2 km).

The receiver spacing on the individual subarrays in DI and JS was consistent with the POST lines. This allowed us to evaluate how well the individual subarrays detected

the 180-kHz tags given the tags' reduced power and range, and also allowed us to compare the 69-kHz DE for individual lines in this tidally extreme area with that of single-line 69-kHz POST arrays in other parts of the study area. Maintaining this spacing also prevented overbuilding of the individual subarrays for 69-kHz tags while ensuring that the two subarrays combined resulted in adequate detection of the 180-kHz tags.

All receivers were successfully offloaded from DI and JS arrays between Aug 30th and Sept 3rd, 2015. OTN offloaded data from NSOG, QCS, and JDF in November 2015.

Acoustic tags

Fish were double-tagged with 69-kHz V9-1H and 180-kHz V4-1H transmitters (Fig. 1a). The V9-1H tags (9 mm diameter, 24 mm long, 3.6 g in air, 151 dB; hereafter 69-kHz tags) were programmed to transmit an acoustic signal at random intervals between 30 and 90 s (60 s average) until battery death or until transmissions were programmed to turn off, 107 days after activation. VEMCO estimated that 95% of 69-kHz tags would still be active 102 days after activation (estimated tag lifespan). The V4-1H tags (3.6 mm diameter, 11 mm long, 0.42 g in air, 134 dB; hereafter 180-kHz tags) were programmed to remain silent for the first four days after activation to conserve battery power prior to fish release (although fish were held beyond four days; see below). On day five they began transmitting randomly every 13 to 27 s (20 s average) until battery death or until transmissions were turned off 54 days after activation. VEMCO estimated that 95% of 180-kHz tags would still be active 36 days after activation, and that 50% would be active 42 days after activation.

Tagging

Fifty summer-run, hatchery-origin steelhead from the Seymour River Hatchery, British Columbia, were surgically implanted with one of each tag type on May 13–14th, 2015. Fish were approximately 14 months of age and ranged between 175 and 236 mm fork length at tagging. The combined tag weight in air was 4.0 g and the average tag burden (weight of the transmitters relative to the weight of the fish) was 4.8%. Tag burdens did not exceed 7%. Smolts selected for tagging were reflective of the size frequency of the overall hatchery population. Tags were implanted using Kintama's standard surgical protocols [18]. In brief, fish were anesthetized individually in 75 ppm (mg/L) of MS-222 buffered with 140 ppm NaHCO_3 . A maintenance dose of 50 ppm anesthetic buffered with 100 ppm NaHCO_3 was pumped through the fish's mouth and over the gills while an incision was made at the ventral midline, midway between the pelvic and

pectoral fins. Two transmitters (180-kHz and 69-kHz) were inserted through the incision into the peritoneal cavity, and two absorbable sutures were used to close the incision (Fig. 1b). The fish were held for several weeks at the hatchery because the release date was postponed to accommodate another field study we were conducting (not reported here). No mortalities were observed.

Transport and release

Tagged steelhead were transported to a more northern location along their migration route to avoid elevated levels of mortality which have been documented in Burrard Inlet and the lower Strait of Georgia [8, 38] and boost the sample size used to evaluate array performance. Several weeks after tagging, we loaded the tagged smolts into an aerated fish-transportation tank filled with fresh water along with ~150 unmarked individuals, moved them by truck for 2.5 h, loaded the tank onto a chartered commercial fishing vessel, then transited north for a further eight hours for release in Malaspina Strait (Fig. 2) on June 16th, 2015. Fish were released on a flooding tide and in darkness (at 1:00 am) to encourage northward migration and to minimize predation. Fish were released directly into the ocean via a large diameter hose connected to the side of the transport tank at a release site located 19 km south of the NSOG array. Tank temperature (11.7–12.8 °C) and dissolved oxygen concentration (7.3–13.7 ppm) were monitored and maintained throughout the transportation process.

Data management

Prior to analysis, we screened all data for false detections [32]. Although false detections are rare, they may occur as a result of environmental conditions creating noise similar to those used for telemetry, or from collisions between acoustic-tag transmissions that reach the receiver from direct or reflected paths (echoes). Fish with two or more detections of either tag within 0.5 h and with more detections spaced with short intervals (<0.5 h spacing) than with long intervals (>0.5 h spacing) were passed. Detections that failed this first step were assessed individually and were passed if the migration sequence was reasonable and if the travel time for the segment (i.e., between receiver lines) was within the 10th–90th percentiles of travel times calculated for each treatment using all detections. None of the 9226 detections were classified as false.

We also examined the sequence of detections to identify fish milling between subarrays: we classified 894 detections of four fish as out of sequence relative to the expectation of linear northward migration (all these fish were detected at NSOG after being detected at DI). These detections were excluded from estimates of detection

efficiency and survival, but were included in the visualization of the migration [31].

Data analyses

Detection efficiency of 69-kHz tags

The detection efficiency (DE) of 69-kHz tags for NSOG, DI, and JS was calculated as the number of tagged fish detected at each array divided by the number of tagged fish known to have been there (fish detected + fish not detected but detected at any subsequent array in the migration). The uncertainty in measurements of DE was calculated as the standard error of a proportion, $SE(p) = \sqrt{p(1-p)/N}$, where p is the detection efficiency and N is the sample size. When detection rates are less than perfect, we typically use Cormack–Jolly–Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) models to estimate detection probabilities and the associated error around these parameters; however, it was not necessary for the 69-kHz tags because the DE was 100% (see “Results”), so the CJS estimates converge on the binomial probability result.

To compare the 69-kHz tag DE of single-line to double-line configurations, we calculated the 69-kHz tag DE for each subarray in the DI and JS arrays using the same procedure described above (the number of tagged fish detected at each array divided by the number of tagged fish known to have been present), but also including any detections from the other line forming the pair in calculating the number of fish known to have been present (i.e., we assumed that mortality was zero in the short [<4 km] distance between the paired lines). Like the double line configuration of DI, single line configurations combine all three sections (DP, SC and DS) of the DI array but the three northern subarrays were combined to form DI north and the southern subarrays were combined to form DI south.

Detection efficiency of 180-kHz tags (raw and corrected)

Our analyses focus on the performance of the DI array at detecting 180-kHz tags. Our original objective was to assess performance using both the DI and JS array design; however, fish transport and release was inadvertently delayed by several weeks, resulting in many of the 180-kHz tag batteries weakening or expiring by the time smolts reached JS (Fig. 4). Although battery expiry had begun by the time smolts reached DI, we were able to correct the DE estimates. We did not assess the 180-kHz tag DE at NSOG, QCS, or JDF because these arrays were not equipped to detect 180-kHz tags.

The presence or absence of tagged smolts was established using the 69-kHz tag data, making it possible to calculate the raw proportion of the paired 180-kHz tags that were detected on the DI array and its components

by counting the number of 180-kHz tag codes detected relative to the 69-kHz count. The uncertainty for measurements of DE for the 180-kHz tag was calculated using the formula for the standard error of a proportion. We excluded fish that milled over the DI array from the proportion because milling behavior could provide additional opportunities for the 180-kHz tag to be detected and the resulting DE estimates would then be biased upwards. We reduced this bias by calculating the difference in the arrival times between each 180-kHz tag and its paired 69-kHz tag and then excluding all 180-kHz tag detections that were recorded >24 h after their paired 69-kHz tag were recorded ($N=3$ at DI and DI north; $N=5$ at DI south).

Detection efficiency as calculated above probably underestimates the true DE of the 180-kHz tags because the 180-kHz (but not the 69-kHz tags) tags began to expire while the smolts were still in the study area (Fig. 4). To account for tag expiry, we weighted the count of 180-kHz tag detections in each 12-h period by the reciprocal of the tag lifespan curve. VEMCO has measured tag lifespan for large numbers of 180-kHz tags and reports that the tag failure time distribution is closely Gaussian, and well fitted by the mean time of failure, \bar{t} , and the standard deviation, σ_t (Drs. D. Webber and R. Vallee, VEMCO, pers. comm.). Thus, the cumulative normal function ($N(\bar{t}, \sigma_t)$) describes the percentage of tags expected to have expired before time t . The weighting function $\omega(t) = 1 - N(t|\bar{t}, \sigma_t)$ then describes the predicted proportion of 180-kHz tags expected to still be active at time t , and the reciprocal $\omega^{-1}(t)$ provides a multiplicative weight to inflate the observed 180-kHz tags detected on a given day to compensate for tags that have expired. For example, at the mean time of failure, 50% of the tags are predicted to have expired, so the corrected number of 180-kHz tags detected on that day would be double.

There are a few cautions associated with this correction factor. First, VEMCO notes that there is some variability in the tag lifespan curve across tag production batches and the specific tags that we implanted were not tested. Second, because the detected time of arrival was not exactly the same between the 180 and 69-kHz tags, we used the arrival time of the 69-kHz tags as t . The disparity likely occurs because of the smaller potential detection area around a receiver for the 180-kHz tag, so it takes longer for the tagged fish to enter the region where it can be detected. Finally, the inflation factors lying in the right hand tail of the distribution (i.e., applied to tag detections occurring later in the observational record, when few tags are predicted to be still active), are likely to incur substantial errors due to even slight departures from normality. To establish a cut off in the right tail of the distribution, we calculated the cumulative DE for these tags by

progressively including more and more of the detection record until their kill date (day 54). The corrected estimates were stable for a few days beyond the mean date of tag expiry (day 42) and then became increasingly erratic, presumably due to breakdown in the correction. Thus, we included detections up to day 42 in the corrected estimates of DE for 180-kHz tags.

Survival and confidence intervals using 69-kHz tags

Detection efficiency was 100% for the 69-kHz transmitters at the NSOG, DI, and JS arrays; therefore, survival could be calculated simply as the number of fish detected at each array divided by the number of fish released, and the uncertainty calculated as the standard error of a proportion ($S = \sqrt{S(1-S)/N}$, where S is survival and N is the sample size. The Wald 95% confidence interval is $S \pm 1.96 * SE$.

Survival and confidence intervals using 180-kHz tags: CJS method for comparison

Typical survival studies do not have any additional information to confirm fish survival (i.e., fish are not generally double-tagged with a more powerful transmitter, as they were in this study), so we wanted to estimate the error that was obtained using only the 180-kHz tags where DE is uncertain, and where survival and DE (and their variances) are estimated using spatial variants of the CJS model. These models are used for live-recaptured animals where each array of acoustic receivers that the smolts encounter is considered a recapture event. This framework jointly estimates survival and detection probability and their variances within a maximum likelihood framework and is used when the true detection rate is unknown or less than one. Standard CJS model assumptions are: (1) every tagged individual of each group has equal survival probability and equal probability of detection following release, (2) sampling periods are instantaneous, (3) emigration is permanent, and (4) tags are not lost.

Our data from the 180-kHz tags violate CJS model assumption (1), that every tagged individual has equal probability of detection following release, because some tags expired during the study period. Therefore, we simulated a 180-kHz tag detection dataset unaffected by tag expiry. To do so, we used the values in Table 3 (detection probabilities for 180-kHz tags corrected for tag expiry) and 69-kHz survival estimates to generate capture histories using a custom script in R [39]. In this simulated dataset, each fish ($N=50$ to equal the sample size at release) was designated as 'detected', or 'not detected', at each array in the migration sequence (DI and JS). Because tag expiry prevented us from estimating the detection probability of 180-kHz tags for JS, the final recapture site

in our field study, we assumed in our model that the DE at JS would equal the DE at DI. This assumption is reasonable because both arrays were deployed with the same geometry and had zero gear loss; however, unknown site-specific differences in environmental conditions may alter performance. By setting the DE of JS equal to DI, we could generate capture history sequences that would allow us to estimate survival and detection probability at DI. We used the simulated capture histories and Program Mark [40] to construct CJS models using the R [39] package RMark [41]. Standard error was estimated using the profile-likelihood option available in Program Mark.

We then compared CIs calculated using the powerful 69-kHz tags to the CJS estimates produced using the more difficult to detect 180-kHz tags to determine by how much the precision of the survival estimate degrades when detection probability is less than perfect. The standard error of a survival proportion (used for the 69-kHz tag data) takes into account only the sample size because detection is perfect, while the CJS survival estimate accounts for reduced (imperfect) detection performance as well as sample size. In practice, most telemetry array studies have less than perfect detection performance, so the latter methodology is more common for telemetry-based studies of survival.

Detections per fish per tag type

We further assessed the performance of the DI array by summing the number of 69-kHz and 180-kHz tag transmissions recorded for each individual fish arriving at DI before day 42 (when 50% of 180-kHz tags were predicted to have expired; $N=22$). We subdivided the total detections per tag into “zero”, “single”, “2–5”, and “>5” detections per tag. Validity of single and zero detections from the 180-kHz tags were verified by multiple detections of the more powerful 69-kHz transmitter.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s40317-020-00205-z>.

Additional file 1: Figure S1. Detection probability of acoustic tag transmissions as a function of tag depth and tag-to-receiver distance.

Abbreviations

CI: Confidence interval; CJS: Cormack–Jolly–Seber model; DE: Detection efficiency; DI: Discovery Islands array; JDF: Juan de Fuca array; JS: Johnstone Strait array; JSATS: Juvenile Salmon Acoustic Telemetry System; NSOG: North Strait of Georgia array; OTN: Ocean Tracking Network; POST: Pacific Ocean Shelf Tracking; SE: Standard error; QCS: Queen Charlotte Strait array.

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Authors' contributions

ER and DW conceived of the study and designed the array. ER and PW tagged and transported the fish. PW deployed the acoustic receivers and offloaded fish detection data. AP and ER performed data analyses. ER and AP wrote the manuscript with input from DW. All authors read and approved the final manuscript.

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Availability of data and materials

The fish tagging metadata, detection data, and R scripts supporting the conclusions of this article are available in the Dryad repository, <https://doi.org/10.5061/dryad.8w9ghx3j8>. Array metadata and data are available at Ocean Tracking Network <https://members.oceantrack.org/project?ccode=NEPKRS>.

Ethics approval and consent to participate

All work involving live fish met the standards laid out by the Canadian Council on Animal Care.

Consent for publication

Not applicable.

Competing interests

DWW is president and owner of Kintama Research Services, an environmental consultancy that designed and operates the main elements of the acoustic telemetry array described in this article.

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