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Identifying when tagged fishes have been consumed by piscivorous predators: application of multivariate mixture models to movement parameters of telemetered fishes

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Abstract

Background: Consumption of telemetered fishes by piscivores is problematic for telemetry studies because tag detections from the piscivore could introduce bias into the analysis of telemetry data. We illustrate the use of multivariate mixture models to estimate group membership (smolt or predator) of telemetered juvenile Chinook salmon (*Oncorhynchus tshawytscha*), juvenile steelhead trout (*O. mykiss*), striped bass (*Morone saxatilis*), smallmouth bass (*Micropterus dolomieu*) and spotted bass (*M. punctulatus*) in the Sacramento River, CA, USA. First, we estimated two types of track statistics from spatially explicit two-dimensional movement tracks of telemetered fishes: the Lévy exponent (b) and tortuosity (τ). Second, we hypothesized that the distribution of each track statistic would differ between predators and smolts. To estimate the distribution of track statistics for putative predators and smolts, we fitted a bivariate normal mixture model to the mixed distribution of track statistics. Lastly, we classified each track as a smolt or predator using parameter estimates from the mixture model to estimate the probability that each track was that of a predator or smolt.

Results: Tracks classified as predators exhibited movement that was tortuous and consistent with prey searching tactics, whereas tracks classified as smolts were characterized by directed, linear downstream movement. The estimated mean tortuosity was 0.565 (SD = 0.07) for predators and 0.944 (SD = 0.001) for smolts. The estimated mean Lévy exponent was 1.84 (SD = 1.23) for predators and -0.304 (SD = 1.46) for smolts. We correctly classified 90% of the *Micropterus* species and 72% of the striped bass as predators. For tagged smolts, 80% of Chinook salmon and 74% of steelhead trout were not classified as predators.

Conclusions: Mixture models proved valuable as a means to differentiate between salmonid smolts and predators that consumed salmonid smolts. However, successful application of this method requires that telemetered fishes and their predators exhibit measurable differences in movement behavior. Our approach is flexible, allows inclusion of multiple track statistics and improves upon rule-based manual classification methods.

Keywords: Telemetry, Predation, Survival, Chinook salmon smolt, Steelhead trout smolt, Striped bass, Smallmouth bass, Spotted bass, Sacramento River Delta

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Background

An inherent issue with telemetry of fishes is that they may be preyed upon during the course of telemetry studies [1-4] potentially leading to incorrect conclusions about movement, behavior or survival. This problem is especially acute in western rivers of the United States where telemetered migrating juvenile salmonids may experience high mortality rates due to predation from piscivorous fishes [5-7]. More specifically, our concern is with predation of telemetered emigrating juvenile salmonids by non-native striped bass (*Morone saxatilis*) and two species of non-native black basses, smallmouth bass (*Micropterus dolomieu*) and spotted bass (*Micropterus punctulatus*), in the Sacramento-San Joaquin River Delta (Figure 1). Here, telemetry-based survival studies (for example, [6]) assume that tag detections are from live juvenile salmonids, rather than tagged salmonids consumed by predatory fishes (hereafter, consumed smolts). Consumed smolts subsequently detected at downstream locations may lead to inflated survival estimates. Thus, in this example, it is important to differentiate between detections of live tagged smolts and consumed smolts to avoid bias in survival estimates.

Few quantitative methods have been developed to distinguish between telemetry detections of live study fishes and consumed fishes in situations where recapture of the study species is infeasible. Several studies have taken different approaches to resolving this issue, but most rely on subjective classification rules based on expert opinion rather than objective quantitative methods. For example, Vogel [8] proposed that tag detections be examined at three scales of resolution to classify an acoustic tag as a live or consumed smolt: 1) examining the acoustic pattern of a tag as it passes a hydrophone, 2) comparing movement direction relative to flow direction (typically, emigrating smolts move with the flow) and 3) comparing the movement rate of a given tag against the movement rates of the entire tagged population. Friedl *et al.* [9] used three criteria for determining natural mortality of telemetered juvenile spot (*Leiostomus xanthurus*) in estuarine creeks. Tagged fish were considered moribund or consumed if: 1) the tag ceased to move, 2) swim speeds were not within the normal range for the study fish or 3) the fish failed to emigrate from the rearing habitat. Thorstad *et al.* [2] examined depth profiles produced by pressure tags to identify Atlantic salmon (*Salmo salar*) smolts thought to have been consumed by predators. They hypothesized that sudden changes in the vertical distribution of the tag indicated predation events. Kawabata *et al.* [3] used atypical behavior based on detection patterns of telemetered black-spot tuskfish (*Choerodon schoenleinii*) to predict predation events.

The aforementioned studies relied on subjective opinion to some degree to classify predation manually based

on the expected behavior of the tagged fish species. Because such methods are based on expert opinion, they could introduce bias or systematic variation among individual observers examining the detection histories. Furthermore, manual classification methods can be prohibitively laborious for large telemetry studies using thousands of tags because they require visual inspection of the entire detection history of each tag.

In contrast to user-defined classification rules, statistical classification methods can objectively classify different patterns in telemetry data. Specifically, when spatially explicit two-dimensional telemetry data are collected, mathematical characteristics of the time series of x - y positions (hereafter, fish tracks) may be useful in identifying behaviors indicative of tagged fish and their predators. For example, Morales *et al.* [10] used turning angles and daily movement rates to classify movement patterns of telemetered elk (*Cervus elaphus*) into two behaviors: encamped and exploratory. The encamped behavior was characterized by short movements between relocations and somewhat randomly distributed turning angles, whereas the exploratory behavior was characterized by longer, more consistent unidirectional movement.

As with the elk example, if tagged fish and predators exhibit different movement behaviors, then track statistics such as movement rate and turning angle would likely differ between the two groups [5,11,12]. For example, to maximize efficiency of their seaward migration, emigrating smolts will likely exhibit linear movement that is oriented with the direction of flow [12]. This movement would be characterized by shallow turning angles [13,14] and is similar to the exploratory behavior found by Morales *et al.* [10]. In contrast, the track of a foraging predator would likely exhibit steep turning angles and a non-linear trajectory, consistent with patrolling or prey-searching tactics or an encamped behavior characteristic of a fish holding in feeding lanes or eddies. These differences in track characteristics present are an opportunity to use quantitative methods to classify tracks as being from a smolt or predator.

While turning angles provide information about track complexity, other movement statistics may capture different aspects of behavior, which can be used to inform track classification. For example, in areas where prey are patchily distributed or in low abundance, predators often exhibit Lévy walk-type behavior [15], which may increase prey encounter rates compared to using a simple correlated random walk search [16,17]. Lévy walks are characterized by clusters of short, seemingly random steps followed by less frequent and longer directed steps [17,18]. Thus piscivorous predators constrained by abiotic conditions such as flow, may exhibit similar behavior, choosing to hold in optimal feeding lanes, moving small

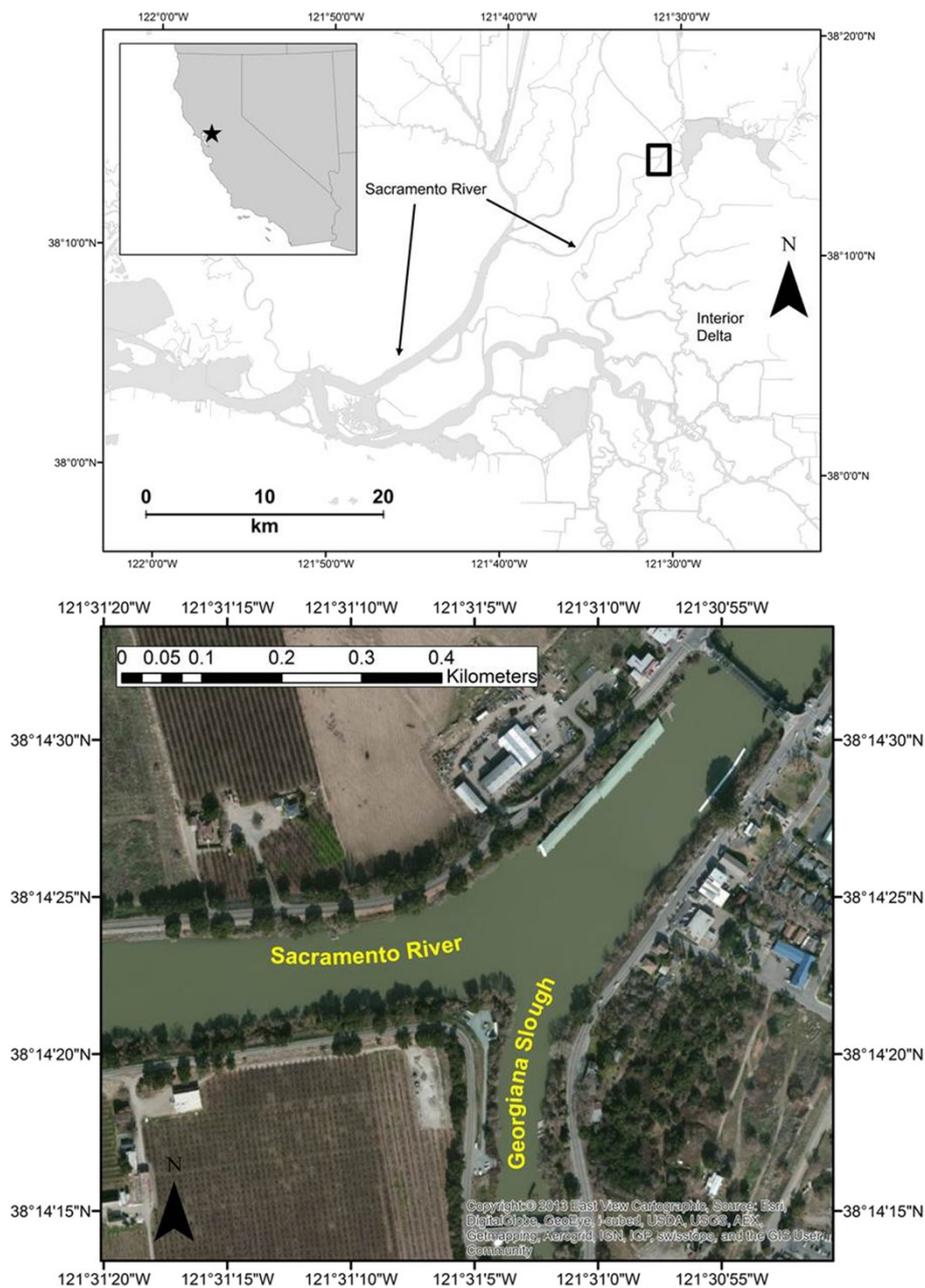


Figure 1 Map showing location of the study area. The box in the top panel shows the location of the study area in the Sacramento-San Joaquin River Delta. The bottom panel shows the detail of the study area.

distances and only making periodic directed forays to other feeding areas (for example, in response to changing hydrodynamics caused by the tides). In contrast, we would expect the distribution of step lengths of a smolt emigrating through a telemetry array to be normally distributed [12] and unrepresentative of a Lévy walk.

The work presented here was motivated by a larger study designed to evaluate whether a non-physical barrier reduced entrainment of juvenile salmonids into a low-survival migration route (see [19] for the experimental

design and description). However, prior to analysis of the telemetry data, it was necessary to identify and remove the telemetry tracks of tagged smolts that may have been consumed by predators, as tracks of consumed smolts could bias the results. In Perry *et al.* [19], predators were identified through manual examination of the telemetry tracks using a rule-based classification. To reduce the amount of manual labor and eliminate the subjective nature of rule-based classification, we developed a statistical approach to identify consumed smolts, which were then removed from

the dataset used for analyses in the larger study. To differentiate tracks of live tagged smolts from tagged smolts consumed by predators, we fitted multivariate mixture models to track statistics from a telemetry study conducted in the Sacramento-San Joaquin River Delta. We first estimated the Lévy exponent and tortuosity for each track. We then fitted a bivariate normal mixture model to these statistics to estimate the parameters of the smolt- and predator-specific distributions from the combined bivariate distribution of the track statistics. Given these distributions, we then quantified the probability that any given track exhibited characteristics that were consistent with predator- or smolt-like movement and used this information to classify the track as due to a predator or smolt.

Results

In total, 1,413 Chinook salmon (*Oncorhynchus tshawytscha*), 259 steelhead trout (*O. mykiss*), 14 smallmouth bass (*Micropterus dolomieu*), 6 spotted bass (*M. punctulatus*) and 29 striped bass (*Morone saxatilis*) tracks were analyzed. Of these, 155 chinook salmon, 41 steelhead trout, 13 smallmouth bass, 6 spotted bass and 20 striped bass tracks consisted of multiple segments (the fish departed the study area and then returned). In total, 1,852 Chinook salmon, 356 steelhead trout, 443 smallmouth bass, 232 spotted bass and 129 striped bass track segments were pooled and analyzed. Our *a priori* hypotheses about the distributions of track statistics were supported by the estimated distributions from the mixture model and the observed distribution of track statistics for known predators (Figure 2). The mixture model classified 50.6% and 49.4% of the track segments as predators (λ_p) and smolts (λ_s), respectively. The fitted distributions for the Lévy parameter were centered at -0.304 ($SD = 1.46$) for smolt-like and 1.84 ($SD = 1.23$; Table 1) for predator-like behavior, which is consistent with our expectations of smolt-like and predator-like behavior. The distribution of Lévy coefficients for known predators (mean = 2.10, $SD = 1.12$) was similar to that estimated by the mixture model, lending further support to this approach. Examples of tracks for putative predators and smolts show how the step length distributions for predators typically followed a power function, characterized by a greater frequency of short steps than longer steps (Figure 3). In contrast, step lengths of smolt-like tracks were approximately normally distributed with a slope close to zero (Figure 3).

The fitted distributions for tortuosity were centered at 0.944 ($SD = 0.001$) and 0.565 ($SD = 0.070$), with an order of magnitude difference in the standard deviation of these distributions (Table 1). The distribution of tortuosity for known predators (mean = 0.523, $SD = 0.281$) was similar to the distribution estimated for predators by the mixture model. These findings support our *a priori*

hypothesis that smolts would have more linear, less tortuous tracks than predators.

Our approach using the mixture model accurately classified 72% of the striped bass, 86% of the smallmouth bass and 100% of the spotted bass as predators (Table 2). Of the 1,413 Chinook salmon tracks analyzed, our approach classified 281 (20%) tracks as being predators and 1,131 (80%) tracks as being smolts. Of the 259 steelhead trout tracks analyzed, 68 (26%) tracks were classified as predators and 191 (74%) were classified as smolts. Unlike known predator tags, we were not able to validate the classification of tags implanted in smolts because tagged smolts could not be recaptured.

The total probability for tracks consisting of multiple segments was estimated as:

$$P_{\text{total},k} = 1 - \left(1 - p_{i,j,k}\right) \times \left(1 - p_{i+1,j,k}\right) \times \dots \times \left(1 - p_{n,j,k}\right)$$

where $p_{i,j,k}$ is the probability of the i th segment ($i = 1, \dots, n$) of track j belonging to group k (smolt or predator).

The distribution of probabilities of being a predator was bimodal with distinct modes near zero and one (Figure 4). These findings show that most tracks could be assigned as predator or smolt with little uncertainty in the classification. In contrast, a few track segments had probabilities in the range 0.3 to 0.7 where uncertainty about classification is greater. The majority of salmonid tags that moved through the telemetry array multiple times were classified as predators, which was consistent with the movement pattern of tags known to be implanted to predators (see the example of a multiple-pass track in Figure 5). Of the 154 Chinook salmon tracks that consisted of multiple track segments, 106 (68.8%) were classified as predators. Of the 259 steelhead trout tags, 41 tracks consisted of multiple segments, 31 (75.6%) of which were classified as predators. Consistent with these findings, tagged predators made many forays through the array. The 49 tagged predators (49 tracks) produced 809 track segments, of which 13.3% of these track segments were misclassified as smolts. Most tracks consisting of more than four segments were classified as predators.

Discussion

In telemetry studies of fishes, predation by piscivores may result in erroneous conclusions because the tracks reflect the predator movements rather than the fish originally tagged. Researchers will seldom have information to verify whether detections from tags actually arise from movements of a predator that has consumed a tagged fish. Our mixture model approach explicitly accounts for the unknown state of tags (predator or smolt,

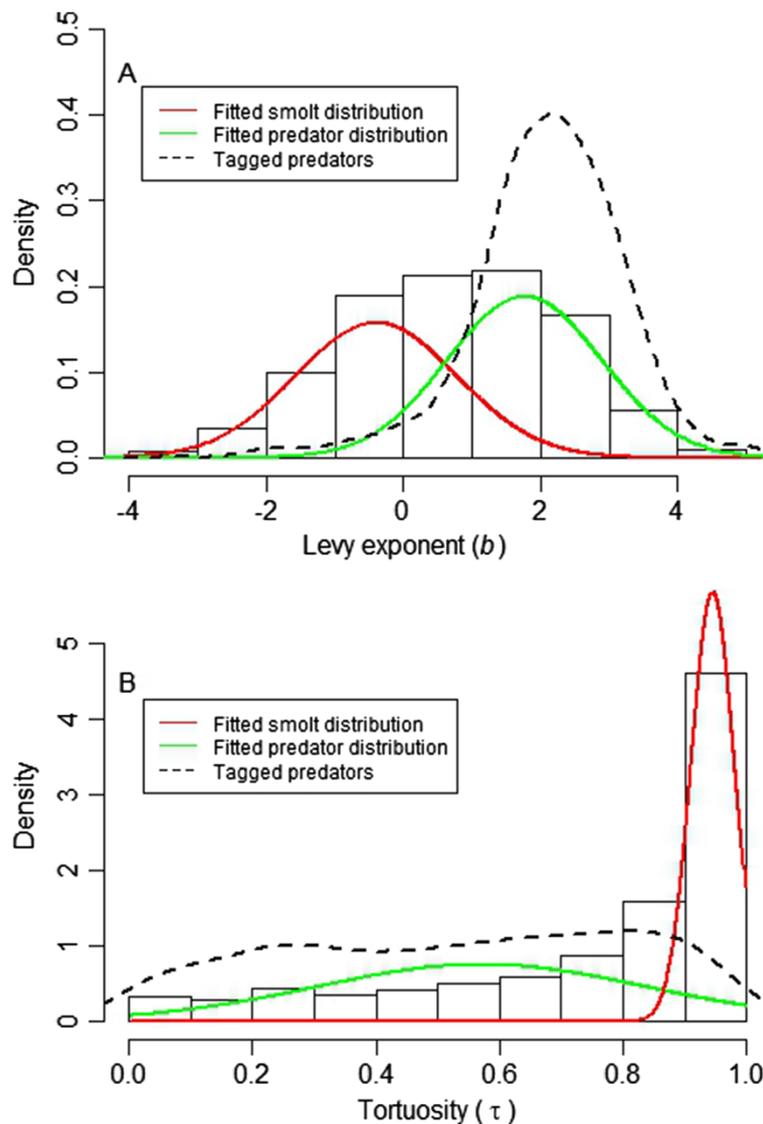
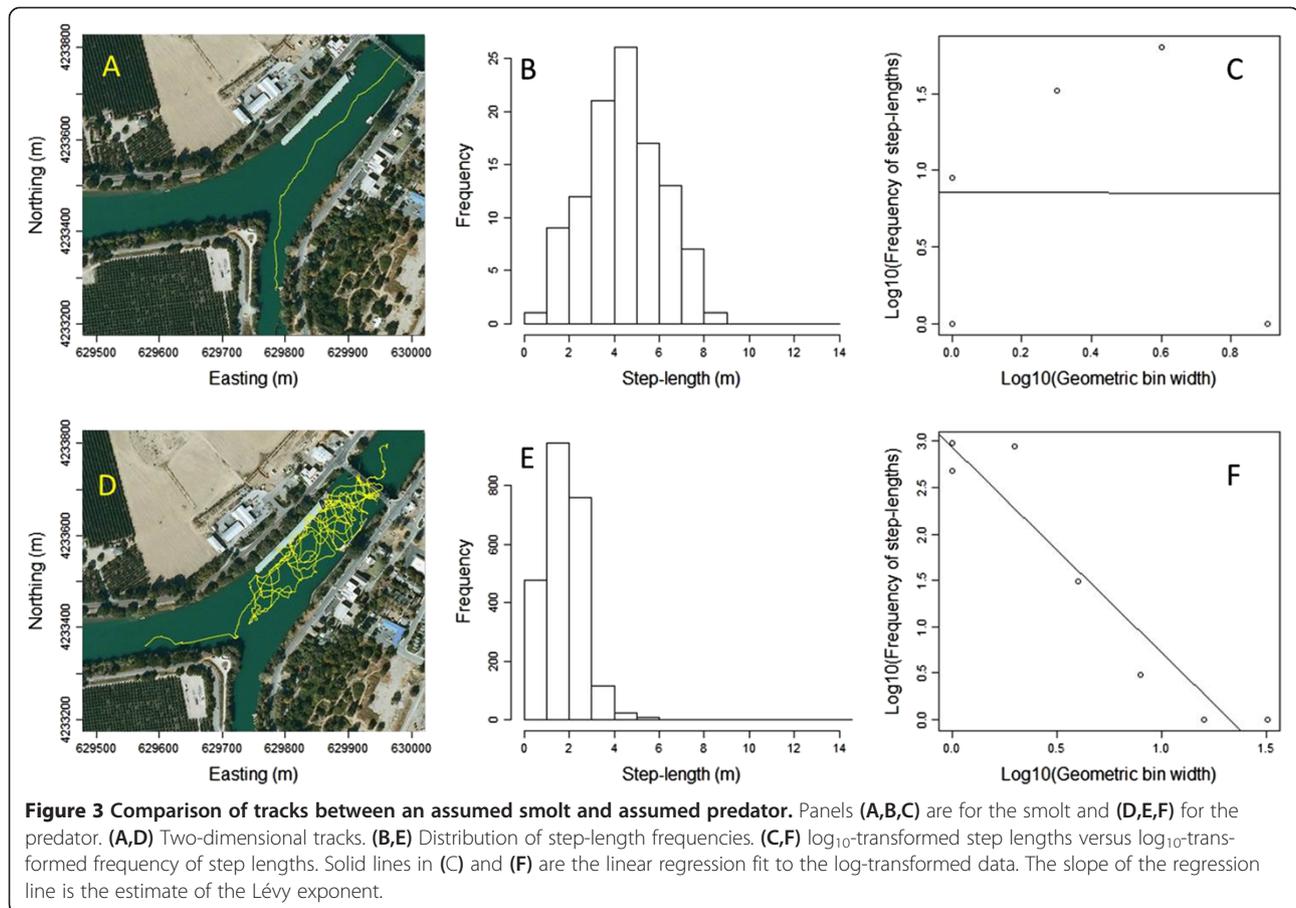


Figure 2 Distributions of the Lévy exponent (A) and tortuosity (B) for smolt (red line) and predator (green line) populations estimated using a bivariate mixture model of normal distributions. The histogram shows the mixed empirical distribution of track statistics for which the true population assignment is unknown (that is, predator or smolt). The black dashed line shows the distribution of track statistics for known predators.

Table 1 Parameter estimates from the mixture model

Parameter	Mean	Estimate ^a	Standard deviation	Estimate ^a
Lévy exponent, predators	$\mu_{P,b}$	1.84 (0.033)	$\sigma_{P,b}$	1.23 (0.048)
Lévy exponent, smolts	$\mu_{S,b}$	-0.304 (0.008)	$\sigma_{S,b}$	1.46 (0.003)
Tortuosity, predators	$\mu_{P,\tau}$	0.565 (0.037)	$\sigma_{P,\tau}$	0.070 (0.048)
Tortuosity, smolts	$\mu_{S,\tau}$	0.944 (0.001)	$\sigma_{S,\tau}$	0.001 (0.0001)

^aThe parameters were estimated from the entire population of track segments (tagged salmonids and tagged predators). Values in parentheses are standard errors estimated from 500 bootstrap simulations.



in this case) by using behavioral characteristics of movement paths to segregate smolt-like versus predator-like behavior. The mixture model was able to separate clearly distributions of track statistics that were consistent with hypothesized smolt and predator behavior. The mixture model also provides a probabilistic estimate of whether a given track segment arises from a predator or smolt. Furthermore, relative to the manual review of tracks, which requires considerable labor, the processing time for the mixture model is of the scale of hours.

We believe the mixture model approach is a sound alternative to the manual review of each track, but our

Table 2 Final classification of tags moving through the acoustic array

	Model classification	
	Smolt	Predator
Striped bass	8	21
Smallmouth bass	2	12
Spotted bass	0	6
Chinook salmon	1,131	281
Steelhead trout	191	68

approach need not eliminate classification schemes that include some level of manual review. Because the mixture model yields a probabilistic estimate of a track's source population, there will be regions of high certainty where a track's characteristics are consistent with those for a smolt or predator, and regions of relative uncertainty where manual review may still provide a useful "second opinion" for a track's classification (Figure 4). For example, one approach would be to divide the probability space into three equal-size regions (that is, 0 to 0.33, 0.33 to 0.66 and 0.66 to 1). Tracks falling in the central region, where the classification is less certain, could be manually reviewed and auxiliary information (for example, movement against the flow) could help inform the classification. Such an approach would provide a more systematic, quantitative method for classifying tracks while still retaining some level of manual review.

It is important to recognize that any classification method, whether statistical or manual, will be unlikely to classify tracks with 100% accuracy because both predators and smolts may exhibit multiple behavioral modes that lead to misclassification. That is, sometimes a predator track may look like a smolt track and sometimes a smolt may act like a predator. This aspect of fish behavior is

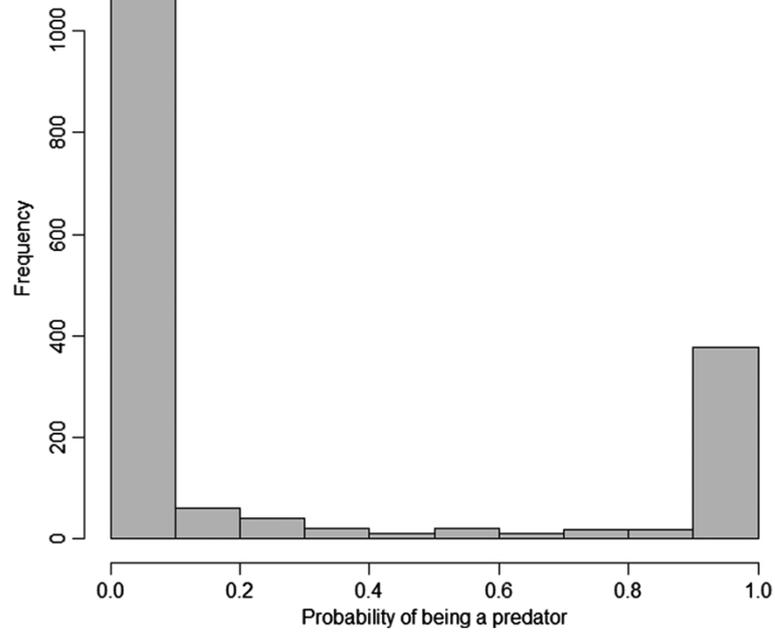


Figure 4 Results from the mixture model illustrating the probability of tracks being classified as predators.

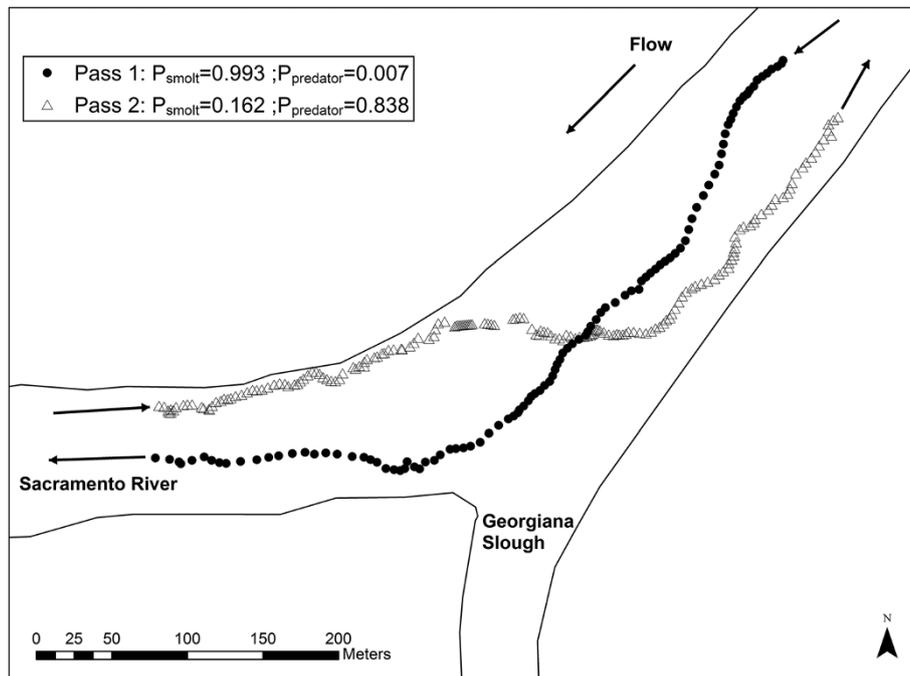


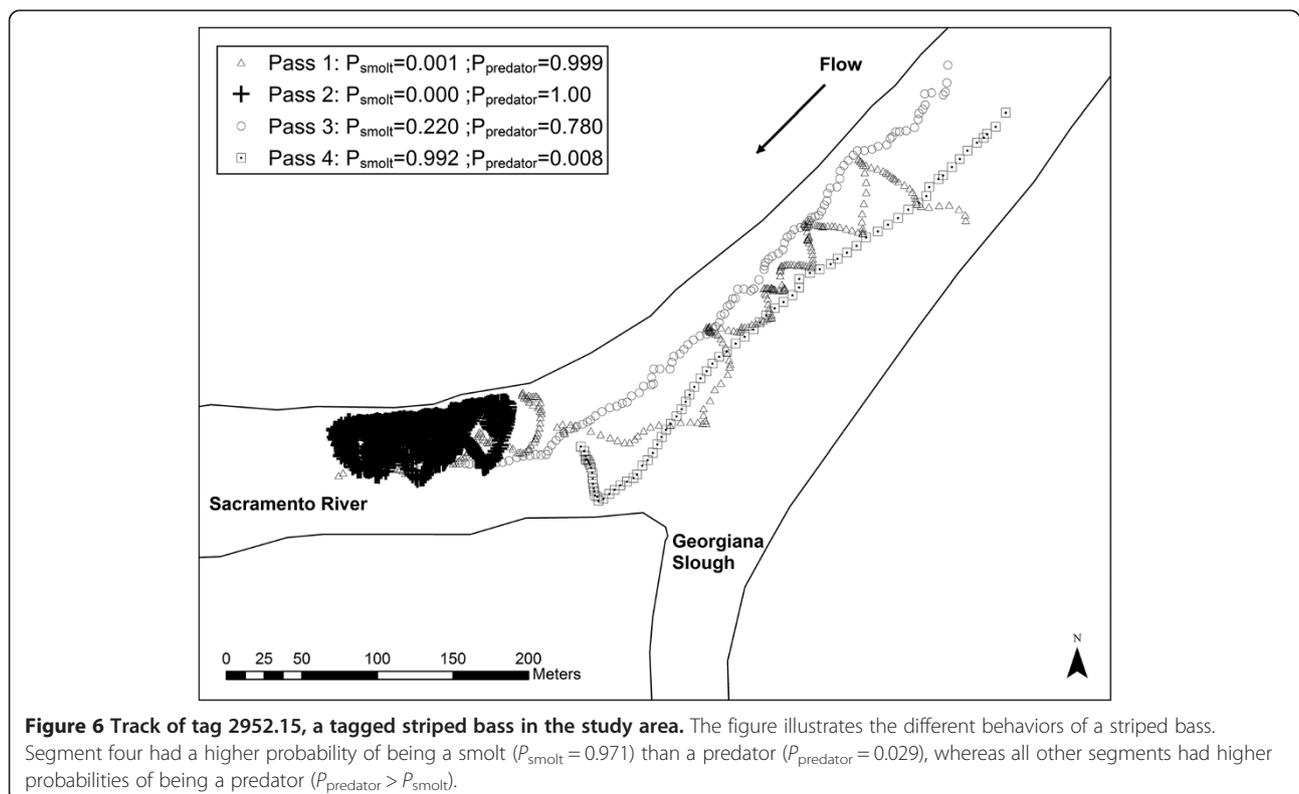
Figure 5 Example of a multiple segment track (acoustic tag 2007.01) in the study area. The first segment (solid circles) had a higher probability of being a smolt ($P_{smolt} = 0.986$) and the second segment with an upstream movement (triangles) had a greater probability of being a predator ($P_{predator} = 0.738$).

captured in our mixing model as the overlap in the distributions of track statistics for predator and prey (Figure 2). Specifically, the predator distribution overlaps the smolt distribution, indicating that predator tracks sometimes resemble a smolt track. For example, one striped bass had four distinct track segments and each track segment had different characteristics leading to its classification as both a smolt and predator (Figure 6). The first two track segments were classified as a predator with near certainty, and the third was also classified as a predator but with less certainty. In contrast, the final track segment was classified as a smolt because the striped bass moved quickly through the array in a linear fashion. In practice, tracks from known tagged predators would always be classified as predators despite their similarity to smolt tracks. However, including tagged predators in the analysis was important for informing parameter estimates of predator tracks and validating our classification methods for known predators.

Likewise, it is possible for smolts to exhibit movement behavior that may be mistaken for a predator. For example, under low river flows, Chinook salmon smolts may hold in areas of suitable habitat along migration pathways, a behavior similar to predator holding behavior [20,21]. In addition, predator avoidance behavior could cause the tracks of smolts to be classified as those of predators. Chapman *et al.* [22] found significant differences in

migration rates during the day and night for Chinook salmon smolts in the Sacramento River. Chinook salmon migrated further during the night than during daytime hours, suggesting some smolts in our study may have exhibited holding behavior similar to predators during the day when migration may have slowed. Bradford and Higgins [23] also reported lower activity levels for both juvenile Chinook salmon and steelhead trout during the day. Furthermore, Atlantic salmon have also been shown to have a preference for migrating during the nighttime hours rather than during the day [24]. Notwithstanding multiple modes of behavior that would pose difficulty for any classification scheme, our mixture model approach provides a quantitative method for classifying behaviors that are most commonly associated with the movement of predators and smolts.

As previously stated, our approach does not eliminate the misclassification of smolts as predators, but does provide a quantitative probabilistic technique to reduce this error. Nevertheless, misclassification can introduce bias into survival estimates when this method is applied for large survival studies. For example, Buchanan *et al.* [25] provided two estimates of survival for out-migrating Chinook salmon smolts in the Sacramento-San Joaquin River Delta in 2010: one estimate was calculated where the data for putative predators was removed and the other included data for putative predators. Survival estimated



for the dataset without predators was 0.05, whereas survival estimated from the dataset with predators was 0.11. The excessive misclassification of smolts as predators could result in negatively biased survival estimates, whereas failure to remove predators may result in positive bias. Given that no method can completely eliminate uncertainty associated with identifying predators, short of recapture, researchers should present the sensitivity of their results to the classification methods used.

We used two statistics to characterize movement behavior in our analysis, but our approach can be easily extended to incorporate more than two track statistics. In our case, the use of both tortuosity and the Lévy exponent in the multivariate mixture model led to high certainty in the classification of predator- or smolt-like behavior (Figure 4). We considered additional types of movement statistics (for example, swimming speed and turning angle), but they failed to improve the analysis because they were highly correlated with the other track statistics. Including additional types of track statistic should improve the analysis when the distribution of the statistic differs between the tagged fish and its predator, and the candidate statistic has a low correlation with the other track statistics in the analysis.

Although our approach provides a sound basis for estimating predation on juvenile salmonids from two-dimensional movement tracks, we had no mechanism to verify whether after tagging smolts, the tracks classified as smolts or predators were indeed from smolts or predators. In contrast, Svendsen *et al.* [14] utilized a trap below a water diversion to verify that after tagging Atlantic salmon smolts, the fish tracks were indeed from tagged smolts. Given the dynamics of our study area, the recapture of tagged fishes was impractical. Although recapture of study fish in most cases will likely be impossible, our classification methods could be further tested in studies where tagged fish can be recaptured. However, we did observe 12 smolt tags that appeared to have been defecated within the array, suggesting the fish may have been consumed. These tags initially showed the expected movement then ceased forward movement for the duration of the tag's battery life. The mixture model classified these tags as predators. These tags do provide some support for our methods, but we could not rule out other explanations. Lab studies have shown gut evacuation rates of consumed tagged smolts to be of the order of days to weeks (SVJ, unpublished data). Other possible causes include tag shedding or mortality from other causes. However, tag shedding would be highly unlikely (Liedtke, unpublished data). Other approaches for verification of our methods might include the coupling of an intensive acoustic array and single hydrophones in adjacent areas. This would provide insights into the migratory behavior of the tag, which could be used to

support or refute classifications assigned by the mixture model.

Conclusion

The approach we have presented here provides the researcher with a flexible and quantitative method to distinguish between behavioral modes of prey and predator as observed through two-dimensional telemetry tracks. This is an improvement upon previous subjective smolt and consumed smolt classification schemes and should be considered when examining two-dimensional telemetry data from small-bodied fishes. In addition to providing a quantitative means to classifying telemetry tracks, the approach includes a measure of uncertainty through the estimation of group membership probabilities. As seen in Figure 4, the distribution of predator probabilities was skewed to zero or one, suggesting smolt- and predator-like behavior could be identified with little uncertainty using the multivariate mixture model approach. Furthermore, the method is flexible and allows for multiple track statistics or behavioral estimates to be used in the model fitting. In our analysis, we only used two statistics, tortuosity and the Lévy exponent. However, more metrics could be used. This study takes an important step in furthering the methods of telemetry data analysis where predation of telemetered fishes is a concern.

Methods

Study area

The study area was located 36 km south of Sacramento, CA, where the Georgiana Slough branches off the Sacramento River (Figure 1). The average water depth within the study area was 6.3 m and the width of the channel was 100 m. Discharge in this area ranges from negative (an upstream flow caused by tidal forcing) to $1,132 \text{ m}^3 \cdot \text{s}^{-1}$ during spring floods. During the study flows ranged from $-127 \text{ m}^3 \cdot \text{s}^{-1}$ to $849 \text{ m}^3 \cdot \text{s}^{-1}$. This area is a critical junction for out-migrating juvenile salmonids because emigrating smolts that are entrained into the Georgiana Slough have much lower survival rates than those that remain in the Sacramento River [6].

Acoustic telemetry

Juvenile salmonids were telemetered with acoustic tags that operated at 307 kHz (Hydroacoustic Technology Inc (HTI), Seattle, WA). The tags were 6.5 mm in diameter and 16.3 mm in length and averaged 0.67 g in air. The expected battery life was 15 days (HTI Model 795 Lm). Predators were telemetered using tags that operated at 307 kHz, were 11.0 mm in diameter, 25.0 mm in length and averaged 4.5 g in air. The expected battery life was 105 days (HTI Model 795 Lg). Each tag emitted a unique acoustic signal composed of a primary and secondary pulse. The pulse rate of tags ranged from 2.003 s

to 3.474 s and the pulse length of the transmitted signal was 0.003 s.

The acoustic array consisted of 34 hydrophones (HTI, Model 590) installed throughout the study site. Hydrophones were installed near the surface and bed of the river and were arranged to enable three-dimensional positioning of the acoustic transmitters (hereafter referred to as tags) as fish moved through the study area. Hydrophones were connected via cable to receivers (HTI Model 290 Acoustic Tag Receivers) located on shore. Two receivers were used to collect and store acoustic data from the 34 hydrophones. Telemetry data were processed using vendor-supplied software to acquire, store and identify the acoustic signals.

Positions of tags were identified by calculating the differences in arrival times of tag transmissions at individual hydrophones in the array. Positioning required transmissions to be recorded by a minimum of four hydrophones. Successive locations formed tracks of individual tags.

Fish tagging and release

The salmonid fishes used in the study were juvenile late fall-run Chinook salmon and steelhead trout smolts obtained from the Coleman National Fish Hatchery operated by the US Fish and Wildlife Service (USFWS). The fork length of fishes selected for tagging ranged from 110 mm to 140 mm. The tag burden (tag weight relative to fish weight) for fishes in this size range was less than 5%. The fishes used in the study were transported daily from the hatchery to the tagging and release site located 9 km upstream of the study site. At the release site, the fishes were placed in flow-through containers submerged in the Sacramento River and held there for 18 hr to 24 hr prior to tagging. Following tagging, the fishes were returned to the flow-through containers and held for another 18 hr to 30 hr prior to release.

The fish-tagging protocols were based on Liedtke and Wargo-Rub [26]. Fish were anesthetized using buffered tricaine methanesulfonate (MS-222, 50 to 70 mg.L⁻¹) until loss of equilibrium. The fish were then weighed, measured and placed ventral side up on a submerged surgical platform for 5 min or until non-responsive. Their gills were irrigated with MS-222 (20 mg L⁻¹) during the 2-to-3-min surgical procedure. A small incision was made anterior to the pelvic girdle and a disinfected transmitter was placed within the body cavity. The incision was then closed using two interrupted sutures with Vicryl + 5-0 absorbable suture material. Following surgery, the fish were moved to a recovery container until they had regained equilibrium. After the fish had recovered, they were placed in flow-through containers at a density of four to five fish per container. Tagging operations were conducted twice daily and fish were released

approximately every 3 hr during the study period. Fish releases started on 6 March 2012 and continued until 2 May 2012.

Smallmouth bass, spotted bass and striped bass were captured using a hook-and-line. Sampling for predators was confined to a 1.6 km radius from the divergence of the Georgiana Slough and the Sacramento River. However, capture efforts were focused within the immediate study area to avoid transporting and introducing more predators into the study area. Only *Micropterus* species greater than 300 mm in total length and striped bass greater than 360 mm in total length were retained for the study. Fish deemed fit for tagging were immediately placed in an aerated livewell and transported to in-river flow-through containers at the tagging location.

Bass were anesthetized using diffused carbon dioxide in a surgery station livewell. The oxygen level within the surgery station livewell was maintained near saturation via a diffuser and approximately 7 to 10 g of salt was added per liter of water to reduce gill irritation and help control blood hematology and chemistry [27]. The fish became unresponsive within 3 to 5 min following immersion in the carbon dioxide bath and were removed from the immersion bath and inspected for anomalies (for example, general condition of eyes, scales and fins) and general health; unfit individuals were rejected for tagging.

Tags were implanted by making a 10 mm to 12 mm incision parallel to and 2 mm perpendicular to the ventral midline anterior to the pelvic girdle. A sterilized tag was inserted into the peritoneal cavity of the fish and the incision was closed with two simple interrupted sutures using a 26 mm (FS-1) reverse cutting, 9.5 mm circle needle with 3/0 monofilament suture material. Immediately after completion of surgery, the fish were placed in recovery tubes submerged in post-surgery livewells containing freshwater saturated with oxygen. The fish were removed from the recovery tubes after approximately 10 min, but kept in the post-surgery recovery livewell for an additional 20 min. During this time, the fish were observed closely for recovery progress and behavior. After 30 min, if it was determined a fish was fully recovered and exhibiting normal behavior it was moved to an in-river livewell. After 2 hr in the in-river livewell, if it was determined the fish was fully recovered and exhibiting normal behavior it was released into the Sacramento River and the release time noted. Individuals that did not recover or exhibited impaired behavior were euthanized and the tag was retrieved for reuse.

Data analysis

Fish tracks encompassing the entire detection history of Chinook salmon smolts, steelhead trout smolts, striped bass, smallmouth bass and spotted bass were used in the analysis. Tracks were broken into discrete track

segments if the time between successive detections was greater than 30 min. Each track segment was analyzed separately. In other words, a tag that moved through the array, out of the study area, and then returned after 30 min or more was treated as two separate track segments. This resulted in some tracks consisting of multiple track segments. Tracks with fewer than 60 two-dimensional positions were omitted from the analyses. The ping rates of tags varied from 2 to 4 s. Therefore, we discretized track segments at a time step of 8 s using the *adehabitatLT* package in R [28] to normalize telemetry data and avoid potential bias in track statistics that might arise due to different ping rates between tags [29]. Discretizing uses linear interpolation to estimate a tag's location based on the measured locations occurring prior to and after the 'missing' location. Track segments that had an average speed of less than $0.0009 \text{ m}\cdot\text{s}^{-1}$ over the span of 4 days were also removed from the analyses as these were motionless tags that were likely defecated by predators or were post-release mortalities.

Two statistics were estimated for each track segment for each fish, tortuosity (τ) and the Lévy exponent (b). Tortuosity (τ) was calculated as a function of the turning angle (θ):

$$\tau = \sqrt{\bar{x}^2 + \bar{y}^2}$$

where

$$\bar{x} = \frac{1}{n} \sum_{i=1}^n \cos(\theta_i)$$

and

$$\bar{y} = \frac{1}{n} \sum_{i=1}^n \sin(\theta_i)$$

Here n is the number of relocations and the turning angle (θ) is the change in direction between three successive relocations. A track with tortuosity close to one is considered linear whereas a track with tortuosity near 0.5 is more tortuous or complex.

In Lévy walks, the relation between step length (l) and the frequency of occurrence of a step length follows a power function, $f(l) = al^{-b}$, where a is an intercept parameter and b is the Lévy exponent. Lévy exponents were estimated using the logarithmic binning method following Sims *et al.* [30]. The Lévy exponent was estimated from the slope of the linear regression between log-transformed geometric bin widths and log-transformed bin frequencies of step lengths. A step length is the distance between two successive locations, and the frequency is the number of occurrences of each step length.

After track statistics were estimated for tagged smolts and predators, finite mixture models were fitted to the

distributions of track statistics using the *mixtools* package for R [31]. Finite mixture models are a form of model-based clustering, which uses the expectation maximization algorithm to maximize the likelihood function and estimate parameters of mixed distributions for observations with unknown group membership. In our case, the bivariate distribution of track statistics (the tortuosity τ and the Lévy exponent b) was formed from a mixture of two underlying bivariate normal distributions — one for predators and one for smolts. Our goal was to use the finite mixture model to estimate the parameters of each assumed Gaussian component of the distribution, which then allowed us to estimate the probability that a track segment came from a predator or smolt from the posterior probability distribution.

A priori we assumed that predators would exhibit the encamped behavior described by Morales *et al.* [10], which has larger turning angles resulting in more tortuous tracks and Lévy exponents in the range of one to three (Table 3). In contrast, we hypothesized that smolts would exhibit a more directed path of movement or exploratory behavior, resulting in turning angles close to zero and a resulting tortuosity estimate close to one, which is indicative of a linear path. Furthermore, a lower estimate of the Lévy exponent is indicative of a smolt swimming at a constant speed through the telemetry array.

We used a mixture model and assumed that the distribution was a mixture of two bivariate normal distributions, each with an associated mean (μ) and standard deviation (σ). Thus, the mixture model estimated the parameters of a normal distribution for smolt- and predator-specific tortuosity and the Lévy exponents, resulting in eight parameters: $\mu_{S,b}$, $\sigma_{S,b}$, $\mu_{P,b}$, $\sigma_{P,b}$, $\mu_{S,\tau}$, $\sigma_{S,\tau}$, $\mu_{P,\tau}$ and $\sigma_{P,\tau}$. Here, $\mu_{j,k}$ and $\sigma_{j,k}$ are the mean and standard deviation of a normal distribution for population j (for the predator (P) or smolt (S)) and for track statistic k (the Lévy exponent b or tortuosity τ). In addition, the model also estimates λ_P the proportion of track segments that are from predators ($1 - \lambda_P = \lambda_S$ is the proportion of track segments that are from smolts). To classify track segments as from a predator or smolt, we used the estimated parameters and the observed track statistics of each track segment to estimate p_{ik} , the probability that track segment (i) could have been produced by a smolt ($k = S$) or predator ($k = P$, see Equation two in [29]). Track segments were then classified as from a

Table 3 *A priori* assumptions for track statistics for smolts and predators

Track statistic	Smolt	Predator
Tortuosity (τ)	Higher	Lower
Lévy exponent (b)	Lower	Higher

predator if $p_{i,P} > p_{i,S}$ or from a smolt if $p_{i,P} \leq p_{i,S}$. The standard errors for the parameter estimates were estimated from 500 parametric bootstrap runs. Each bootstrap sample was randomly drawn from the distributions described by the maximum likelihood estimates. The model was then fitted to each bootstrap sample. This was repeated 500 times to generate estimates of the standard error for the parameter estimates [31]. This algorithm was implemented using the `boot.se` function in the `mixtools` package for R. We were able to validate our methods via the misclassification of tagged predators as smolts. For tagged predators, we simply calculated the percentage of segments that were correctly identified as from predators. However, we were unable to validate the classification for tagged smolts since it was impossible to recapture tagged smolts to verify their status.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

JR performed the analyses and wrote the initial drafts of the manuscript. RP contributed to the analyses and writing of the initial drafts of the manuscript. SJ performed fieldwork, processed the acoustic data and provided comments on the initial drafts. CF and SP performed fieldwork and contributed to the initial drafts. AB conducted fieldwork, processed acoustic data and provided critical comments on the initial drafts. All authors read and approved the final manuscript.

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