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Characterizing activity and assessing bycatch survival of Pacific halibut with accelerometer Pop-up Satellite Archival Tags

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Abstract

Background: Pacific halibut support high-value commercial and sport fisheries in the north Pacific Ocean, making survival of Pacific halibut bycatch in trawl fisheries an important management concern. We present a method for characterizing activity and inferring survival of Pacific halibut based on accelerometer data from Pop-up Satellite Archival Tags (PSATs). A PSAT attached to a fish with a dart and tether floats freely above the fish in a vertical orientation when the fish is stationary, but switches to a more horizontal orientation when towed behind an active fish. We hypothesized that characteristic changes in PSAT orientation associated with activity could be detected by accelerometers and summarized for transmission by PSATs to provide valuable information on fish activity.

Results: We developed procedures for inferring survival of Pacific halibut with accelerometer PSATs based on a progression of analysis steps that linked PSAT orientation, PSAT acceleration data, and Pacific halibut activity patterns. Relationships between PSAT orientation and Pacific halibut activity were confirmed by observations of PSAT orientation on Pacific halibut swimming in the laboratory and comparisons with depth data from tags on free-ranging Pacific halibut. We developed two metrics summarizing 1 Hz acceleration data for transmission to the Argos satellite network. The "knockdown" metric records abrupt changes in vertical acceleration, indicating both initiation of swimming bouts and sustained swimming behavior, and is robust to the effects of tidal currents. The "%tilt" metric records the amount of time the tag tilts past a vertical orientation threshold and captures the proportion of each time bin that the fish is active. These PSAT metrics revealed diel behavior and three activity modes present in free-ranging Pacific halibut that allowed inference of survival when compared to PSAT data from fish carcasses and weighted tags.

Conclusions: Accelerometer PSAT metrics developed in this study revealed Pacific halibut activity patterns, and thus survival, and may be extended to other fish species. Economical accelerometer PSATs can allow larger sample sizes that enhance bycatch survival studies while detecting fish activity in flat study areas. PSAT advantages over other survival estimation methods include providing outcomes for all specimens during exposure to natural conditions.

Keywords: Acceleration, Activity, Bycatch survival, Discard mortality, Pacific halibut, Pop-up Satellite Archival Tags, PSATs

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Background

Incidental capture and subsequent release of fish while targeting other species (bycatch) is a source of mortality that can only be effectively managed using valid estimates of both the number of fish that are returned to the sea and the mortality rates of those returned fish. Bycatch of Pacific halibut (Hippoglossus stenolepis) in groundfish trawls is an economically important case of this issue, both for its effects on the directed fishery for Pacific halibut and the constraints that it places on trawl fisheries in which retention of Pacific halibut is prohibited and total mortality is limited by regulation. Discard mortality rates (DMR) currently applied to Pacific halibut bycatch in eastern Pacific groundfish trawl fisheries are largely based on a mark-recapture study of Pacific halibut released from British Columbian trawlers in 1970 [1-3]. Thus, confirming the accuracy of Pacific halibut DMRs using updated technology would greatly benefit the management of this high-value species.

Under existing handling requirements, Pacific halibut caught by trawlers that process their catch onboard cannot be released until after they are made available for scientific sampling in the vessel's factory. The resulting delays in release have the potential to increase total mortality rates of the bycatch, and perhaps markedly so. Bering Sea bottom trawlers, organized by the Alaska Seafood Cooperative (AKSC), have been developing methods for sorting Pacific halibut from their catches quickly while allowing effective accounting of their numbers, size, and physical condition. Deck-sorting trials are authorized only for vessels participating under an exempted fishing permit issued to the AKSC by the US National Marine Fisheries Service (NMFS), Alaska Region. In the decksorting trials, fish are handled carefully and released quickly and are therefore expected to have much higher survival rates compared to fish released under current handling regulations. The need to assess the effectiveness of handling changes in deck-sorting trials has motivated the current study to use satellite-tagging technology to study survival of Pacific halibut released from trawls and to validate current methods for estimating DMRs.

Pop-up Satellite Archival Tags (PSATs) can provide the ability to observe behavior and infer the fate of tagged bycatch fish in their natural environment. PSATs are devices attached to fishes that record sensor readings until they detach, float to the surface, and report those data via satellite uplinks. Survival outcomes are typically inferred from variability in depth or temperature beyond that which was considered reasonable for a dead animal [4]. Survival studies need large sample sizes to provide statistically reliable estimates and are thus constrained by per-unit tag costs as well as performance requirements. As the choice of installed sensors is the most adjustable cost component for PSATs, this prioritizes selection of the least expensive sensor package that can still be used to infer survival.

PSATs that contain three-axis accelerometer sensors, one of the more recent sensors to be installed in PSATs, may be valuable for bycatch survival studies. Accelerometers detect static acceleration due to gravity as well as changes in velocity of the tag, decomposing these accelerations across three axes. High-resolution accelerometers (e.g., >30 Hz) have been used to detect survival of sharks [5] by detecting the dynamic accelerations associated with tail beats [6]. Tags with high-resolution accelerometers are typically rigidly attached to the fish so that all acceleration data recorded by the tags corresponds entirely to the movement of the fish. However, the tilt of a free-floating PSAT attached to a fish with a dart and tether can also serve as an indication of the movement of the fish [7]. When the fish is not active, the positively buoyant tag floats freely in a vertical orientation above the fish. During active swimming, drag forces tilt the tag increasingly toward a horizontal orientation with higher swimming speeds. The vertical acceleration sensor on board the PSAT provides information about the vertical orientation (tilt) of the PSAT when static (e.g., measuring only acceleration due to gravity) as the arccosine of vertical acceleration relative to gravity. When a static tag is vertical, the vertical acceleration sensor measures the full force of gravity (1 g). Thus, the magnitude of the vertical component of acceleration measured by the PSAT (in units of gravity) provides information about tag changes in tilt that may occur in response to swimming motion. Changes in acceleration induced by swimming were demonstrated for adult Pacific halibut in a previous study in Glacier Bay, Alaska, in which detailed (4-min interval) acceleration and depth data from physically recovered PSATs revealed that changes in depth unrelated to tidal influence occurred in conjunction with change in tag tilt from vertical to horizontal (J. Nielsen, unpublished). Therefore, we hypothesized that tag tilt can provide valuable information on activity and survivorship of free-ranging Pacific halibut, provided that metrics are developed to summarize activity. Onboard processing and summarization of the raw data are necessary for PSATs, because the high-resolution data archive cannot be transmitted via satellite due to throughput constraints. Therefore, algorithms must be developed to meaningfully summarize or compress those data into a biologically relevant metric that can be transmitted.

The overall goal of this study was to develop methods and analytic support for inferring survival of Pacific halibut released from trawl catches in the Bering Sea with acceleration-based PSATs. Assessing survival of Pacific halibut based on depth data is difficult due to the flat topography of the Bering Sea and potentially extended periods of sedentary behavior of Pacific halibut. Including only accelerometers as primary PSAT sensors minimizes per-tag costs and facilitates the substantial sample sizes needed for an informative survival study. To accomplish this goal, we conducted baseline research to link PSAT tilt measurements to Pacific halibut activity and to characterize activity patterns in free-ranging Pacific halibut. Then we used knowledge of activity patterns provided by PSAT data to develop procedures for inferring survival or mortality of Pacific halibut bycatch in the Bering Sea. Our research consisted of four specific objectives: (1) relate PSAT tilt to Pacific halibut activity, (2) obtain detailed acceleration data sets and characterize activity patterns for free-ranging fish, (3) develop metrics to summarize fish activity measured by accelerometers on board PSATs, and (4) develop procedures for using summarized PSAT acceleration data to infer survival of Pacific halibut bycatch.

Methods

Pop-up Satellite Archival Tags

PSATs employed in this study (MiniPAT and sPAT-Benthic-354) were manufactured by Wildlife Computers, Inc. ("WC", Redmond, Washington, USA). Tags had a length of 124 mm, a width of 38 mm, weighed 60 g in air and were slightly buoyant in water. Both tags contained triaxial accelerometers (range -2 to 2 g, resolution 0.05 g) and wet-dry sensors, and MiniPAT tags additionally contained depth, temperature, and light sensors. The Mini-PAT accelerometer vertical sensor recorded a value of -1 g when the PSAT was static and vertical. Data were recorded at a frequency of 1 record per second (1 Hz). PSATs were attached to Pacific halibut with an anchoring dart through the pterygiophores of the dorsal fin from the eyed side and a 130 kg monofilament fishing line tether with length 15 cm (Objectives 1-3) or 9 cm (Objective 4).

Objective 1: Relate PSAT tilt to Pacific halibut activity

To verify that swimming behavior of Pacific halibut causes a change in PSAT tilt (i.e., vertical when stationary to approaching horizontal when active), we observed a Pacific halibut (78 cm fork length) tagged with an inactive WC MiniPAT in the laboratory. Observations were conducted in a seawater tank (4.5 m diameter, 1 m depth) with 14 other Pacific halibut at the Oregon Coast Aquarium, Newport, OR, USA. The orientation of the tag during swimming and resting events was observed directly and video-recorded.

To link tilt data recorded by the PSAT accelerometers to speed of PSAT movement through water, we conducted additional laboratory tests at the Behavioral Ecology Laboratory of the US National Marine Fisheries Service Alaska Fisheries Science Center, Newport, OR, USA. Four accelerometer-equipped PSATs were attached with a 15-cm, 130-kg monofilament fishing line tether to a support armature suspended downward from an electrically powered rotating arm that circled above a 4.5-m-diameter seawater tank. A range of mechanical towing speeds through water was implemented and calculated from measured path radii and arm rotation rates, which were then matched to vertical acceleration readings through time codes. Readings were averaged over the first 10 s after vertical acceleration readings had stabilized, limiting effects of dynamic accelerations or any water circulation generated by the tags and armature. All water movement was stopped between tests at different speeds.

Objective 2: Characterize activity patterns of free-ranging fish

Detailed (1 Hz) acceleration and depth records from freeranging fish were needed to confirm the links between PSAT orientation, acceleration data, and activity for wild fish and to develop metrics for summarizing acceleration datasets for PSAT transmission. In July 2015, we deployed three MiniPAT PSATs on Pacific halibut caught on longlines in Port Frederick, a mostly enclosed bay in southeastern Alaska (Fig. 1). Tags were set to collect data for 24 days and release from the fish after 28-30 days. PSATs were physically recovered using an Argos goniometer that detects signal strength and direction to a transmitting PSAT (The Woods Hole Group, Inc., Falmouth, MA, USA), making available the full archived datasets. These detailed (1 Hz) data sets obtained from free-ranging fish are subsequently referred to as "Port Frederick fish" and are referred to individually by the prefix "PF".

First, we characterized global properties of detailed acceleration data sets for all three Port Frederick fish. Acceleration data sets typically contain a mixture of static values, which measure only gravity and thus provide information about the orientation of the tag, and dynamic values, which measure any acceleration due to changes in velocity of the tag itself. An acceleration measurement is static if the total acceleration (the square root of the sum of squared values from each of the three axes) has a value of 1. We determined the proportion of static observations in each data set based on the number of observations with total acceleration values <1.1 and > 0.9 g. For all observations determined to be static, we fit a Gaussian mixture model to the tilt (vertical axis) data to estimate the mean, standard deviation, and proportion of observations for a vertical mode (inactive, approximately -1 g), and tilted mode (active, > -1 g) using the R package "mixtools" [8, 9].



Second, to link PSAT tilt data to activity of free-ranging fish, we visually identified swimming bouts in detailed tilt records from the Port Frederick fish. Swimming bouts were defined as abrupt departures from a vertical orientation with a duration of more than 10 s followed by at least 10 s of vertical orientation before the next bout began. We categorized types of activity modes based on frequency and duration of swimming bouts.

Third, we quantified the relationship between swimming bouts identified by acceleration data and the simultaneous occurrence of non-tidal depth changes by examining hourly subsets of the detailed data sets from the three Port Frederick fish. We plotted detailed tilt and depth records for each hour of the day for a subset of 5 days spaced throughout the archival records for each fish (July 11, 16, 20, 25, and August 1). For each hour, we counted the number of swimming bouts identified by tilt data and recorded whether each bout corresponded to changes in depth beyond the change in tide height or whether change in depth occurred when no activity was identified by tilt data.

Objective 3: Develop PSAT summary metrics of fish activity

We examined and analyzed the detailed (1 Hz) acceleration data from the three free-ranging Port Frederick fish to develop and test summary metrics that could compress the raw data into a readily transmittable number of observations. The amount of PSAT data that can be transmitted to the satellites is limited by Argos message size (32 bytes) and battery capacity. Given the transmission constraints and the expected success rate of Argos message transmissions, we developed onboard processing algorithms to calculate two survival metrics for Pacific halibut for 2-h time bins for a period of 60 days (a total of 1440 Argos messages). Because the velocity of currents in areas inhabited by Pacific halibut could not be known in advance, it was important to consider some metrics that would differentiate Pacific halibut swimming bouts from gradual changes in PSAT tilt that could occur in response to local seafloor currents.

Assessing performance of PSAT metrics

To assess overall performance of acceleration-based PSAT summary metrics, we first compared the PSAT activity metrics to hourly changes in depth. We assumed that changes in depth greater than those explainable by tides or sensor variability were due to voluntary fish movements. Given the depth sensor resolution of 0.5 m and tidal variation in Port Frederick of up to 1 m per hour (US National Oceanographic and Atmospheric Administration tidal tables, Elfin Cove, Alaska), we considered that depth changes of more than 3 m in an hour should indicate that swimming had occurred during that period. A converse relationship was not assumed (i.e., that constant depth represented sedentary behavior), as voluntary swimming could occur without substantial depth changes. Therefore, we determined the proportion of 1-h periods with depth changes > 3 m in which activity was also detected by movement metrics. We used a twosample *t* test to test for differences in the average depth change between periods with zero-value metrics and those with positive metrics.

Performance of PSAT summary metrics was also assessed within hourly binning periods during the examination of a subset of the detailed tilt and depth records described above, under Objective 2, for confirming relationships between acceleration and activity. For each hour of subset data (n = 120 h per fish), we compared the activity reported by PSAT metrics to the number of swimming bouts that were identified in the high-resolution data. We assessed whether PSAT metrics reported false activity or did not detect some activity, as indicated by the relative number of movement events detected by each method (i.e., summary versus visual), during each hourly interval.

Characterizing activity with PSAT metrics

We developed criteria for classifying activity modes for free-ranging fish based on PSAT metrics. During the examination of a subset of the detailed tilt and depth records for Port Frederick fish (n=120 per fish), each hour was classified by activity mode based on swimming bout frequency and duration. For each fish, PSAT metrics for hourly subset data were normalized by the maximum value in each data set and grouped by activity mode to determine which values of PSAT metrics were

representative of each activity mode. PSAT metric activity criteria were then applied to the full data sets.

To visualize temporal patterns in activity and depth over entire data sets, heat maps were produced by plotting activity or depth values by hour of the day (*Y* axis) for each day that data were collected (*X* axis) and coding values by color to indicate their magnitude. These plots allowed visualization of diel patterns, tidal patterns, and general increases or decreases in activity over time. In all heat maps, afternoon is the lowest portion of the plot, night is the region between two horizontal white lines (times of civil dusk and dawn obtained from the maptools package in R [10]), and morning to mid-day is the upper portion. Midnight UTC (00:00) corresponds to 16:00 local time. Heat maps were produced for the PSAT metrics, activity modes, and mean depth for Port Frederick fish.

Objective 4: Develop procedures for assessing survival of Pacific halibut bycatch

In the summer of 2016, PSATs developed in accordance with the results from Objective 3 (Wildlife Computers sPAT-Benthic-354) were deployed in the Bering Sea as part of a larger project to assess survival of Pacific halibut trawl bycatch. Herein, we describe only procedures for determining survivorship or mortality based on PSAT data from controls in the study area, while the broader results of the study as they pertain to survival of fish released from trawls will be published subsequently (C. Rose, unpublished). The PSATs deployed in 2016 contained only triaxial accelerometer and conductivity sensors (i.e., did not contain depth sensors) and calculated the two activity metrics developed in Objective 3 over 2-h time bins for 60 days. For tags that released from the fish prior to 60 days, data transmission was initiated after 'dry' readings from the conductivity sensor indicated that the tags were floating on the sea surface.

Our strategy for inferring bycatch survival involved establishing criteria for classification of survival or mortality based on PSAT data obtained from healthy Pacific halibut, Pacific halibut carcasses, and weighted tags in the study area. To obtain information about activity patterns characteristic of healthy Pacific halibut in the study area, PSATs were deployed on 10 fish captured with longline gear in the vicinity of St. Paul Island, southeast Bering Sea. Previous tagging studies have demonstrated that fish captured with longline gear and handled carefully have excellent survival rates [11–13]. Tagged specimens were selected as the most vigorous and healthy-appearing of those captured in a size range matching that of Pacific halibut commonly taken as trawl bycatch in the Bering Sea (50-100 cm length, Table 1). The ten data sets of summarized PSAT data from Bering Sea longline fish

Fish#	PTT ID	Length (cm)	Capture date	Capture latitude	Capture Iongitude	Capture depth (m)	Pop-up date	Pop-up latitude	Pop-up longitude
Port Fre	ederick								
PF-1	151,765	99.5	7/10/15	57.9974	- 135.6207	88	8/7/15	57.9890	- 135.6490
PF-2	151,767	82.0	7/10/15	57.9993	- 135.6185	68	8/8/15	57.9915	- 135.6143
PF-3	151,766	104.0	7/10/15	57.9994	- 135.6180	69	8/9/15	57.9985	- 135.6242
Bering S	Sea								
BS-1	159,584	75.0	7/1/16	57.3368	- 170.3199	64	8/31/16	57.4686	- 170.8756
BS-2	159,586	78.0	7/1/16	57.3380	- 170.3161	62	8/31/16	57.3256	- 170.3124
BS-3	159,587	74.5	7/1/16	57.3384	- 170.3159	62	8/31/16	57.2395	- 170.9571
BS-4	159,592	79.5	7/1/16	57.3388	- 170.3157	62	8/25/16	58.2785	- 170.0106
BS-5	159,597	59.4	7/1/16	57.3399	- 170.3147	62	8/31/16	57.4170	- 170.0256
BS-6	159,591	56.5	7/1/16	57.3402	- 170.3150	62	8/31/16	57.5071	- 170.3141
BS-7	159,599	67.1	7/1/16	57.3408	- 170.3137	62	8/31/16	57.3380	- 170.3367
BS-8	159,473	67.8	7/1/16	57.3439	- 170.3113	62	8/31/16	57.5488	- 171.0054
BS-9	159,589	67.5	7/1/16	57.3519	- 170.3053	63	8/31/16	56.7769	- 170.9311
BS-10	159,475	56.4	7/1/16	57.3556	- 170.3078	63	8/31/16	57.3557	- 170.5043

Table 1 Capture information for Pacific halibut (*Hippoglossus stenolepis*) tagged with accelerometer Pop-up Satellite Archival Tags (PSATs)

Platform transmitter (PTT) ID, total fish length, capture date, location and depth, and PSAT pop-up date and location for longline-caught Pacific halibut in Port Frederick (PF), Alaska, (Objectives 2 and 3) and the southeastern Bering Sea (BS; Objective 4). Port Frederick data sets contain high-resolution (1 Hz) triaxial accelerometer and depth data, while Bering Sea data sets contain PSAT metrics summarized in 2-h time bins

are referred to subsequently as "healthy fish" and referred to individually with the prefix "BS". To obtain examples of data sets characteristic of mortalities, PSATs were deployed on four dead Pacific halibut captured by the regional trawl fishery at four sites on the eastern Bering Sea continental shelf. These four data sets of summarized PSAT data are referred to subsequently as "carcass tags". Finally, to assess potential influence of tidal action on PSAT metrics, we characterized patterns from PSATs deployed on fixed stationary tags in the study area. These tags were tethered to weights (approximately 1 kg of bundled steel chain) on the seafloor at the same locations and times as trawl-caught fish were released to record the effects of seafloor currents. Additional stationary tags were deployed near the release locations of longlinecaught halibut and at another location on the continental shelf. These six data sets of summarized PSAT data are referred to subsequently as "weighted tags". To interpret tidal patterns in relation to the weighted tag PSAT metrics, water level data were obtained from NOAA station 9464212 (Village Cove, St Paul Island, AK) at a frequency of 6 min (tidesandcurrents.noaa.gov). Wave height data were obtained from the National Data Buoy Center for station 46035 (central Bering Sea) at 1-h intervals (http:// www.ndbc.noaa.gov).

To facilitate comparisons between healthy fish, carcass tags, and weighted tags, we generated six types of plots depicting PSAT metric data. Plots consisted of (1) time series of 2-h bins, (2) daily sum, (3) the cumulative density function (CDF), (4) heat maps (color-coded by magnitude) for each hour of the day and each day of the archival data set, (5) a "close-up" of PSAT metric time series for the 5 days prior to the end of the data set, and (6) plotting KDs and %tilt against each other, color-coded by time period. For plot types 1–3 and 6, polygons that indicated typical ranges observed for healthy fish were added to each plot. Plots were produced that depicted each tag's full 60-day programmed deployment period (full data set) in addition to close-up plots that focused only on the first 20 days of each archival tag record. Plots were produced for all healthy fish, carcass tags, and weighted tags and patterns in activity were visually assessed based on the plots (additional details provided in Additional file 1).

Results

Objective 1: Relate PSAT tilt to Pacific halibut activity

Qualitative observations of the PSAT on a 78-cm long captive Pacific halibut in the Newport aquarium confirmed the expectation that these tags tilt significantly during movement bouts and remain vertical when fish are stationary (video provided in Additional file 2). During a typical swimming bout, fish accelerated from rest with several (2–5) tail beats, continued swimming with a mixture of lower-amplitude tail beats and gliding, and ended bouts by gliding to a stop. Tag orientation was vertical when the fish was stationary, but was abruptly tugged into a horizontal position as the fish began to swim. The tag remained tilted during swimming, but gradually returned to the vertical position when the fish glided to a stop.

Tilt values measured by the PSATs (the vertical acceleration component) during mechanical towing experiments followed a sigmoidal relationship with towing speed. As towing speed increased, tag tilt values increased rapidly from a value of -1 g (the value that corresponds to vertical orientation for the MiniPAT acceleration sensor) to an inflection point at -0.5 g at 0.5 m/s. Tilt values reached an asymptote at -0.25 g and approximately 1 m/s (Fig. 2).

Objective 2: Characterize activity patterns of free-ranging fish

PSATs from the three Pacific halibut released in Port Frederick were recovered within 1-2 km of their release locations after deployments of 28–30 days (Table 1, Fig. 1). Tags recorded data for 24 days. Depths and temperatures while on the fish ranged from 25 to 159 m and 6.4-9.2 °C.

In all three Port Frederick data sets, the acceleration measurements were mostly static (e.g., not measuring a change in tag velocity). Total accelerations (vector sums across X, Y, and Z axes) were tightly clustered around 1 (99% between 0.9 and 1.1). Therefore, almost all vertical accelerometer measurements provided information

about PSAT tilt rather than change in velocity of the PSAT. For all three fish, overall PSAT tilt values followed a bimodal distribution (Fig. 3). The vast majority (>90%) of tilt measurements were associated with a stationary (vertical) mode near -1 g. Stationary mode means (0.94, -0.99, and -1.01 g) were similar among all three fish. However, means for the active (tilted) modes (-0.54, -0.68, and -0.43 g) were more variable among fish.

Analysis of detailed acceleration and depth records from the free-ranging Port Frederick fish confirmed links between PSAT tilt and fish activity. Initiation of a typical swimming bout consisted of an abrupt change in PSAT tilt from vertical (-1 g) toward horizontal (0 g) where it oscillated until it more gradually returned to vertical (Fig. 4a). Instantaneous changes in depth (beyond the gradual influence of tide) generally accompanied initiation and duration of swimming bouts identified by PSAT tilt (Fig. 4b). Simultaneous changes in depth were observed for 83% of the 1164 swimming bouts identified in hourly analyses of subset data for all three fish combined (120 h per fish). In contrast, when PSAT tilt data indicated that the fish were stationary (-1 g), only very gradual changes in depth due to tide were observed. In the examination of hourly subsets, only one instance of a very slight change in depth (approximately 1 m) was observed without a simultaneous increase in tilt data relative to the vertical tag orientation.

When fish were active, two different activity modes were observed in the detailed tilt data. The first mode,





normal mixture model indicate that the proportion (lambda) of observations assigned to the stationary modes exceeds 90% for all three fish. To visualize the tilt distribution for smaller active modes, zoomed in plots are also shown for each fish (right). The threshold (-0.75 g) chosen to define activity for the %tilt PSAT algorithm is shown by a thick black dashed line

referred to subsequently as "hopping", consisted of saltatory movement events with durations of less than 3 min interspersed with longer sedentary periods (Fig. 5a). This was the dominant activity pattern observed for all three Port Frederick fish during the subsample analysis of detailed data sets (Table 2); the median standard deviation in depth during hours classified as hopping ranged from 0.8 to 1.2 m (Table 3). The second pattern, referred to as "sustained swimming", consisted of movement events longer than 3 min, during which sedentary periods were more infrequent (Fig. 5b). This was the least frequent activity pattern observed during subsample



- 0.75 g (horizontal dashed line) that classifies movement as active

in the %tilt PSAT algorithm. The knockdown (KD) algorithm (vertical

dashed line) detects the change from vertical (inactive) to more horizontal (active) tilt values when movement bouts are initiated

(here, n = 7 KDs)

analysis of detailed data sets (Table 2). For hours classified as sustained swimming, median standard deviation of depth ranged from 2.5 to 4.9 m (Table 3).

Objective 3: Develop PSAT summary metrics of fish activity Based on PSAT tilt observations from laboratory and field deployments, two metrics were developed to identify and summarize halibut activity patterns present in detailed acceleration data sets (Fig. 4a). The first metric, "knockdown" (KD), was designed to detect the abrupt switch from vertical to horizontal that occurs when a swimming bout is initiated. First, the difference between the maximum and minimum tilt in a 10-s window is calculated. If the difference is greater than a threshold value of 0.5 g, the maximum occurs after the minimum, and the window starting in the previous second did not include such an event, a KD is recorded. The numbers of KDs per time bin are tallied for transmission to satellites. Because this metric measures large changes in tilt that occur over very short time periods, it does not detect the gradual changes in tilt that may occur when stationary tags are subjected to tidal influence in areas with high tidal currents. The second metric, "%tilt", was designed to measure the duration of swimming bouts. This metric calculates the percentage of each time bin that tags are tilted past a threshold value of -0.75 g. The threshold value for the %tilt metric was chosen based on the bimodal distribution of tilt values (Fig. 3), where 100% of detailed observations assigned to the stationary (vertical) mode would be classified as stationary with the PSAT metric and the majority of detailed observations assigned to the active (tilted) mode would be classified as active. However, a proportion of measurements from the active mode ranging from 8% (Fish PF-3) to 37% (Fish PF-2) would be classified by the PSAT metric as stationary with the %tilt threshold set at -0.75. The %tilt metric is also sensitive to the action of tidal currents, as tidal current speeds greater than 0.7 m/s (Fig. 2) may tilt the tag past this threshold and record activity when the fish is inactive.

Assessing PSAT metric performance

In general, activity of free-ranging Port Frederick fish detected by PSAT acceleration metrics corresponded to activity determined by depth changes. Of the 1-h datasummary periods displaying more than 3 m of depth change (e.g., a greater change than tidal fluctuation), 95% (962/1018) contained at least one KD, 96% contained %tilt values > 0, and 100% contained at least 1 KD or values of %tilt > 0. For periods during which < 3 m of depth change occurred, the percentages with at least one KD



or %tilt >0 were 21 and 30%, respectively. Hourly depth changes when PSAT metrics detected activity (mean 9.0 m, 8.3 s.d.) were significantly greater (p < 0.00001) than hourly depth changes when no activity was detected by PSAT metrics (mean 2.1 m, 0.4 s.d.).

In addition to the general correspondence of acceleration PSAT metrics to depth-derived activity, hourly examination of a subset of detailed acceleration and depth data indicated that PSAT acceleration metrics were able to detect the majority of fish activity. For all three free-ranging Port Frederick fish, both PSAT metrics tracked trends in the number of swimming bouts identified in the detailed data sets (Fig. 6a). Out of 5 days (120 h) examined for each tag record, only one instance of a possible spurious knockdown and one change in depth that was not identified as a swimming bout by tilt data were observed (Table 2). Hours with at least some spurious %tilt values ranged from 3% (Fish PF-2) to 8% (Fish PF-1). The percentage of hours during which at least one swimming bout was not detected with the KD metric ranged from 2% (Fish PF-3) to 36% (Fish PF-2). The percentage of hours during which at least some activity was counted as sedentary by the %tilt metric ranged from 6% (Fish PF-1) to 52% (Fish PF-2).

Characterizing activity with PSAT metrics

PSAT acceleration metrics were able to distinguish between hopping and sustained swimming activity modes. In the hourly subsets examined, the magnitude of both KD and %tilt metrics differed between activity modes. Median KDs per hour for the hopping mode ranged from 3 to 5.5 and were significantly lower than

 Table 2 PSAT metric performance and activity mode frequency for hourly subset data from Port Frederick fish

Fish PF-1	Fish PF-2	Fish PF-3
0	0.8	0
7.5	3.3	5
10	35.8	1.7
5.8	51.7	21.7
0	0.8	0
29.2	37.5	36.7
56.7	52.5	45
14.1	10	18.3
	Fish PF-1 0 7.5 10 5.8 0 29.2 56.7 14.1	Fish PF-1 Fish PF-2 0 0.8 7.5 3.3 10 35.8 5.8 51.7 0 0.8 29.2 37.5 56.7 52.5 14.1 10

Results from hourly examination of detailed (1 Hz) acceleration and depth data from three Pacific halibut (*Hippoglossus stenolepis*) tagged with Pop-up Satellite Archival Tags in Port Frederick (PF), Alaska. Hourly data (n = 120 per fish) were examined from five separate 24-h periods throughout the duration of deployment. Percentage occurrence of hours with any spurious knockdowns (KD, count of abrupt changes in tilt) and %tilt (proportion of time spent active), hours where KDs or %tilt did not detect activity (under-detection), hours where change in depth occurred without tilt of PSAT, and proportion of hours classified as stationary, hopping, or sustained swimming activity modes are indicated

median KDs for the sustained swimming mode (range 4–21.5) for Fish PF-2 and Fish PF-3 (Table 3). All three fish had significantly lower values of median %tilt per hour during the hopping mode (range 2.3–5) compared to the sustained swimming mode (range 12.3–47.9). The number of KDs was approximately equivalent to the number of movement bouts each hour during hopping activity, but was significantly higher in the sustained swimming mode for all three fish.

To objectively identify activity modes (stationary, hopping, or sustained swimming), criteria were developed based on PSAT data. Plots of normalized KD versus normalized %tilt grouped by activity mode from the hourly subset analysis (Fig. 6c) revealed that the primary difference between the hopping and sustained swimming activity modes was the magnitude of the %tilt metric. We chose a normalized %tilt value of 0.2 for a threshold that differentiated the hopping from the sustained swimming activity mode for all three Port Frederick fish. The stationary mode was defined as KD values of 0 or 1.

In the full data sets for Port Frederick fish, activity patterns were found to have a strong diel component. Heat maps for KD and %tilt indicate that the sustained swimming activity mode occurred primarily in the daytime, whereas the hopping activity mode occurred mostly at night (Fig. 7). Sustained swimming activity occurred in shallower depths (approximately 80 m) compared to the hopping mode (100–120 m).

In addition to diel activity patterns, trends in activity type and magnitude were observed over the course of tag deployment. All three Port Frederick fish displayed relatively low activity levels during the first 5 days after release and activity levels increased throughout the 3-week deployment. Some fish (e.g., Fish PF-2) switched from an initial pattern of hopping at night and stationary during the day to hopping at night and sustained swimming during the day during the second half of the deployment. Other fish were more consistent in type of activity observed over the course of tag deployment. For example, after the initial period of low activity following release, activity modes for Fish PF-3 tended to be either stationary or hopping at night and sustained swimming during the day.

Table 3	Characteristics of two a	activity modes observed	d for Pacific halibut	(Hippoglossus ster	<i>iolepis</i>) in Port F	rederick,
Alaska						

	Fish PF-1	Fish PF-2	Fish PF-3
Hopping			
Median KDs (range)	5.5 (0–21)	3 (0–12)***	3 (1-18)***
Median %tilt (range)	5.0 (0.6–25.8)***	2.5 (0.2–14.8)***	2.3 (0.3-29.6)***
Median ratio KDs: movement events (range)	1 (0–3)**	0.9 (0-2.5)***	1.1 (1–3)***
Median SD Depth (m) per hour (range)	1.2 (0.1–6.7) **	0.9 (0.3-4.3)***	0.8 (0.3-5.1)***
% Movement events with change in depth	79	84	74
Sustained swimming			
Median KDs (range)	4 (1–16)	12.5 (0–20)	21.5 (4–48)
Median %tilt (range)	12.3 (3.7–70.2)	47.2 (3.8–76.1)	47.9 (9.9–91.5)
Median ratio KDs: movement events (range)	2 (0.8–11)	2.4 (0–6)	2.8 (1.2–12)
Median SD Depth (m) per hour (range)	2.5 (0.7–10.2)	3.4 (1.0–7.7)	4.9 (0.7–9.5)
% Movement events with change in depth	88	100	89

Hourly characteristics of the hopping and sustained swimming activity modes observed for Pacific halibut (*Hippoglossus stenolepis*) tagged with accelerometer Pop-up Satellite Archival Tags in Port Frederick (PF), Alaska, as determined from acceleration data, including: median and range number of tag knockdowns (KDs, count of abrupt changes in tilt), %tilt (proportion of time spent active), ratio of KDs to number of visually identified movement events per hour, standard deviation of depths, and percent of overall movement events that were accompanied by a detectable (> 0.5 m) change in depth. Asterisks denote significant difference between movement states for individual fish (Wilcoxon rank-sum tests), where *p < 0.02, **p < 0.01, and ***p < 0.001



Fig. 7c)

Objective 4: Develop procedures for assessing survival of Pacific halibut bycatch Patterns for healthy fish

Activity patterns from PSATs deployed on ten healthy fish (3 in 55–60 cm range, 3 in 65–70 cm range, and 4 in 75–80 cm range) in the Bering Sea were similar to those from the three Port Frederick fish (Objective 3).

Nine fish provided full 60-day data sets and one provided data for 55 days. Strong diel patterns (activity predominantly during night, predominantly during the day, or differences between night and day) in both KD and %tilt were present throughout the deployment period for healthy fish and were easily detected in the activity heat maps (Fig. 8a). Hopping and sustained swimming activity



modes could also be distinguished. In addition to daily patterns, increases and decreases in activity over several days to weeks was also apparent in data from live fish (Additional file 1: Fig. 4). Values of KD and %tilt for all ten fish during the first 3 weeks of the deployment were lower than the last half of the deployment period. During the first few weeks, some fish recorded low levels of %tilt but no KDs in a tidal pattern (manifested in the heat map as a diagonal pattern that results from the shift of tidal current maximum exchange by approximately 1 h each day; Fig. 8a). A similar tidal activity pattern in KD but not %tilt was observed for weighted tags (Fig. 8b). The median length of stationary behavior periods (consecutive time bins with KD=0 or 1) was 4 h (two 2-h time bins), and 95% of stationary behavior periods had a duration of less than 10 h (Fig. 9).

Patterns for weighted tags

Patterns in PSAT data for weighted tags were characterized by long periods of no activity punctuated by occasional low-level activity consistent with periods of maximum tidal exchange or storms. All six weighted tags recorded data for all 60 days. Tags deployed at Stations 1, 3, 5, and 6 recorded %tilt values of up to 21% during periods of maximal tidal flow (Fig. 10) but KD values were low (maximum of 4) during these times. However, tags deployed at Stations 2 and 4 had both KD and %tilt uniformly at or near zero, even during tidal maxima. The tag at Station 5 (depth 62 m) was deployed during five storms: one with wave heights > 5 m in mid-August and four with wave heights > 6 m in late September and early October. Higher values of KDs and %tilt were observed during this period but %tilt and KD values did not correspond consistently with each other or wave height, as elevated metrics did not occur during two other 6-m wave height storms.

Patterns for carcass tags

Data sets from PSATs deployed on carcasses were characterized by short deployment times, long periods of no activity, and combinations of KD and %tilt values that were not observed for live fish. PSATs deployed on



carcasses surfaced after 0.6, 4.2, 9.5, and 22.7 days. Some patterns for carcass tags were similar to weighted tags, with long periods of inactivity and occasional low-level tidal current signals. However, some of the carcass tags recorded continuous periods with %tilt values that were much higher than observed for healthy fish (Fig. 8c, d). The duration of stationary periods (consecutive time bins with KD=0 or 1) was much longer for carcass tags than

for the healthy fish. For the three tags that were on carcasses longer than 1 day, the median durations of their stationary periods were 24, 30, and 52 h, respectively. In general, KDs for carcasses were low-level and sporadic, KDs and %tilt values did not vary in tandem with each other, and no diel patterns were observed (Additional file 1: Fig. 10).



Criteria for survival classification

Differences in temporal patterns, patterns in KD versus %tilt, length of periods of inactivity, and length of deployment between healthy fish, carcass tags, and weighted tags were used to set criteria for assessing survival of Pacific halibut bycatch in future work. Detailed information on these characteristics for each deployment type is provided in Additional file 1. Healthy fish tended to exhibit regular increases and decreases in activity (both KD and %tilt metrics) over multiple time scales. Within each day, activity tended to increase to KD values generally greater than 10 and %tilt values generally greater than 5, then returned to KD values of 0 or 1 and %tilt values near zero. These daily alternations of activity and inactivity created characteristic spiky patterns in simple graphs of KD and %tilt against time (Additional file 1: Fig. 1). Increases and decreases in activity were also observed at tidal and semilunar scales. In contrast, temporal patterns were restricted to tidal for the weighted and carcass tags and tended to be present in the %tilt metric only. For healthy fish, KD and %tilt were strongly related and varied in tandem with each other over time. High values of %tilt were always observed with high values of KD in healthy fish. In contrast, very high values of tilt were observed to occur without KDs for tagged carcasses, and low levels of tilt (related to tidal currents) occurred without KDs in both weighted and carcass tags. Therefore, either high values of KD combined with high values of %tilt (sustained swimming activity mode) or low to moderate values of KD combined with low values of %tilt (hopping activity mode) were suggestive of a live fish, whereas either very high values of tilt (>80%) or low values of %tilt during periods of high tidal flow that occurred without KDs were suggestive of a dead fish.

Taken together, the patterns in acceleration data that we obtained from apparently healthy, active Pacific halibut observed in situ and from carcass tags and weighted tags suggest that a screening procedure can be used to infer survival of Pacific halibut. A full data set with strong diel patterns and weekly increases and decreases in activity would be classified as alive for the full 60 days. Partial data sets could have resulted from scavenging and subsequent release of a tag from the carcass or the tag could have been shed from a live fish. Partial data sets without any activity patterns characteristic of a live fish or combinations of KD and tilt not characteristic of live fish would be classified as dead at time of release. Partial data sets with initial activity patterns characteristic of live fish followed by combinations of KD and tilt not characteristic of live fish would be classified as dead, with the date of mortality being the last day where patterns of increases and decreases in both KD and %tilt were observed. Because stationary behavior (consecutive time bins with KD = 0 or 1) was also observed for healthy fish, a threshold duration of stationary behavior greater than that observed for healthy fish at the end of partial data sets would also lead to a classification of mortality. Justifiable threshold durations could include 16 h (8×2 -h periods, longer than 99% of stationary periods on healthy, live fish) and 40 h (20×2 -h periods, longer than any such rest periods observed). Threshold selection should consider that our reference data did not include any live but significantly impaired fish. Partial data sets with initial activity patterns characteristic of a live fish followed by a period less than the threshold duration of stationary behavior at the end of the data set would be classified as alive until the last day of the partial data set. Misclassification using these criteria could include mortality events occurring during the first and last 4 h of deployment and, as indicated from some carcass tag and weighted tag data, some periods of storm and high tidal current.



Discussion

By demonstrating how PSAT tilt is related to fish activity and developing methods for summarizing accelerometer tilt data for satellite transmission, our work has resulted in a new method for characterizing activity and assessing survival of Pacific halibut that is likely adaptable to a variety of benthic fish species. Our approach to assessing survival, which features comparing activity patterns between healthy fish, carcass tags, and weighted tags, is necessary for determining survival of Pacific halibut due to the sedentary nature of healthy fish and the flat terrain of the Bering Sea study area. Other PSAT methods for determining survival based on depth and temperature data alone (e.g., [7]) would not be effective under these conditions. Therefore, in addition to the ability to distinguish survival from mortality, this baseline study has also provided a valuable new method for obtaining information about Pacific halibut activity patterns that has a broad range of future applications.

Objective 1: Relating PSAT tilt to Pacific halibut activity

This study confirms that implementing accelerometerbased PSATs can provide direct measurements of Pacific halibut activity without the need to recapture tagged fish. PSAT tilt, actuated by swimming movement, was shown by direct observation in the laboratory and analysis of data from free-ranging fish to clearly delineate swimming activity. The majority of swimming bouts identified by tilt were accompanied by simultaneous changes in depth. However, even though our research to link PSAT tilt to Pacific halibut activity was conducted in an area with heterogeneous bathymetry, approximately 20% of the tilt-indicated movement events were not accompanied by depth changes. This is not surprising, considering that fish often swim at constant depth and may follow isobaths in high-relief habitat. For low-gradient terrain like the Bering Sea, the percentage of movement events that would only be detectable via acceleration would be expected to be much higher than observed in our initial study area in southeast Alaska.

PSAT tilt data provided a stronger signal than change in depth for detecting the hopping activity mode, which was the dominant activity mode for all three fish from Port Frederick. Most of the swimming bouts that were not accompanied by changes in depth occurred during the hopping activity pattern. Even when change in depth did accompany swimming bouts identified by PSAT tilt, depth changes were often close to the limit of tag measurement resolution and hourly changes were similar to tide-related depth changes. Therefore, the use of accelerometer PSATs provides the ability to identify an important behavior that could be missed with tags that measure only depth.

Objective 2: Characterize activity patterns of free-ranging fish

Our finding that free-ranging tagged Pacific halibut in Port Frederick, and the Bering Sea, displayed prominently diel activity patterns during the summer is similar to the results of a previous study on the behavior of Pacific halibut that employed depth-only archival tags. Scott et al. [14] found that individual Pacific halibut were active primarily during either day, night, or dusk/dawn during the summer foraging period. This strong tendency toward diel behavior produced clear patterns in acceleration data that greatly facilitated the identification of live, healthy fish with accelerometer PSATs.

Stationary behavior was a dominant activity mode for the fish tagged in Port Frederick. Pacific halibut are ambush predators and known to lie motionless on the seafloor, but the duration of completely stationary behavior has not been previously quantified. Scott et al. [14] identified a "tidal" mode in depth data that was prominent during summer months (along with diel behavior), where change in depth was related only to tidal cycles, and hypothesized that fish were inactive on the seafloor during this mode. In this scenario, the depth measured by the tag will fluctuate in direct relation to changes in water column height above the stationary fish resulting from tides. Based on the information from our study, activity identified as "tidal" by depth data alone could have resulted from completely stationary behavior. However, it could also have resulted from the hopping activity pattern, where changes in depth are infrequent and subtle. Thus, our study offers the first insights into the frequency and duration of stationary behavior that can be distinguished from movement that occurs at a constant depth.

The "hopping" and "sustained swimming" activity patterns identified in this study could result from different modes of foraging. Hopping behavior has been observed in juvenile Pacific halibut in a laboratory setting (C. Ryer, Alaska Fisheries Science Center, Newport, Oregon, personal communication) associated with foraging. Pacific halibut are visual foragers, and foraging activity is strongly related to light levels [15]. However, they may also detect prey by olfaction [16], allowing them to forage in low-visibility settings, at low light levels, and at night. It is possible that different activity patterns correspond to foraging strategies in different visibility conditions, or vary according to prey targets.

The ability to characterize activity patterns with PSATs has many potential applications beyond assessing survival. For example, PSAT data could be used to estimate vulnerability to capture in the day versus night, in correlation with tidal flux, or link activity patterns to PSAT depth and temperature data. Information on activity patterns from PSATs could also be used to improve geolocation models through inclusion of directly measured behavioral states [17].

Objective 3: Develop PSAT summary metrics of fish activity Well-designed summary metrics are critical for obtaining information on behavior without the need for physical recovery of tags. The KD metric detected activity and was robust to tidal currents whereas %tilt metric could be affected by tidal currents. Still, tidally influenced periods were easily identified because increased %tilt was accompanied by few or no knockdowns. When fish were active, the activity reported by the %tilt metric was much greater than the signal from tidal currents and varied at other temporal scales than tidal (e.g., diel, or semilunar). Finally, high values of %tilt is one characteristic of the sustained swimming movement pattern. Therefore, we consider the %tilt metric to be a valuable component for assessing activity patterns and survival even though it is occasionally vulnerable to detecting tilt that is caused by tidal currents.

In addition to possible effects of tidal currents on the tilt of PSATs, two other issues should be acknowledged. First, a tag on a fish that is swimming steeply downward is likely to retain a relatively vertical orientation thus might provide the same acceleration signal as a stationary fish. Some of the underdetections of both KD and %tilt metrics in the Port Frederick fish appear to have been due to steep downward movements. However, despite the chances for under-detection of individual movement bouts, overall activity patterns were still clearly evident in the KD and %tilt because extended periods of steep downward movements were relatively infrequent.

Additionally, tags on individual fish differed in the distribution of tilts measured during swimming bouts. Of the Port Frederick fish, Fish PF-1 and Fish PF-3 had tilt distributions centered at higher values than Fish PF-2. While some of these differences may relate to very slight variations among tags in sensor orientation relative to tag orientation, it is likely that fish vary in the distributions of their swimming speeds. Because of this variability among individuals in magnitude of tilt values when swimming, data sets should be compared to a range of known values or patterns in metrics rather than simply comparing among individuals. This can ultimately affect the choice of tilt threshold, as a chosen value must apply to all tags used in a given setting; in this study we chose a value that would intentionally allow some real movement to be missed while minimizing false indications of movement. Here, the choice was a matter of study context: the desire to develop protocols that would reduce the probability of inferring survival when fish have in fact died during the deployment period in the context of discard mortality rate estimation. For other subject populations and questions, different thresholds may be chosen to satisfy research objectives.

Our methods for summarizing accelerometer data based on simple tilt measurements have provided a simple, effective, low-cost PSAT that can be used to assess bycatch survival. Other methods for assessing survival of bycatch based on high-resolution accelerometer data have recently been developed [5]. However, these methods require the physical recovery of tags after they release from the fish, and are therefore not feasible for remote locations such as the Bering Sea. Methods for summarizing high-resolution acceleration data for transmission to satellites have been developed to describe diving activity of a marine mammal [18]. However, this

approach requires more processing capability than our metrics do and requires the tag to be rigidly attached to the animal. Our approach is less computationally expensive and practical for application to fish as opposed to marine mammals.

Objective 4: Develop procedures for assessing survival of Pacific halibut bycatch

Based on the ability of PSATs to provide information on typical activity patterns of live Pacific halibut, procedures were developed for assessing survival of Pacific halibut bycatch. A substantial deployment of these tags on Pacific halibut released from Bering Sea trawlers using expedited release (i.e., deck-sorting) procedures has already been completed and a manuscript describing results has been submitted for publication (C. Rose, unpublished).

Ideally, guidelines chosen for assessing survival could be coded into an automated screening algorithm that would largely eliminate biases associated with relying upon individual interpretations, which are likely to vary according to the experience of the screener. However, while the evaluation steps detailed above are clear and objective, a large variation in activity patterns should be expected from large samples of at-large, potentially stressed fish. Distinguishing between mortality and premature tag release from a live fish may be challenging for short data sets, particularly given the period of low activity observed in healthy fish during the first few days following release. Our control data sets could not include observations of confirmed delayed mortality, so the current recommendations are based solely upon observations of acceleration profiles of healthy versus dead individuals. It is likely that the stress-induced death of a fish will produce data that take additional forms than have been detailed herein. Therefore, assessments should initially be made with these results as guidelines and then take into consideration the range of observations that emerge from the collection of additional data. Tag data should be examined in plots at a range of resolutions that allow assessment to be conducted across days and timeof-day (see example plots and additional details in Additional file 1).

Adapting methods for other applications (species, geographic regions)

The ability of the PSAT metrics to detect Pacific halibut activity patterns is important for assessing bycatch survival. The methods reported here are likely to be readily applicable to the closely related Atlantic halibut (*Hippoglossus hippoglossus*) as well as to other large flatfishes such as Greenland halibut (*Reinhardtius hippoglossoides*) and California halibut (*Paralichthys californicus*). Similar protocols might be developed for a host of other species that are sufficiently large to bear these tags. While these tags were successfully deployed on Pacific halibut as small as 55 cm in length, tag stress and setting appropriate thresholds to differentiate activity would likely be more difficult with smaller, weaker, and slower-swimming fish.

We found control data collected from tags on healthy fish, weighted tags, and carcasses to be critical for understanding and interpreting tag data and recommend similar procedures for other studies. Tags on fish that were known to be healthy when released were needed to characterize the normal range of activity patterns. Weighted tags provided the response of metrics to tides and wave action in the area of release. While our study was conducted in the summer with few storms, data from one weighted tag indicated that storm activity could produce significant KD values. Studies conducted in shallower waters than our study (range 53–366 m) during a storm season might be greatly affected. Likewise, %tilt values can certainly be affected by bottom currents, particularly if current speeds approach the normal swimming speeds of the subject fish. However, we found the %tilt metric to be valuable in detecting orientations of the PSAT that were not typical of live fish (e.g., extended periods of maximum tilt that could occur if a PSAT was lodged between the carcass and the substrate). Carcass tags were particularly informative, as the variety of patterns manifested by dead fish (e.g., scavenging action or the tag pinned underneath a carcass) is potentially much larger than for weighted tags and could be increased by wave or current action.

For more general application of methods developed here, we strongly recommend laboratory studies or retrieval of detailed data sets from free-ranging fish to understand the way that the PSAT moves when the fish swims and to set appropriate values for (1) the change in vertical acceleration needed to define a KD, and (2) the threshold value for %tilt used to define activity. These values would need to be adapted to the swimming characteristics and physical requirements of each subject species and study environment. For example, many shark species (*Elasmobranchii*) need to move constantly, so any period of time during which such a fish can be determined to be stationary should likely be interpreted as mortality. Other demersal species could have more extended periods of stationary behavior that would need to be accounted for in determination of mortality or slower swimming starts that could make a KD-like metric hard to establish. Different tag or tag attachment configurations would change tilt/speed relationships relative to those reported here and would therefore require unique threshold calibrations.

For our application for Pacific halibut, the vast majority of the acceleration measurements were static, allowing the data to be treated as tilt measurements. Dynamic accelerations, which could occur with species that move the tag more vigorously, or if the tag measurement resolution is increased above 1 Hz, could confound the use of tilt-based metrics by introducing excessive noise in the acceleration-tilt relationship.

Utility of PSATs for assessing survival of Pacific halibut

Utilization of PSATs for determining bycatch survival solves many issues encountered by other survival estimation methods. Mark-recapture studies, which infer mortality from the relative return rates of different classes of fish, require knowledge or assumptions about reporting rates, natural mortality, migration, and survival of the best-surviving class. They may also require intensive recovery efforts lasting years to obtain sufficient returns. Studies that retain the affected animals in enclosures (e.g., [19-21]), where their fates can be determined, can be affected by stressors that are added (e.g., limited movement, crowding, unfamiliar environmental conditions, insufficient food, and inability to avoid sand flea, Amphipoda spp., predation) or excluded (e.g., predators) by the enclosures or holding conditions. Holding studies also become increasingly difficult with larger and more mobile animals. By using PSATs, the tagged fish can be fully exposed to the same post-release environment they would experience if not tagged. Therefore, results more accurately reflect the untagged population compared to post-capture holding studies. Barring tag or transmission failure, data are received on all subject animals without the need for physical tag recovery, and are available for analysis soon after the tags release. This eliminates recovery rate and selectivity assumptions necessary to estimate survival with conventional tagging, as well as requiring lower initial tagged samples sizes to ensure a given level of recovery data and producing a much shorter and more-predictable timeline for obtaining those data than can be accomplished with conventional markrecapture methods.

The development of accelerometer PSATs in this study provides several advantages for bycatch survival

studies. Using only accelerometer sensors and relatively simple metric algorithms reduces tag costs, allowing for the use of larger sample sizes than would be employed using more expensive archival tags. This consideration is particularly important for bycatch survival experiments. In addition, accelerometer PSATs are valuable in areas with flat terrain, where changes in depth may not be an adequate signal for fish survival.

Knowledge of Pacific halibut bycatch survival is of particular concern considering the magnitude of bycatch and the cultural and economic importance of the directed fisheries. Bycatch mortality of Pacific halibut was estimated to be 3.2 M kg compared to the commercial harvest of 11.3 M kg in 2016 [22]; however, actual survival and mortality rates of released bycatch are currently poorly understood considering the number of confounding variables involved in previous studies [1–3]. In light of recent declines in estimated Pacific halibut stock biomass [22], improved understanding of bycatch survival will provide valuable information for setting future harvest limits for commercial and recreational halibut fisheries and Prohibited Species Catch limits for non-target fisheries.

Conclusions

We developed a method for characterizing activity of Pacific halibut based on tilt measurements from accelerometer PSATs. This method allows detection of three distinct activity modes (stationary, hopping, and sustained swimming) in live fish in addition to the ability to infer post-release survival or mortality. The lower cost of the sPAT-Benthic-354 PSAT developed as a result of this research compared to similar PSATs with more sensors allows deployment of larger sample sizes needed for bycatch survival studies. Accelerometer PSATs are also valuable for use in study areas with flat terrain, where change in depth may not provide an adequate signal for assessing fish activity or survival.

Additional files

Additional file 1. Detailed description of plots used to assess Pacific halibut bycatch survival in Bering Sea trawl fisheries. File format..pdf. Detailed analyses of PSAT data from healthy fish, carcass tags, and weighted tags in the Bering Sea along with additional details on procedures for inferring survival or mortality based on PSAT data.

Additional file 2. Video of tagged Pacific halibut in the laboratory. File format..mp4. The video demonstrates a change in tilt of the PSAT from vertical (stationary) to horizontal (active) as a tagged fish initiates a swimming bout.

Authors' contributions

All authors participated in study design. TL and JN conducted laboratory visual observations of PSAT tilt on live fish. CR conducted laboratory research to link PSAT tilt to tow speed. JN and PD conducted Port Frederick fieldwork, while CR and PD conducted Bering Sea fieldwork. MC conducted data processing and produced metadata for the project. Analyses and manuscript writing were conducted primarily by JN and CR with assistance from AS, TL, and MC. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets generated and/or analyzed during the current study will be available through the North Pacific Research Board Project Search and Database page, http://projects.nprb.org, referenced under Project 1510.

Consent for publication

Not applicable.

Ethics approval and consent to participate

Deployment of PSATs on live Pacific halibut was conducted under University of Alaska Fairbanks IACUC Protocol Number 775145-1 and by permit from the International Pacific Halibut Commission.

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