

**Estimation of post-release longline mortality in Pacific halibut using acceleration-logging tags**

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## ABSTRACT

Pacific halibut (*Hippoglossus stenolepis*) captured in directed commercial longline fisheries in Canada and the United States of America that are below the legal minimum size for retention must be returned to the sea without incurring additional injury. Estimates of mortality caused by discarding sublegal-size fish are included in annual estimates of total mortality from all sources and affect the results of stock assessment and the yield available to fisheries. Currently, an average discard mortality rate (DMR) of 16% is applied to all sublegal-sized longline discards. These discards consist of fish that suffer injuries ranging from minor to severe. The 16% DMR that is currently applied was derived by averaging injury-specific DMRs that in turn assume 3.5% mortality of Pacific halibut that are released to the sea with only minor injuries. The latter has been derived experimentally, but only in captivity. Here, we used acceleration-logging pop-up archival transmitting tags to infer individual survival outcomes for Pacific halibut released *in situ* following capture on longline gear. Post-release behavioral data were evaluated for 75 fish that were at liberty for 2-96 days. Three fish were confidently inferred to have died after periods at liberty of 41-80 days and another three fish may have died 96 days after release; resulting in minimum and maximum estimated 96-day post-release DMRs of 4.2% (range = 0.0-8.7%) and 8.4% (range = 1.7-14.6%), respectively. These ranges are consistent with the currently-applied value of 3.5%. However, the observation that no mortalities occurred until >40 days post-release departs from captive studies in which the majority of capture-induced mortality occurred within 20 days of release.

## INTRODUCTION

Pacific halibut (*Hippoglossus stenolepis*) supports a directed commercial fishery in North American waters whose total economic impact was estimated at 280 million US Dollars in 2018 (Hutniczak 2021). The directed commercial fishery is limited to capture using benthic longlines (and pots in some areas). Coastwide harvests are distributed among International Pacific Halibut Commission (IPHC) regulatory areas with a requirement that all commercially-captured Pacific halibut <81.3 cm fork length (FL) must be returned to the sea with a minimum of injury. Still, injuries and stress associated with the capture and handling of these fish results in mortality for a portion of released individuals (Kaimmer and Trumble 1998; Trumble et al. 2000; Davis and Olla 2001). Pacific halibut lack a swim bladder but have been observed to inhabit depths >800 m (Seitz et al. 2011) and may therefore be subject to barotrauma affecting other organ systems (Carlson 2012). Additionally, their vision may be adversely affected by bright light (Magel et al. 2017) and exposure to temperature changes and air have been shown to influence post-release survival (Davis and Olla 2001).

To establish appropriate target harvest levels for the directed fishery, the IPHC's stock assessment and harvest policies must account for all sources of mortality. For longline-captured Pacific halibut, the IPHC estimates discard levels using a combination of fishery-independent longline survey, fisheries-observer, and fishery logbook data to estimate the quantity and size distribution of discards on a regional basis. Total discard mortality is subsequently estimated by applying a mean discard mortality rate (DMR) of 16% to the estimated volume of discards. For Pacific halibut that are directly observed prior to release, individual viability assessments can be conducted that allow these fish to be assigned to one of four injury categories (minor, moderate,

severe, or dead) that are associated with category-specific mortality rates (Trumble et al. 2000). During 2020, mandatory discard of sublegal-sized Pacific halibut in the directed commercial fishery was estimated to represent 2.2% of total fishery-induced mortality (Stewart and Webster 2021).

The DMRs that are currently employed for longline-captured Pacific halibut were derived from experimental data that have included captive holding (Peltonen 1969), tagging (Peltonen 1969; Kaimmer et al. 2012), and physiological research (Davis and Olla 2001). Foundational research on longline DMRs was composed of a pair of holding studies conducted in 1958 and 1960 (Peltonen 1969). Pacific halibut were captured via longline, tagged with opercular metal strap tags, and placed in at-sea benthic live boxes, without feeding, for subsequent observation. Survival outcomes were obtained for 235 fish ranging from 75-119 cm FL that had been held for periods ranging from 14-77 days, although predominantly <30 days (92% of the fish). Mortality rates varied broadly by treatment group (cage) but were estimated at a maximum of 23% among all treatments and 20% for fish held for  $\leq 20$  days. After restricting the post-capture mortality period to 14 days to control for environmental variability, and accounting for presumed tagging-induced and natural mortality, Peltonen (1969) estimated a capture-induced instantaneous mortality rate of 3.8%. Ultimately, the 3.5% DMR that is currently applied to longline-captured Pacific halibut released after suffering only minor injuries rests on this work and represents the baseline mortality rate from which injury-specific (moderate = 36.3%, severe = 66.2%, dead = 100%) and mean fishery-wide (16%) DMRs are derived. Injury-specific and mean fishery-wide values represent the results of tag-recovery analyses (Hoag 1975; Clark et al. 1993; Trumble et al. 2000), based predominantly upon trawl-caught fish, in which Pacific halibut

have been assigned to injury categories, tagged, and released. Relative recovery rates by category have been inferred to represent the effects of differential discard mortality, assuming 3.5% capture-induced mortality of Pacific halibut released with only minor injuries. As such, if the DMR for fish suffering minor injuries is mis-specified, that error will be carried through the mortality-estimation process and total fishery removals from all injury categories will be inaccurately estimated.

Unfortunately, the ability of captive studies to represent the course of recovery of free-ranging animals following transient stress is limited. Pacific halibut occupy daily home foraging ranges on the order of square kilometers (Nielsen et al. 2014) and have meso-scale dispersal capabilities (i.e., over the course of months) on the order of hundreds of kilometers (Loher and Seitz 2006; Seitz et al. 2011). No holding experiment can allow for the degree of movement that is likely to be exhibited by individuals released from fisheries. Confinement and captivity may impart stress on teleosts (Pankhurst and Sharples 1992; Clearwater 1997; Bolasina 2011) and Peltonen (1969) reported behavior in caged Pacific halibut consistent with adverse reactions to confinement. These effects have included biased distribution of individuals at the edge of enclosures, injury and abrasion from persistent contact with the enclosure materials, and mortality occurring in distinct pulses suggestive of external stressors from which the fish could not escape (Peltonen 1969). Peltonen's (1969) decision to limit mortality estimation to a 14-day period was motivated by observations of variability in ambient temperature and salinity which could not be controlled and was inferred to have induced direct mortality. As such, it remains unclear to what extent the mortality rates observed by Peltonen (1969) represent the relative contributions of capture-induced versus holding-stress mortality.

In the current study, we used acceleration-logging pop-up archival transmitting (PAT) tags to infer individual survival outcomes for Pacific halibut released *in situ* following capture on longlines. PAT tags have proven effective for studying a variety of aspects of the biology of marine fishes (Thorstad et al. 2013). The tags used in the current study were capable of detecting and recording acceleration for periods in excess of three months, allowing for individual fish activity to be inferred. Possessing a programmable release mechanism and satellite-transmission capabilities, tagged fish can be released into the wild and the data characterizing their at-liberty periods can be retrieved and analyzed without the need to recapture the fish. The ability of these tags to index survival outcomes in Pacific halibut has been experimentally validated (Nielsen et al. 2018) and the technology has been used to investigate mortality of Pacific halibut (Rose et al. 2019) and green sturgeon (*Acipenser medirostrus*; Doukakis et al. 2020) following release from trawls. Here, we use these tags to examine post-release mortality and survival of longline-captured Pacific halibut that were released to the sea with minimal injury (IPHC 2021) after being subjected to capture conditions typical of the directed commercial fishery.

## **METHODS**

The Pacific halibut that were used in this study were captured between October 20 and November 2, 2017. A commercial Pacific halibut longline vessel (the F/V *Kema Sue*: 25 m length overall) with an experienced captain holding Pacific halibut quota shares was chartered for this work. An experienced commercial longlining crew conducted all fishing using gear, soak times, and fish-handling techniques commonly employed in the directed Pacific halibut fishery. Fish were captured using benthic longline gear rigged with 16/0 circle hooks attached without swivels to 72-thread-count gangions (i.e., leaders) measuring 60-120 cm in length, fixed 5.5 m

apart along the groundline, and baited with chum salmon (*Oncorhynchus keta*). Sets consisted of eight skates measuring 549 m (1800 ft) each, rigged with 100 hooks per skate, with 2-5 kg weights attached between skate junctions, and soak durations (defined as the interval between deployment of the longline's first anchor and the commencement of gear retrieval) of at least three hours. A single Vemco (InnovaSea, Bedford, Nova Scotia, Canada) Minilog-II-T temperature data logger was affixed to the anchor at the beginning of each set. The loggers were set to record temperature at a resolution of 0.01 °C at 15-second frequency. Fishing was constrained to daylight hours to minimize impacts of benthic invertebrate depredation upon the captured fish (*sensu* Stepien and Brusca 1985).

Pacific halibut were randomly assigned to one of two hook-removal treatments: 1) careful shake, in which a gaff was used to quickly twist the hook to remove it from the fish's mouth; 2) gangion cutting, in which the leader was severed and the fish was returned to the water without removing the hook from its mouth. In normal fishing operations, fish that are released via careful shake are returned directly to the water without being brought aboard the vessel. In the current study, careful shake was executed by positioning the roller (i.e., the point at which fish are first handled) inside the rail of the vessel rather than at the rail (i.e., the roller's normal location), such that fish could be released onto a gently sloped deck slide instead of overboard. Gangion cutting may be employed when large snarls of groundline containing hooked fish are retrieved under conditions that require rapid disentanglement of the snarl and may result in fish being released directly into the water or onto the deck before being returned to the sea.

The physical condition of each Pacific halibut was assessed upon its removal from the longline gear. Only fish that had been subjected to minor injuries were tagged. Minor injuries

were defined as those in which very little or no bleeding was observed; the hooking injury affected only the lip or cheek regions of the mouth and did not result in damage to the jaw (i.e., injures to only skin and soft tissue); and there was no evidence of damage or penetration of the head or body by sand fleas (benthic isopods). The selected fish were tagged with Wildlife Computers (Redmond, Washington, USA) Benthic Survivorship Pop-up Archival Transmitting (sPAT) tags using a dart-and-tether mechanism (Figure 1) following procedures described in Rose et al. (2019). Tag assemblies weighed approximately 70 g in air, representing 0.9-4.3% of the body weights (i.e., 1.6-7.9 kg) of the tagged fish, but were slightly (<5 g) buoyant in water. Note that tag buoyancy alone is insufficient to cause a properly-applied sPAT tag from being shed from the fish.

For each Pacific halibut, biological and handling data were collected that included individual fork length, weight, duration of each longline set, and the average depth of the skate of longline gear upon which the fish had been captured. Time out of water for each fish was recorded as the time elapsed between the fish reaching the sea surface and the time when it was returned to the sea following processing and tagging. Air temperature was taken as a single reading during the processing of each fish, using a Tifictour (Shenzen Hao Yi Wie Technology, Shenzen, China) 038-DTH94 digital thermometer. Fish surface temperature was determined immediately prior to release using a Ceenwes (Englewood, Colorado, USA) GM 550 contactless digital infrared thermometer. Mean bottom temperature of each set was calculated as the average of Minilog-II-T temperature readings beginning five minutes after the setting of the gear (to allow the instruments to acclimatize) to five minutes prior to commencement of gear retrieval. Caudal fin



clips measuring 0.5 cm<sup>2</sup> were collected from each fish for sex identification via established genetic techniques (Drinan et al. 2018).

Tag parameterization and data-transmission protocols followed the methods established in Nielsen et al. (2018) for the detection of activity and mortality in captive, longline-, and trawl-captured Pacific halibut. The tags were programmed to record triaxial acceleration (-2 to 2 g at 0.05 g resolution) at 1 Hz and subsequently compile those data into 2-hour binning periods over the course of deployment. For each binning period, internal software summarized the percentage of time during which the tag was tilted past a vertical acceleration threshold of >-0.7 g (i.e., “percentage tilt”), where fully-vertical = -1.0 g; and the number of times per summary period that the absolute magnitude of vertical acceleration increased by >0.5 g within 10 seconds (i.e., tag “knockdowns”). The percentage of time that the tag remains tilted has been shown to be an indicator of the proportion of time that Pacific halibut are engaged in sustained swimming. Knockdowns are indicative of the tag’s change in orientation at the commencement of swimming bouts that are initiated from a resting position and are more indicative of activity type (i.e., “hopping” versus “cruising”; Nielsen et al. 2018) than time spent swimming *per se*. The chosen acceleration thresholds have been shown to resolve between swimming activity and near-bottom tidal currents in Alaskan coastal habitats wherein current speeds do not exceed 0.7 m s<sup>-1</sup> (Nielsen et al. 2018).

Tags were programmed to remain attached to their host fish for 96 days (i.e., 2,304 hours: the maximum data-logging duration for the given tag parameterization) and to then automatically detach, float to the surface, and broadcast the percentage tilt and knockdown data via satellite. Tags were equipped with a wet-dry sensor to detect deployment and subsequent surfacing. The

recording period was initiated automatically when the tagged fish was placed into the sea and the tags initiated broadcast when surfacing was detected. For all tags, a tag-detachment designation of either “interval” (i.e., detachment was initiated electronically upon completion of the programmed period of retention) or “floater” (i.e., premature surfacing was detected) was obtained. Tag locations upon surfacing were estimated by the receiving satellite(s) from the Doppler shift of the transmitted radio frequency (Keating 1995). Each satellite-generated position estimate was assigned a “location class” by the satellite data-processing service (CLS/Argos, Toulouse, France) that indicated the positional accuracy of the estimate; locations reported herein represent the first broadcast for each tag for which positional accuracy was reported to be <1000 m.

Following Nielsen et al. (2018), death of a Pacific halibut is assumed to result in tag knockdowns declining to zero accompanied by percentage tag tilt that is either near-zero (i.e., tag persistently vertical) or 100% (tag horizontal; either underneath the dead fish or indicating consumption by a large predator). Herein, tag detachment was assumed to occur via one of three most-plausible mechanisms: 1) the programmed retention period was reached, and the tag released electronically; 2) the fish died and either decayed or was scavenged such that the tagging dart was released from its body, or; 3) the tag was shed by force, either through hydraulic drag, fouling on fixed benthic material (e.g., kelp), or removal by an external source (e.g., pulled from the fish by a predator that perceived the tag to be a prey item). Automatic release after 96 days yields data that terminate 2,304 hours after deployment and an “interval” status designation. The second and third forms of detachment produce “floater” designations, wherein the record of a dead fish terminates with a series of zero-knockdown/invariant-tilt data, and a live fish is

expected to shed its tag during a period of positive acceleration. Although live Pacific halibut can become quiescent for periods in excess of two hours (i.e., the minimum temporal resolution possible in this study due to aggregation of the acceleration data into two-hour periods for satellite broadcast), there is no *a priori* reason to expect an sPAT tag to be shed from a live fish in the absence of positive acceleration. As such, the default assumption for tag shedding in the absence of acceleration is that the animal has died.

For fish whose tags successfully broadcast data, two sets of criteria were used to infer death of individuals during the tagged period at liberty and to then calculate two separate, but plausible, mortality rates expressed as a percentage of inferred deaths per 96 days at liberty. First, it was assumed that all fish that retained their tags for 96 days and returned an “interval” detachment designation had survived the tagging period. For any tag that released prematurely, the fish was assumed to have been alive when the tag was shed if its acceleration data demonstrated positive values (swimming) upon tag detachment. Fish were “confidently” inferred to have died if their tag-knockdown values declined to zero and tag-tilt percentages were either near-zero or 100% in the 2-hr summary bin that immediately preceded tag detachment. These deaths were then used to calculate a minimum plausible DMR. However, assuming that any fish that retains its tag for the full 96-day programmed retention period must be alive at the end of that period can produce “false positives” if the fish dies sufficiently close to programmed tag release that the tag does not have time to detach from the carcass, due to the fish’s physical deterioration, before detaching electronically. Therefore, a second criterion assigned “potential death” in fish bearing full-period tags (i.e., “interval” designation) for which data were received that described the end of their periods at liberty and which failed to demonstrate activity during

the final 2-hr binning period immediately preceding programmed tag detachment. These potential deaths were then added to the “confidently” inferred deaths to calculate a maximum plausible DMR.

For attributes describing the conditions under which fish were captured and the characteristics of the study population, errors are reported as one standard deviation about the reported mean. Statistical tests comparing attributes with each other (Pearson correlation) and between sexes (t-tests for continuous data or Mann-Whitney nonparametric tests for highly skewed data) were conducted using R statistical software (R Core Team 2020). The Kaplan-Meier method (Kaplan and Meier 1958) was implemented using the survival package in R to estimate both the minimum and maximum plausible DMRs, with 95% confidence intervals.

## **RESULTS**

The Pacific halibut described in this study were captured on 26 individual sets of longline gear conducted at two locations located southwest of Kodiak Island in the Gulf of Alaska, USA (Figure 2). Sets on which tagged fish were captured employed soak times of 3.0-9.4 (mean  $\pm$  SD =  $5.4 \pm 1.88$ ) hours and were conducted in waters ranging from 69-411 (mean  $\pm$  SD =  $120 \pm 74.8$ ) m in depth with mean bottom temperatures of 4.0-8.7 °C (mean  $\pm$  SD =  $6.8 \pm 1.28$ ). A total of 79 Pacific halibut with minor injuries measuring 53-81 (mean  $\pm$  SD =  $70 \pm 7.4$ ) cm FL and weighing 1.6-7.9 (mean  $\pm$  SD =  $4.6 \pm 1.51$ ) kg were tagged. Time out of water ranged from 91-253 (mean  $\pm$  SD =  $136 \pm 32.0$ ) seconds.

None of the tagged Pacific halibut were recaptured prior to programmed tag reporting; all tags successfully reported to Argos satellites. One tag detached from its host fish within six hours of deployment and was eliminated from the analysis on the assumption that it represented

attachment failure unrepresentative of survival or fish behavior. Three additional tags suffered from data corruption during either data recording or satellite transmission and were also eliminated from the analyses. The remaining 75 tags reported via satellite after periods at liberty ranging from 2-96 days.

The 75 fish that generated usable acceleration data ranged from 53-81 cm FL (Supplement 1) with a relatively even distribution of females ( $n = 35$ ) and males ( $n = 39$ ) with one fish of unknown sex. Fifty-seven of these fish (29 females and 28 males) were released from the hook using careful shake and 17 (7 females and 10 males) via gangion cutting; the fish with unknown sex was released using careful shake. Females and males did not differ significantly from one another with respect to the bottom depths at which they were captured ( $p = 0.10$ ), gear-soak times employed ( $p = 0.18$ ), mean fork length ( $p = 0.54$ ), mean weight ( $p = 0.96$ ), or time out of water while being processed and tagged ( $p = 0.29$ ). Females were captured at significantly warmer mean bottom temperatures than males ( $p = 0.003$ ) and experienced significantly lower air temperatures ( $p = 0.004$ ) on average than males (Table 1) and bottom temperature was negatively correlated with depth (Pearson's  $r = -0.76$ ; Supplement 1). Although the minor differences in bottom and air temperature experienced by male and female Pacific halibut were observed to be statistically significant at  $p \leq 0.05$ , all observed temperatures were well within the range likely to be commonly experienced by fish during capture in the directed commercial fishery and biological significance is therefore unlikely.

Of the 75 successful deployments, 68 fish retained their tags throughout the 96-day programmed period and seven tags detached prematurely. Four of the seven fish with premature tag detachments were consistently active throughout their periods at liberty and generated

positive acceleration data at the time of tag detachment, consistent with having shed their tags while alive and swimming. Periods at liberty for these fish were 2, 25, 31, and 88 days (Figure 3). The remaining three premature tag detachments occurred during zero-knockdown periods that were consistent with mortality of the fish, after 41, 58, and 80 days at liberty (Figure 4). For two of those individuals (tags S-17131 and S-17136), the quiescent (i.e., zero-knockdown) periods immediately preceding tag detachment were relatively short (i.e., 2 and 4 hours, respectively; Figure 4a-b); for the third individual (S-17123), zero-knockdown data were generated for 50 consecutive hours prior to tag detachment (Figure 4c). All three individuals were female; two had been released from the hook via careful shake (S-17123, S-17136) and one (S-17131) by gangion cutting.

Of the 68 Pacific halibut that retained their tags throughout the 96-day programmed period, data that characterized 100% of their times at liberty (i.e., 1,152 consecutive summary periods beginning at deployment) were received for 44 individuals. Incomplete data (i.e., due to gaps in the transmitted record) were received for the remaining 24 fish. For four of these fish the data describing the end of their periods at liberty were not received; thus, it could not be determined whether any of these individuals might have died immediately prior to the programmed detachment of their tags. For the remaining 20 fish whose data records were incomplete, the minimum period prior to tag detachment over which contiguous data were received was 20 hours, thereby allowing robust evaluations of whether or not these fish were active when their tags detached. The proportion of data received for tags displaying data gaps ranged from 55-99% and averaged  $83 \pm 24.3\%$ . Data coverage was  $<90\%$  for 14 tags.

For the 64 fish that retained their tags throughout the 96-day programmed period and for which data describing the end of their periods at liberty were received, 61 (95%) displayed continuous activity throughout their data series, terminating with positive knockdown and percent tilt values (e.g., Figure 5a), and were inferred to have survived. The acceleration data for the three remaining individuals terminated with periods of inactivity (in particular, consecutive zero-knockdown bins) suggesting that the fish may have died immediately prior to tag detachment. For these fish, pre-detachment inactivity (i.e., quiescence) lasted from 8-12 hours. Relative activity in one of these fish (S-17124) declined considerably over its final nine days at liberty (Figure 5d). For the other two fish (S-17155, S-17157), activity was reduced to a lesser extent over the final week at liberty (Figure 5b-c). All three individuals had been released from the hook via careful shake; two were female (S-17155, S-17157) and one was male (S-17124).

In summary, out of 75 Pacific halibut that were successfully tagged and their data recovered, an inferred minimum of three fish suffered mortality (all females) as indicated by premature tag release; and an inferred maximum of six fish suffered mortality (five females and one male) if terminal quiescence in tags that reported as programmed is included as an indication of death (Table 2). Although data describing factors that might contribute to post-release mortality were collected, meaningful analyses relating mortality rates to covariates such as sex, fork length, depth, temperature, and on-deck conditions were not possible because of the relative paucity of confidently-assigned deaths, the small overall sample size, the small number of mortalities, and confounding of covariates (Supplementary Figure 1). Pooling all data and performing a Kaplan-Meier survival analysis resulted in a maximum estimated 96-day mortality rate of 8.4% with a 95% confidence interval ranging from 1.7% to 14.6%. Five of the inferred mortalities

occurred in fish that had been released by careful shake (within a sample of 58 carefully-shaken individuals) and one (out of 17) by gangion cutting (Table 2). Assuming a mortality rate of 8.4%, the binomial probability of observing one mortality in a sample size of 17 is 0.58. Therefore, it cannot be concluded from these observations that gangion cutting resulted in a lower (or higher) mortality rate than careful shake. Repeating the Kaplan-Meier analysis and assuming that the only mortalities were the three fish that were confidently determined to have died (as indicated by premature tag releases; all were released by careful shake) resulted in a minimum estimated mortality rate of 4.2% with a 95% confidence interval ranging from 0.0% to 8.7%.

In addition to the period leading up to their final scheduled summary bins (i.e., 2,304 hours post-deployment), the tags continued to record and summarize data for periods that represented the time lag between the initiation of electronic pin-burn and each tag's physical release from its tether and subsequent surfacing (hereafter, "detachment delay"). These detachment delays ranged from 0-22 hours and averaged  $8 \pm 4.6$  hours. For ten fish, the summary bin associated with hours 2,302-2,304 (i.e., the final scheduled period) was populated with a zero-knockdown value (i.e., the fish were quiescent when the tags were programmed to detach) but activity clearly resumed during the detachment delay. This was close to expectation based upon the behavior of individuals that were inferred to have survived the full observation period. Analysis of the frequency of occurrence and duration of zero-knockdown quiescent periods could be conducted for the 42 surviving individuals (20 females, 21 males, one of unknown sex) for which 100% of their acceleration data was received. Among these individuals, 3,013 quiescent periods were observed, ranging from 18-160 events (mean  $\pm$  SD =  $71.7 \pm 30.06$ ) per individual. The duration of these periods was biased towards relatively short duration (Figure 6). However, twenty fish



exhibited quiescent periods lasting  $\geq 12$  hours and nine individuals displayed quiescence  $\geq 24$  hours in duration. In the most extreme case, an individual remained quiescent in excess of four days (58 hours) before resuming its activity. The mean duration of quiescent periods was highly skewed and there was a slight difference in mean duration of quiescent periods between females and males (Mann-Whitney  $p$ -value = 0.04), with females spending on average 3.86 hours in quiescence during each period whereas male quiescent periods averaged 3.79 hours (Figure 7a). The number of quiescence periods was significantly ( $p = 0.001$ ) more frequent in females (mean  $\pm$  SD =  $87.1 \pm 27.23$ ) than males (mean  $\pm$  SD =  $56.8 \pm 26.02$ ; Figure 7b). Quiescent periods represented 2.2-31.4% of each individual's time at liberty (mean  $\pm$  SD =  $11.9 \pm 5.77\%$ ) and 11.8% of all summary periods. As such, it is estimated that for the 64 Pacific halibut that retained their tags for 96 days, the final knockdown summary bins of seven or eight individuals should have been expected to be populated with zero values even if all fish had survived the full observation period.

Satellite-derived final locations were obtained for 72 tags. A position was not obtained for one of the fish that retained its tag for 96 days. Additionally, broadcasts for two fish that shed their tags prematurely while active were not initiated until the end of the programmed period at liberty and the resulting locations therefore could not be assumed to represent the location of the fish when the tags were shed. Linear geographic displacement among the 72 remaining individuals was highly variable (Figure 2), ranging from 0-1,042 km. Fish that survived ( $n = 69$ ) displayed greater variability in displacement (0-1,042 km) than those that may have died ( $n = 6$ ; 73-282 km), but mean linear displacement was not significantly ( $p = 0.08$ ) different by mortality outcome.

## DISCUSSION

The range of 96-day DMRs obtained in the current study (i.e., spanning 0.0-14.6% under different assumptions of mortality) is consistent with the 3.5% DMR that is currently assumed for longline-captured Pacific halibut released after suffering only minor injuries, and suggest that much larger values are implausible. The temporal nature of the current data is consistent with the hypothesis that capture-induced mortality of Pacific halibut may be lower than 3.5% when careful-release protocols are adhered to and fish are released in excellent condition. In particular, the post-release mortality observed herein was substantially delayed relative to that which has been either observed (holding studies: Peltonen 1969; Davis and Olla 2001) or inferred (*in situ* remote sensing: Rose et al. 2019) from prior research while the dispersal of individuals that were inferred to have died was considerable. It is therefore unclear to what extent the current results were capture-induced as opposed to being associated with natural sources of mortality.

Time-to-event modelling was an explicit feature of the discard mortality analyses conducted by Rose et al. (2019) for trawl-captured Pacific halibut. Those fish had been subjected to variable tow durations, times on deck, exposure temperatures, and catch composition; and progression of mortality was modelled separately for fish within each of three viability categories (excellent, poor, or dead). Despite experiencing a broad range of potential stressors, nearly all mortalities in trawl-captured fish that were returned to the water in excellent condition occurred within 15 days of capture, and mortality ceased within 10 days for two of the three fishing trips that were conducted. These results were consistent with captive experiments predicting that trawl-capture-induced mortality should occur within 30 days of release (Davis and Olla 2001). Similarly, although Peltonen (1969) observed mortality over a range of 6-73 days for

longline-captured fish, the observed median time to death was only 13 days and ~80% of all observed mortalities occurred within the study's typical 14-20 day holding periods. The relatively long time-lags observed in the current study between fish capture and mortality call into question the degree to which the mortality observed by Peltonen (1969) was the direct result of fish capture or, rather, due to post-capture handling (e.g., transit) and captivity in a setting in which recovery from such stressors may have been limited. Setting either a 20- or 30-day mortality window for the current work, to be directly comparable to Peltonen (1969) and Davis and Olla (2001), respectively, would have yielded no mortalities: fish that were confidently inferred to have died did so 41-80 days after release.

For fish that were inferred to have only potentially died (i.e., exactly 96 days after release), the long delay and synchrony among individuals calls into question the likelihood that they truly succumbed to capture stress or hooking injuries. Short-term holding experiments have demonstrated high survival of fish with severe injuries (Kaimmer and Trumble 1998) and approximate 3% IPHC's Fishery Independent Setline Survey of all individuals sustain and recover from minor hooking injuries; an additional 1% recover from injuries more severe than those considered in the current study. In summary, evidence suggests that recovery from minor hooking injuries is common and that Pacific halibut that die from hooking injuries are most likely to do so soon after capture. In contrast, the fact that three fish were inactive at the end of the programmed observation period was consistent with the frequency of occurrence of intermittent activity that was observed among all tagged fish. Therefore, we believe that these fish were probably alive and quiescent when their tags detached. Additionally, the total number of deaths inferred in the current study, both minimum and maximum, were consistent with

expectations based on currently-assumed rates of natural mortality in Pacific halibut (Stewart and Hicks 2020).

The precise magnitude and nature of natural mortality ( $M$ ) in the species is not well-understood. However, estimates of  $M$  used for historical assessment and policy analyses have ranged from approximately 7-30% annually, based on catch analyses (IPHC 1960), tag-recovery data (Myhre 1967), and life-history theory (Clark and Hare 2006) relating maturation and reproductive investment to mortality rates in iteroparous fishes (Lester et al. 2004). Currently,  $M$  for Pacific halibut is believed to be similar for females and males at approximately 14-22% per year (Stewart and Hicks 2020). This range is consistent with estimates of 14% derived from tag-recovery analysis (Webster et al. 2013). Similarly, tag recoveries for Atlantic halibut (*Hippoglossus hippoglossus*) produced estimates of 19% and 16% for females and males, respectively, on the Scotian Shelf and Grand Banks (den Heyer et al. 2013). Natural mortality in fishes is likely to be age- and size-dependent (Jørgensen and Holt 2013) as well as seasonally-variable (*sensu* Hurst 2007; Raimondo 2012). However, little is known regarding mortality-at-age for Pacific halibut and seasonal patterns may be demographically-dependent. For example, mortality may be linked to reproductive investment for spawning individuals (Lester 2004; Jørgensen and Holt 2013) and therefore expected to increase during the post-spawning period (i.e., spring) when individual physiological condition is lowest (*sensu* Mello and Rose 2005; Barnes et al. 2015). In contrast, pre-reproductive individuals may be most susceptible to mortality agents that peak in late summer, such as temperature-dependent predation (Morley and Bucknell 2014; Öhlund et al. 2015) or pathogen transmission (Karvonen et al. 2010; Claar and Wood 2020).

Ultimately, we have no empirical data with which to evaluate seasonal dynamics in physiological condition and natural mortality of Pacific halibut. Therefore, if we assume constant instantaneous natural mortality of 15-22% annually over a 96-day observation period, between 0 and 8 deaths would be expected to occur due to natural causes with 95% confidence within a sample of 75 Pacific halibut. This estimate fully encompasses that which was inferred in the current study. It is difficult to disentangle the confounding effects of natural and capture-induced mortality, especially when natural causes of mortality, such as predation, may be the result of changes in behavior or susceptibility to predation post-capture. However, the minimum DMR that was calculated in the current study is not inconsistent with Kaimmer et al.'s (2012) estimate of 0.18% handling mortality for fish in excellent condition, as derived by captive holding following tagging with Passive Integrated Transponders (PIT tags).

Stock assessment models and management procedures are commonly developed on the assumption that mortality is known (Quinn and Deriso 1999). Where discarding is rare and mortality rates are well understood, these represent a minor source of uncertainty for biological understanding and management efficacy. However, for Pacific halibut, discards (live and dead) are common, and improved understanding of mortality rates could affect model results and therefore management decisions. This study was designed to detect DMRs grossly different from the status quo estimates: roughly three times greater (or more) than the current DMR of 3.5% which, through the linkage among rates assigned to different conditions, could change the overall estimated mortality by an influential amount. We did not find evidence for such differences using modern technology (i.e., sPAT tags) to update historical DMR estimates. However, the range of values derived in the current study (0 - 8.7%) would encompass a substantial range in discard

mortalities relative to that which is currently estimated. For example, total Pacific halibut discard mortality within IPHC Convention Waters was estimated to be approximately 347 tonnes in 2020 based on the assumption of 3.5% baseline mortality for fish released in excellent condition. This value would decrease to 282 tonnes (81% of the current estimate) if the baseline DMR were reduced to 0% (i.e., the lowest bound of the minimum DMR estimated herein), would increase to 445 tonnes (1.3 times the current estimate) if the baseline were increased to 8.7% (i.e., the upper confidence interval of the minimum DMR), and would further increase to 557 tonnes (1.6 times the current estimate) using a baseline DMR of 14.6% (i.e., the upper confidence interval of the maximum DMR estimate). As such, the selection of a baseline DMR even within the range of values estimated by the current study can substantially influence results of the stock assessment and the yield that would be available to the directed Pacific halibut fishery.

This study highlights the need for large sample sizes when attempting to detect small differences in mortality rates and for relating mortality to handling practices and environmental covariates. While sufficient for detecting large differences between the status quo DMR estimate (i.e., 3.5%) and the true discard mortality rate of fish released with minor injuries, the sample size was too small to confidently differentiate between status quo and 4.2% (i.e., the rate observed for fish confidently inferred to have died). We were also unable to conduct covariate analyses such as those found in Rose et al. (2019). In that study, fish length and air exposure time were found to be significantly related to mortality rates. However, that study investigated the survival of fish that were, on average, smaller than those captured in the current study, following capture in trawls, and included fish of all injury classes. Resultant survivorship was one to two orders of magnitude lower than observed herein, allowing for greater resolution regarding

potential causes of mortality. In order to conduct similar analyses with respect to longline DMR (e.g., allowing consideration of length, sex, or soak time), one would likely need to tag a large number of fish and likely need to invoke distinct contrasts in the underlying covariates.

The current study does provide a model for investigating the rates assigned to other fisheries (e.g., recreational), updating rates as future biological, environmental, and management conditions change for Pacific halibut, and investigating differences in DMRs between fisheries, sexes, release condition, and many other covariates. For example, it has been demonstrated experimentally that thermal stress can affect post-release mortality in Pacific halibut (Davis and Olla 2001). For longline-captured fish, the difference between sea bottom and surface temperatures, in conjunction with mixed-layer depth (i.e., governing the time during which fish are exposed to any temperature differential) will likely define the thermal stress because the fish are only briefly (i.e., typically a few seconds) exposed to air temperatures while being “shaken” from the hook. Herein, we were unable to mimic the range of sea temperature conditions to which longline-captured Pacific halibut are likely to be subjected, coastwide, over the course of a nine-month directed commercial fishing season and, therefore, we were unable to relate water temperature to post-release survival. Similarly, the trawl-discard mortality experiment (Rose et al. 2019) that employed approximately three times as many tags as the current study was also unable to detect consistent effects of water temperature on post-release survival. Understanding these effects *in situ* would require an experiment of considerable magnitude that is specifically designed to invoke a meaningful degree of thermal variance while controlling for other environmental and handling effects.

Depredation by marine mammals is known to be common in North Pacific longline fisheries (Peterson et al. 2014) and may represent another substantial form of discard mortality that we were unable to quantify. Surveys of Alaskan longline fishermen suggest that 10-25% of sets may be affected by killer whales (*Orcinus orca*) (Peterson and Carothers 2013) and sperm whales (*Physeter macrocephalus*) also affect longline fisheries in the Gulf of Alaska (Hanselman et al. 2018). However, published research has focused on removal of fish directly from longlines during soak and retrieval (Hamer et al. 2012), which would not be considered discard mortality in the context of the current study. We observed no marine mammals during tag release and the cause of the inferred post-release mortalities could not be identified. Quantifying rates of discard mortality that might result from marine mammals would be logistically challenging but represents an important avenue for future investigation. A variety of remote-sensing techniques have been used to quantify interactions between marine mammals and longline fisheries (Straley et al. 2014; Gaëtan et al. 2019) and to characterize foraging behavior (Tennessen et al. 2019), and the use of fishery discards as a food source by marine mammals has received attention from a theoretical perspective (Heath et al. 2014).

Finally, long-term deployments of acceleration-logging archival tags may provide a mechanism for further investigating aspects of natural mortality and allow for the simultaneous modeling of capture effects and natural processes (*sensu* Kneebone et al. 2021). For satellite-broadcasting tags, study duration may be limited by the amount of data that can be reliably received over the duration of the tag's broadcast life. However, some combination of reduced sampling frequency and longer binning periods may allow researchers to increase observation periods to lengths that are sufficient to obtain such data.



## ACKNOWLEDGMENTS

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### **Table captions**

TABLE 1. Mean  $\pm$  SD, by sex, of various metrics collected for Pacific halibut (*Hippoglossus stenolepis*) that were tagged with acceleration-logging pop-up archival tags for which usable acceleration data were obtained and sex was determined (n = 74). Attributes denoted with an asterisk were significantly different ( $p < 0.05$ ) between sexes.

TABLE 2. Summary of inferred outcomes (alive or dead) for Pacific halibut (*Hippoglossus stenolepis*) that were tagged with acceleration-logging pop-up archival tags, by tag-reporting type (Prog = programmed electronic reporting after 96 days; Prem = earlier detachment and reporting), hook-removal method (SH = careful shake; GC = gangion cut), and sex (F = female, M = male, U = unknown) for fish for which usable acceleration data were obtained (n = 75).

## **Figure captions**

FIGURE 1. An acceleration-logging pop-up archival tag affixed to a dart-and-tether mechanism that is configured for use on Pacific halibut (*Hippoglossus stenolepis*).

FIGURE 2. Tagging locations and dispersal of Pacific halibut (*Hippoglossus stenolepis*) that were captured by benthic longline and released bearing acceleration-logging pop-up archival tags in order to assess post-release activity and survival. Fish were tagged at the two locations depicted with black squares. Open red diamonds indicate fish whose acceleration data suggest that they died 41-80 days after release. Open green diamonds depict fish that shed their tags while active, 61 and 88 days after release. Orange circles are fish whose tags were retained for 96 days and detached electronically.

FIGURE 3. Time series of “tag knockdowns” (i.e., abrupt changes in tag tilt) for tags that detached from four Pacific halibut (*Hippoglossus stenolepis*) prematurely (i.e., prior to their programmed 96-day retention period) while displaying positive tag-knockdown readings. Acceleration-logging pop-up archival tag data for Pacific halibut captured by benthic longline were summed over two-hour data-binning periods. Codes after each panel designation indicate the fish numbers that are referred to in the text.

FIGURE 4. Time series of “tag knockdowns” (i.e., abrupt changes in tag tilt) for tags that detached from three Pacific halibut (*Hippoglossus stenolepis*) prematurely (i.e., prior to their programmed 96-day retention period) during zero-knockdown quiescent periods. Right-hand panels for each fish display the final seven days (84 hours) prior to tag release with the final quiescent period depicted in red. Acceleration-logging pop-up archival tag data for Pacific

halibut captured by benthic longline were summed over two-hour data-binning periods. Codes after each panel designation indicate the fish numbers that are referred to in the text.

FIGURE 5. Time series of “tag knockdowns” (i.e., abrupt changes in tag tilt) for tags that detached from three Pacific halibut (*Hippoglossus stenolepis*) whose tags detached from the fish electronically after programmed 96-day retention. Tag release for **the fish depicted in the first panel** occurred while displaying positive acceleration readings; for individuals depicted in the subsequent panels, the tags detached during zero-knockdown quiescent periods. Right-hand panels for each fish display the final seven days (84 hours) prior to tag release with the final quiescent period depicted in red. Acceleration-logging pop-up archival tag data for Pacific halibut captured by benthic longline were summed over two-hour data-binning periods. Codes after each panel designation indicate the fish numbers that are referred to in the text.

FIGURE 6. Frequency distribution of the duration of individual quiescent periods (i.e., during which no abrupt changes in tag orientation were observed over consecutive 2-hour summary intervals; n = 3,013) for 42 Pacific halibut (*Hippoglossus stenolepis*) that were captured on benthic longline gear, were released bearing acceleration-logging pop-up archival tags, and retained their tags for a full 96-day programmed retention period and for which 100% of the summarized acceleration data were received.

FIGURE 7. (A) Duration and (B) number of quiescent periods (i.e., during which no abrupt changes in tag orientation were observed over consecutive 2-hour summary intervals; n = 3,013), by sex (n = 20 females and 21 males) observed during 96 days of observation for Pacific halibut (*Hippoglossus stenolepis*) that were captured on benthic longline gear and released bearing

acceleration-logging pop-up archival tags and for which 100% of the summarized acceleration data were received.

SUPPLEMENTARY FIGURE 1. Plots of fork length (cm), capture depth (m), gear soak time (s), mean bottom temperature (°C), air temperature (°C), and fish temperature at release (°C) for Pacific halibut (*Hippoglossus stenolepis*) that were captured by benthic longline and released bearing acceleration-logging pop-up archival tags. Shown are the relationship with each other (lower left panels), a histogram of the occurrence of each variable (diagonal), and the Pearson's correlations with each other (upper right panels). Females are shown in red and with circles. Males are shown in blue and with triangles.



Figure 1

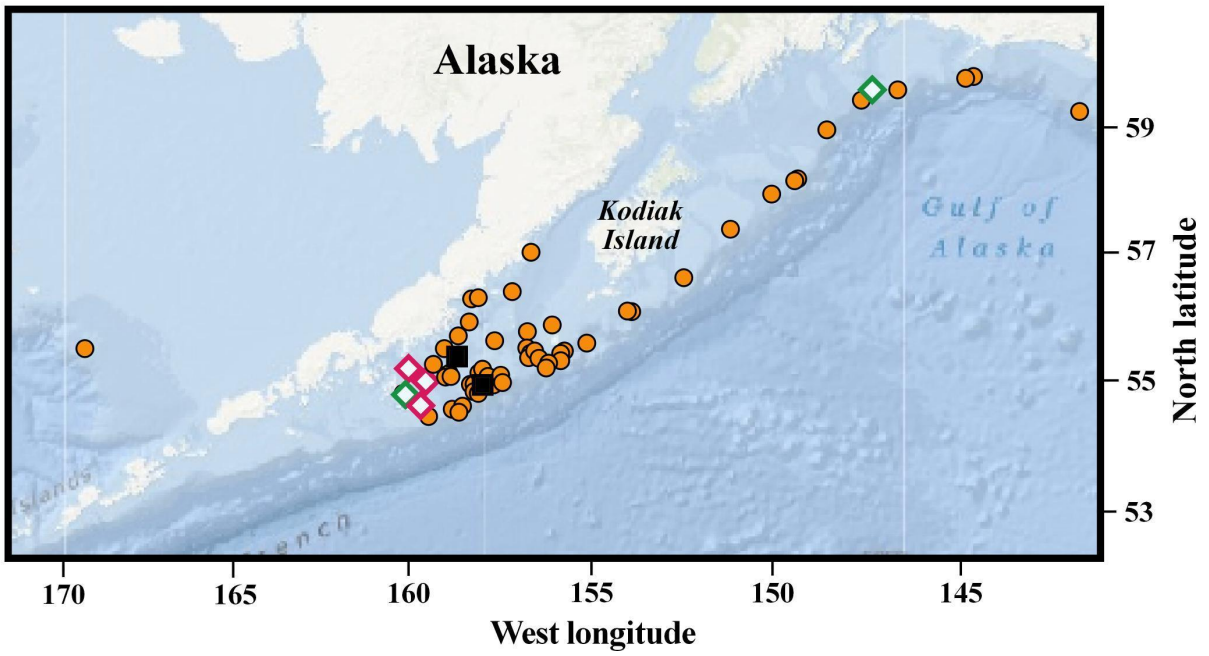


Figure 2

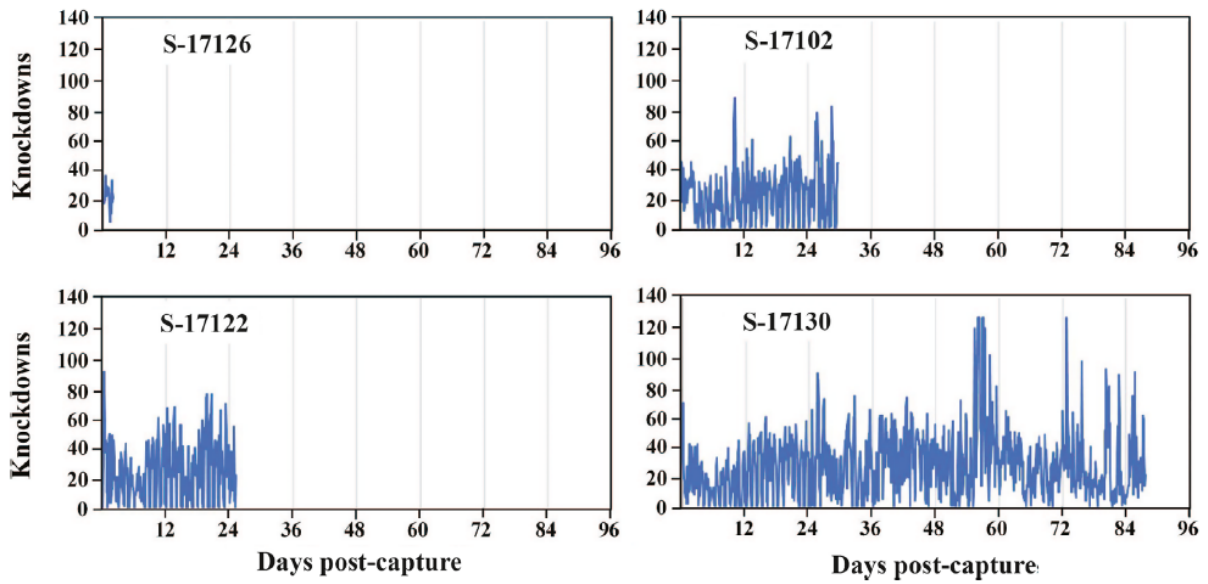
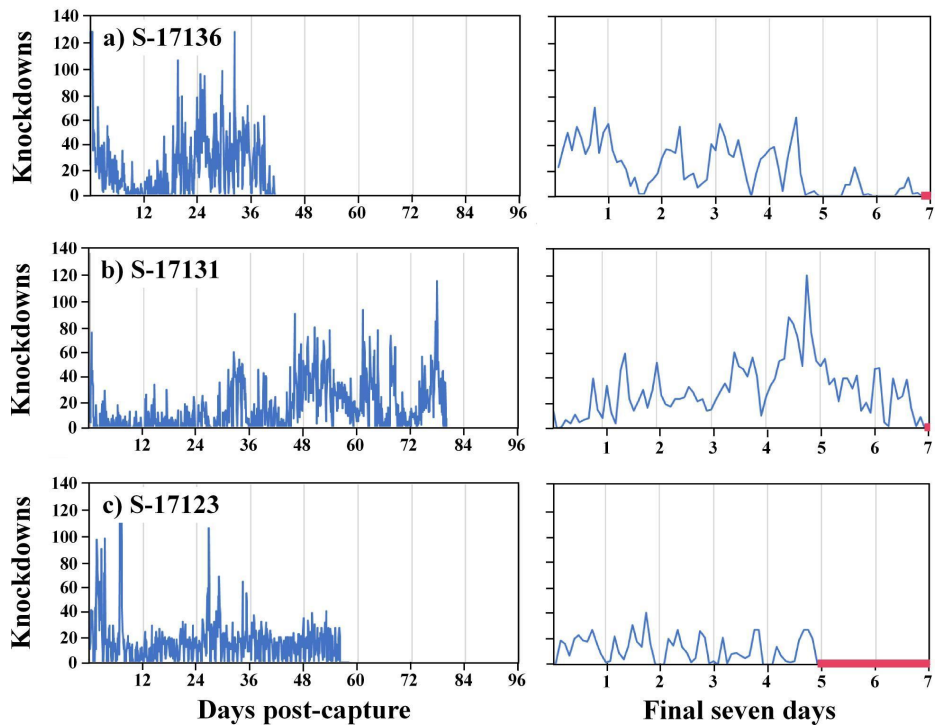


Figure 3





**Figure 4**

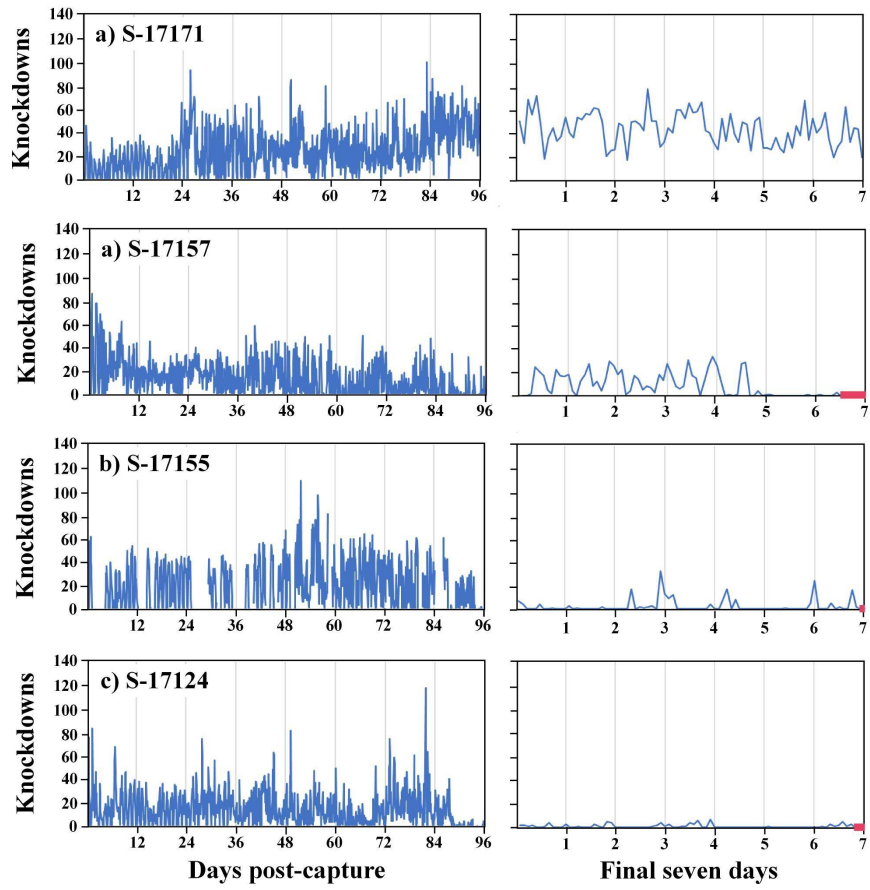


Figure 5

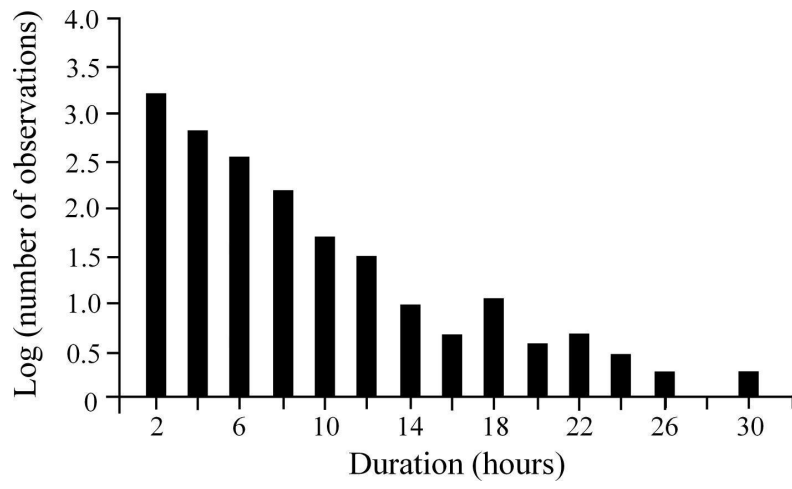


Figure 6

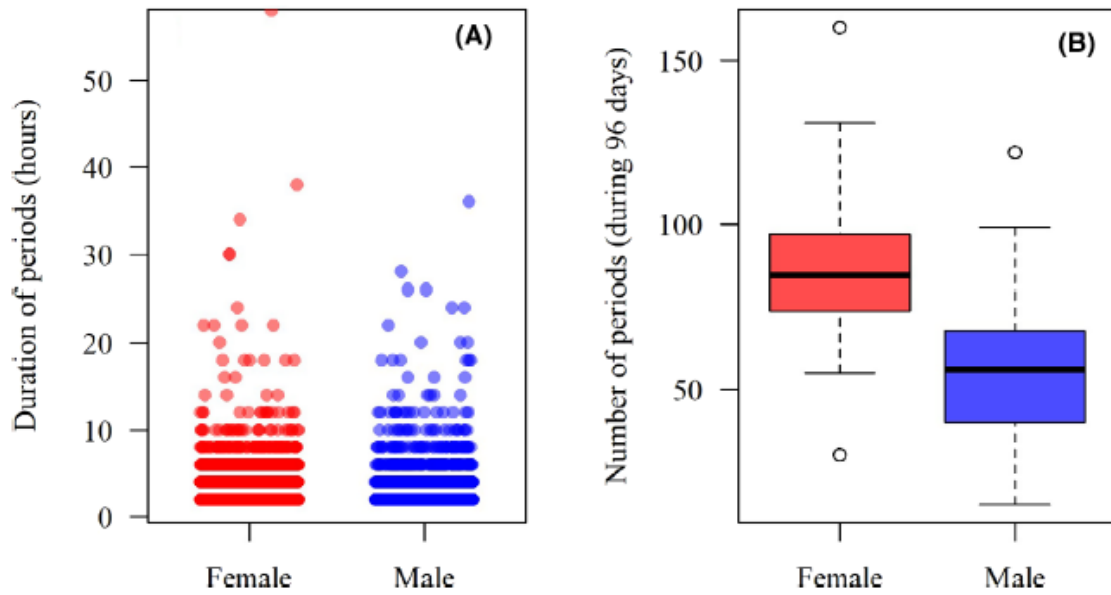
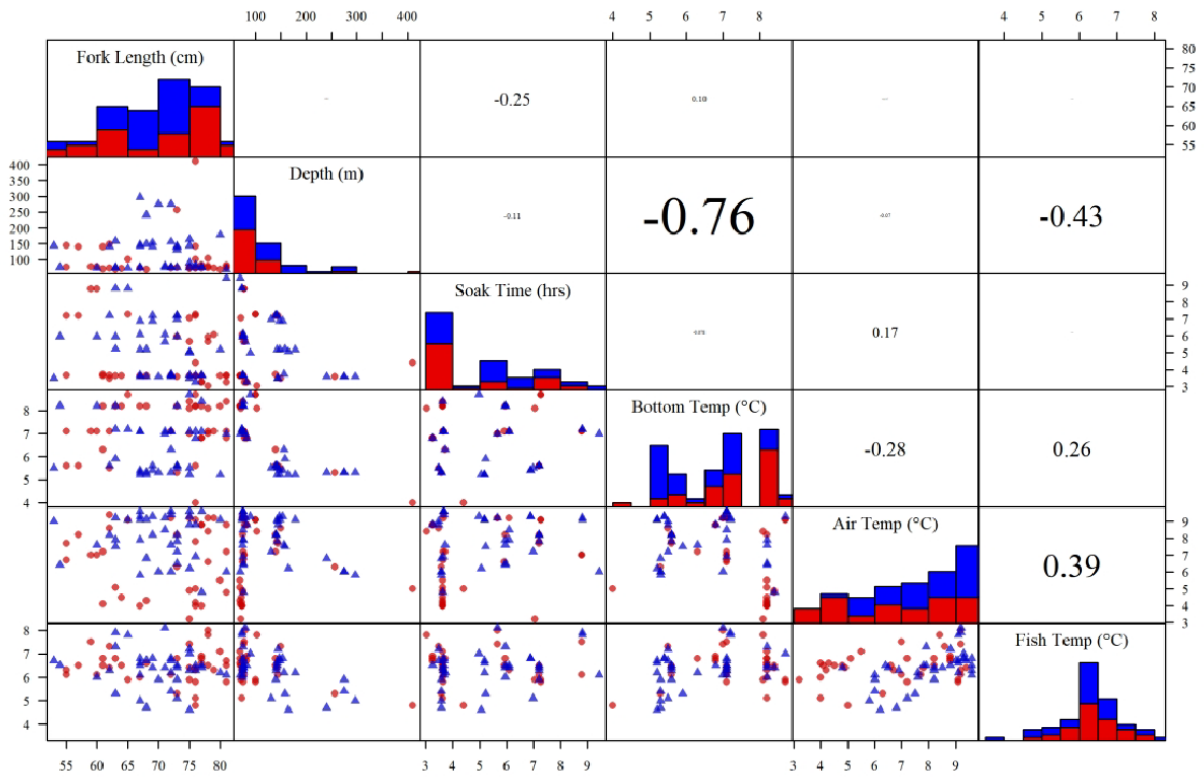


Figure 7



Supplementary Figure 1