

NOTE

Pacific herring response to surface predators in Prince William Sound, Alaska, USA

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ABSTRACT: An *in situ* method was applied to monitor the responses of adult Pacific herring *Clupea pallasii* to predators. An autonomous, upward-facing echosounder was deployed on the seabed at 40 m just prior to the peak of the herring spawning season in Port Gravina, Prince William Sound, Alaska, USA. Monitoring took place over a continuous 4 d period (9–12 April 2016), during which herring and predators (seabirds and Steller sea lions *Eumetopias jubatus*) were tracked. Herring speeds varied (mean = 33.1 cm s⁻¹, range = 0.02–127.1 cm s⁻¹) and were significantly lower than predator speeds (mean = 56.3 cm s⁻¹, range = 13.7–144.6 cm s⁻¹). Swim speeds of herring and predators were positively correlated when regressions were lagged to 2.5 min and indicate a link between activity states of prey and predator. Changes in depth of herring were correlated positively with predator depths over a period of up to 5 min, which corresponds with seabird dive durations. This monitoring method can increase our understanding of sub-lethal effects of predators on Pacific herring and provide a direct method to quantify predation intensity on this critical life history stage.

KEY WORDS: Adult *Clupea pallasii* · Predation · Swim speeds · Depth · Prince William Sound · Alaska

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INTRODUCTION

Pacific herring *Clupea pallasii* of Prince William Sound (PWS), Alaska, USA, have not recovered from a 1993 decline following the 'Exxon Valdez' oil spill. Several hypotheses have been evaluated to understand the causes of the decline and the lack of recovery (Deriso et al. 2008, Pearson et al. 2012, Ward et al. 2017). One of the key uncertainties in the stock assessment used to manage the fishery is adult mortality from disease, predation, competition and oil spill effects (Muradian et al. 2017). The role of predation in limiting the recovery of PWS herring has been debated (e.g. Rice et al. 2011, Moran et al. 2018).

Here I evaluate a new approach to monitoring predation on Pacific herring using an autonomous echosounder. This approach has been applied in other systems and has provided insight into fine-

scale behavior and distribution patterns of pelagic fishes (Axenrot et al. 2004, Taylor et al. 2007), but to my knowledge, no previous studies in PWS have observed and described patterns in both herring and predators. The objective of this study was to evaluate the feasibility of continuous monitoring of adult, pre-spawn herring schools and their response to the presence of diving, surface predators in PWS. Based on 3-dimensional tracking of acoustic targets, I tested whether there were (1) differences in swim speeds between herring and predators, (2) effects of depth on swim speed and (3) correlations of swim speeds between herring and predators. Changes in the abundance-weighted mean depths occupied by herring and predators and were also tested and examined to determine whether predator depths affected the distribution of herring across different time scales.

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MATERIALS AND METHODS

Study area and direct capture

Sampling took place in Port Gravina in eastern Prince William Sound during a 4 d period (9–12 April 2016, Fig. 1). I determined the species of fish making up schools in the study area by gillnet sampling during the evening of 11 April 2016 at a location within 3 km of my monitoring site. The gill net (48.7 × 4.8 m) was deployed for 4 h after sunset along the vessel at anchor (20 m depth). The net consisted of panels of 1.91, 2.54, 3.18 and 3.81 cm square mesh. Captured fish were frozen immediately following capture. Fish were later thawed, identified to species and measured (standard length, in mm) in the laboratory.

Hydroacoustic sampling and data analysis

An autonomous echosounder (BioSonics DTX-SUB) mounted on a benthic tripod (Sea Spider seafloor platform, Fondriest Environmental) was deployed in 40 m of water off Hell's Hole in Port Gravina, approximately 40 km northwest of Cordova, Alaska (Figs. 1 & 2). The transducer (124 kHz, 7.6° split beam) was mounted facing upward. To conserve battery power, a duty cycle was programmed to 1 h on, 2 h off at a ping rate of 2 s^{-1} (0.4 ms pulse duration, source level 219.6 dB re μPa at 1 m).

The acoustic data were analyzed using Echoview 3.0 (Sonar Data). Prior to analysis, a -60.0 dB threshold was applied to remove backscatter originating from smaller targets (e.g. zooplankton) in the water

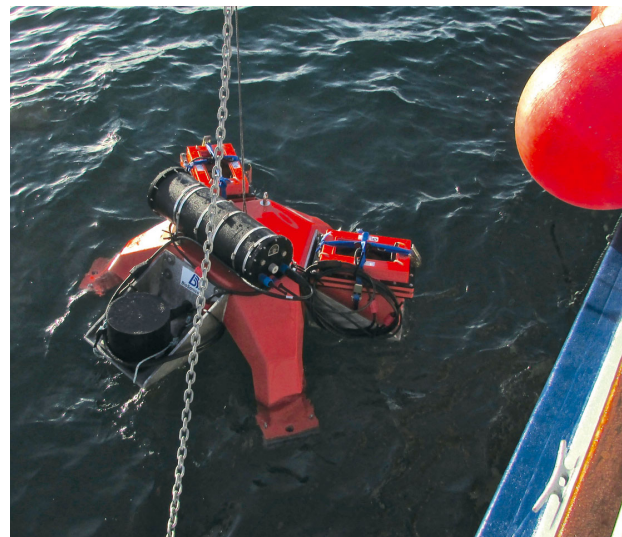


Fig. 2. BioSonics DTX-SUB used in the study. The echosounder electronics were housed in a waterproof cylinder positioned on a benthic tripod. Two marine batteries powered the unit (top and right in the photo), and a 124 kHz split-beam transducer was positioned in an upward-facing orientation (lower left position). Photo: David Janka, Auklet Charter Services

column. A line was established at 25 m range from the transducer (approximately 15 m below the sea surface) that initially demarcated predator (above) and prey (below, Fig. 3) zones. The acoustic records were visually examined and the line was edited in cases where either predator or prey targets intersected this line. Predators were identified as strong targets exhibiting diving behaviors and sinusoidal swimming patterns, while herring were weaker targets and tended to be associated with schools

in deeper water. Individual targets were identified within each discrete zone by applying a tracking algorithm within Echoview (4D setting parameters: $\alpha = 0.7$, $\beta = 0.5$, exclusion axis distance [m] = 4, range exclusion distance [m] = 0.4, minimum number of targets in track = 5 and maximum gap between targets [pings] = 5). These parameters reduce the likelihood that more than 1 fish target is included in a single track. Because of the likelihood of smaller fishes and other targets in surface waters, I applied a target strength threshold of -35 dB to limit my analysis to larger targets that are more likely to be predators. Note that many targets (particularly herring) are schooled,

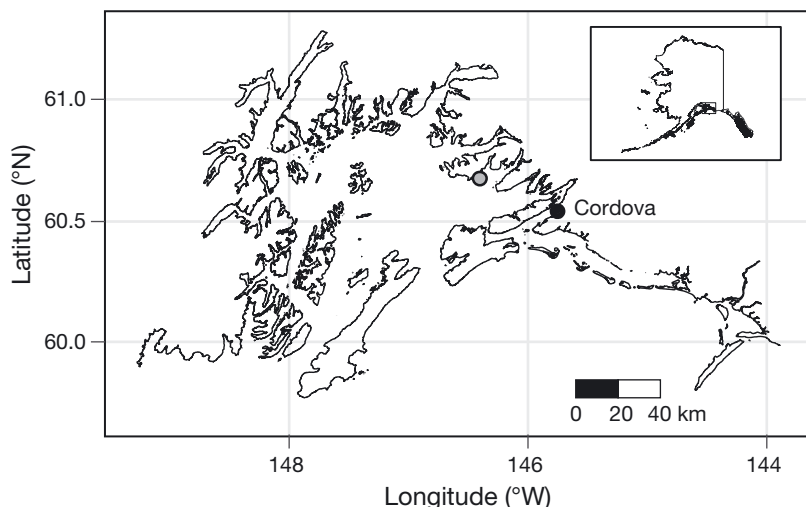


Fig. 1. Location of the study site (●) in eastern Prince William Sound, Alaska, USA

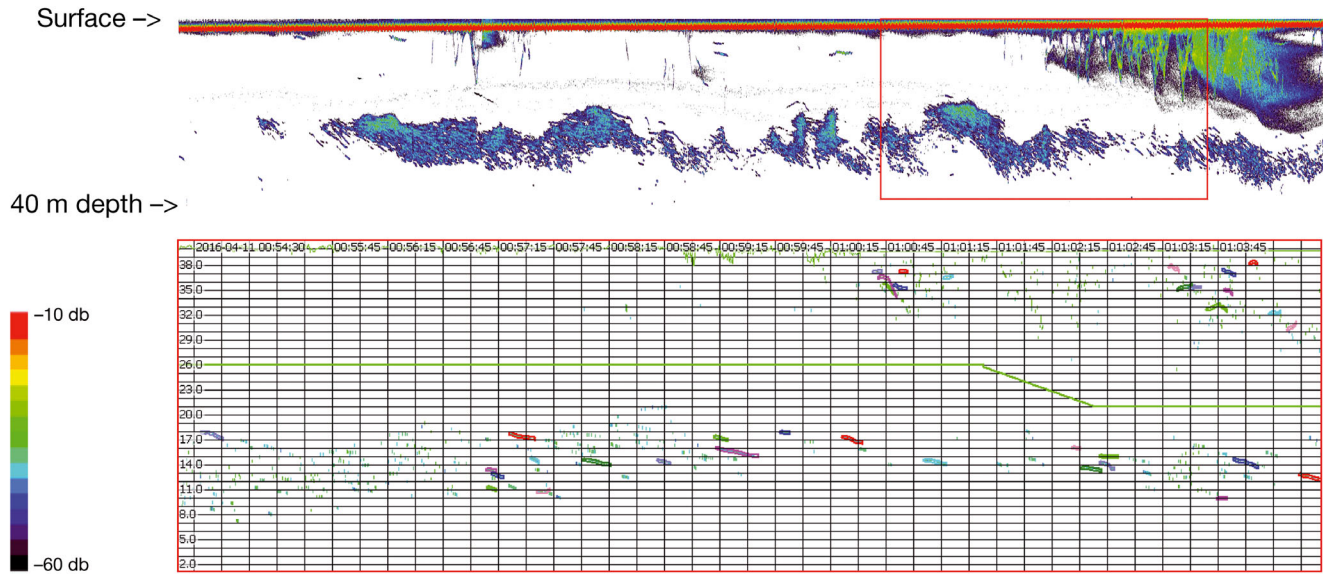


Fig. 3. Echogram depicting 1 h of recording off Hell's Hole in Port Gravina, Prince William Sound, Alaska, during 00:11–01:10 h on 11 April 2016. Diving predators, characterized by strong backscatter, are evident in the top 20 m of the water column. A section of the echogram is expanded with a grid overlay (1 m depth by 15 s) and predator–prey line interface (green). Target tracks identified as herring (below interface) and predators (above interface) are shown with different colors

and thus it was not possible to discriminate individual tracks. As a result, the tracking approach used for characterizing responses of herring to predators is more representative of individuals that are spatially displaced from schools.

Data on swim speed were positively skewed and leptokurtic. I carried out a Box-Cox transformation (library MASS in R) to normalize the swim speed measures prior to statistical analysis and limited this analysis to hour-long recording intervals with >10 targets recorded. Analysis of variance and general linear model regression ('aov' and 'glm' in R) were applied to test for differences in prey and predator speeds and whether depth influenced swim speeds. Significance was determined at $p < 0.05$.

The degree of coherence between herring and predator swim speeds was determined by testing for autocorrelation between the swim speed time series at a temporal resolution of 15 s. I used the cross correlation function (CCF) in R and determined under what range of time lags regressions were statistically significant out to 64 lags (± 16 min).

Acoustic data were echo integrated in Echoview 3.0 and were output in the form of the nautical area scattering coefficient (NASC, m^2 nautical mile $^{-2}$, as in MacLennan et al. 2002). Cells for echointegration were delineated by time (15 s) and depth (1 m intervals), and a weighted mean depth of backscatter (in m) for each 15 s time interval was computed.

I tested for effects of day (blocking variable: hour) on weighted mean depths for herring and predators using Friedman's test ('friedman.test' in R) to determine shifts in depth distribution over the entire recording period. Comparisons between days were performed using Dunn's test. Lagged regressions were applied to test if changes in occupied depths of herring were related to depth changes observed for predators applied to days when herring schools were more commonly observed. I used CCF and determined under what range of time lags regressions were statistically significant out to 64 lags (± 16 min). All statistical analyses were conducted in R version 3.3.2 (2016-10-31).

RESULTS

Results of gillnet catches and a qualitative examination of the acoustic recordings indicated that I recorded pre-spawn herring subjected to punctuated periods of surface predation (Fig. 3). The gillnet catch consisted entirely of adult, pre-spawn Pacific herring with an average standard length of 177 mm ($N = 402$). I quantified 900 tracks in the acoustic data for herring and 84 acoustic tracks for predators. Based on observations from the vessel, the diving tracks of predators likely included Pacific loons *Gavia pacifica*, common murre *Uria aalge*, pelagic cormorants

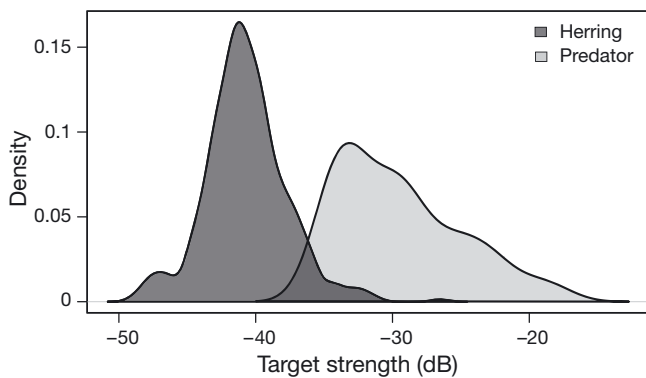


Fig. 4. Probability density of target strengths assigned to herring (dark gray) and surface predators (light gray) during 9–12 April 2016 off Hell's Hole in Port Gravina, Prince William Sound, Alaska

Phalacrocorax pelagicus and Steller sea lions *Eumetopias jubatus*. Over 99 and 72% of the tracks were observed during crepuscular and night time hours for herring and predators, respectively (Hours 0, 3, 6, and 21). Mean target strengths of herring and predators were estimated to be -40.7 and -29.5 dB, respectively (Fig. 4). The target strength (dorsal aspect) for herring of this size (converted from standard length to a fork length of 198 mm) based on the model of Thomas et al. (2002) is -41.0 dB, which is a relatively small departure from the value obtained from the ventral aspect in this study (0.3 dB difference).

Herring swim speeds were more variable compared to predator speeds. Average speed of herring was 33.1 cm s^{-1} (~ 1.9 body lengths s^{-1} , range = 0.02 – 127.1 cm s^{-1}) compared to 56.3 cm s^{-1} (range = 13.7 – 144.6 cm s^{-1}) for predators. Swim speeds of predators were significantly higher than herring swim speeds ($p < 0.05$, ANOVA). The highest swim speed recorded for herring was 127.1 cm s^{-1} , which exceeds a rate of 7 body lengths s^{-1} . It is important to note here that my analytical approach reduces the likelihood of combining positions from multiple targets that might result in inflated swim speeds (see 'Materials and methods'). While several herring exceeded a swim speed of 100 cm s^{-1} , it is certainly within the range of published values for fast-start swimming in fishes that is often associated with escape responses to predators (Domenici & Blake 1997). Herring swim speeds were related to depth ($p < 0.05$, Fig. 5), but depth was not significant in explaining predator speeds ($p > 0.05$, Fig. 5). Herring swim speed was higher closer to the sea surface (Fig. 5). I found no relationship between herring and predator swim speeds observed during the same sampling interval (15 s), but I documented a positive association

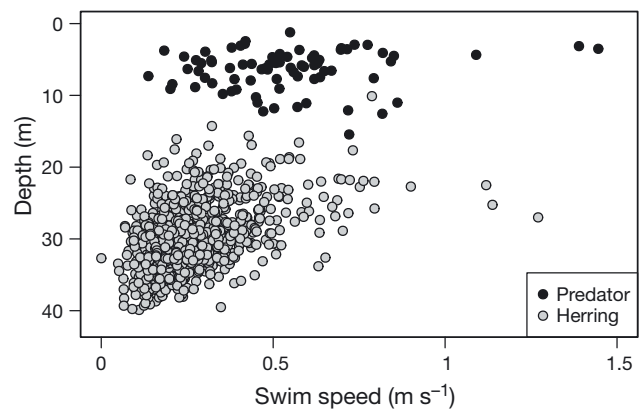


Fig. 5. Swimming speeds (m s^{-1}) of herring (gray) and surface predators (black) during 9–12 April 2016 at a range of depths

between swim speeds of herring and their predators at lags. The association occurred at short time lags and was consistently positive out to 10 time lags (~ 2.5 min, Fig. 6).

Backscatter-weighted mean depth of herring and predators did not significantly shift over hour of day, but there was a significant effect of day after blocking for hour of day ($p < 0.05$, Friedman's test). The herring occupied shallower depths on 12 April compared to 9 April (weighted mean depth 28.3 m compared to 36.4 m , $p < 0.05$), and predators occupied shallower water on 11 April compared to 10 April (weighted mean depth 8.8 m compared to 4.9 m , $p < 0.05$). During the 2 d on which herring schools were more commonly observed (11–12 April 2016), the time series of mean depth of herring and surface predators (weighted by backscatter) was positively correlated out to approximately 20 lags (encompassing a period of 5 min, Fig. 7).

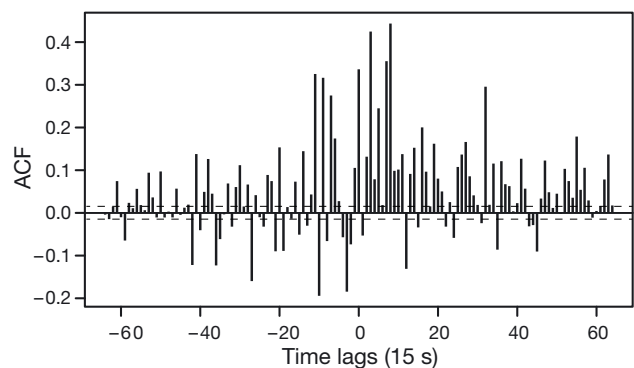


Fig. 6. Temporal autocorrelation function (ACF) between the time series of herring and predator swim speeds. A series of stronger, positive associations between the time series is evident during lags out to approximately 2.5 min. Bars exceeding the dashed lines indicate statistical significance

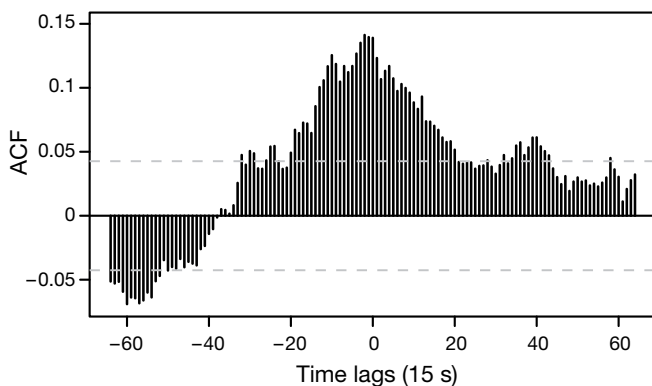


Fig. 7. Temporal autocorrelation function (ACF) of weighted mean depth of herring and predators indicating a positive association over a lagged interval of approximately 5 min. Bars exceeding the dashed lines indicate statistical significance

DISCUSSION

This is the first effort to quantify swim speeds of Pacific herring in PWS and evaluate their behavioral response to diving predators. The predators likely included both seabirds (characterized by sinusoidal swim patterns) and sea lions (strong targets from air-filled lungs and evidence of entrained air bubbles near the surface). Herring appear to be responding to the presence of surface predators. Based on results of the autocorrelation in swim speeds, there is evidence of an association. This is not surprising, given that I likely captured predation events involving predators tracking prey. Herring speeds were highly skewed right and were greatest (exceeding 7 body lengths s^{-1}) near the surface, suggesting periodic escape responses when in close contact with predators. Herring were primarily found between 15 m and the sea floor at 40 m depth. The fish ultimately spawn closer to shore in shallower water (approximately 5–10 m depth). A significant shift to shallower water occurred on the final day of sampling (12 April) despite the presence of surface predators, and this may have been related to movements to spawning beds (often associated with kelp in shallower water) as the peak of spawning occurred within 24 h of the last interval recording on 12 April based on aerial surveys conducted by Alaska Department of Fish & Game (S. Moffitt pers. comm.).

I found that shifts in depths of herring were a dynamic indicator of predation. Depth of predators, weighted by abundance, was positively associated with herring depths. Based on the autocorrelation analysis, changes in depths of herring positively tracked changes in predator depths over a series of

time lags encompassing a period of approximately 5 min, suggesting that fish moved deeper under predation threat from the surface. This dynamic is evident near the final minutes of the interval recording during 00:11–01:10 h shown in Fig. 3. Based on the literature, dive times of individual sea birds last for approximately 1 min (e.g. median of 52 s for pelagic cormorants in the Gulf of Alaska; Kotzerka et al. 2011), and one could envision multiple dives from a group of predators that would result in associated shifts in herring over a period extending over multiple minutes as documented in this study. It is important to note that there are likely a number of fish predators also preying on herring during this stage in their life cycle, and thus this approach does have limitations in understanding their role.

I can make only limited inferences about the herring population based on a single sampling site, but this technology can provide new insight into predator–prey dynamics in this ecosystem. I envision a more rigorous sampling design with multiple acoustic observatories in the region where the herring stage prior to spawning. These stationary observations, combined with a mobile survey conducted each year in this system (Rand & Thorne 2017), could provide a new perspective on how herring respond to predators in both space and time and how their abundance may change over time as a result of predatory impact.

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