Behavioural responses of wild Pacific salmon and herring to boat noise

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ABSTRACT

There is growing concern about impacts of ship and small boat noise on marine wildlife. Few studies have quantified impacts of anthropogenic noise on ecologically, economically, and culturally important fish. We conducted open net pen experiments to measure Pacific herring (Clupea pallasii) and juvenile salmon (pink, Oncorhynchus gorbuscha, and chum, Oncorhynchus keta) behavioural response to noise generated by three boats travelling at different speeds. Dose-response curves for herring and salmon estimated 50% probability of eliciting a response at broadband received levels of 123 and 140 dB (re 1 μPa), respectively. Composite responses (yes/no behaviour change) were evaluated. Both genera spent more time exhibiting behaviours consistent with anti-predator response during boat passings. Repeated elicitation of vigilance or anti-predatory responses could result in increased energy expenditure or decreased foraging. These experiments form an important step toward assessing population-level consequences of noise, and its ecological costs and benefits to predators and prey.

1. Introduction

Concerns surrounding the influx of anthropogenic noise, particularly behavioural and physiological impacts on a wide variety of marine taxa, have increased considerably in recent decades (Cox et al., 2018; Duarte et al., 2021; Simpson et al., 2016; Slabbekoorn et al., 2010). Broadly speaking, fish are underrepresented in studies on the ecological effects of anthropogenic noise (Williams et al., 2015a), even though fish are ecologically, culturally, and economically important. In recent years, a number of studies have established how different fish species can respond to anthropogenic noise by moving away from the noise source or changing their behaviour (Popper and Hawkins, 2019). One anthropogenic noise source that is widespread in the marine environment is produced by vessels. Vessel noise can affect fish presence in an area; Atlantic herring (Clupea harengus) and Atlantic cod (Gadus morhua) have been found to make horizontal and vertical movements away from vessels (Vabo et al., 2002; Handegard et al., 2003). Vessel noise also affects fish behaviour by increasing predation risk (Simpson et al., 2016), reducing the size of a fish’s home range (Ivanova et al., 2020), or changing day-night activity patterns (van der Knaap et al., 2021). All fish species are capable of detecting sound via particle motion, but only some species (primarily those with swim bladders, and particularly species with swim bladders in close proximity to the inner ear) can also receive acoustic signals from changes in sound pressure that are then translated to particle motion (Popper et al., 2003). A growing body of research is showing that noise from shipping and other human activities can reduce the acoustic communication space of fishes (Putland et al., 2018), affect the behaviour and physiology of individuals (Hawkins and Popper, 2017; Weilgart, 2018), and could affect survival, reproduction, and population growth (Soudijn et al., 2020; Watson et al., 2020).

In the northeast Pacific Ocean, wild Pacific herring are known to respond to sounds from vessels, killer whales, and sonar (Schwarz and Greer, 1984), but in order to set quantitative targets for allowable noise levels or desirable levels of mitigation, managers need dose-response studies that measure the probability of a response to the same stimulus across a range of intensity (Hawkins et al., 2014; Miller et al., 2014; Southall et al., 2007). Juvenile salmon, including Chinook salmon (Oncorhynchus tshawytscha) demonstrate strong avoidance responses to
infrasound (Knudsen et al., 1997), but few studies have measured re-

sponses of free-ranging fish across a range of received ship noise levels (Hawkins et al., 2014). Survival of juveniles is of conservation concern. In addition to pressures associated with noise pollution and habitat quality, research has indicated that predators may target this life stage at certain times of the year (Lance et al., 2012; Thomas et al., 2016).

In addition to the importance of fish in their own right, maintaining the health of some fish species is essential to the survival and recovery of endangered and legally protected populations of whales. The trans-

boundary waters of the Salish Sea, located between British Columbia (BC), Canada and Washington state, USA, represents an important feeding habitat for critically endangered southern resident killer whales (Orcinus Orca). One of the main factors affecting the decline of this population is the limitation of Chinook salmon (Ford et al., 2010; Ward et al., 2009; Lacy et al., 2017). Humpback whales (Megaptera novaeangliae) in Canada’s Pacific region are recovering rapidly from commercial whaling (Ashe et al., 2013), but continued recovery of humpback whales requires healthy stocks of zooplankton and forage fish, including Pacific herring (Fisheries and Oceans Canada, 2013). Vessel noise can inhibit whale foraging through behavioural disruption of feeding activities (Blair et al., 2016; Lusseau et al., 2009; Williams et al., 2006), and possibly through acoustic masking (Clark et al., 2009; Erbe et al., 2016; Williams et al., 2014a).

Shipping and other human activities have already made chronic ocean noise a persistent feature of the Salish Sea (Erbe et al., 2012). Although some parts of Canada’s Pacific region are less urbanized than others and may lend themselves to area-based management efforts to maintain acoustic integrity, the Salish Sea experiences high levels of chronic noise from shipping (Erbe et al., 2014; Williams et al., 2015b). Anticipated trends in regional shipping (Kaplan and Solomon, 2016) and multiple proposed fossil fuel-related and port development projects (Gaydos et al., 2015) are poised to increase noise levels in the Salish Sea. Canada’s legal framework, under the Oceans Act, Fisheries Act, and Species at Risk Act, requires use of “best available science” in decision making regarding effects of ocean noise on marine habitat and wildlife (Mooers et al., 2010; Williams et al., 2014b). This creates an incentive to assess whether noise affects fish—both for conservation of fish habitat and for recovery of endangered whales—to evaluate whether ocean noise warrants additional consideration in environmental impact assessments, prioritizing research funding, or mitigating effects of indus-
trial development in Canada’s Pacific region.

In this study, we measured schooling behaviour of wild juvenile Pacific salmon (pink, Oncorhynchus gorbuscha, and chum, Oncorhynchus keta) and herring (Clupea pallasiis) schools in response to boat noise produced by three experimental vessels. Fish were caught from the wild and kept in net pens where their schooling behaviour was observed during experimental trials. Our primary goal was to understand how the schooling behaviour of these three common fish species is affected by boat noise. To accomplish this, we measured responses by identifying changes in typical schooling behaviours (school cohesion, swimming speed, and orientation) and comparing baseline (control) periods to exposure trials when the fish were in the presence of boat noise. Based on the theoretical framework developed by Frid and Dill (2002) in which anthropogenic disturbance can be thought of as a form of predation risk, we expected the fish to respond to vessel noise and disturbance in ways similar to natural predators (De Robertis and Handegard, 2013; Pitcher, 1986; Pitcher et al., 1996). We hypothesized that exposure to boat noise would increase school cohesion, as well as fish swimming speed, and that schools would move down the water column during the exposure period.

2. Materials and methods

2.1. Study site and observation platform

The study site was located in the Broughton Archipelago, a remote fjord system in BC, Canada, between northern Vancouver Island and the BC mainland. All data were collected from the Salmon Coast Field Sta-
tion (SCFS), a field research station located on Gilford Island, BC (Fig. 1).

Noise exposure trials were conducted during two consecutive field seasons in the summers of 2014 and 2015. One pen contained mixed schools of wild juvenile Pacific salmon (pink, Oncorhynchus gorbuscha, and chum, Oncorhynchus keta), and a second pen contained Pacific herring (Clupea pallasiis). A third net pen contained Yellowtail rockfish (Sebastes flavidus), however low visibility prevented us from measuring behavioural responses, so this is not discussed further. Net pens were suspended in the water of a floating observation platform, constructed near the research station inside an enclosed, tidal rocky bay similar to the environment of the fish catch sites (vertical tidal difference of 2–4 m, max depth 8 m). This construction was part of the research equipment available at SCFS and specifically designed to house fish. The location was chosen for its proximity to the SCFS and for its relative isolation from the typical travel routes of recreational boaters. The observation platform was constructed to optimize observations of swimming fish schools in the presence and absence of vessel noise from local vessel traffic.

The observation platform allowed for temporary containment of the three fish species collected for the experiment. Captured fish were contained inside mesh-lined, open net pens hung from the platform (Fig. 2). Anti-predator nets covered the top of the net pens to mitigate predation from piscivorous birds. Salmon (pink, Oncorhynchus gorbuscha, and chum, Oncorhynchus keta) and herring (Clupea pallasiis) schools were separated and given a minimum of 24 h to acclimate to the enclosures before trials were initiated. The captured fish were retained inside the net pens for no longer than eight consecutive days, after which they were released back into the wild. No supplementary food was provided as the fish foraged freely from prey moving through the pens.

2.2. Fish collection and containment methods

Live fish collection was carried out by experienced local fisherman under the supervision of SCFS staff. All fish used in the study were caught within 8 nautical miles (13 km) of the experimental site to limit transportation time and distance, and to minimise stress to the fish. Fish were housed in square containers (approximately 1.0 m, 1.0 m, 0.5 m) filled with water from the catch site which was oxygenated during transport. Water temperatures in the containers were the same as local water temperatures. Depending on the distance of the catch site from the net pens, the time between catch and release varied between 15 and 60 min. Catch methods were genera-specific and were designed to cause as little damage to the fish as possible. Juvenile salmon are known to shoal close to the shoreline. In both years, mixed species schools of ju-
vendile pink and chum salmon were captured using a beach seine (Table 1). Herring “bait balls” were targeted and the herring were captured using a fine mesh dip net. This approach maximised the number of herring captured while minimising handling (Table 1). One school of each fish type (one herring and one salmon) were caught in both years of the study for a total of four schools that were repeatedly exposed to boat noise.

2.3. Acoustic recording and analysis methods

A hydrophone (Reson TC4032; Teledyne RESON Inc., Daytona Beach, Florida, USA) was installed inside the net pen at 1 m depth (approximately mid-net depth) to measure the received level from the experimental vessel inside the net pens and to record any fish vocalisations. The hydrophone was connected to a recorder (Sound Device 722; Sound Devices, LLC, Reedsburg, Wisconsin, USA) as well as an amplifier, which allowed real-time monitoring of sounds. The sampling rate was set at 48 kHz with 24-bit samples and recordings were stored on 32 GB compact flash cards and backed up onto a 1 TB hard drive daily. Acoustic system calibration was carried out using a GRAS pistophone
(Type 42) (GRAS Sound & Vibration, Holte, Denmark) before the start and at the end of each field season and accounted for frequency dependent hydrophone sensitivity (JASCO Applied Sciences in Victoria, BC, Canada). The raw recordings were processed using PAMlab (JASCO Applied Sciences, Canada) to calculate sound pressure level (SPL) each second in decidecade (1/3-octave base 10) frequency bands (10 Hz to 20 kHz) from the averaged pairs of spectra computed from 50% overlapped Hanning-windowed one second FFTs (fast Fourier transformation). The octave-band SPL was calculated by summing three adjacent decidecade bands. The weighted broadband (per genera) SPL

Fig. 1. Map of study and catch locations in the Broughton Archipelago, British Columbia, Canada. Salmon Coast Field Station (50.7459° N, 126.4983° W) and associated open-net fish pens were located on Gilford Island.

Fig. 2. (a) Two net pens suspended from the floating platform covered with anti-predator nets. The docking station of the tender vessel, used to create the boat noise, is located at the far back next to the net pens. (b) Experimental setup; net size 4.3 m × 3.5 m × 2.8 m.
was calculated by subtracting a weighting value, representing fish audiogram values (Hawkins and Johnstone, 1978; Nedwell et al., 2004), in dB from each octave-band level before summing to obtain broadband measurements. Broadband weighted and unweighted SPLs were time-averaged for each exposure and control trial period for further analysis. Descriptive statistics (average ± standard deviation (SD)) were calculated for the unweighted broadband received level of ambient noise and vessel treatments.

Vessel noise experiments used one of the three vessels of varying length and engine horsepower (Fig. 3). A noise exposure trial was conducted by monitoring the fish behaviour in the absence of any boats within the bay for a minimum of 15 min (control period), then operating the treatment vessel past the fish nets at randomly varying speeds and distances (~5–40 m from the hydrophone), and monitoring fish behaviour during a 3-minute noise treatment session. After 3 min, the engine was shut down and fish were allowed to recover for at least 1 h before another trial was initiated.

Fish school behaviour was recorded continuously (i.e., before, during, and after boat transit) using three underwater cameras (GoPro Hero 4 silver, GoPro Hero 4 silver, and a GoPro Hero silver) mounted on a pole at 23 cm depth in the corner of each net pen (Fig. 2). Schooling behaviour was assessed simultaneously from playbacks of video recordings for each separate trial since the fish school was generally only visible on one of the cameras. All video processing was completed in Windows Media Player (2013 Microsoft).

### 2.4. Behavioural data

Behavioural categories and their descriptions were defined using an ethogram developed a priori (Table 2). Video recordings were analysed without sound to avoid observer bias. Three schooling behavioural categories were identified, each divided into two response options (Table 2) that were all given a unique key code used to connect the behaviour to a certain time in the video using a simple PC behavioural analysis program called JWatcher (version 1.0, 2000–2006 (Blumstein et al., 2006)).

During each trial, there were times (of varying duration) when the fish were out of camera view. An “out of sight” code, mutually exclusive to all other behaviours (i.e., none of the other behaviours could co-occur when the fish were “out of sight”), was created in JWatcher to account for the proportion of time the fish were not captured on video.

Behavioural rates were standardized to the proportion of time the fish were in view of the cameras. Overall changes in schooling behaviour of the fish were used to describe the response(s) of the fish from the control period to the noise treatment during boat passage and to the received SPL changes throughout the trials. The decision to conduct an experimental treatment was governed by the availability of boats and drivers, while they were conducting other research projects in the area. Although the treatments were not applied in a random fashion, neither were they applied in an “ordered” way in which fish could be sensitized to increasing noise levels over time. Instead, the use of the small, medium, and large vessels was staggered throughout the field seasons.

#### 2.5. Dose-response curve

The response variable of interest was not the behaviour (e.g., swimming speed or orientation) itself, but rather the change in behaviour between the experimental control and the treatment period.

Each of the three behavioural metrics (school cohesion, swimming speed, and school orientation) was defined such that it could either change or not change during the vessel exposure period. If no change occurred in any of the three behavioural metrics from before to during exposure, then the trial resulted in a score of 0. If the fish schooling behaviour changed for more than 20% of the time for one, two or all three behaviours, then the trial resulted in a score of 1, 2 or 3. Although the sum of behavioural changes can be used to assess severity of behavioural responses (e.g., Miller et al., 2012; Southall et al., 2007), modelling severity of ordered, categorical responses results in a suite of dose-response curves that require policy-makers to decide what constitutes a response large enough to warrant concern. Similarly, we could have used a different threshold for the duration of a behavioural change required to constitute a response (e.g., from 20% to 50% of the observation period). We chose a 20% threshold because it was long enough to convince us that it represented a true change in behaviour, rather than

<table>
<thead>
<tr>
<th>Number of trials</th>
<th>Species group</th>
<th>Fish number</th>
<th>Fish length (cm)</th>
<th>Catch method</th>
<th>Catch date</th>
<th>Catch site</th>
</tr>
</thead>
<tbody>
<tr>
<td>24</td>
<td>Pacific Pink salmon (O. gorbuscha) and Chum salmon (O. keta)</td>
<td>&gt;200</td>
<td>12–17</td>
<td>Beach seine</td>
<td>07/30/2014</td>
<td>Rocky shore close to Wicklow Salmon Farm</td>
</tr>
<tr>
<td>24</td>
<td>Pacific herring (C. pallasi)</td>
<td>&gt;250</td>
<td>15–20</td>
<td>Dip net</td>
<td>08/05/2014</td>
<td>Water surface close to SCFS</td>
</tr>
<tr>
<td>24</td>
<td>Pacific Pink salmon (O. gorbuscha) and Chum salmon (O. keta)</td>
<td>49</td>
<td>15–18</td>
<td>Beach seine</td>
<td>08/20/2015</td>
<td>Rocky shore close to Wicklow Salmon Farm</td>
</tr>
<tr>
<td>13</td>
<td>Pacific herring (C. pallasi)</td>
<td>&gt;200</td>
<td>19–25</td>
<td>Dip net</td>
<td>09/01/2015</td>
<td>Black fish sound</td>
</tr>
</tbody>
</table>

Fig. 3. Photographs of each of the “treatment”, or sound exposure vessels used: (a) Tenderoni, 4.5 m aluminium skiff with 8 hp. outboard Mercury; (b) Broughton, 5.5 m fiberglass runabout with outboard 115 hp. Evinrude E-tec engine; (c) Wishart, 9.4 m Sargo with a 370 hp. Volvo Penta diesel inboard engine.
variability, without being so high a threshold that it could not be triggered by the modest noise sources (small boats) we were testing. Ultimately, policy-makers may set thresholds that are linked to biologically significant effects. In the absence of any policy guidance, we followed previous recommendations that reduce multivariate behavioural data into a binary (response/no-response) outcome for each trial, depending on: a change in one or some combination of behaviours according to expert opinion (Miller et al., 2014); exceeding some modest threshold (Williams et al., 2014c); or change in a biologically significant behaviour such as feeding (Moretti et al., 2014). Binning involved some loss of information, but facilitated the primary objective of the study, which was to be able to inform managers of the point at which 50% of fish were likely to respond to a given received noise level. In this case, a score of 0 or 1 (i.e. a change in none or one of the three behavioural metrics) was considered a non-response, and a score of 2 or 3 (i.e. a change in two or three of the three behavioural metrics) was considered a response. This allowed the data to be modelled as a generalised linear model (GLM) (R stats version 3.6.2) (Faraway, 2005) with a binomial outcome.

The probability of a behavioural change was modelled as a function of fish group, trial number, vessel used, audiogram-weighted broadband received level (dB SPL re: 1 µPa), unweighted broadband received level, or the change in received level between the control and treatment stages of each trial. All statistical analyses were conducted in R (version 3.2.3 (R Core Team, 2015)). We used AICc to select the model that had the most support from the data. Additional models were tested with narrower frequency bands, but several models failed to converge because they had nearly as many parameters as data.

3. Results

A total of 79 noise exposure trials were performed on herring and juvenile salmon schools (Table 1). On average, ambient noise (i.e. no vessels) was 105.2 dB and small, medium, and large vessel treatments increased ambient noise by 12.4 dB, 18.0 dB, and 41.4 dB, respectively (Table 3, Fig. 4). On average, fish were within sight of the camera for 61% of the time (SD 28%). During five trials, fish remained out of camera sight for the entire trial and these were removed from further analysis. The top two models (binomial GLMs with a probit link function) included the broadband (unweighted) received sound level with both genera combined, or with a genera interaction term (Table 4). The AIC values for the two models (77.21 and 78.17, respectively) were effectively tied (Δ < 2). The model with the genera interaction term was ultimately chosen, because it explained slightly more of the residual deviance when the genera interaction was included (0.23 vs 0.21, R package ‘modEvA’ version 2.0; Barbosa et al., 2013). The selected model was used to predict the dose-response relationship, including 95% confidence intervals, of both herring and salmon to the received sound pressure levels (dB re: 1 µPa) of boat noise across the range of received levels recorded in the study (Fig. 5). Results showed that 50% of the herring or salmon schools responded when sound levels reached above 123 dB or 140 dB, respectively, but that there is considerable variability around this relationship (Fig. 5). The binomial GLM with a probit link function allows the two genera to exhibit similar sigmoidal shapes, but allows differences in the scale parameter that governs steepness. As a result, the herring curve shows a characteristic sigmoidal shape, whereas the salmon curve is shallower—resulting in a 17 dB difference between the noise level most likely to trigger a response by 50% of the fish.

Recall that the binary response (yes/no) variable is a composite variable that contains information on school cohesion, orientation, and swimming speed (Table 2). The analysis was not conducted on the raw data, but rather on the response or lack of response of the school in each experimental trial. A typical response to boat noise involved increasing swimming speeds, forming tight schools, and diving, which are all consistent with predator avoidance.

4. Discussion

When exposed to boat noise, wild Pacific herring and juvenile pink and chum salmon schools showed stereotyped responses that are consistent with classic vigilance behaviours associated with anti-predator tactics (Magurran, 1990). During exposure trials (in the presence of boat noise) both fish groups spent more time in behaviours considered to be a response to predators. These composite response findings suggest that salmon and herring respond to boat noise as a non-lethal predator (Beale and Monaghan, 2004; Frid and Dill, 2002). Flight responses to predators, including perceived predators, are adaptive. Once a predator is detected, schooling behaviour decreases any one individual’s probability of being eaten (Pitcher, 1986). But repeated responses to predation risk can carry costs. If fish are repeatedly replacing foraging activities with vigilance and anti-predator behaviour, this can reduce their energetic intake and fitness. Simply living in a “landscape of fear” of predation risk can carry population-level consequences, even in the absence of actual predation (Lima and Dill, 1990).

In fact, fish exposed to boat noise are responding to perceived and actual predation risk. In addition to disrupting normal behaviour in response to anthropogenic disturbance, juvenile salmon and herring in the Salish Sea face a gauntlet of predators (Chasco et al., 2017).

Although both marine mammals and fish are capable of producing and detecting sounds, marine mammal predators and their prey have co-evolved in what has been termed an acoustic arms race (Twyack and Clark, 2000). If whales are better equipped to detect fish in a noisy environment than fish are at detecting predators, then the fishes’ anti-

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### Table 2

<table>
<thead>
<tr>
<th>Category</th>
<th>Response value</th>
<th>Behaviour</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>School cohesion</td>
<td>0</td>
<td>Loose school</td>
<td>Individuals form a loose group; swimming in all directions at different swim speeds</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Polarisated school</td>
<td>Individuals form a tight group; oriented in the same direction and swimming at approximately the same speed</td>
</tr>
<tr>
<td>Swimming speed</td>
<td>0</td>
<td>Slow swimming</td>
<td>Normal swim behaviour, no increase observed</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Fast movement/burst swimming</td>
<td>Increase of swim speeds of short duration</td>
</tr>
<tr>
<td>School orientation</td>
<td>0</td>
<td>Horizontal</td>
<td>Swimming at constant depth</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Vertical</td>
<td>Movement directed toward the water surface or net bottom (upward or downward)</td>
</tr>
</tbody>
</table>

### Table 3

Mean ± standard deviation of received level (RL) (dB re: 1 µPa) and the change in RL between control and vessel treatments.

<table>
<thead>
<tr>
<th>Vessel</th>
<th>Treatment</th>
<th>RL (dB re: 1 µPa)</th>
<th>SD</th>
<th>Δ RL (dB re: 1 µPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>Control</td>
<td>106.1</td>
<td>6.6</td>
<td>12.4</td>
</tr>
<tr>
<td>Small</td>
<td>Small</td>
<td>118.5</td>
<td>3.7</td>
<td></td>
</tr>
<tr>
<td>Medium</td>
<td>Control</td>
<td>107.2</td>
<td>6.7</td>
<td>18.0</td>
</tr>
<tr>
<td>Medium</td>
<td>Medium</td>
<td>125.2</td>
<td>6.3</td>
<td></td>
</tr>
<tr>
<td>Large</td>
<td>Control</td>
<td>102.4</td>
<td>8.5</td>
<td>41.4</td>
</tr>
<tr>
<td>Large</td>
<td>Large</td>
<td>143.7</td>
<td>13.4</td>
<td></td>
</tr>
</tbody>
</table>
predatory behaviour may prove to be maladaptive. That is to say, evasive tactics that were adaptive over evolutionary time may now be disadvantageous to fish when compared to pre-industrial acoustic conditions (i.e., providing whales with higher foraging success, or ability to capture larger schools of fish). This reliance on evolutionary responses that are maladaptive today is a hallmark of Ehrenfeld’s hypothetical “most endangered animal” (Ehrenfeld, 1970).

It is always a challenge to extrapolate from captive or semi-captive controlled experiments to wild scenarios, but several questions remain. Were fish responding to sound pressure level, particle motion, or something else? These are some of the questions that need to be answered to fully understand the impact of human activities on marine life.

Table 4

<table>
<thead>
<tr>
<th>Model</th>
<th>Formula</th>
<th>K</th>
<th>AICc</th>
<th>deltaAIC</th>
<th>Akaike weights</th>
<th>Cumulative Akaike weights</th>
<th>Log-likelihood</th>
<th>Deviance explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>glm.all2</td>
<td>Response ~ received level + genera</td>
<td>3</td>
<td>77.2109</td>
<td>0.0000</td>
<td>0.5875</td>
<td>0.5875</td>
<td>-35.4340</td>
<td>0.21</td>
</tr>
<tr>
<td>glm.all3</td>
<td>Response ~ received level * genera</td>
<td>4</td>
<td>78.1706</td>
<td>0.9597</td>
<td>0.3636</td>
<td>1.00</td>
<td>-34.7954</td>
<td>0.23</td>
</tr>
<tr>
<td>glm.all</td>
<td>Response ~ received level</td>
<td>2</td>
<td>82.1854</td>
<td>4.9745</td>
<td>0.0488</td>
<td>1.00</td>
<td>-39.0082</td>
<td>0.13</td>
</tr>
</tbody>
</table>

Fig. 4. Grouped bar plot of unweighted broadband received level of control (no vessels) and small, medium, and large vessel treatments. Lines are 95% confidence intervals.

Fig. 5. Predicted dose-response curves for herring (red line) and juvenile salmon (blue line). The lighter red and blue polygons represent the 95% confidence interval on the dose-response relationship for herring and salmon, respectively. The observed response values for both genera are shown as black points. The dotted line indicates the 50% response probability that occurs at a received sound pressure level (SPL dB re: 1 μPa). For herring, this unweighted received level is 123 dB, and for salmon, this level is 140 dB. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
wake or current produced by passing boats, bubbles generated by pro-
ellar cavitation, or shadows caused by the boat? This does not alter the
conclusions of the study, but it does affect whether a manager could look
up a ship track on an automatic identification system (AIS) and ship
source characteristics (Veirs et al., 2016) to predict a zone of influence
along the ship’s path (Erbe, 2002). How often do we think fish could be
exposed to received levels of 123–140 dB in the Salish Sea? With large
ships passing through Haro Strait, the channel connecting the Strait of
Juan de Fuca with the Strait of Georgia, every 20 min or so (Erbe et al.,
2012), it is reasonable to think that fish may be exposed to noise levels
high enough to cause disturbance throughout much of their time in the
region. As a non-exhaustive example, we use available data on source
characteristics of ships in the local fleet (Veirs et al., 2016; Wladichuk
et al., 2019) to illustrate scenarios that could result in received levels of
123 dB and 140 dB (Table 5). Empirical noise measurements off Lime
Kiln, San Juan Island in 2019 suggest that noise levels in Haro Strait
exceeded a 123 dB threshold for herring 46% of the time, but rarely
(<1%) exceed the 140 dB threshold needed to elicit behavioural re-
sponses of salmon (see Fig. 24 in JASCO Applied Sciences and SMRU
Consulting, 2020).

Initially, our aim was to include a broader range of fish species in our
experiment. In addition to the herring and juvenile salmon species, we
captured adult pink salmon and yellowtail, quillback and copper rock-
fish. Unfortunately, adult salmon sustained heavy injuries during
catching. These injuries were too severe for the animals to be used in the
experiments and they were therefore excluded from further analysis.
Rockfish are a demersal species, which meant that we had to be very
careful in bringing the animals up to the water’s surface after hooking
them. Both quillback and copper rockfish could not withstand the
pressure difference and died shortly after capture. Yellowtail turned out
to be more resilient and sustained no observable injuries. However, as
soon as the animals were set inside the net pen they disappeared be-
tween the folds and stayed on the bottom of the net, making it impos-
ible to follow their behaviour by camera. Even the Pacific herring and
juvenile salmon schools were captured on film only 30–88% and
34–86% of the time, respectively, over the trial durations. The length of
time the fish were out of view did not allow for individual focal follows
and subsequent behavioural analyses at the scale of the individual were
not tenable given the schooling behaviour of these species at the juvenile
stage. Future studies on rockfish would benefit from higher-quality
video cameras now available, and the use of passive acoustic moni-
toring to detect changes in vocal behaviour. Conducting the study dur-
ing a season with improved visibility or using acoustic telemetry would
allow for observations of demersal fish.

The shallower dose-response curve of salmon relative to herring has
some interesting implications. Either juvenile salmon appear more
tolerant than herring to noise, or salmon respond only when noise levels
reach some threshold (e.g., the received level of a dolphin or killer whale
echolocation click). The distinct curve shapes predicted for the two
genera can also be explained by the significant differences seen between
salmonid and clupeid auditory anatomy and sensitivity. Salmonids are
considered “hearing generalists” as the swim bladder is not believed to
be involved in sound detection (Popper and Hawkins, 2019). They are
therefore most sensitive to particle motion and have a much more
restricted frequency range of hearing and higher sensitivity thresholds
(Hawkins and Johnstone, 1978; Popper and Hawkins, 2019) when
compared to “hearing specialists” such as clupeids. Herring and other
clupeids are considered specialists because they possess anatomical
structures joining the swim bladder to the ear (Popper and Fay, 1999),
leading to an expanded hearing range (both in frequency and relative
sensitivity) aided by sound pressure detection capabilities (Enger, 1967;
Popper et al., 2003). Therefore, our results showing a 50% response
probability for received levels of 123 dB for herring and 140 dB for ju-
venile salmon are consistent with hearing data available for these fishes
(Nedwell et al., 2004; Matsuda, 2021). Herring use sound to commu-
nicate (Wilson et al., 2004), and their reliance on acoustic cues could
mean they are more sensitive to anthropogenic noise than salmon.

Received level is an important predictor describing the probability
that an animal will respond to noise, in part because this quantitative
framework lends itself to implementation through establishing safety
zones around noise-generating activities (Barlow and Gisiner, 2006).
However, received level is not the only factor determining an animal’s
responsiveness to sound. Behavioural context (Clark et al., 2009; Ellison
et al., 2012; Williams et al., 2006) may be a far more important deter-
minant than received level alone. A previous study showed startle re-
sponses of Pacific herring to qualitatively different sounds ranging from
98 to 120 dB (Schwarz and Greer, 1984). Nevertheless, simple experi-
ments like these offer a valuable starting point to gauge, however
roughly, the level of noise that fish may tolerate.

This study showed that ecologically, economically, and culturally
important schooling fish species exhibited changes in behaviours
consistent with an anti predator response such as increased swimming
speed, polarisation of schools, and diving, in response to relatively
modest levels of boat noise. As we move from net pens to more
ecologically relevant settings, we intend to assess whether ocean noise
may be disrupting predator-prey pathways. Ecologically, noise could
make herring and salmon more vulnerable to predators such as killer
whales, humpback whales, seals, and Pacific white-sided dolphins.
Rising ocean noise levels are likely to be picking evolutionary winners
and losers in the acoustic arms race between marine predators and their
prey. Larger-scale experiments will be needed to assess whether the anti-
predatory behaviour of fishes seen in this study are successful in the face
of real-world predation risk.

CRediT authorship contribution statement

Inge van der Knaap: Conceptualization, Methodology, Validation,
Formal analysis, Investigation, Data curation, Writing – original draft,
Writing – review & editing, Visualization, Project administration. Erin
Ashe: Conceptualization, Methodology, Validation, Investigation, Re-
sources, Writing – original draft, Writing – review & editing, Supervi-
sion, Project administration, Funding acquisition. Dave Hannay:
Conceptualization, Methodology, Software, Validation, Resources, Data
curation, Writing – original draft, Writing – review & editing, Supervi-
sion, Project administration, Funding acquisition. Asila Ghoul Berg-
man: Writing – original draft. Kimberly A. Nielsen: Formal analysis,
Data curation, Writing – original draft, Writing – review & editing,
Visualization. Catherine F. Lo: Formal analysis, Data curation, Writing –
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liams: Conceptualization, Methodology, Validation, Investigation, Re-
sources, Writing – original draft, Writing – review & editing, Supervi-
sion, Project administration, Funding acquisition.

Table 5
Illustrative examples of vessel traffic scenarios that could result in a received
level of 123 dB and 140 dB using published ship source characteristics, speeds,
and transmission loss data from the Salish Sea. Mean broadband source levels
(dB re: 1 μPa) are shown for container, tanker, tug, and fishing vessels (Veirs
et al., 2016) and pleasure craft vessels (Wladichuk et al., 2019).

<table>
<thead>
<tr>
<th>Vessel type</th>
<th>Mean source level (dB)</th>
<th>Mean speed (knots)</th>
<th>Range (m) resulting in 123 dB received level</th>
<th>Range (m) resulting in 140 dB received level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Container</td>
<td>178</td>
<td>19</td>
<td>905</td>
<td>110</td>
</tr>
<tr>
<td>Tanker</td>
<td>174</td>
<td>14</td>
<td>552</td>
<td>67</td>
</tr>
<tr>
<td>Tug</td>
<td>170</td>
<td>8</td>
<td>356</td>
<td>41</td>
</tr>
<tr>
<td>Fishing</td>
<td>164</td>
<td>0</td>
<td>160</td>
<td>20</td>
</tr>
<tr>
<td>Pleasure craft</td>
<td>166</td>
<td>11</td>
<td>205</td>
<td>25</td>
</tr>
</tbody>
</table>
Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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