Behavioural responses of wild Pacific salmon and herring to boat noise

Inge van der Knaap [a], Erin Ashe [b], Dave Hannay [c], Asila Ghoul Bergman [b], Kimberly A. Nielsen [b], Catherine F. Lo [b], Rob Williams [b,*]

[a] Leiden University, Institute of Biology, Sylvius, Sylviusweg 72, 2333 BE Leiden, Netherlands
[b] Oceans Initiative, 117 E Louisa St #135, Seattle, WA 98102, USA
[c] JASCO Applied Sciences, 2305-4464 Markham Street, Victoria, BC V8Z 7X8, Canada

ARTICLE INFO

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 (Vabø 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 (Nedwell et al., 2004; Popper and Hawkins, 2019). When particle motion reaches a fish's inner ear, the sensory cells in the inner ear move with the motion, while the far denser otolith structures move at a different amplitude and phase which results in a signal being sent to the brain (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 responses 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 transboundary 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 industrial 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 pallasii*) 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 Station (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 pallasii*). 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 pallasii*) 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 juvenile 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 pistonphone
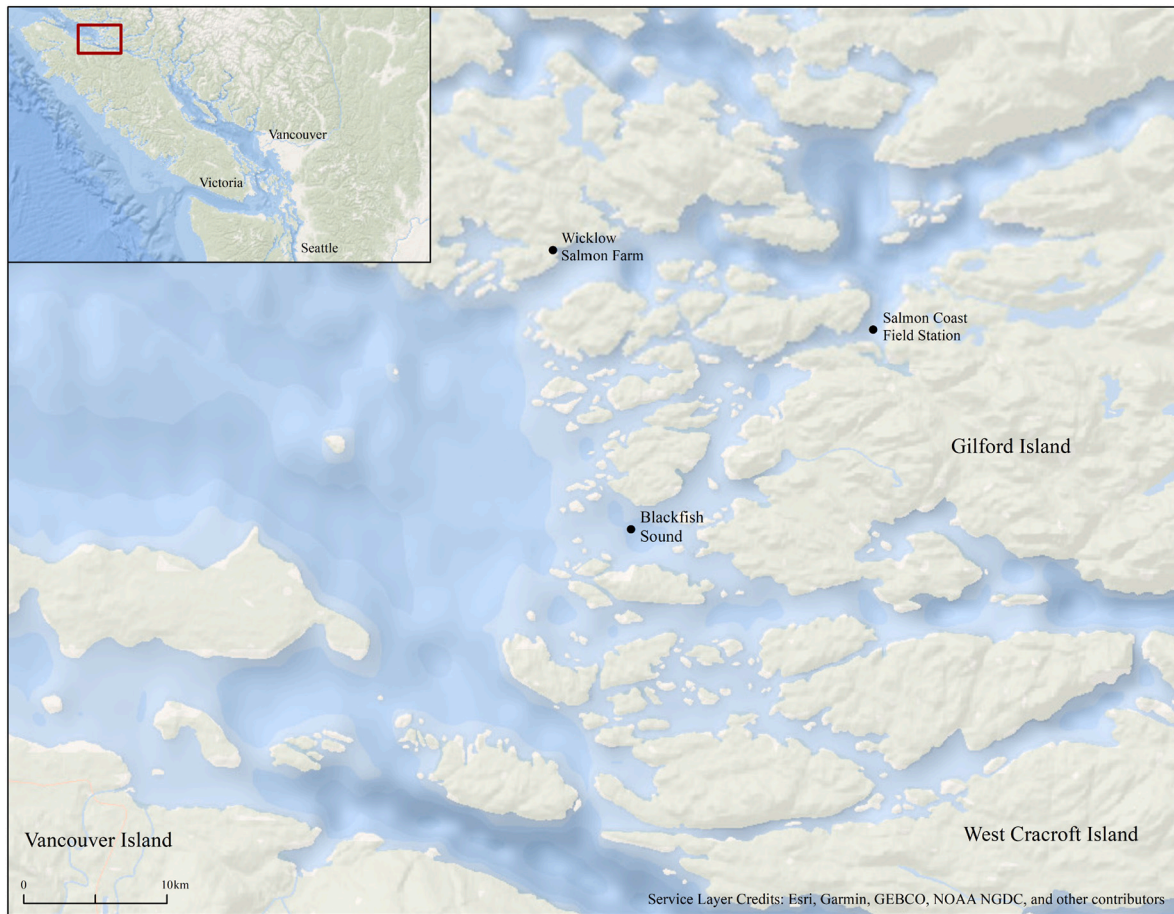
Fig. 1. Map of study and catch locations in the Broughton Archipelago, British Columbia, Canada.
Salmon Coast Field Station (50.7459° N, 126.4983° W) and associated open-net fish pens were located on Gilford Island.
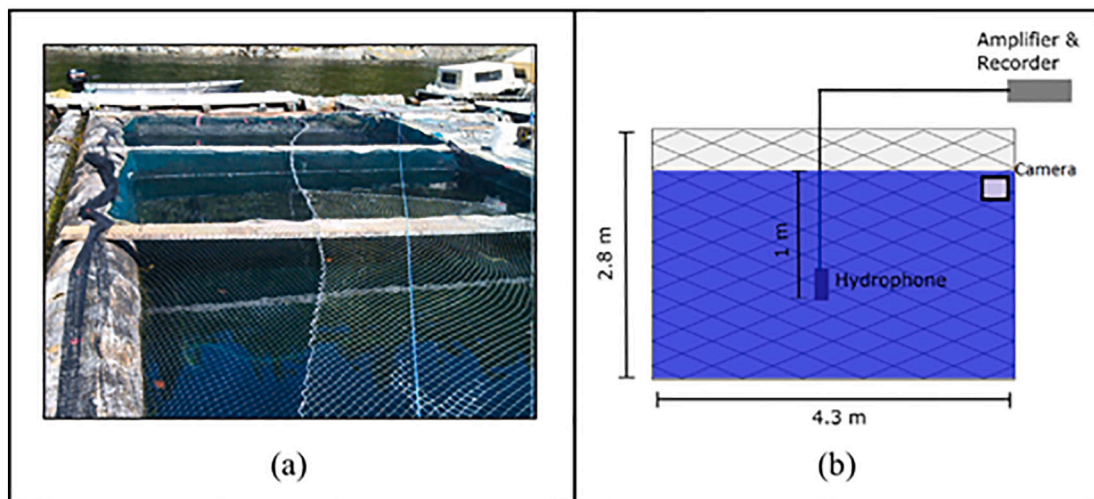
Fig. 2. (a) Two net pens suspended from the floating platform covered with anti-predator nets.
The docking station of the tender vessel, used to create the boat noise, is located at the far back next to the net pens. (b) Experimental setup; net size 4.3 m × 3.5 m × 2.8 m.

(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% over-lapped Hanning-windowed one second FFTs (fast Fourier trans-formation). The octave-band SPL was calculated by summing three adjacent decidecade bands. The weighted broadband (per genera) SPL

Table 1

The number of trials, catch site, and associated fish composition of each noise-fish exposure trial. Total lengths of the juvenile salmon and herring are estimations based on a sample of 10 individuals.

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

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 trail 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

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.

Table 2
Ethogram describing the behaviour exhibited by the Pacific herring and juvenile salmon schools. Each behaviour has a response value, which indicates the severity of the response; 0 for no response, 1 for response (defined as ≥50% of the school responding).

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

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 generalized 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

Table 3
Mean ± standard deviation of received level (RL) (dB re: 1 μPa) and the change in RL between control and vessel treatments.

Vessel	Treatment	RL (dB re: 1 μPa)	SD	Δ RL (dB re: 1 μPa)
Small	Control	106.1	6.6	12.4
Small	Small	118.5	3.7	
Medium	Control	107.2	6.7	18.0
Medium	Medium	125.2	6.3	
Large	Control	102.4	8.5	41.4
Large	Large	143.7	13.4	

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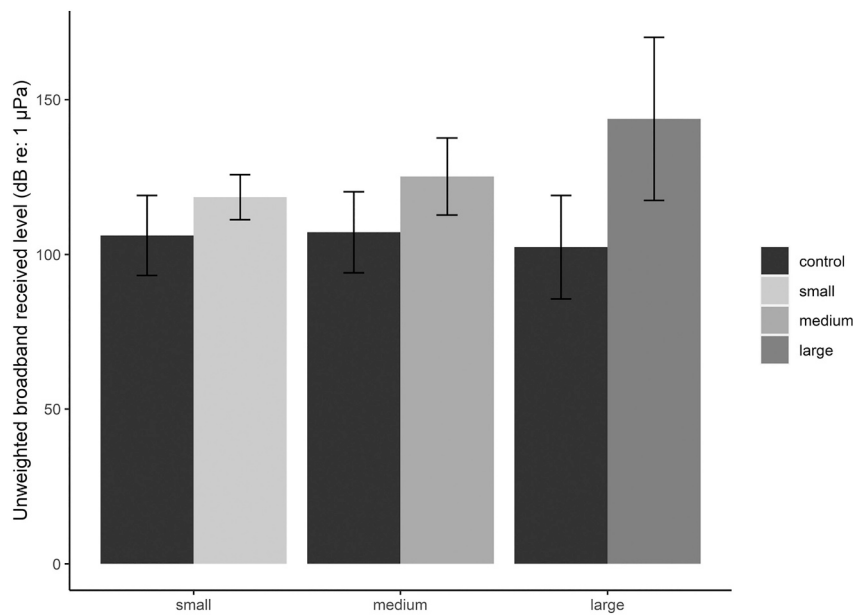
Fig. 4. Grouped bar plot of unweighted broadband received level of control (no vessels) and small, medium, and large vessel treatments. Lines are 95% confidence intervals.

Table 4
Model summaries. GLMs have a binary response with probit link functions. Model selection was performed by balancing minimised AICc score and maximised deviance explained. The final model is indicated in bold.

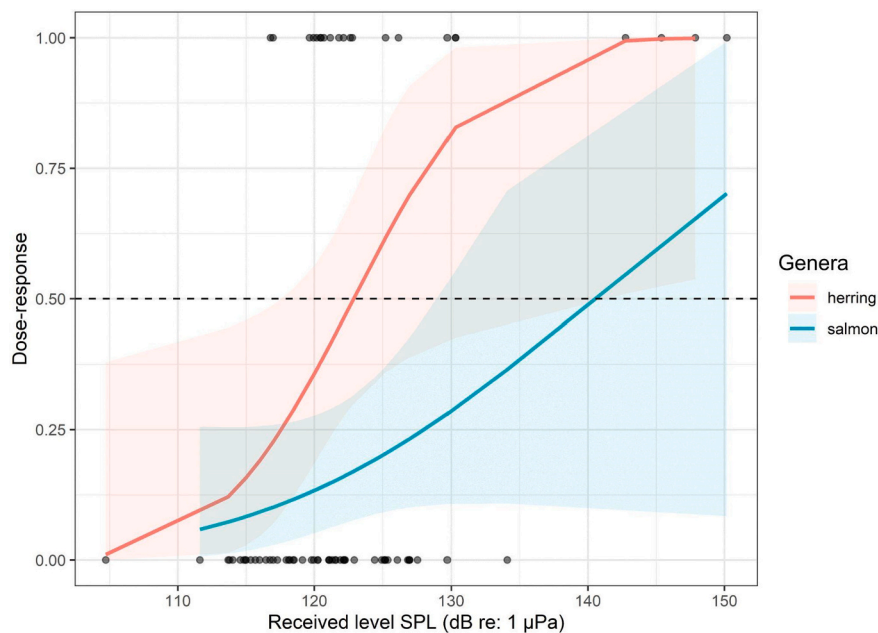| Model	Formula	K	AICc	deltaAIC	Akaike weights	Cumulative Akaike weights	Log-likelihood	Deviance explained
glm.all2	Response ~ received level + genera	3	77.2109	0.0000	0.5875	0.5875	−35.4340	0.21
glm.all3	**Response ~ received level * genera**	**4**	**78.1706**	**0.9597**	**0.3636**	**1.000**	**−34.7954**	**0.23**
glm.all	Response ~ received level	2	82.1854	4.9745	0.0488	1.000	−39.0082	0.13

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.)

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,

wake or current produced by passing boats, bubbles generated by propeller 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 responses 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 rockfish. 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 between the folds and stayed on the bottom of the net, making it impossible 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 monitoring to detect changes in vocal behaviour. Conducting the study during 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 juvenile salmon are consistent with hearing data available for these fishes (Nedwell et al., 2004; Matsuda, 2021). Herring use sound to communicate (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 determinant than received level alone. A previous study showed startle responses of Pacific herring to qualitatively different sounds ranging from 98 to 120 dB (Schwarz and Greer, 1984). Nevertheless, simple experiments 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, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Dave Hannay:** Conceptualization, Methodology, Software, Validation, Resources, Data curation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Asila Ghoul Bergman:** 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 – original draft, Writing – review & editing, Visualization. **Rob Williams:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – original draft, Writing – review & editing, Supervision, 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).

Vessel type	Mean source level (dB)	Mean speed (knots)	Range (m) resulting in 123 dB received level	Range (m) resulting in 140 dB received level
Container	178	19	905	110
Tanker	174	14	552	67
Tug	170	8	336	41
Fishing	164	9	160	20
Pleasure craft	166	11	205	25

Declaration of competing interest

Acknowledgments

References

Ashe, E., Wray, J., Picard, C.R., Williams, R., 2013. Abundance and survival of Pacific humpback whales in a proposed critical habitat area. PLoS ONE 8, e75228.

Barbosa, A.M., Real, R., Munoz, A.R., Brown, J.A., 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. Divers. Distrib. 19, 1333–1338. https://doi.org/10.1111/ddi.12100.

Barlow, J., Gisiner, R., 2006. Mitigating, monitoring and assessing the effects of anthropogenic sound on beaked whales. J. Cetacean Res. Manag. 7, 239–249.

Beale, C.M., Monaghan, P., 2004. Human disturbance: people as predation- free predators? J. Appl. Ecol. 41, 335–343.

Blair, H.B., Merchant, N.D., Friedlaender, A.S., Wiley, D.N., Parks, S.E., 2016. Evidence for ship noise impacts on humpback whale foraging behaviour. Biol. Lett. 12.

Blumstein, D.T., Evans, C.S., Daniel, J.C., 2006. JWatcher 1.0.. http://www.jwatcher.ucla.edu.

Chasco, B., Kaplan, I.C., Thomas, A., Acevedo-Gutiérrez, A., Noren, D., Ford, M.J., Hanson, M.B., Scordino, J., Jeffries, S., Pearson, S., Marshall, K.N., 2017. Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. Can. J. Fish. Aquat. Sci. 74 (8), 1173–1194.

Clark, C.W., Ellison, W.T., Southall, B.L., Hatch, L., Van Parijs, S.M., Frankel, A., Ponirakis, D., 2009. Acoustic masking in marine ecosystems: intuitions, analysis, and implication. Mar. Ecol. Prog. Ser. 395, 201–222.

Cox, K., Brennan, L.P., Gerwing, T.G., Dudas, S.E., Juanes, F., 2018. Sound the alarm: a meta-analysis on the effect of aquatic noise on fish behavior and physiology. https://doi.org/10.1111/gcb.14106.

De Robertis, A., Handegard, N.O., 2013. Fish avoidance of research vessels and the efficacy of noise-reduced vessels: a review. ICES J. Mar. Sci. 70, 34–45. https://doi.org/10.1093/ICESJMS/FSS155.

Duarte, C.M., Chapuis, L., Collin, S.P., Costa, D.P., Devassy, R.P., Eguiluz, V.M., Erbe, C., Gordon, T.A.C., Halpern, B.S., Harding, H.R., Havlik, M.N., Meekan, M., Merchant, N.D., Miksis-Olds, J.L., Parsons, M., Predragovic, M., Radford, A.N., Radford, C.A., Simpson, S.D., Slabbekoorn, H., Staaterman, E., Van Opzeeland, I.C., Winderen, J., Zhang, X., Juanes, F., 2021. The soundscape of the Anthropocene Ocean. Science 371. https://doi.org/10.1126/science.aba4658.

Ehrenfeld, D.W., 1970. Biological Conservation. Holt, Rinehart, and Winston. Inc, New York.

Ellison, W.T., Southall, B.L., Clark, C.W., Frankel, A.S., 2012. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. Conserv. Biol. 26 (1), 21–28.

Enger, P.S., 1967. Hearing in herring. In: Comparative Biochemistry and Physiology, 22. Pergamon Press, Great Britain, pp. 527–538. https://doi.org/10.1016/0010-406X(67)90615-9 (Issue 2. ISSN 0010-406X).

Erbe, C., 2002. Underwater noise of whale-watching boats and its effects on killer whales (Orcinus orca). Mar. Mamm. Sci. 18, 394–418.

Erbe, C., MacGillivray, A.O., Williams, R., 2012. Mapping cumulative noise from shipping to inform marine spatial planning. J. Acoust. Soc. Am. 132, EL 423–428.

Erbe, C., Williams, R., Sandilands, D., Ashe, E., 2014. Identifying modelled ship noise hotspots for marine mammals of Canada's Pacific region. PLOS ONE 9, e89820.

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., Dooling, R., 2016. Communication masking in marine mammals: a review and research strategy. Mar. Pollut. Bull. 103, 15–38.

Faraway, J.J., 2005. Extending the Linear Model With R: Generalized Linear, Mixed Effects And Nonparametric Regression Models. CRC Press.

Fisheries and Oceans Canada, 2013. In: <collab>Canada, F.a.O.</collab> (Ed.), Recovery Strategy for the North Pacific Humpback Whale (Megaptera novaeangliae) in Canada, Species at Risk Act Recovery Strategy Series, Ottawa, p. 67.

Ford, J.K.B., Ellis, G.M., Olesiuk, P.F., Balcomb, K.C., 2010. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? Biol. Lett. 6, 139–142.

Frid, A., Dill, L.M., 2002. Human-caused Disturbance Stimuli as a Form of Predation Risk.

Gaydos, J.K., Thixton, S., Donatuto, J., 2015. Evaluating threats in multinational marine ecosystems: a coast Salish first nations and tribal perspective. PLoS ONE 10, e0144861.

Handegard, N.O., Michalsen, K., Tjøstheim, D., 2003. Avoidance behaviour in cod (Gadus morhua) to a bottom-trawling vessel. Aquat. Living Resour. 16, 265–270.

Hawkins, A.D., Johnstone, A.D.F., 1978. The hearing of the Atlantic salmon, Salmo salar. J. Fish Biol. 13, 655–673.

Hawkins, A.D., Popper, A.N., 2017. A sound approach to assessing the impact of underwater noise on marine fishes and invertebrates. ICES J. Mar. Sci. 74, 635–651. https://doi.org/10.1093/ICESJMS/FSW205.

Hawkins, A.D., Roberts, L., Cheesman, S., 2014. Responses of free-living coastal pelagic fish to impulsive sounds. J. Acoust. Soc. Am. 135, 3101–3116.

Ivanova, S.V., Kessel, S.T., Espinoza, M., McLean, M.F., O'Neill, C., Landry, J., Hussey, N. E., Williams, R., Vagle, S., Fisk, A.T., 2020. Shipping alters the movement and behavior of Arctic cod (Boreogadus saida), a keystone fish in Arctic marine ecosystems. Ecol. Appl. 30 (3), e02050 https://doi.org/10.1002/eap.2050.

JASCO Applied Sciences and SMRU Consulting, 2020. ECHO Program 2019 Voluntary Vessel Slowdown Hydroacoustic Studies: Final Report. Document 01994, Version 1.0. Technical report by JASCO Applied Sciences and SMRU Consulting for Vancouver Fraser Port Authority.

Kaplan, M.B., Solomon, S., 2016. A coming boom in commercial shipping? The potential for rapid growth of noise from commercial ships by 2030. Mar. Policy 73, 119–121.

Knudsen, F.R., Schreck, C.B., Knapp, S.M., Enger, P.S., Sand, O., 1997. Infrasound produces flight and avoidance responses in Pacific juvenile salmonids. J. Fish Biol. 51, 824–829.

Lacy, R.C., Williams, R., Ashe, E., Balcomb III, K.C., Brent, L.J., Clark, C.W., Croft, D.P., Giles, D.A., MacDuffee, M., Paquet, P.C., 2017. Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. Sci. Rep. 7 (1), 1–12.

Lance, M.M., Chang, W., Jeffries, S.J., Pearson, S.F., Acevedo-Gutiérrez, A., 2012. Harbor seal diet in northern Puget Sound: implications for the recovery of depressed fish stocks. Mar. Ecol. Prog. Ser. 464, 257–271.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Lusseau, D., Bain, D.E., Williams, R., Smith, J.C., 2009. Vessel traffic disrupts the foraging behavior of southern resident killer whales Orcinus orca. Endanger. Species Res. 6, 211–221.

Magurran, A.E., 1990. The adaptive significance of schooling as an anti-predator defence in fish. JSTOR 51–66.

Matsuda, K., 2021. A comparison of avoidance to acoustic stimuli in fish with different auditory capabilities: juvenile chum salmon (Oncorhynchus keta) and common carp (Cyprinus carpio). J. Fish Biol. 98, 1459–1464.

Miller, P.J., Kvadsheim, P.H., Lam, F.-P.A., Wensveen, P.J., Antunes, R., Alves, A.C., Visser, F., Kleivane, L., Tyack, P.L., Sivle, L.D., 2012. The severity of behavioral changes observed during experimental exposures of killer (Orcinus orca), long-finned pilot (Globicephala melas), and sperm (Physeter macrocephalus) whales to naval sonar. Aquat. Mamm. 38, 362–401.

Miller, P.J.O., Antunes, R.N., Wensveen, P.J., Samarra, F.I.P., Alves, A.C., Tyack, P.L., Kvadsheim, P.H., Kleivane, L., Lam, F.-P.A., Ainslie, M.A., 2014. Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. J. Acoust. Soc. Am. 135, 975–993.

Mooers, A.O., Doak, D.F., Findlay, C.S., Green, D.M., Grouios, C., Manne, L.L., Rashvand, A., Rudd, M.A., Whitton, J., 2010. Science, policy, and species at risk in Canada. Bioscience 60, 843–849.

Moretti, D., Thomas, L., Marques, T., Harwood, J., Dilley, A., Neales, B., Shaffer, J., McCarthy, E., New, L., Jarvis, S., 2014. A risk function for behavioral disruption of Blainville's beaked whales (Mesoplodon densirostris) from mid-frequency active sonar. PloS one 9, e85064.

Nedwell, J.R., Edwards, B., Turnpenny, A.W.H., Gordon, J., 2004. Fish And Marine Mammal Audiograms: A Summary of Available Information (Subacoustech Report ref: 534R0214).

Pitcher, T.J., 1986. Functions of shoaling behaviour in teleosts. In: The Behaviour of Teleost Fishes. Springer, pp. 294–337.

Pitcher, T.J., Misund, O.A., Fernö, A., Totland, B., Melle, V., 1996. Adaptive behaviour of herring schools in the Norwegian Sea as revealed by high-resolution sonar. ICES J. Mar. Sci. 53, 449–452.

Popper, A.N., Fay, R.R., 1999. The auditory periphery in fishes. In: Fay, R.R., Popper, A. N. (Eds.), Comparative Hearing: Fish And Amphibians. Springer Handbook of Auditory Research, vol 11. Springer, New York, NY. https://doi.org/10.1007/978-1-4612-0533-3_3.

Popper, A.N., Hawkins, A.D., 2019. An overview of fish bioacoustics and the impacts of anthropogenic sounds on fishes. J. Fish Biol. 1–22 https://doi.org/10.1111/jfb.13948.

Popper, A.N., Fay, R.R., Platt, C., Sand, O., 2003. Sound detection mechanisms and capabilities of teleost fishes. In: Collin, S.P., Marshall, N.J. (Eds.), Sensory Processing in Aquatic Environments. Springer, New York, NY. https://doi.org/10.1007/978-0-387-22628-6_1.

Putland, R.L., Merchant, N.D., Farcas, A., Radford, C.A., 2018. Vessel noise cuts down communication space for vocalizing fish and marine mammals. Glob. Chang. Biol. https://doi.org/10.1111/gcb.13996.

R Core Team, 2015. R: A Language And Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Schwarz, A.L., Greer, G.L., 1984. Responses of Pacific herring, Clupea harengus pallasi, to some underwater sounds. Can. J. Fish. Aquat. Sci. 41, 1183–1192.

Simpson, S.D., Radford, A.N., Nedelec, S.L., Ferrari, M.C.O., Chivers, D.P., McCormick, M.I., Meekan, M.G., 2016. Anthropogenic noise increases fish mortality by predation. Nat. Commun. 7 (1), 1–7.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., Popper, A.N., 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. Trends Ecol. 25 (7), 419–427.

Soudijn, F.H., van Kooten, T., Slabbekoorn, H., de Roos, A.M., 2020. Population-level effects of acoustic disturbance in Atlantic cod: a size-structured analysis based on energy budgets. Proc. R. Soc. B Biol. Sci. https://doi.org/10.1098/rspb.2020.0490.

Southall, B., Bowles, A., Ellison, W., Finneran, J., Gentry, R., Greene, C., Kastak, D., Ketten, D., Miller, J., Nachtigall, P., 2007. Marine mammal noise exposure criteria: initial scientific recommendations. Aquat. Mamm. 33, 411–521.

Thomas, A.C., Nelson, B.W., Lance, M.M., Deagle, B.E., Trites, A.W., 2016. Harbour seals target juvenile salmon of conservation concern. Can. J. Fish. Aquat. Sci. 74 (6), 907–921.

Tyack, P.L., Clark, C.W., 2000. Communication and acoustic behavior of dolphins and whales. In: Springer Handbook of Auditory Research, 12, pp. 156–224.

Vabø, R., Olsen, K., Huse, I., 2002. The effect of vessel avoidance of wintering Norwegian spring spawning herring. Fish. Res. 58, 59–77.

van der Knaap, I., Reubens, J., Thomas, L., Ainslie, M.A., Winter, H.V., Hubert, J., Martin, B., Slabbekoorn, H., 2021. Effects of a seismic survey on movement of free-ranging Atlantic cod. Curr. Biol. 31 (7), 1555–1562. https://doi.org/10.1016/j.cub.2021.01.050.

Veirs, S., Veirs, V., Wood, J.D., 2016. Ship noise extends to frequencies used for echolocation by endangered killer whales. PeerJ 4, e1657.

Ward, E.J., Holmes, E.E., Balcomb, K.C., 2009. Quantifying the effects of prey abundance on killer whale reproduction. J. Appl. Ecol. 46, 632–640.

Watson, J.W., Hyder, K., Boyd, R., Thorpe, R., Weltersbach, M.S., Ferter, K., Cooke, S.J., Roy, S., Sibly, R.M., 2020. Assessing the sublethal impacts of anthropogenic stressors on fish: an energy-budget approach. Fish Fish. https://doi.org/10.1111/faf.12487.

Weilgart, L.S., 2018. The Impact of Ocean Noise Pollution on Fish And Invertebrate. OceanCare.

Williams, R., Lusseau, D., Hammond, P.S., 2006. Estimating relative energetic costs of human disturbance to killer whales (Orcinus orca). Biol. Conserv. 133, 301–311.

Williams, R., Clark, C.W., Ponirakis, D., Ashe, E., 2014a. Acoustic quality of critical habitats for three threatened whale populations. Anim. Conserv. 17, 174–185.

Williams, R., Ashe, E., Blight, L., Jasny, M., Nowlan, L., 2014b. Marine mammals and ocean noise: future directions and information needs with respect to science, policy and law in Canada. Mar. Pollut. Bull. 86, 29–38.

Williams, R., Erbe, C., Ashe, E., Beerman, A., Smith, J., 2014c. Severity of killer whale behavioral responses to ship noise: a dose–response study. Mar. Pollut. Bull. 79, 254–260.

Williams, R., Wright, A.J., Ashe, E., Blight, L.K., Bruintjes, R., Canessa, R., Clark, C.W., Cullis-Suzuki, S., Dakin, D.T., Erbe, C., 2015a. Impacts of anthropogenic noise on marine life: publication patterns, new discoveries, and future directions in research and management. Ocean Coast. Manag. 115, 17–24.

Williams, R., Erbe, C., Ashe, E., Clark, C.W., 2015b. Quiet(er) marine protected areas. Mar. Pollut. Bull. 100, 154–161.

Wilson, B., Batty, R.S., Dill, L.M., 2004. Pacific and Atlantic herring produce burst pulse sounds. Proc. R. Soc. B Biol. Sci. 271 (suppl_3), S95–S97. https://doi.org/10.1098/rsbl.2003.0107.

Wladichuk, J., Hannay, D.E., Macgillivray, A.O., Li, Z., Thornton, SJ., 2019. Systematic source level measurements of whale watching vessels and other small boats. J. Ocean Technol. 14, 110–126.