Fish avoidance of research vessels and the efficacy of noise-reduced vessels: a review

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It has long been recognized that fish can avoid approaching vessels and that these behaviours can bias fishery surveys. Underwater noise is considered the primary stimulus, and standards for research vessel noise have been established to minimize fish reactions. We review the literature on fish reactions to vessels appearing since these recommendations were made, focusing on acoustic surveys, and compare how fish react to noise-reduced and conventional vessels. Reactions to approaching vessels are variable and difficult to predict. However, the behaviour can bias acoustic abundance measurements, and should be considered when performing acoustic surveys. The few comparisons of acoustic abundance measurements from noise-reduced and conventional vessels are contradictory, but demonstrate that the sound pressure level, on which the noise-reduction criterion is based, is insufficient to explain how fish react to survey vessels. Further research is needed to identify the stimuli fish perceive from approaching vessels and the factors affecting whether fish perceiving these stimuli will react before further recommendations to reduce vessel-avoidance reactions can be made. In the interim, measurement of the biases introduced by fish avoidance reactions during surveys, and timing of surveys when fish are in a less reactive state, may reduce errors introduced by vessel avoidance.

Keywords: acoustic surveys, behaviour, noise-reduced vessel, ship, underwater radiated noise, vessel avoidance.

Introduction

The presence of a moving survey vessel can impact the behaviour of fish, which may in turn influence vessel-based observations of fish. For the purpose of this review, a vessel-induced fish reaction is defined as a change in behaviour in response to the approach of a moving survey vessel. Reactions to approaching vessels are of general concern as a range of species have been documented to react to vessels including large ships (Olsen, 1990; Mitson 1995), small boats (Xie et al., 2008), and underwater vehicles (Stoner et al., 2008). Although biases introduced by behavioural reactions to the vessel or the sampling gear certainly affect other sampling methods, such as trawling (Handegard and Tjøstheim, 2005; Kaartvedt et al., 2012), this review focuses primarily on large research vessels making acoustic measurements. The reason for focusing on acoustic surveys is that they can, in theory, make unobtrusive observations at ranges longer than the reaction distance of fish. However, the acoustic method is sensitive to changes in fish behaviour (Mitson, 1995; Fréon and Misund, 1999), and behavioural disturbances caused by the survey vessel can introduce a substantial bias in abundance estimates of commercially important stocks (Løland et al., 2007; Hjellvik et al., 2008).

Fish reactions to approaching vessels were reported by Olsen (1971), where vessel-induced fish behaviour adversely affected fishing success in Norwegian purse-seine fisheries for herring. Subsequent studies provided increasing evidence that fish can exhibit responses consistent with avoidance of vessels (e.g. Olsen et al., 1983a; Ona and Godø, 1990). The reactions, which can be dramatic, can occur at separation distances between the fish and the vessel of several hundred metres (Figure 1), which suggests that the stimulus propagates well ahead of the vessel. The most likely stimulus causing a reaction at long range is thought to be

underwater radiated noise, as vessels produce high levels of radiated noise in the frequency range of fish hearing that propagates far from the vessel (Engås *et al.*, 1995; Mitson, 1995). Fish are known to be attracted to or to avoid visual stimuli from vessels, but visual stimuli are unlikely to be the cause of reactions at long range, particularly during the day (Fréon and Misund, 1999).

In response to mounting concern about the influence of vessel-induced reactions of fish on abundance surveys, low-frequency (1–1000 Hz) limits for research vessel underwater radiated noise were formulated to minimize vessel avoidance in ICES cooperative research report 209 (Mitson, 1995), hereafter denoted 'CRR 209'. Recommendations were also made at frequencies >1000 Hz to maximize the performance of acoustic instruments (Mitson, 1995). Although noise-reduced vessels conforming to these recommendations are substantially quieter than their conventionally designed (i.e. not noise reduced) counterparts over a broad frequency range (Mitson and Knudsen, 2003), there has been no overarching evaluation of the efficacy of noise-quieting measures on reducing fish reactions to survey vessels.

The approach taken in this paper is to review the recent literature on avoidance of vessels by fish, and the discussion is intended to follow the approach of CRR 209. We focus primarily on the body of work appearing after CRR 209, as reviews of the work conducted prior to that publication are available elsewhere (Olsen, 1990; Aglen 1994; Mitson, 1995; Fréon and Misund, 1999), and emphasize studies that provide quantitative estimates of the impacts of fish reactions to survey vessels on acoustic abundance estimates. We first summarize what is known about how fish react to approaching vessels, and then examine how these behaviours may influence abundance estimation. We then review studies comparing noise-reduced and conventional research vessels to determine whether noise reduction (as proposed in CRR 209) minimizes avoidance reactions. Finally, we examine which stimuli produced by an approaching vessel may be causing fish to react, and consider the mechanisms that may influence whether fish that have detected the presence of a vessel will in fact react.
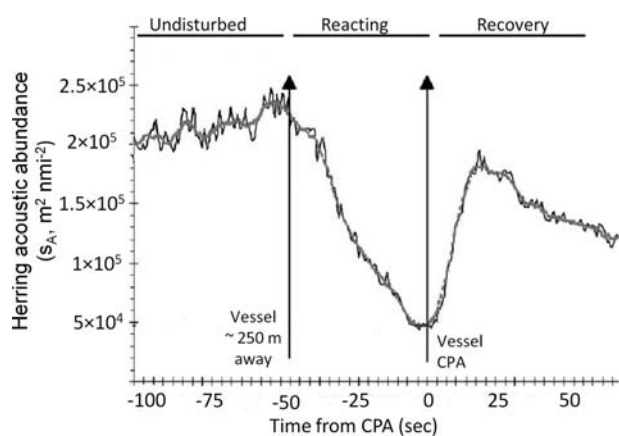

Figure 1. Mean backscatter of Atlantic herring measured by a stationary echosounder as the aggregation is approached and then passed by a research vessel (mean of 14 night-time vessel runs). A substantial reduction in backscatter is evident at the vessel's closest point of approach (CPA) to the echosounder; this is what a vessel-mounted echosounder would detect. Modified from Vabø *et al.* (2002) with permission from Elsevier.

What behavioural changes are triggered by approaching vessels?

When fish are observed to react to moving research vessels, the reaction is generally consistent with an avoidance response. Typical reactions are diving, horizontal movements, and altered tilt angle distributions (Mitson, 1995; Simmonds and MacLennan, 2005). Strong diving responses have been reported for overwintering Norwegian spring spawning herring (Vabø *et al.*, 2002; Ona *et al.*, 2007), and demersal gadoids responding to a trawling vessel in the Barents Sea (Handegard and Tjøstheim, 2005). Walleye pollock have been observed to exhibit diving responses, but vertical displacements are modest, typically <5 m (De Robertis *et al.*, 2008; De Robertis and Wilson 2010, 2011). Gerlotto *et al.* (2004) showed that anchovy and common sardine exhibited a moderate diving response (from the surface to the 5–10 m depth layer).

Lateral avoidance has been inferred from tracking schools with sonars (Misund *et al.*, 1996), counting the number of detected schools in the athwartship direction (Soria *et al.*, 1996), and tracking individual fish using split-beam echosounders (Handegard and Tjøstheim, 2005). Lateral avoidance appears to be situation specific; for example, Gerlotto *et al.* (2004) reported no difference in school counts as a function of athwartship distance, indicating that no lateral avoidance occurred, whereas other studies have reported elevated densities of fish schools from lateral-looking sonars compared with downwards-looking echosounders (e.g. Pitcher *et al.*, 1996; O'Driscoll and McClatchie, 1998) which indicates lateral avoidance. Ona *et al.* (2007) used an acoustic Doppler current profiler to estimate the mean horizontal movement of the fish layer during vessel approach and passage, but no clear signal was observed (R. Patel, pers. comm.).

Fish well ahead of approaching vessels have been documented to move towards the vessel path (e.g. Gerlotto and Freon, 1992; Misund and Aglen, 1992; Misund *et al.*, 1996; Soria *et al.*, 1996; Handegard and Tjøstheim, 2005). This pattern may be explained by the fish reacting to the sound field, as ships can produce a non-uniform 'butterfly' pattern of radiated noise in the lateral plane. This occurs at higher frequencies, with a minimum in front of the vessel and maxima to each side due to shading of propeller noise by the hull (Urick, 1983). Thus, observations of fish herding towards the vessel track ahead of the vessel could be explained by the fish moving away from areas of high radiated noise (Misund *et al.*, 1996). This suggests that radiated noise produced in the area of the propeller may be an important stimulus, at least at longer ranges (Misund *et al.*, 1996). However, fish to the side of a moving vessel have also been observed to move towards the vessel (Røstad *et al.*, 2006), which is inconsistent with movement away from noise radiating in the 'butterfly' pattern described above.

How do these behaviours affect acoustic measurements?

Diving behaviour changes the orientation of fish, which will impact acoustic measurements of abundance. At the frequencies used by echosounders, backscattering is highly dependent on the tilt angle of the fish relative to the acoustic beam (Foote, 1985; Hazen and Horne, 2004). Thus, large changes in backscatter can result from a general diving response (e.g. Ona *et al.*, 2007), polarization of an aggregation (fish orienting to each other, e.g. Gerlotto *et al.*, 2006), or any other behaviour altering fish tilt angle distributions. In many species, maximum backscattering

strength is observed with the head tilted slightly down as the swim-bladder has the highest projected area at this orientation (e.g. Nakken and Olsen, 1977; Foote, 1985; Hazen and Horne, 2004). Thus, backscatter has the potential to increase or decrease depending on the change in tilt angle at the time of measurement. In some cases, a small increase in backscatter strength is observed prior to vessel passage (e.g. figures 3–5 of Vabø *et al.*, 2002; see also Figure 1), which is consistent with an increase in target strength as fish alter their tilt angles as they begin to dive.

In addition to changing orientation, diving can have indirect effects on acoustic measurements. If the change in pressure experienced by the fish is substantial, the swimbladder will be compressed, which will change the target strength of the individuals. For example, if herring dive from 50 to 90 m depth, an 11% reduction in backscatter is expected (Ona, 2003). This will be the case not only for physostome fish such as herring, which cannot inflate their swimbladder underwater, but also for physoclist fish which are able to inflate their swimbladders via gas exchange from the blood, but cannot do so over the short time-scale of behavioural reactions (Edwards and Armstrong, 1984). If demersal fish dive towards the seabed where an echosounder is not capable of discriminating between the echo from the fish and the bottom (the acoustic blind zone, e.g. Ona and Mitson, 1996), an additional negative bias will occur.

Lateral avoidance is a concern for acoustic measurements as even modest displacements can impact the probability that fish will be detected within a narrow acoustic beam. The angular half power points (one-way) of a typical echosounder are $\sim 3.5°$, and fish at 100 m depth must only move ~ 6 m from the centre of the beam to be located outside of the nominal beam width. Given that fish can react well before the vessel arrives [~ 300– 500 m in the case of Vabø *et al.*, (2002) and De Robertis and Wilson (2010)], and that the beam widths are small compared with the distances reacting fish can travel before the vessel passes, the bias caused by even relatively modest horizontal displacements from the vessel is potentially very large.

Along with the strength of the reaction, the timing of the reaction pattern can have an important effect on acoustic measurements. If the reaction occurs primarily after the fish have been measured by the shipboard echosounder, the impact on the measurements will be minor. Although Ona *et al.* (2007) detected a strong reaction after the passage of the vessel-mounted transducer (Figure 2), the reaction did not lead to changes in herring backscatter at the time of vessel passage. However, in other cases, this herring stock has been observed to react well before vessel passage, with large decreases in backscatter observed at the time of vessel passage (Figure 2). This illustrates that measurements with a shipboard echosounder, which observes events only at the time of vessel passage, are sensitive to the timing of the fish reaction relative to vessel passage. Consequently, small variations in the timing of the reaction, e.g. due to small changes in the motivation to react or in sound propagation, can result in large variations in backscatter observed from a survey vessel.

How do fish reactions influence acoustic abundance estimates?

As reviewed above, the reactions of fish to approaching vessels have the potential to affect acoustic measurements of fish abundance. In some cases, this bias can be large (e.g. Figure 1). Vabø *et al.* (2002) report that for Atlantic herring in the upper 100 m at night, an average of 16% of the undisturbed acoustic abundance
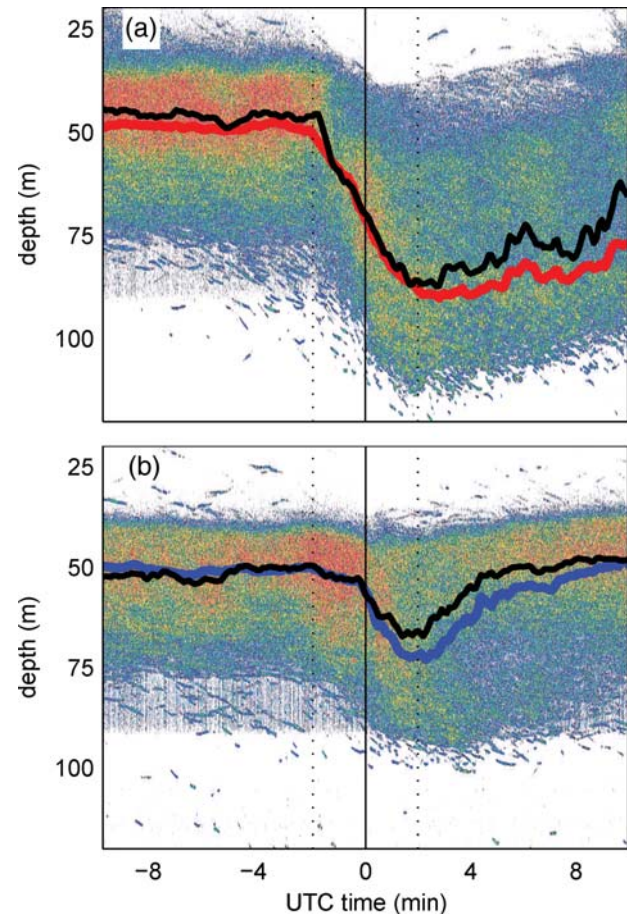

Figure 2. Echogram for a single passage of the (a) noise-reduced "G.O Sars" and (b) conventional "Johan Hjort" over a moored echosounder. The black line is the median depth distribution for this passage, and the blue and red lines are the means of the median depth distribution for all passages in the experiment for "Johan Hjort" and "G.O. Sars", respectively. From ~ 2 min before passage and to 2 min after passage a median diving response of ~ 20 m is observed for "Johan Hjort" and ~ 40 m for "G.O. Sars". Reproduced from Ona *et al.* (2007) with permission from the Acoustical Society of America.

was observed at vessel passage, with the bias decreasing strongly with depth. The impact of the biases introduced by fish reactions to survey vessels ultimately depends on how the abundance estimate is used. Acoustic surveys are generally used as an index tracking the trends in abundance in stock assessments (e.g. Dorn *et al.*, 2008). In this context, the concern is not the mean bias introduced by avoidance reactions, but the variable bias among years. However, if acoustic measurements are used as a measure of absolute abundance either in a stock assessment (Gjøsæter *et al.*, 2002) or as an input to an ecosystem model (Handegard *et al.*, 2012b), the mean value is of concern, and the model will be sensitive to both the mean bias and the variability among years.

Given the potential impacts of avoidance reactions on abundance estimates, experiments have been conducted to characterize impacts of vessel-induced fish reactions on acoustic abundance estimates relative to undisturbed states. Quantitative measurements have been published for herring, capelin, anchovy and sardine, walleye pollock, and Antarctic krill. These measurements

are summarized in Figure 3, and are discussed in turn below. Although the studies employ diverse methods, they all produce estimates of the ratio of the abundance observed by the vessel and the undisturbed abundance. Of the 26 cases with replicates examined, 7 cases exhibited a statistically significant negative bias and 2 exhibited a positive bias associated with vessel passage (see Supplementary material). The studies indicate that fish reactions can introduce substantial bias into acoustic abundance estimates compared with the undisturbed state, with the largest biases occurring in cases where the fish are more shallowly distributed. However, the results are highly variable, even within a species.

Studies conducted on Norwegian overwintering herring show that substantially lower backscatter is observed during vessel passage due to avoidance reactions, with large effects for shallow herring. One experiment for shallow (67 m) Norwegian overwintering herring differed from this general trend, but, as discussed above, these fish exhibited a strong reaction which started primarily after they had been measured by the shipboard echosounder (Figure 2). Experiments on the same stock of herring when spawning revealed little evidence of avoidance behaviour (Skaret *et al.*, 2005, 2006), and similar results are reported for North Sea herring in summer (Fernandes *et al.*, 2000a, b). Observations of walleye pollock in Alaska at depths of 50−200 m suggest that reductions in backscatter can be associated with vessel passage (De Robertis and Wilson, 2010, 2011; C. Wilson, unpublished data), although this response is fairly modest, with a 0−30% decrease in acoustic backscatter during vessel passage. A diving response was observed in all cases where a significant decrease in backscatter was observed at vessel passage.

Observations of small pelagic fish indicate that they can exhibit strong reactions to approaching vessels. Soria *et al.* (1996) studied
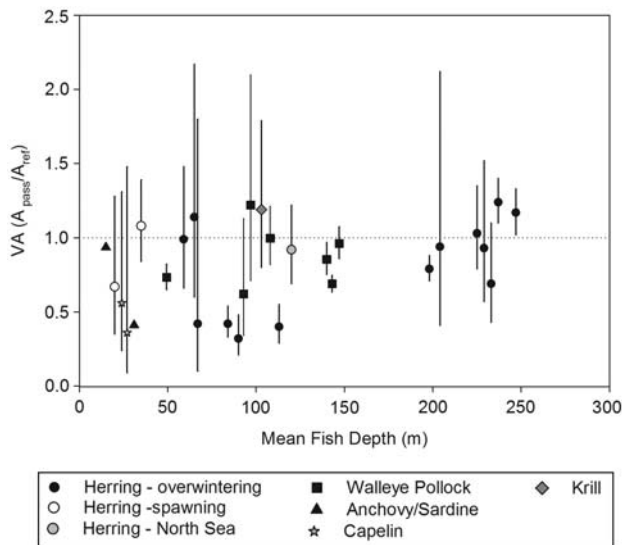
the fraction of anchovy and sardine schools available to a downwards-looking echosounder in the Mediterranean Sea with a multibeam sonar and estimated that only 41% of the schools detected by the sonar would be observed by an echosounder due to a lateral shift of fish schools away from the vessel. In contrast, similar sonar observations in Peru of different species of anchovy and sardine indicated that fish reactions were limited to 5−10 m from the vessel and had limited effects on echosounder measurements (Gerlotto *et al.*, 2004).

Experiments on shallowly distributed capelin (Jørgensen *et al.*, 2004) revealed highly variable changes in backscatter among repeat vessel passes and did not exhibit a statistically significant change in backscatter at the time of vessel passage. However, the authors do not discount the possibility of an avoidance response given that a trend towards less backscatter during passage was observed in one area and the experiment had low statistical power due to low replication and a patchy fish distribution (Jørgensen *et al.*, 2004). In the only published measurement of reactions of invertebrates to an acoustic survey vessel (Brierley *et al.*, 2003), equivalent backscatter from Antarctic krill was observed with a quiet autonomous vehicle assumed to be unobtrusive and the survey vessel.

One should be cautious when generalizing from this body of work as many of the measurements of the effects of fish reactions to vessels are not directly comparable. These observations are the consequences of responses to different vessels, which vary substantially in a variety of aspects including size (44−78 m), displacement (700−4100 t), and noise emission characteristics (see Supplementary material). In addition, the measurements were made under different hydrographic conditions, which will differ in their sound propagation characteristics and levels of background noise. Consequently, the stimuli received by the fish are not consistent (Popper and Hastings, 2009). Finally, as discussed below, environmental factors such as predation risk, time of day, and physiological state, all of which may affect the probability that fish will react to an approaching vessel, probably differ among experiments. Since the studies differ in multiple respects, it is prudent not to read too much into comparisons of specific reports.

Many of the observations of fish reactions to vessels have been made in situations that are amenable to measurement, but which may not be representative of the population or survey area. For example, observations of fish reactions to approaching vessels made from stationary echosounders can be very informative, but this approach is only practical in cases where fish distributions are relatively uniform and the perturbation due to vessel passage is larger than the background fluctuations in abundance (e.g. Figures 1 and 2). Alternatively, in areas where fish are sparsely distributed, individuals can be tracked to assess behavioural changes caused by an approaching vessel (e.g. Handegard and Tjøstheim, 2005). In many cases, fish do not exhibit such distributions (e.g. patchy schools), and if the reaction is different in these 'unobservable' situations, it is unclear whether the observations in Figure 3 will be representative. It has also been suggested that surface buoys may aggregate fish and bias measurements of avoidance (Røstad *et al.*, 2006). Finally, one must also keep the potential of publication bias in mind, as dramatic but not necessarily typical cases of avoidance may be more likely to lead to reports in the literature.

The quantitative body of work on reactions to approaching survey vessels indicates that avoidance behaviour can substantially impact acoustic measurement of abundance. For all taxa studied other than Antarctic krill, there appears to be some indication

Figure 3. Published comparisons of fish backscatter from undisturbed fish and during vessel passage. Symbols indicate the mean ratio of an abundance measurement made during vessel passage to the undisturbed abundance (VA). Each experiment is plotted against the mean depth of the animals in the experiment. The 95% confidence intervals for VA are given where available. See Supplementary material for data sources and methods.

that vessel-avoidance reactions reduce acoustic abundance estimates at the time of passage, with the strongest effects tending to occur when the animals are shallow (Figure 3). When reactions are observed, the reactions are often strongly depth dependent, with the shallower animals exhibiting a stronger response (e.g. Vabø et al., 2002; De Robertis and Wilson, 2010, 2011).

Do noise-reduced vessels reduce fish reactions?

With the construction of noise-reduced vessels conforming to the recommendations of CRR 209, direct comparisons of measurements from noise-reduced and conventional (i.e. not noise-reduced) vessels have been possible. Fernandes et al. (2000a, b) compared herring backscatter from an autonomous vehicle producing low radiated noise and a noise-reduced vessel, and demonstrated no avoidance of the noise-reduced vessel. The lack of avoidance was attributed to noise reduction of the survey vessel. However, it is ambiguous whether the absence of a reaction in this experiment can be attributed to the noise-reduced design of the vessel, or if the herring would not have responded to a louder conventional vessel.

Only a few studies have simultaneously measured fish avoidance of conventional and noise-reduced vessels. Ona et al. (2007) show that contrary to expectations, herring exhibited a much stronger reaction to a noise-reduced vessel. However, much of the reaction occurred after vessel passage (Figure 2), and measurements of herring backscatter made on the noise-reduced and conventional vessels were similar (Figure 4a) despite the difference in reaction. Our re-analysis of experiments 4–6 in Hjellvik et al. (2008), which were conducted with the same vessels as used by Ona et al. (2007), support the conclusion of this study as there were no consistent differences in herring backscatter recorded from the vessels (Figure 5a).

A series of comparisons of acoustic backscatter from walleye pollock from a noise-reduced and a conventional research vessel produced a different result: when differences were observed, fish reacted less to the noise-reduced vessel. The reaction differed among the situations studied. There was a strong diel pattern in the case of the Bering Sea only, with the noise-reduced vessel detecting ∼40% higher pollock backscatter from fish at <140 m, but only at night (Figure 4b). Although the pollock were ∼10 m deeper during the day than at night, the reaction in specific depth layers increased at night, and the difference in reaction is attributable primarily to stronger avoidance reactions at night rather the change in vertical distribution (De Robertis and Wilson, 2011). Experiments in three spawning areas revealed that in the two areas with shallower walleye pollock distributions (fish depths ∼100–200 and 200–300 m) the noise-reduced vessel detected ∼31% and ∼13% higher pollock biomass due to differences in fish avoidance behaviour (De Robertis et al., 2010; Figure 4b). Measurements with a free-drifting echosounder confirmed that pollock performed a stronger avoidance response to the conventional vessel, with the strongest response observed for shallower fish (Figure 5b; De Robertis and Wilson, 2010). In a third survey area where the fish were deeper (400–700 m), survey estimates from the vessels were equivalent (Figure 4b).

The pattern in vessel differences among sites cannot be explained by pollock depth alone: the fish in the eastern Bering Sea are the shallowest, but acoustic measurements from both vessels are equivalent during the day (De Robertis and Wilson, 2011; Figure 4b). However, at a site, the vessel discrepancy, if present, decreases with fish depth (De Robertis et al., 2010, De

Robertis and Wilson, 2011). This indicates that the magnitude of the difference in reaction to the vessels differed among sites, but at a given location the reaction was depth dependent, as might be expected from a stimulus propagating from a surface vessel. Together, these studies demonstrate that the noise-reduced vessel produced higher abundance estimates due to weaker reactions to the noise-reduced vessel. The pollock surveys described above have transitioned to the noise-reduced vessel, and the results of the vessel comparisons have been incorporated into the stock assessment (Dorn et al., 2008).

The comparisons of noise-reduced and conventional vessels to date have yielded equivocal results regarding the degree to which noise reduction of vessels minimizes vessel avoidance. Although the work on pollock demonstrates that a noise-reduced vessel is associated with decreased avoidance, the work on herring indicates that is not always the case. A response primarily to radiated noise as hypothesized in CRR 209 is consistent with the cases in which the noise-reduced vessel detected more pollock, but not the observation of herring performing a stronger or equivalent avoidance reaction to a noise-reduced vessel (Ona et al., 2007; Hjellvik et al., 2008). What is clear is that there are vessel effects on fish behaviour, and that this can bias abundance estimates and time-series. These vessel differences are probably not limited to comparisons of noise-reduced and conventional vessels, as conventionally designed vessels differ widely in many respects including radiated noise (e.g. Mitson and Knudsen, 2003).

Which stimuli are fish reacting to?

An important aspect of understanding vessel avoidance is identifying the nature of the stimuli that cause fish to react. In CRR 209, the primary stimulus causing reaction at distances >20 m was assumed to be the sound pressure level in the 1–1000 Hz frequency range averaged into 1/3 octave bands (Mitson, 1995). The recommendation linked perception to reaction assuming that a stimulus 30 dB above the hearing threshold would cause fish to react. However, prior to that time, other hypotheses had also been proposed. Olsen et al. (1983b) hypothesized different ways the fish could respond to vessel noise, including the perceived gradient of the sound pressure amplitude given a vessel speed and directivity pattern of the vessel noise, both including and excluding the fish's own movement. Other potential stimuli include visual cues, ship bow wave, particle acceleration, and stimulated bioluminescence, and some of these were summarized in the CRR 209. Wood (2011) considered the potential impact of narrowband tones in ship radiated noise and concluded that the logic in CRR 209 would provide similar estimates of the distance at which fish would be able to hear the vessel. Although the nature of the primary stimulus causing fish reactions remains poorly characterized, results from several recent experiments have shed some light on potential factors.

The available evidence demonstrates that fish reactions cannot be predicted solely on the basis of pressure-based radiated noise. As discussed above, Ona et al. (2007) show that herring exhibit a larger reaction when approached by a noise-reduced vessel than by a conventional vessel. This is inconsistent with the hypothesis that 1/3 octave band radiated noise as described in Mitson (1995) is the sole stimulus for vessel avoidance. In addition, the vessel comparison estimates of pollock vessel-avoidance behaviour cannot be explained by considering sound pressure level alone, as the fish in the eastern Bering Sea exhibit a diel response that cannot be explained by a changing pressure stimulus (De
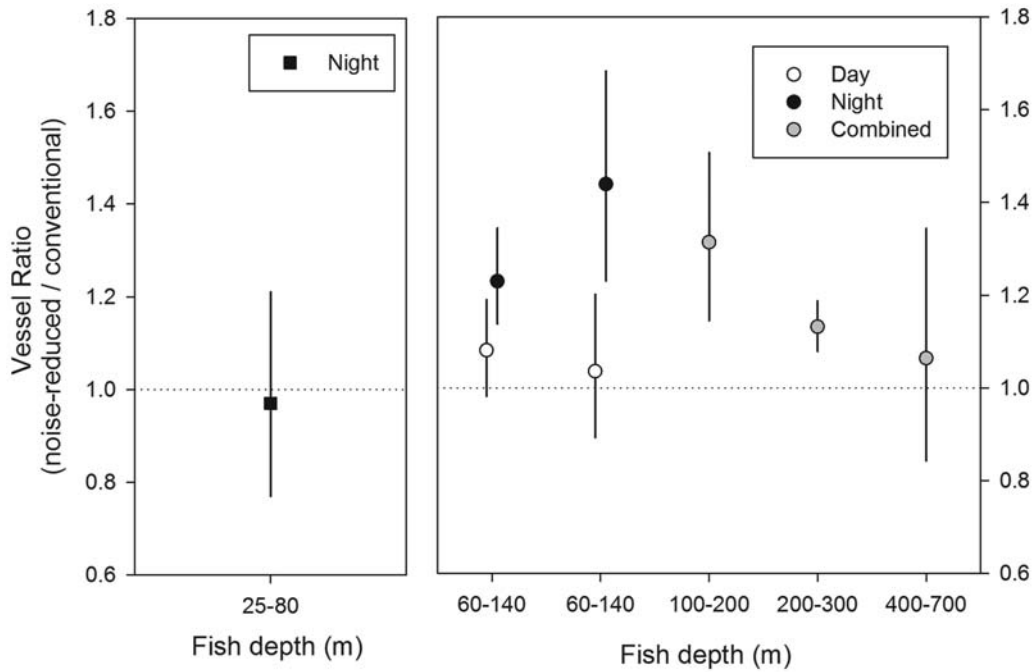
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Figure 4. Summary of experiments making direct comparisons of backscatter measurements made from noise-reduced and conventional research vessels. The vessel ratio ($\pm$ 95% confidence interval) describes the ratio in observed backscatter from the noise-reduced compared with the conventional vessel. (a) Measurements on overwintering herring by "Johan Hjort" and "G.O. Sars", and (b) measurements of walleye pollock in Alaska by "Oscar Dyson" and "Miller Freeman". Experiments with pollock depths of 60–140 m are during the feeding season in the eastern Bering Sea, while experiments on fish at depths of 100–200, 200–300, and 400–700 m are during the winter spawning season. Results for experiments of the summer measurements in the Bering Sea are given for night and day separately as diel differences in the vessel ratio are observed in these cases. See Supplementary material for data sources and methods.
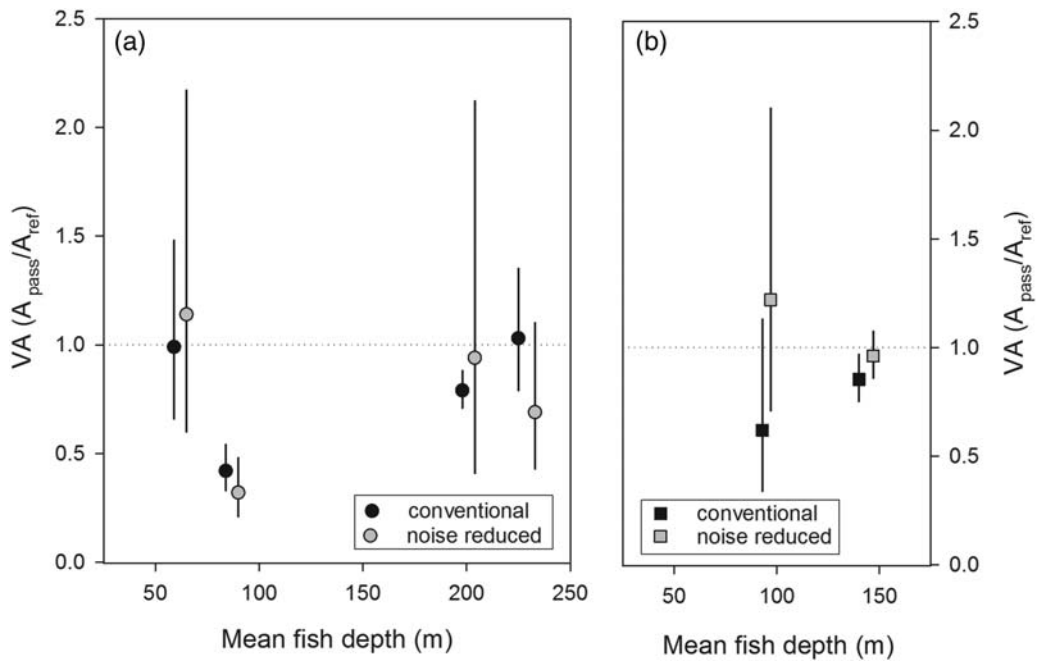

Figure 5. Published pairwise comparisons (under similar experimental conditions) of backscatter from undisturbed fish and fish passed by conventional and noise-reduced ships made with free-drifting or moored echosounders. Results for (a) Atlantic herring and (b) walleye pollock are shown separately. Symbols indicate mean depth of fish and mean ratio of an abundance measurement made during vessel passage to the undisturbed abundance (VA), where vertical bars are 95% confidence intervals and solid symbols and grey symbols denote conventional and noise-reduced vessels, respectively. See Supplementary material for data sources and methods.

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Robertis and Wilson, 2011). Handegard and Tjøstheim (2005) showed that the reaction of demersal gadoids to a trawling vessel was not stimulated by the gradual increase in sound pressure level of the approaching vessel. Prior to vessel passage, the reaction was associated with the sudden change in vessel noise caused by changes in propeller pitch when deploying the trawl, which is consistent with the gradient stimulus of Olsen et al. (1983b). After vessel passage, a strong reaction was initiated by the trawl warps (which vibrate primarily at 7 and 14 Hz) after vessel passage.

Fish exhibit strong reactions to low-frequency sound (e.g. Enger et al., 1993; Sonny et al., 2006), and low-frequency sources have been used to induce fish avoidance responses to improve fish passage at dams and power plant intakes (Sand et al., 2001; Sonny et al., 2006). Similar to the strong reaction of gadoids to trawl warps (Handegard and Tjøstheim, 2005), salmonids reacted strongly to low-frequency (5–10 Hz) sounds, but not to 100–150 Hz sounds, which are in the range of maximum pressure-based hearing sensitivity (Knudsen et al. 1992; Sand et al., 2001). In the acoustic far field, particle velocity and pressure are in phase, and the (time-averaged) intensity measuring the energy flow through a unit area can be described by pressure alone (Carey, 2006). This justifies the use of more easily measured sound pressure levels to estimate the stimuli perceived by fish from an approaching vessel. In the acoustic nearfield, however, the sound is not propagating as a simple plane wave. and particle velocity is no longer proportional to pressure. In addition, the source (in this case the ship) sets up hydrodynamic flows with particle motions stronger than those from the compressional sound wave that dominates the far field (Sand et al., 2008). This effect can be understood by assuming that water is incompressible and then imagining a body that increases in volume or changes in shape. The moving or vibrating boundary of the body will cause water movements, i.e. hydrodynamic flows. Ships exhibit low-frequency excitation of the hull, with strong tones caused by rotating machinery and oscillating propeller thrust at shaft or blade rate (typically in the range of 1 Hz to tens of Hertz; Urick, 1983; Ross, 1987; Wood, 2011), which will produce low-frequency particle motion.

The auditory system of fish is sensitive to particle motion at low frequency (Enger et al., 1993; Sand et al., 2001). Fish are highly sensitive to particle acceleration, and exhibit a flat frequency response at low frequency (i.e. 0.1–100 Hz; Enger et al., 1993; Sand et al., 2001). In CRR 209, the relevance of low-frequency sound for vessel avoidance was assessed by converting sensitivity to particle acceleration into units of pressure. This was accomplished by converting sensitivity to particle acceleration at 0.1 Hz to pressure sensitivity using the frequency-dependent ratio between pressure and particle acceleration (Enger et al., 1993). However, it is important to note that this relationship is only valid in the far field. In the nearfield, pressure cannot be used to estimate particle acceleration (see discussion above). Low-frequency radiation from ships follows a dipole radiation pattern (Arveseon and Vendittis, 2000), with the nearfield extending to a distance of λ/π where λ is the wavelength (Sand et al., 2008). Thus, for 10 Hz, the nearfield extends to 50 m and at 5 Hz to 100 m, which is well within the ranges relevant to fish avoidance, for example the experiment of Ona et al. (2007). Thus, the far-field assumption made in CRR 209 may have underestimated the relevance of the low-frequency particle acceleration stimulus produced in the nearfield of approaching vessels.

Sand et al. (2008) point out that in the experiment of Ona et al. (2007) the noise-reduced vessel was more than twice as large by displacement as the conventional vessel, and suggest that the noise-reduced vessel may have produced a stronger particle acceleration signal which may have contributed to the stronger reaction. Sand et al. (2008) suggest that particle motion produced by vessels should be measured directly (Sigray and Andersson, 2011) in the nearfield to investigate if particle motion is causing fish to react to vessels in ways that cannot be predicted on the basis of pressure measurements. Fish may also use the phase difference between pressure and particle velocity to detect range to a sound source (Schuijf and Hawkins, 1983), and it is possible that the perception of range rather than the magnitude of particle motion itself could be a stimulus causing reactions.

In some cases, properties of the sound such as the frequency content and how sudden the sounds are have been shown to be better predictors of fish behaviour than measures of energy (Doksæter et al., 2012). One way to interpret this is in the context of the information content. Low-frequency sounds may be alarming as they are indicative of close range predator approaches (Karlsen et al., 2004; Sand et al., 2008). More subtle differences may also be important: Doksæter et al. (2009) show that although herring did not respond to a towed (1–2 or 6–7 kHz) sonar source, there was a reaction to killer whale playback with frequency content and modulation similar to the sonar. Engås et al. (1995) found that herring and cod reacted more strongly to playbacks of vessel noise than smoothed, and thus more constant, versions of these signals projected at a similar level. The playback experiments of Schwartz and Greer (1984) on Pacific herring support these conclusions as responses were stronger to sounds that are of higher level, of lower frequency, and more irregular. Koslow et al. (1995) noted that demersal aggregations of orange roughy dispersed when a camera was lowered within ~130 m of the aggregations. The fish also responded to a small free-falling iron bar dropped from the vessel at a range of ~60 m. This indicates that the response cannot be attributed to the cable used to lower the camera alone, and serves as a caution that fish can respond to seemingly minor stimuli. Non-auditory stimuli should also not be discounted, as changes in light have been shown to modulate an avoidance response (Lévénez et al., 1990).

Animals can also respond indirectly to a threat by responding to other individuals (Treherne and Foster, 1981). Such collective behaviours can either amplify or inhibit the responses of individuals (Couzin, 2009). For example, fish schools can perform coordinated escape responses, with the decision to flee propagated by neighbours in a school, resulting in a 'wave of agitation' (Radakov, 1973; Gerlotto et al., 2006; Handegard et al., 2012a), which is consistent with the coordinated avoidance behaviour observed in dense concentrations of herring (e.g. Figures 1 and 2).

Thus, the specific stimuli causing fish to react to vessels remain unclear. Radiated noise is likely to be important, but there have been observations that suggest that characteristics of sound other than pressure levels should also be considered. A larger number of potential stimuli and their directionality need to be measured for the various vessels and considered in the context of how they are perceived by fish.

What is the link between perception and reaction?

The CRR 209 recommendation was constructed such that two species (cod and herring) will not encounter radiated noise

30 dB above their hearing threshold at distances >20 m. The "30 dB above hearing threshold" criterion for initiation of vessel avoidance reactions was used because it was considered that "Evidence is overwhelming that fish show a positive avoidance reaction to vessels when the radiated noise levels exceed their threshold of hearing by 30 dB or more." (Mitson, 1995, p. 18). It is worth noting that the CRR 209 does not address what happens below the 30 dB threshold. However, since CRR 209 aimed to reduce the avoidance reaction to <20 m (Mitson, 1995, p. 23), it is implicitly assumed that limiting pressure stimuli to <30 dB above the hearing threshold would mitigate the problem. This is a key point, as it means that fish will be able to perceive acoustic stimuli from compliant vessels at relatively long distances, but implies that fish will not react because the level of the stimulus is too low. A CRR 209 compliant vessel would produce radiated noise that is 30 dB above the hearing threshold of cod and herring at 20 m which is likely to be audible at a separation distance of several hundred metres (e.g. Mann *et al.*, 2009). Thus, the specifications in CRR 209, and other efforts to reduce vessel avoidance, rest heavily on understanding the link between perception and reaction, as it will be very difficult to build vessels that produce stimuli that cannot be perceived by fish at the ranges required for unbiased measurement of fish abundance. Given the mixed results of initial comparisons of noise-reduced and conventional research vessels, it is worth re-examining this key assumption since the mechanism behind the reaction is likely to be complex.

Although little is known about the factors influencing how fish react to approaching vessels, there is a rich literature describing how animals respond to predation risk. Many species have been shown to respond to human-induced disturbances as though these disturbances represent a predator (Frid and Dill, 2002). Vessel avoidance reactions are likely responses to a sensory stimulus perceived as a predatory threat. Thus, studies of decision-making under predation risk may provide a context that can be used to improve our understanding of how fish react when they encounter survey vessels. As described by Blumstein and Bouksilla (1996), the link between perception of a stimulus and an observed behaviour can be separated into three stages. (i) Detection: information about the risk is gained by reception of sensory information. (ii) Assessment: information is processed into an assessment of the perceived level of risk. (iii) Decision: this assessment of the sensory information is combined with information about the environment and the state of the animal to produce a decision that results in observable behaviour.

By definition, the ICES CRR 209 limits on radiated noise are well above the hearing threshold of many fish (Mitson, 1995), and noise reduction cannot be expected to eliminate detection of vessels at the ranges over which acoustic measurements are made. Thus, the response of fish to an approaching vessel depends largely on the assessment of the risk posed by the stimuli from the vessel and the factors influencing the decision to react. Framed in this context, the attempt to reduce fish avoidance of research vessels by not exceeding the hearing threshold of fish by 30 dB (Mitson, 1995) can be viewed as an effort to influence the risk assessed by a fish when it detects a vessel, in order to minimize the probability of reaction.

It is difficult to understand how fish assess the level of risk from an approaching vessel. Ships produce a wide range of potential stimuli (cf. the previous section), all of which may influence whether the stimuli received from the vessel are assessed as a

threat. One would expect that stimuli more consistent with those generated by a known predator, and those whose approach appears more direct, sudden, and intense, are likely to be perceived as more threatening (e.g. Doksæter *et al.*, 2009).

In many cases, animals engage in antipredator behaviour in response to stimuli in situations in which there is no actual predation threat (Frid and Dill, 2002). This suggests that animals are faced with making decisions with imperfect information, and may thus make decisions using 'rules of thumb' (e.g. Bouksilla and Blumstein, 1992). For example, stimuli such as low-frequency particle acceleration consistent with a large approaching object might be assessed as high risk, and this may trigger the decision to react as these stimuli are likely to be consistent with those from predators (Sand *et al.*, 2001). Pitcher *et al.* (1996) report that herring schools responded to an approaching research vessel in a similar fashion as to attacks by predators. As reviewed above, responses to vessels are stereotyped; for example, a diving reaction is almost always observed when fish are disturbed. In the case of fish exposed to a bottom trawl, this diving increases mortality by causing fish to dive into the net (e.g. Aglen, 1996; Handegard *et al.*, 2003; Hjellvik *et al.*, 2003; Handegard and Tjøstheim, 2005). The poor outcome of this decision is consistent with the concept that fish are making the decision to dive based on rules of thumb rather than perfect information.

When animals perceive uncertain stimuli consistent with predation risk, there is pressure to make decisions rapidly with imperfect information. Delaying a decision to escape in order to better assess risk is associated with a high cost: not reacting to a predator greatly increases mortality when predators are present. The consequences of failing to react are asymmetric: a poor decision leads to death, while the cost of a false alarm is the energetic expenditure and the time lost for other activities such as feeding and mating. Thus, erring on the side of caution when faced with imperfect information about predation risk is expected to be advantageous (Bouksilla and Blumstein, 1992). Strong avoidance responses are expected to be most common for intense but infrequent stimuli (Lima and Bednekoff, 1999), as there is much at risk, but comparatively little downside to a strong reaction. In many fish populations, short-range encounters with vessels will occur infrequently, and vessel approach is likely to elicit strong reactions. It is tempting to conjecture that in populations highly exploited by vessel-based fisheries, fishing mortality may select for stronger avoidance behaviour (e.g. Uusi-Heikkila *et al.*, 2008), while in cases of consistent exposure to vessels not associated with mortality (e.g. shipping lanes) the costs of reaction will increase (i.e. energetic and lost feeding opportunities), leading to habituation and fewer or weaker reactions.

Many factors related to environmental conditions or the internal state of the organism, such as physiological state, parasite load, or exposure to predators, have been shown to affect the decision-making of fish and other organisms under predation risk (reviewed in Lima and Dill, 1990; Millinski, 1990; Lima, 1998). For example, feeding history and recent encounters with predators are well known to affect antipredator behaviour: hungry organisms and those with little recent exposure to predators tend to be less risk averse. As described above, there is evidence that the degree to which a given species of fish reacts to vessels depends on the time and place of the experiment as well as the species and its depth distribution. The work on herring suggests that the physiological state may play a role: overwintering

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herring appear to be more reactive than feeding or pre-spawning herring (Fernandes *et al.*, 2000a, b; Skaret *et al.*, 2005; Hjellvik *et al.*, 2008). However, these studies may not be directly comparable as the hydrographic conditions probably were different and the ships used for the non-spawning measurements were smaller than the ones used in the overwintering studies, and may have produced a weaker stimulus. Walleye pollock appear to be more reactive during the winter than during daytime in the summer, but they exhibit a strong diel difference in summer (Figure 4). This is consistent with the idea that factors such as environmental conditions and the internal state of the fish (e.g. physiological state of the fish, recent exposure to predators, etc.) differ among areas which will affect how fish will react to the approach of a vessel.

Priorities for future work

When changing the vessel that is used to obtain an acoustic survey time series, one should expect differences in how fish will react, and, in some cases, different survey results. This will also be the case if the behaviour of a species relative to an individual vessel changes (e.g. due to a change in depth distribution), or if the stimuli produced by the vessel change over time. To maintain survey performance, it is advisable to use consistent vessels for a survey time-series, and conduct intercalibration experiments when the survey transitions to a new vessel (De Robertis and Wilson, 2011). In addition, it is important to monitor vessel noise or other stimuli over time to make sure that as many variables as possible are kept constant. Given the substantial investment in noise-reduced vessels by several nations, and the operation of noise-reduced vessels for more than a decade (Fernandes *et al.*, 2000a; Mitson and Knudsen, 2003), it is surprising that so few comparisons of noise-reduced and conventional research vessels have been conducted. Additional work in this area is likely to be informative and should be supported.

There are situations where using a single vessel for a particular survey is not possible. To minimize the impact on survey results, a classification system and design recommendations for research vessels could be developed based on the eliciting stimuli. As most survey results are used as relative indices of abundance, it may be sufficient to ensure that the characteristics of the vessels are as similar as possible to maintain interannual consistency and not to eliminate vessel avoidance as is required for absolute abundance estimates. However, a standard sufficient to either minimize or standardize vessel avoidance will be difficult to develop as long as the primary stimuli causing fish to react remain poorly understood. Controlled experiments, similar to those of Doksæter *et al.* (2012), where different aspects of the stimuli produced by vessels are studied, should be a focus of future research.

The link between perception and reaction remains a key unresolved issue, and the literature on predator avoidance may provide useful concepts to develop and test specific predictions that may explain some of the variability in how fish react to vessels. Fish will be able to hear even a noise-reduced vessel at a substantial distance (Mann *et al.*, 2009), and the resulting behaviour depends on the decision to react rather than whether the stimulus will be perceived. The trade-offs between predator avoidance and other activities such as feeding, mating, and habitat choice are well known, and this body of knowledge has produced a series of generalizations that, if applicable to vessel–fish encounters, may serve as a basis to better predict vessel avoidance.

There is, however, a discrepancy between our ability to predict fish reactions to vessels and the specific requirements of stock abundance surveys. At the current level of understanding, stimulus–response models are unlikely to produce predictions sufficiently accurate for correcting for vessel avoidance. They may, however, provide a basis for understanding the avoidance reaction to minimize the effect, by surveying the stock in favourable, non-responding situations (e.g. survey Bering Sea pollock during the day only). In many applications, this may be more effective than engineering controls such as vessel noise reduction.

For the relatively narrow goal of correcting abundance estimates, it may be more pragmatic to measure rather than predict how fish will react to vessels. Fish behaviour is difficult to measure, and, in many situations, the degree to which fish react to survey vessels is unknown. Although much has been learned from the use of stationary acoustic instruments such as moorings, buoys, and vessel comparisons (Olsen, 1990; Ona *et al.*, 2007; De Robertis and Wilson., 2011), these types of experiments are time consuming and resource intensive. The development of a reliable methodology to establish the degree of vessel avoidance routinely during a survey would constitute a major advance and would be likely to lead to many new insights. For example, by operating an instrumented autonomous vehicle (Fernandes *et al.*, 2000, Bingham *et al.*, 2012) together with the survey vessel, the observations can be compared and a correction factor can be obtained. Vessel-based systems, such as sonar measurements of avoidance (Soria *et al.*, 1996; Cutter and Demer, 2007; Patel and Ona, 2009), and Doppler measurements of fish reactions (Holliday, 1974; Demer *et al.*, 2000), are attractive as they will provide continuous measurements requiring little additional infrastructure. Refinement and application of these approaches would be valuable because they would potentially allow the contribution of vessel avoidance to survey error to be established in the context of an error budget (e.g. O'Driscoll, 2004; Løland *et al.*, 2007). Even if it is only possible to pursue this approach in a qualitative manner, it has merit because it could be used to identify situations where vessel avoidance is a major concern, and would allow evaluation of whether efforts to mitigate vessel avoidance (e.g. changes to vessel stimuli, survey timing, or design) have been successful.

Conclusions

Fish avoidance of approaching vessels has the potential to introduce substantial bias (cf. Figure 3) in acoustic measurements of fish abundance, and should be considered when designing and performing acoustic surveys. Estimates of vessel avoidance are highly variable, and it is clear that current understanding of how fish react to vessels is inadequate to predict the impact of these reactions on abundance measurements with much certainty (e.g. Hjellvik *et al.*, 2008).

The primary motivation of the recommendations proposed in CRR 209 (for noise below 1000 Hz) was to reduce or avoid the problem of vessel avoidance. Given the investment in noise-reduced research vessels, there have been surprisingly few studies testing if noise reduction of vessels in fact reduces fish avoidance reactions. The sparse literature on this topic shows no clear evidence that this has been achieved. Based on comparison of two pairs of vessels conducting replicate measurements on two species of fish, it appears that a noise-reduced vessel elicited weaker fish reactions in Alaskan pollock (De Robertis and Wilson, 2011), and stronger reactions in Norwegian herring (Ona *et al.*, 2007). Thus, one cannot be assured that noise

reduction of research vessels will universally minimize the problem of fish avoidance.

It is also evident that simple models of behaviour, for example those based on sound pressure level alone, cannot explain the observations of fish avoidance. The stronger response to a noise-reduced vessel (Ona *et al.*, 2007) and the diel and regional differences observed in walleye pollock (De Robertis and Wilson, 2011) could not have been predicted in advance based on current understanding of vessel-avoidance behaviour and the characteristics of the vessels involved. Ona *et al.* (2007) conclude that reducing vessel noise as defined in CRR 209 "may be necessary but is not a sufficient measure to eliminate vessel reactions", and the available evidence supports this view. In our opinion, further insight into the stimuli that fish perceive from approaching vessels, particularly low-frequency infrasound (cf. Sand *et al.*, 2008), and the factors that affect whether fish experiencing these stimuli will react (i.e. their motivation) must be gained before further recommendations can be made. With the state of current knowledge in mind, development of methods to monitor vessel avoidance continuously, and using these tools to correct acoustic abundance measurements for the biases introduced by avoidance and to surveys in situations when fish are known to be less reactive, are key areas where progress can be made in mitigating the problem.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript and consists of definition of the data sources and calculations made to produce Figures 3–5.

Acknowledgements

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Handling editor: David Demer

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