Modeling fish reaction to vessel noise, the significance of the reaction thresholds.

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Abstract

A simple model of fish reaction to vessel noise is made. The fish are assumed to swim directly away from the noise source. The main noise source is assumed to be the propeller. Parameters for endurance and swimming speed are obtained from the literature. The initiating stimuli in the model are the loudness and/or the change in loudness. A sensitivity analysis is used to check the importance of the parameters. The model is very sensitive to vessel noise and the fish reaction thresholds. This is an artefact of the dB-scale used in the loudness measure. However, if the fish interpret the dB-scale as almost linear, this may also explain some of the variability in vessel avoidance problems. A small change in the reaction thresholds, may lead to significant changes in the resulting behaviour. If the task is to model fish reaction to vessels, emphasis should be put on the reaction thresholds and noise field around the vessel, rather than swimming speeds and endurance. In general the parameters describing the physiology are less sensitive than the parameters describing the behaviour.

1 Introduction

Fish vessel avoidance have been reported by Olsen et al. (1983b); Ona (1988a), and may be a significant error source when assessing abundance of fish stocks (Olsen, 1990). If the fish reacts to the measuring platform before it is measured, the estimate may be biased. In order to achieve absolute abundance estimation, this problem must be minimized or corrected.

One solution may be to build a model to predict the avoidance reaction. This paper presents a simple model for fish avoidance. The model is used to determine the most important parameters when vessel avoidance occur. It may be seen as an iterative process. A simple model is made, and the results are evaluated. Which in turn will make the basis for a more refined model.

One of the objectives for the work is also the need for a framework for data on individual behaviour. These behaviour patters are obtained from recorded tracks of avoiding single fish using a split beam echo sounder on a free floating bouy. The velocity pattern obtained from the bouy is used to refine the velocity field in the model.

A more thorough discussion of the model in this paper is given in Handegard (2000).

2 Model

2.1 Vessel noise

It is possible for a fish to detect a vessel if the noise exceeds the ambient noise by 10dB at a given frequency (Buerkle, 1969). In the model, the noise field, LN, from the vessel is given as a function of the position relative to the vessel.

$$LN = LN(\vec{r}) \tag{1}$$

where \vec{r} is the vector from the propeller to the fish *i*'s position. The sources of vessel noise are connected to the propulsion system of the vessel, for example the main engine, gear and propeller. The propeller is a major noise source (Mitson, 1995).

2.1.1 The noise level from R/V Johan Hjort

The noise level measured from R/V Johan Hjort is used in the model, figure 1. The sound field and noise signature were measured by the Royal Norwegian Navy (Anon, 1990). The measurements were taken in Mastrafjorden, with a bottom mounted hydro-phone at 100m depth. The integrated sound levels over different frequency intervals are given in table 1. Measurements of the spatial distribution of the sound field of this particular vessel is given by Misund et al. (1996), figure 2.

Frequency Interval	KN (Source level)
$[10Hz \ 1kHz]$	$169, 6dB//1\mu Pa$
$[10Hz \ 500Hz]$	$168, 8dB//1\mu Pa$
$[10Hz \ 200Hz]$	$164, 1dB//1\mu Pa$
$[10Hz \ 100Hz]$	$159, 5dB//1\mu Pa$

Table 1: Total source level, KN, given in $dB//1\mu Pa$ for different frequency intervals. The noise detected by the fish depends on the frequency interval. The interval between 10Hz and 500Hz is used as a source level in the model, see section 2.2.

2.1.2 Modeling the noise field

A simplified model for the vessel noise is used. The main noise source is assumed to be a single point, the propeller, and the sonar equation, equation (2), is used to calculate the distribution of the noise. The source level is taken from table 1.

$$I = I_r \frac{10^{-\alpha r}}{r^2} b(\theta) \tag{2}$$

Where I is the intesity, I_r is the intensity on the acoustic axis @1m, r is the distance from the source, α is the coefficient of absorbsion and $b(\theta)$ is the directivity at an angle θ from the acoustic axis (Urick, 1975). The absorbsion is low ($\alpha = 0,06dB/km@1000Hz$, from Urick (1975)), and the directivity for these frequencies is also low (Mitson, 1995). The sonar equation in logarithmic form, equation (3), is used as a model for the noise field.

$$LN = KN - 20\log_{10}r\tag{3}$$

KN is the source level in $dB//\mu Pa@1m$, and r is the distance from the source. The change in noise perceived by the fish is given in equation (4).

$$\frac{dLN(\vec{x},t)}{dt} = \frac{\partial LN}{\partial t} + \frac{\partial LN}{\partial \vec{x}} \cdot \frac{\partial \vec{x}}{\partial t} = \frac{\partial LN}{\partial t} + \nabla LN \cdot \vec{v}_{fish}$$
(4)

 $\nabla LN \cdot v_{fish}$ represents the change in noise induced by the fish movement. For simplifications, $\nabla LN \cdot v_{fish}$ is set to zero. When the vessel is surveying at 11knots, the error introduced by this simplification is low. However, if the vessel is trawling at 3knots, this may introduce a significant error. Equation (5) is an approximation of dLN/dt, from equation (4).

$$\frac{\partial LN}{\partial t} = \frac{-20}{ln10} \frac{1}{|\vec{r}|^2} \vec{r} \cdot \frac{\partial \vec{r}}{\partial t}$$
(5)

where

$$\frac{\partial \vec{r}}{\partial t} = -\vec{v}_{vessel}$$

and \vec{r} is the vector from the vessel to the fish.



Figure 1: Noise signature for R/V Johan Hjort at 11knots. SPN is the spectral noise level. The unit is $[dB//1\mu Pa/\sqrt{Hz}@1m]$.

2.1.3 Ambient noise

Ambient noise is defined as sound independent of the observed system (Urick, 1975). The ambient noise in the ocean have increased due to an increase in human activities in the oceans. In some places, the ambient noise has increased more than 10dB (Ross, 1976). The ambient noise level corresponds with ship traffic, weather and depth (Urick, 1975), figure 3, and seasonal changes (Buerkle, 1977).

An approximation of the ambient noise can be achieved by integrating the the ambient noise under the broken line in figure 3. This gives an ambient noise level on $LN_{ambient} < 100 dB//1 \mu Pa$. If the vessel noise is approximately 10 dB above this level, the fish is able to detect the vessel (Mitson, 1995).



Figure 2: Spatial noise distribution for R/V Johan Hjort for different center frequencies and 1/1 octave bands. The center frequency is shown over each panel. The points in the 125kHz figure show the position of the measurements. From Misund et al. (1996).



Figure 3: Average ambient noise at deep water. In shallow water (d < 50m), the ambient noise is more dependent on ship traffic and biological noise. From Urick (1975).

2.2 Fish hearing

Depending on the species, fish have the ability to hear frequencies as high as 2000Hz (Pitcher, 1993). There is also evidence that fish may hear frequencies as low as 0.1Hz (Sand and Karlsen, 1986). Cod (Gadus morhua) detect frequencies up to approximately 500Hz, and are most sensitive to frequencies around 120Hz (Døving and Reimers, 1992). Since the hearing in cod is most sensitive between 10Hz and 500Hz, the measure of the total sound energy, LN, is integrated over this frequency band.

The ability off the fish to discriminate between frequencies is bad, and at the best 3%-10% (Døving and Reimers, 1992). Cod and Haddock (Melanogrammus aeglefinus) have the ability to discriminate signals that differ 1, 3dB in amplitude at 50Hz (Pitcher, 1993, page 150). Fish do have the ability to determine the direction of an acoustic signal (Schellart and de Munch, 1987; Hawkins and Sand, 1977). Experiments show that cod is able to discriminate signals both in the vertical- and transversal-plane (Buwalda et al., 1983).

Observations of the flee response induced by acoustic stimuli show that herring is able to detect the stimulus within 45° (Olsen, 1969; Olsen et al., 1983a; Sorokin, 1989). A directional response within 20° has been shown for reward conditioning of wrasse (Schuijf, 1974). Similar results have been shown for cod for both cardiac and reward conditioning (Chapman and Johnstone, 1974; Schuijf and Siemelink, 1974; Schuijf, 1975).

Engås et al. (1993) showed that cod of different size had different reactions to seismic shooting. Large fish swam out of the area, while smaller fish stayed. This may indicate that small fish are less sensistive to the direction of the signal than large fish, or that small fish have a higher reaction thresholds.

2.3 The model

2.3.1 The basic equations

Every fish, i, is represented by a set of differential equations. Equation (6) show the general equation for fish i. These equations make the framework of the model.

$$\frac{dX_i}{dt} = \vec{f}(t, \vec{X}_1, \vec{X}_2, \dots, \vec{X}_i, \dots, \vec{X}_n)$$
(6)

 \vec{X}_i contains the variables for each fish. The variables in this version of the model are position and energy level, equation (7).

$$\vec{X}_i = \begin{bmatrix} \vec{x}_i \\ e_i \end{bmatrix} \tag{7}$$

$$\frac{d}{dt}\vec{X}_i = \begin{bmatrix} \vec{v}_i \\ \dot{e}_i \end{bmatrix}$$
(8)

The swimming velocity, \vec{v}_i , is modelled in equation (10), and \dot{e}_i is modelled in equation (17). A simple euler forward integration scheme (Atkinson, 1988) is used to solve the system, equation (9).

$$\begin{bmatrix} \vec{X}_1 \\ \vec{X}_2 \\ \vdots \\ \vec{X}_n \end{bmatrix} (t + \Delta t) = \begin{bmatrix} \vec{X}_1 \\ \vec{X}_2 \\ \vdots \\ \vec{X}_n \end{bmatrix} (t) + \frac{d}{dt} \begin{bmatrix} \vec{X}_1 \\ \vec{X}_2 \\ \vdots \\ \vec{X}_n \end{bmatrix} (t) \cdot \Delta t + O(\Delta t^2)$$
(9)

To be able to solve the system, the swimming velocity and endurance for each single fish must be modelled. The modelled velocity, \vec{v}_i , for each fish is divided into swimming speed, $|\vec{v}_i|$, equation (11), and swimming direction, $\vec{e}_{v,i}$, equation (10).

$$\vec{v_i} = |\vec{v_i}| \cdot \vec{e_i} \tag{10}$$

2.3.2 Swimming speed, $|\vec{v}_i|$

The swimming speed is modelled as a function of the stimuli from the vessel, equation (11). In this case the stimuli are loudness, LN, and the rate of change in loudness, dLN/dt. The reaction is initiated when the stimulus exceeds a given threshold. When the fish is undisturbed, the swimming velocity is set to zero. The first reaction is an increase in swimming speed as a function of the level of the stimulus, and the second reaction is a typical flee response, figure 4.

$$|\vec{v_i}| = f(LN, dLN/dt, e_i) \tag{11}$$

The model uses both the absolute noise, LN, and the change rate in noise, dLN/dt, as stimuli for the response. One stimulus function is modelled for each stimulus, and these equations are weighted to get the resulting swimming speed, equation (12). The velocity fields corresponds to the graph in figure 4.

$$|\vec{v}_i| = k_i v_{i,1} + (1 - k_i) v_{i,2} \tag{12}$$

where $v_{i,1}$ is the modelled swimming speed with LN as the stimulus, k_i is the weight between the stimuli, and $v_{i,2}$ is the modelled swimming speed with dLN/dt as the stimulus. If the energy state for fish *i*, is low ($e_i < 0.01$), it will affect the swimming velocity:

$$e_i < 0.01 \implies |v_i| = 0$$



Figure 4: Assumed swimming speed as a function of the stimulus.

2.3.3 Swimming direction, $\vec{e}_{v,i}$

The simplest reaction pattern may be that the fish tries to minimize the magnitude of the stimulus. It has been shown for herring that schools herded in front of the vessel often swim in a zig-zagging pattern (Misund et al., 1996). The noise field are in reality slightly damped in front of the vessel, and this has been used to explain the zig-zagging swimming behaviour. It also indicates that the fish tries to minimize the stimulus to which it is exposed.

To minimize a stimulus, the fish will have to swim in the opposite direction of the gradient. With the simple noise field used in this model, the direction of ∇LN and $\nabla dLN/dt$ is given in equation (13) and (15) respectively. Equation (13) is derived from equation (3).

$$\nabla LN \parallel -\vec{r} \tag{13}$$

where \vec{r} is the vector from fish *i* to the vessel.

$$\frac{dLN(\vec{x},t)}{dt} = \frac{20}{ln(10)} \frac{1}{|\vec{r}|}^2 \left(r_1 \vec{r} \cdot \vec{v}_{vessel} - \vec{r} \cdot \vec{v}_{fish} \right)$$
(14)

where r_1 is the projection of \vec{r} along the vessel track. Minimization of equation (14) will give a swimming direction as shown in equation (15).

$$\vec{v} \parallel \vec{r} \tag{15}$$

If the fish moves away from the stimuli, the stimuli will be minimized.

The swimming direction of the "minimization of the stimuli" is modelled as shown in equation (16).

$$\vec{e}_{m,i} = \frac{\vec{r}}{|\vec{r}|} \tag{16}$$

2.3.4 Endurance

The endurance for each individual is modelled. Endurance, E_i , is defined as the time the fish can sustain a given swimming speed. If the fish swimming speed exceed v_{ms} , the fish will use anaerob metabolism and eventually be exhausted.

An energy state variable is introduced, e_i . Fatigue occurs when e_i is zero. The change in e_i is given in equation (17), and e_i is introduced as a variable in the model.

$$de/dt = \begin{cases} 0 & , v < v_{ms} \\ -\frac{1}{E_p(l,v)} & , v_{ms} < v \le v_{mp} \\ -\frac{1}{E_b(v)} & , v_{mp} < v \le v_{mb} \end{cases}$$
(17)

After exhaustion, the fish will use some time to recover. This recover time will vary between different species. It will take 8 hours for sockeye salmon to recover 63% of the initial state (Brett, 1964). The time scale of the restitution is different for the vessel passage, and will only be important when the fish is exposed to several passings within the restitution time. The restitution is therefore not implemented in the model.

2.4 Parameters

The parameters used in the model are listed in table 3.

2.4.1 Swimming speed parameters

Data on swimming speeds have been obtained from the literature. Large variances between individuals of the same size and species have been reported (Beamish, 1966). Individual differences may be as high as 24% (Bainbridge, 1960; Brett, 1967). Different methods have been used to measure swimming speed, and the experimental setup may differ considerably from the field situation.

Classification of different swimming speeds as defined by Hoar and Randall (1969) was used:

• Sustained swimming, v_{ms} .

Defined as the swimming speed the fish is able to keep for at least 200min without exhaustion. v_{ms} is defined as the maximum sustained swimming speed.

• Prolonged swimming, v_{mp} .

Defined as the swimming speed the fish is able to keep for 20s to 200min without fatigue. v_{mp} is defined as the maximum prolonged swimming speed.

• Burst swimming, v_{mb} .

Defined as the swimming speed the fish is able to keep for 20s. v_{mb} is defined as the maximum burst swimming speed.

Swimming speed data for saithe (Pollachius virens) is well documented as a function of size (He and Wardle, 1988). The experiments for cod lack this size dependency. The size dependency data for saithe is used combined with the temperature dependency data for cod, figure 5 and figure 6. For burst swimming there are no data for cod and the data for saithe is used "as is", figure 7. All swimming speeds are given in body length per second, [bl/s].

2.4.2 Endurance parameters

Endurance has been investigated for saithe (He and Wardle, 1988). Since data for cod are not available, the data for saithe are used, equation 18.

Table 2: Endurance for saithe at prolonged swimming speed (He and Wardle, 1988)

Length (l) $[cm]$	Temp	a	b	Endurance [min]
25	15	-1,17	$5,\!95$	2,0
35	15	-1,36	$6,\!16$	$_{3,0}$
43	15	-1,52	$5,\!91$	$1,\!6$
50	15	$-1,\!63$	$5,\!60$	$1,\!6$

$$log E_p(l, v) = a(l)v + b(l) \text{ when } v_{ms} < v < v_{mp}$$

$$\tag{18}$$

A linear fit of the data in table 2 is used to find a(l) and b(l) in equation (19) and equation (20).

$$a(l) = 0,71 - 0.019 \cdot l \tag{19}$$



Figure 5: Maximal sustained swimming speeds for different fish size. The size dependence for saithe is used in the curves for cod. Data from Saithe is from He and Wardle (1988), and data for cod is from Beamish (1966)



Figure 6: Maximum prolonged swimming speed for different species. The size dependence for saithe is used in the curves for cod. Data from Saithe is from He and Wardle (1988), and data for cod is from Beamish (1966)



Figure 7: v_{mb} for different sizes. Data for saithe from He and Wardle (1988). The temperature has less influence on the burst swimming speed (Blaxter, 1969). v_{mb} is simplified to only be dependent on the fish size. The data for saithe is used as an approximation for cod.

$$b(l) = 6, 5 - 0,014 \cdot l \tag{20}$$

Equation (21) gives the endurance for burst swimming.

$$log E_b(v) = cv + d, \, v > v_{mp} \tag{21}$$

Data for c and d for 35cm cod is taken from Holmstrøm (1993). This is used for all individuals in the model.

$$log E_b = -0,37v + 1,7\tag{22}$$

2.4.3 Parameters in the velocity field

 γ_i govern to what stimuli the fish will react, LN or dLN/dt. There are indications that the fish react to the change rate in the stimulus (Olsen et al., 1983b). The parameter is set to 0.5. The initial velocity, v_0 , is set to 1bl/s.

2.4.4 Reaction thresholds

There is no well documented work on the reactions thresholds, but there have been reported fish reaction to vessel with trawl 200m in front of the vessel (Ona, 1988a), the reaction without trawl was weaker.

The fish is assumed to react somewhere between 150m and 70m before propeller passage, and a flee response is assumed to occur between 30m and 60m before propeller passage. The mean in dB between these distances is used. The reaction thresholds for the change rate in the loudness, dLN/dt, does also depend on depth, position athwarthship and vessel velocity. These reaction thresholds are derived with a vessel speed of 11knots, and for a fish at 40m depth. With the source noise level from R/V Johan Hjort, table 1, this corresponds to the reaction thresholds given in table 3.

2.5 Sensitivity

The model is based on parameters which must be seen as rather coarse approximations. The most sensitive parameters in the model will represent the most important factors in the model. This could, with the limitations of the model, give an indication of what the governing factors in vessel avoidance are, or at least pinpoint important parameters for modeling fish behaviour in relation to vessels. The influence of the errors in the parameters will also be quantified.

A sensitivity analysis is carried out quantify the importance of the parameters. A common measure of the sensitivity is the ratio between the relative change in the result, $\Delta X/X$, and the relative change in the parameter, $\Delta p/p$ (Jørgensen, 1986). If the response is non linear, equation

Parameter	Value	Description
l_i	0.35m	Fish length
$v_{0,i}$	1m/s	Initial swimming speed
$v_{ms,i}$	Figure (5)	Max. sustained swimming speed
$v_{mp,i}$	Figure (6)	Max. prolonged swimming speed
$v_{mb,i}$	Figure (7)	Max. burst speed
LN _{reaction}	$128,7dB//1\mu Pa$	Reaction threshold (LN)
LN_{burst}	$136 dB//1 \mu Pa$	Flee reaction threshold (LN)
$\partial LN_{reak}/\partial t$	$0,376 dB//1 \mu Pa/s$	Reaction threshold (dLN/dt)
$\partial LN_{burst}/\partial t$	$0,599 dB//1 \mu Pa/s$	Flee reaction threshold (dLN/dt)
γ_i	0.5	Stimuli factor for fish i
a_i, b_i	Equation $(19,20)$	Endurance parameters
c_i, d_i	Holmstrøm (1993)	Endurance parameters
$E_{p,i}$	Equation (18)	Endurance, prolonged swimming
$E_{b,i}$	Equation (21)	Endurance, burst swimming
Т	6°	Temperature
v_{vessel}	11knots	Vessel speed
KN	$168, 8dB//1\mu Pa$	Vessel noise source level

Table 3: Parameters used in the model

(23) will give a measure of the sensitivity, $S_{p_n}^2$, as a function of the relative perturbation, n, in parameter p.

$$S_{p_n}^2 = \frac{\Delta X_{p_n}/X}{\Delta p/p} = \frac{X - X'_{p_n}/X}{(p_n - p_{baseline})/p_{baseline}}$$
(23)

where X is the model state before parameter p is perturbated, and X' is the state after parameter p is perturbated.

X is the model state used as a measure of the change caused by the perturbation of the parameters. The model state is in reality a vector (the fish position). In order to use this method, the model state must be converted from a vector to a scalar. The position of fish *i* is given in \vec{x}_i , and the position of fish *i* in the perturbed system is given in \vec{x}'_i . Equation (24) gives a scalar measure of the deviation. A relative measure is given in equation (25).

$$\Delta X_i = |\vec{x}_i - \vec{x}_i'| \tag{24}$$

$$\frac{\Delta X_{p_n,i}}{X_i^1} = \frac{|\vec{x}_i - \vec{x}'_{p_n,i}|}{|\vec{x}_i - \vec{x}_{i0}|} \tag{25}$$

where \vec{x}_{i0} is the starting position for fish *i*.

The sensitivity study must be carried out for several individuals, as the result depends on the initial spatial position. Fish with initial positions between -50m and 50m in x- and y-direction, and between -20m and -60m in depth is chosen. 5 individuals in x- and y-direction, and 3

individuals in the z-direction; alltogether 75 individuals are used in the analysis. The sensitivities for all individuals are then averaged, equation (26).

$$\frac{\Delta X_{p_n}}{X} = \frac{1}{75} \sum_{i=1}^{75} \frac{\Delta X_{p_n,i}}{X_i^{1,2}}$$
(26)

The sensitivity for each parameter can be further simplified as defined in equation (27).

$$S_{p_n}^2 = \frac{p}{\Delta p} \frac{1}{75} \sum_{i=1}^{75} \frac{|\vec{x}_i - \vec{x}'_{p_n,i}|}{|\vec{x}_i - \vec{x}_{i0}|}$$
(27)

Where S_{p_n} is the sensitivity index for parameter p.

3 Results

3.1 Sensitivity

Figure 8 show the sensitivity index for the 11 most sensitive parameters in the model, relative to each other. The parameters are listed in table 3.

 S_p , equation 28, is the average sensitivity for each parameterer. The pertubation from -10% to 10% is used for calculating the mean. Figure 8 compares the different indices.

$$S_p = \frac{1}{m} \sum_{n=1}^{m} S_{p_n}$$
(28)

The source level of the vessel is the most sensitive parameter in the model. Parameters related to the fish behaviour (i.e. LN_{reak} , LN_{burst} , γ_i , dLN/dt_{reak}) are generally more sensitive than parmameters related to the fish physiology (i.e. l_i , v_0 , v_{mb}).

3.2 Model runs

The model have been run with initial setup as shown in table 4. The parameter values are given in table 3.

х	30 fish $x \in [-80\ 80]$
у	20 fish $y \in [-60\ 60]$
\mathbf{Z}	8 fish $z \in [-50 - 90]$

 Table 4: Initial positions

Visualization of the model runs are shown in figure 9 and figure 10. The vessel runs along the x-axis.



Figure 8: Mean sensitivity index S_p . Parameters where $S_{p_n} = 0$ is not shown in the figure.



Figure 9: Transect in x - z-plane for y = 0, propeller at (x, y) = (0, 0)m, standard parameter values. The transect is 16m thick. The fish are herded in front of the vessel. A stronger vertical herding is seen when the propeller is passing.



Figure 10: Transect in y - z-plane for x = 0, vessel at (x, y) = (0, 0)m, standard parameter values. The transect is 16m thick. A typical tunnel is seen where the vessel have passed. This corresponds to the result Ona (1988b) obtained for 0-group cod.

4 Discussion

Models may be used for different purposes. Some models are used to predict an event, and others are used to explain different mechanisms in the nature. Investigating the dynamics of a model is the first step in building a model for vessel avoidance.

The sensitivity of the parameter for the noise level, KN, indicates that a reduction in the vessel noise (in dB) will decrease the vessel induced avoidance reaction. However, the noise level is not critical if the fish reacts to the change rate in the received signal, jf equation (5). Small perturbations in the reaction thresholds will result in large fluctuations in the resulting behaviour. This may be an explanation of the large variability in behaviour seen in vessel avoidance experiments. The reason for this variability is the linear perturbation of the dB-scale in the sound intensity. This explanation of the variance rely upon the use of this dB-scale. Humans percept this scale as "linear", and it is assumed that the fish have a similar (or less) ability to resolve the different intensities. The parameters governing the reaction, and the motivation for reaction, are more sensitive than the parameters governing the physiological limitations for the fish. The values of these parameters are also less accurate.

The vessel may indirectly trigger the reaction. If other fish reacts to the vessel, their reaction may be the stimuli that make other fish react. This vertical herding may be interpreted as polarisation effect. This is not taken into account in the model. The fish density affects the trawl efficiency (Hylen et al., 1994; Godø et al., 1999). This may be an indication of this herding effect.

Obviously the assumptions on the velocity field, swimming direction and that the fish stop reacting when the stimuli cease to exist are rather hypothetical. The relative importance of the parameters is not likely influenced by these assumptions. Since it is *when* the reaction that occur that is most important, the velocity field could have another shape without changing the result significantly. The "herding effect" may be important. But the first reaction must be initiated, and this must be a stimulus from the vessel.

The next step will be to use the model as a framework for target tracking data on individual fish. A mean velocity field will be extracted from the data and used in the model. This will give a mean vessel avoidance reaction, and this may be used to determine the change in density when the vessel is passing.

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