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A method for estimating fish density through the catches of gillnets

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Abstract

We propose a new method for estimating fish density using catches obtained by gillnets of given mesh size. This method builds on work for estimating the number of fish approaching a gillnet by modelling the fish movement that leads to a gillnet encounter. The theoretical framework is developed, and the method is tested on catch data for cod *Gadus morhua* and Dolly Varden *Salvelinus malma* to demonstrate how the method can be applied. The method relies on knowledge of geometric properties of the net, and morphological and behavioural properties of the fish, so we explore the sensitivity of the estimates to some of these parameters. Estimates are most sensitive to the morphological parameter of the angle the mouth is open while swimming and largely invariant to estimates of uncertain parameters like maximum number of fish that can be caught by the particular net.

KEYWORDS
biomass, cod, Dolly varden, estimation, model, movement

1 | INTRODUCTION

Over recent years, concern has increased about human impacts on fish assemblages inhabiting different types of water bodies. Fish populations may be affected by a variety of human activities, including development, pollution, eutrophication, and fisheries (Rijnsdorp et al., 1996). Evaluating, for example, the population status and abundance of a target species requires detailed knowledge of fish population dynamics, which is difficult to obtain without an empirical estimate of species abundance. Fish stock assessment is used in any scientific investigation to determine productivity of a fishery resource, effects of fishing on that resource, and impacts (on the resource and the fishery) of changing patterns of fishing, e.g., from implementation of management or development policies (Gulland, 1983; Leeuw et al., 2003).

Fish stock assessments are based on fish density estimates, which in turn are derived through a variety of approaches, including analysing data recorded during commercial trawl operations (Sant'ana & Perez, 2016; Thomsen et al., 2016), visual observation (McIntyre et al., 2015) or hydroacoustic surveys (Lian et al., 2017; Pollom & Rose, 2016; Tessier et al., 2016). To improve accuracy of

an assessment, different data may be evaluated concurrently, such as trawl and hydroacoustic (Everson et al., 1996) or trawl and visual observation (Trenkel et al., 2004). Fish density can be directly estimated from analysis of catches in active fishing gear, such as trawl or seiners, and area swept. However, fish density is more difficult to estimate from catches in static fishing gear, so studies are mainly concerned with selectivity and catchability of those types of gears (Doll et al., 2014; Hamley & Regier, 1973; Millar & Fryer, 1999; Regier & Robson, 1966). Unfortunately, many water bodies cannot be fished using mobile gear (e.g., trawl or seiners) (Knapp & Matthews, 1998; Olin et al., 2016). In such water bodies, only passive fishing gear can be used, so having an approach to estimate fish density from passive gear catches, such as gillnets, is crucial for monitoring those fish communities for fishery management and ecosystem research purposes.

Gillnets are noiseless, comparatively inexpensive and easy to use. Moreover, gangs of different mesh sizes can be used concurrently to fish different parts of any water body or layers of the water column. Finally, gillnets do not damage bottom ecosystems, unlike trawling gear (Althaus et al., 2009; Kenchington et al., 2001; Olsgard et al., 2008). Gillnet catchability coefficients often used to estimate fish abundance (Borgstrøm et al., 2010; Giacomini et al., 2020). Catchability can be

estimated directly comparing gillnet catches to a known population size, e.g., hydroacoustics (DuFour et al., 2019; György et al., 2012; Hansson & Rudstam, 1995) or using a statistical approach (Griffiths et al., 2007). The main difficulty in estimating fish density is assessing the water volume from which the fish were retrieved. In the case of active fishing gear, the fished volume can be calculated as the product of the area of the trawl opening and the path traversed by the trawl. A gillnet, in contrast, is immobile while fish are moving. To estimate density of fish from catches in gillnets, two questions must be answered: (1) what is the volume of water from which the number of fish were caught and (2) how many fish were in this volume?

Random walk models, which are simple models of diffusion processes, have been adopted in the study of many biological movements (Levin, 1987; Li et al., 1996). Most models for describing dispersal of organisms have been developed using diffusion equations that are based on continuous random walk models (Cantrell & Cosner, 2004; Skalski & Gilliam, 2003; Taylor, 1980). Various types of behaviour of movements have been incorporated into differential models (Okubo & Levin, 2001; Shiyomi & Tsuiki, 1999; Yamamura, 2002). The classical random walk model deals with a particle moving in a series of steps, where length of the step, time between steps, and direction of the step are all independent (Patlak, 1953).

Herein, we present a method for estimating fish density from catches in gillnets by assuming fish swim as randomly moving particles and estimating fishing volume from the region where fish can reach the net and the probability of contact with the net within that volume. We also perform sensitivity analysis to understand the impact of errors of model parameters on density estimates. This approach is an extension of a method, the first part of which is presented in another article devoted to assessment of the number of fish contacting and approaching gillnets of different mesh sizes (Lobyrev & Hoffman, 2018). To estimate the number of fish contacting a gillnet, the method considered geometry of the net and morphology of the fish by splitting the entire interaction between a fish and a gillnet into stages: the probability that a fish approaches a net at an opening, individual probabilities of contacting a thread of mesh and becoming tangled, and individual probabilities of entering a mesh and becoming wedged. Finally, a saturation function describes the changing number of fish retained in the net at a particular time, in relation to the number of fish approaching each gillnet. The method is applied to the number of cod *Gadus morhua* (collected in Kandalaksha Bay on the White Sea, Russia) and Dolly Varden *Salvelinus malma* (collected in Kronotskoe Lake in Eastern Kamchatka, Russia) approaching gill nets of different mesh size, compared with hydroacoustic data for validation.

2 | METHODS

2.1 | Model development

Consider a fish that is initially located at a point (x_0, y_0) in the Cartesian plane at the beginning of the fishing operation. We say that this fish approaches a gillnet in some finite time interval, Δt,
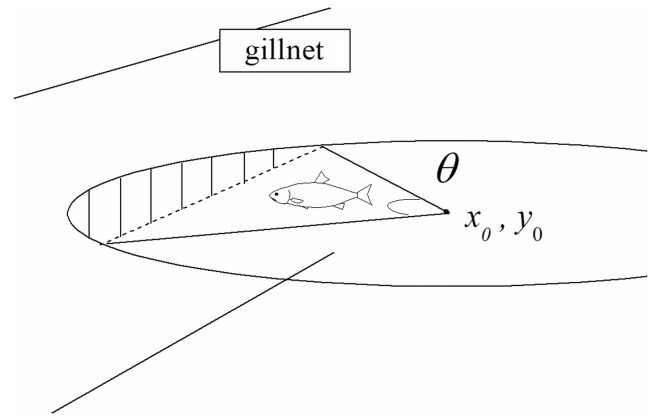

FIGURE 1 The angle θ that determines the $P(\theta)$ probability

when two independent events simultaneously occur: the fish moves in the direction of the net (event 1) and the distance that the fish can swim during the time Δt is *less* than the distance between (x_0, y_0) and some point on the gillnet (event 2).

2.1.1 | Event 1

A fish moves in the direction of the net when it moves within an angle $\theta < 2\pi$ defined as the angle between the two-line segments from (x_0, y_0) to either end of the gillnet. Then the probability, $P(\theta)$, of a random movement being in the direction of the net (Figure 1) is given by:

$$P(\theta) = \frac{\theta}{2\pi} \tag{1}$$

2.1.2 | Event 2

To describe the distance travelled by a fish, two types of motion are possible — direct and random (chaotic). We consider the probability of approach for chaotic motion because fish move chaotically while feeding in almost all lakes and reservoirs (Kim, 2003; Kraus et al., 2018; Railsback et al., 1999; Schulz & Berg, 1992). Most models for describing random movement of living organisms rely on using diffusion equations with a diffusion coefficient (Blackwell, 1997; Bovet & Benhamo, 1988; Li et al., 1996; Wu et al., 2000; Yamamura, 2002). In this formulation, the distance ρ that fish moves during some time t is defined as:

$$\rho = v \cdot \sqrt{t \cdot \tau}, \tag{2}$$

where v is the swimming speed of the fish, τ is the period of time during which the fish moves directly (random movement consists of elementary direct segments), and t is the duration of time the gillnet was fished. If a swimming speed is given in cm/s, and duration of time that the gillnet is fished is in hours, and ρ needs to be estimated in metres, then Equation (2) is $\rho = \left(v \cdot \sqrt{t \cdot 3600 \cdot \tau} \right) / 100$. Clearly, a fish has a nonzero probability of approaching a net, when ρ becomes greater than the initial distance r between (x_0, y_0) and the net. Using

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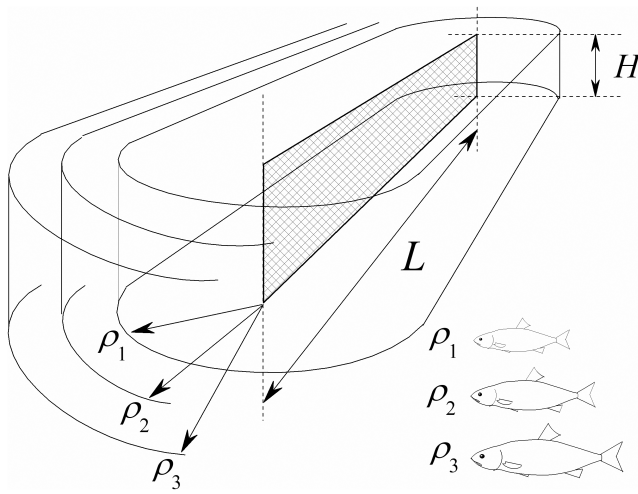
FIGURE 2 The fishing volume estimates, V, for the fish of different length classes

the distance ρ, travelled by a fish of length l, we can characterise the volume fished by the net, V_l, as:

$$V_l, = \left(2 \bullet L \cdot \rho + \pi \cdot \rho^2\right) \cdot H, \tag{3}$$

where L is length of the gillnet and H is height of the net (Figure 2).

Assuming a particle moves chaotically and the (absorbing) screen is located at a certain distance from the particle at initial time t_0, movement is given by a Bernoulli random walk with boundaries (Feller, 1971). In our problem, the fish is the moving particle and the absorbing screen is the gillnet, so the probability P_r of the fish approaching the net can be written as:

$$P_r = \frac{2}{\sqrt{2\pi}} \int_{\frac{r}{\sqrt{t}}}^{\infty} exp\left(-\frac{z^2}{2}\right) dz, \tag{4}$$

where r is a median of triangle abc, $r \leq \rho$ (Figure 3).

Events (1) and (2) are independent because a fish could move towards the net, but not within the angle θ, or a fish could move within the angle θ but with a track ρ that is less that the distance between the fish and the net at the beginning of fishing operation. Hence, the probability $P(x_0, y_0)$ of the fish approaching the net is the product of the two independent probabilities:

$$P(x_0, y_0) = P(\theta) \cdot P_r = \frac{\theta}{2\pi} \cdot \frac{2}{\sqrt{2\pi}} \int_{\frac{r}{\sqrt{t}}}^{\infty} exp\left(-\frac{z^2}{2}\right) dz. \tag{5}$$

The average probability of a fish approaching the net is then the integral of Equation (5) over the horizontal cross-sectional area of the fishing volume, divided by A_F:

$$\overline{P}(A_F) = \frac{\iint_{A_F} P(x_0, y_0) dxdy}{A_F} = \frac{\iint_{A_F} \frac{\theta(z,y)}{2\pi} \cdot \frac{2}{\sqrt{2\pi}} \int_{\frac{r(z,y)}{\sqrt{t}}}^{\infty} exp\left(-\frac{z^2}{2}\right) dzdy}{A_F}, \tag{6}$$

where $A_F = 2 \bullet L \cdot \rho + \pi \cdot \rho^2$. Equation (6) can be computed by discretising the fishing volume into a mesh and summing the $P(x_0, y_0)$ probability for each mesh segment times the area of the segment. The fishing volume can be partitioned into four equal parts, consisting of rectangle and quarter circle (Figure 4), so the computation is only needed for one-fourth of the total fishing volume.

For ease of computation, probabilities can be computed separately for the rectangular region, $\widetilde{P}_R(A_F)$, and the quarter circle region, $\widetilde{P}_Q(A_F)$. For $\widetilde{P}_R(A_F)$, so we partition the region into equal rectangles of size $\Delta_x \times \Delta_y$. The probability $\widetilde{P}_R(A_F)$ at the centre of each grid rectangle can be taken as the probability of the entire grid rectangle:

$$\widetilde{P}_R(A_F) = \frac{\sum_{j=1}^{n_y} \sum_{i=1}^{n_x} \left(\frac{\theta(x_{i,j}, y_{i,j})}{2\pi} \cdot \frac{2}{\sqrt{2\pi}} \int_{\frac{r(x_{i,j}, y_{i,j})}{\sqrt{t}}}^{\infty} exp\left(-\frac{z^2}{2}\right) dz \Delta A_{i,j} \right)}{\frac{L}{2} \rho}, \tag{7}$$

where n_x and n_y are the number of segments in the x and y directions, $(x_{i,j}, y_{i,j})$ are coordinates of the centre of the corresponding grid box, and $\Delta A_{i,j} = \Delta x \Delta y$ is the area of the grid box. Computation for the quarter circle region is simpler in polar coordinates with the region partitioned by equal increments Δs and $\Delta \varphi$ (because the traditional polar variables r and θ already have meanings in this equation). Unlike the rectangular region, the quarter circle is not partitioned into *equal* area segments. Thus, the probability $\widetilde{P}_Q(A_F)$ is computed as:

$$\widetilde{P}_Q(A_F) = \frac{\sum_{j=1}^{n_\varphi} \sum_{i=1}^{n_s} \left(\frac{\theta(s_{i,j}, \varphi_{i,j})}{2\pi} \cdot \frac{2}{\sqrt{2\pi}} \int_{\frac{r(s_{i,j}, \varphi_{i,j})}{\sqrt{t}}}^{\infty} exp\left(-\frac{z^2}{2}\right) dz \Delta A_{i,j} \right)}{\frac{1}{4} \pi \rho^2}, \tag{8}$$

where n_s and n_φ are the number of segments in the s and φ directions, $(s_{i,j}, \varphi_{i,j})$ are coordinates of the centre of the corresponding grid cell, and $\Delta A_{i,j} = \left[\pi \left(s_{i,j} + \frac{\Delta s}{2} \right)^2 - \pi \left(s_{i,j} - \frac{\Delta s}{2} \right)^2 \right] \frac{\Delta \varphi}{2\pi}$ is the area of the grid cell.

The probability $P(A_F)$ is the sum of probabilities of rectangle $\widetilde{P}_R(A_F)$ and quarter circle $\widetilde{P}_Q(A_F)$ regions that are proportional to their areas:

$$\overline{P}(A_F) = \frac{\widetilde{P}_R(A_F) \cdot \frac{L}{2} \rho + \widetilde{P}_Q(A_F) \cdot \frac{1}{4} \pi \rho^2}{\frac{L}{2} \rho + \frac{1}{4} \pi \rho^2}, \tag{9}$$

where sum in the denominarer is a quarter of the fishing volume (Figure 4). Then, the number of fish N_{V_l} of length l in the fishing volume V_l, can be written as:
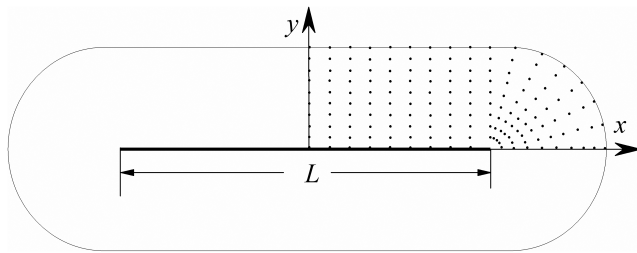
$$N_{V_l} = \frac{N_{AP\_l,\mu}^{(t)}}{P(A_F)_l}, \tag{10}$$

where $N_{AP\_l,\mu}^{(t)}$ is the number of fish of length l, approaching the net of mesh μ during an operation time t. Hence, density N_{D_l} of fish of length l (individuals per cubic metre) is given by:

$$N_{D\_l} = \frac{N_{AP\_l,\mu}^{(t)}}{P(A_F)_l \cdot V_l}, \tag{11}$$
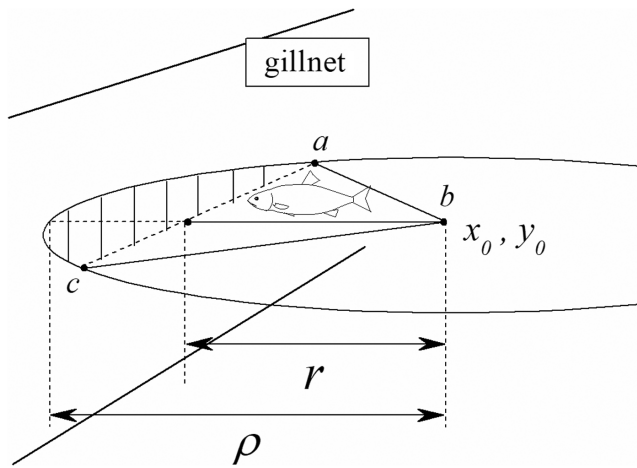
FIGURE 3 A schematic of how the distance r determines the P_r probability

FIGURE 4 A top-down view of the fishing volume with a quarter of the area divided into discrete cells to visualise how the integral in Equation (6) is computed according to Equations (7) and (8)

Six parameters in the proposed method of fish density estimation must be estimated: l = the length of gillnet (m), H = the height of gillnet (m), v = the swimming speed of the fish (body length per sec), τ = the period of time during which the fish moves directly (s), t = the duration of fishing operation (h), and $N^{(t)}_{AP\_l,\mu}$ = the number of fish of length l, approaching the net of mesh μ during time t. Parameters for length and height of the gillnet and duration of fishing are known from records of the fishing operation. The parameter $N^{(t)}_{AP\_l,\mu}$ can be estimated using the method described by Lobyrev and Hoffman (2018); R code by Itai van Rijn is available at GitHub (https://github.com/ItaiVR/Lobyerev-selectivity). The parameter $N^{(t)}_{AP\_l,\mu}$ must be estimated using the expanded version of Equation (20) in Lobyrev and Hoffman (2018):

$$N^{(t)}_{AP\_l,\mu} = \frac{N_{lim\_l,\mu} \cdot 0,63 \cdot e}{\widetilde{\tau}_\mu} \bullet t + \left(\frac{N^{(t)}_{W\_l,\mu}}{P(O|C)_{l,\mu} \cdot P(E|O)_{l,\mu} \cdot P(W|E)_{l,\mu}} - Q^{(t)}_{l,\mu} \right),$$
(12)

where $\widetilde{\tau}_\mu = \frac{t}{\ln\left(1 - \frac{Q^{(t)}_{l,\mu}}{N_{lim\_l,\mu}}\right)}$, $Q^{(t)}_{l,\mu}$ is the total catch of fish of length l (including wedged and tangled fish) in the net of mesh μ during time t, $N^{(t)}_{W\_l,\mu}$ is the numbers of wedged fish of length l, retained in the net of mesh μ during time t, $N_{lim\_l,\mu}$ is the maximum number of fish of length l that can be caught by the net of mesh μ, $0.63 = 1 - exp(-1)$, $e \approx 2.728$, $P(O|C)_{l,\mu}$ is the probability that a fish of length l contacts the net of mesh μ at an opening, $P(E|O)_{l,\mu}$ is the probability a fish l enters the mesh after the contact, and $P(W|E)_{l,\mu}$ is the probability of being wedged after entering. The first term of Equation (12) is the sum of fish in the catch and the fish that backed away from the net due to saturation, and the term in parentheses is the number of fish not being caught due to selectivity (see Lobyrev & Hoffman, 2018). We assumed that on average the same number of fish approached each net during each time unit, and estimated fish density using the average number of fish $\overline{N}^{(t)}_{AP\_l}$ approaching a net of any mesh size:

$$\overline{N}^{(t)}_{AP\_l} = \frac{\sum_{\mu=1}^{n} N^{(t)}_{AP\_l,\mu}}{n},$$
(13)

where n is the number of gillnets of different mesh size.

2.2 | Parameter estimation

Some parameters, such as swimming speed, v, and the time of direct movement, τ, are difficult to estimate, partly because they are species-specific and may depend on factors, such as abiotic conditions of the area fished, time of day and physiological condition of a fish. Swimming speed was taken from literature as an average values from sources. Based on the experiments on cod and Dolly Varden in a 1.5–cubic-metre tank, where food was dispersed to induce chaotic movement, the meantime, τ, during which fish moves directly, was assumed to be 1 sec for both species. Because of the size of the tank, swimming speed was hard to quantify, so we referred to published data to improve accuracy of swimming speed: 0.4 body length per second for cod (BL/s) (Cote et al., 2002; Martínez et al., 2003; Schurmann & Steffensen, 1994; Winger et al., 2002) and 0.8 for Dolly Varden (BL/s) (Christiansen et al., 1992; Courtney et al., 2016; Marchand et al., 2002; Tudorache et al., 2011). All computations of $\overline{P}(A_F)$ used a MATLAB script. To estimate density, a nomogram was developed to facilitate $\overline{P}(A_F)$ probability calculation for different net lengths at different durations of fishing to determine ρ (Figure 5). The probability $P(A_F)$ distribution for given net length was approximated by the following exponential function:
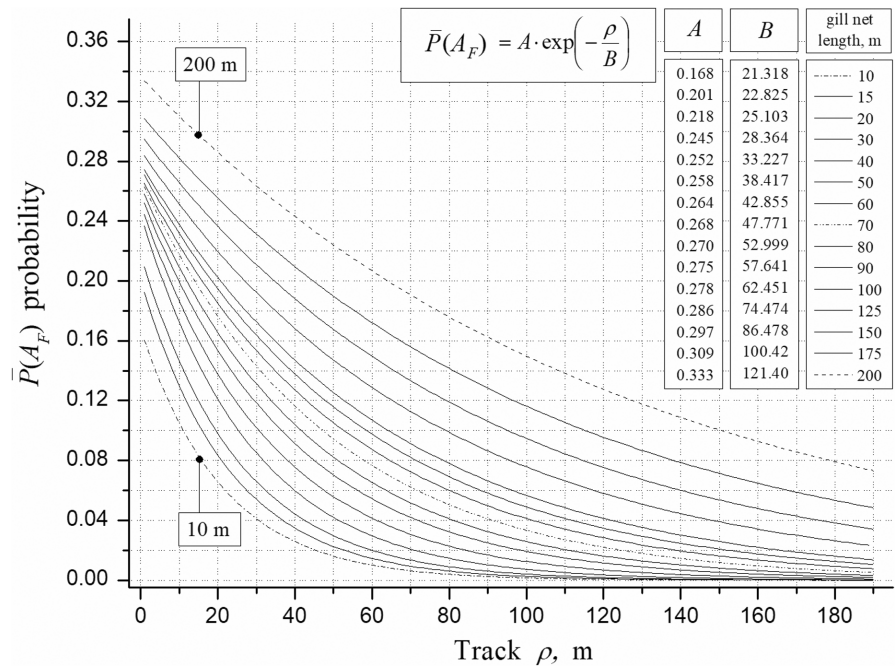
$$\overline{P}(A_F) = A \cdot exp\left(-\frac{\rho}{B}\right); \ R = 0.99 \ ,$$
(14)

where A and B are experimentally obtained parameter values, and ρ is the calculated ρ value. Therefore, $\overline{P}(A_F)$ can be computed from the estimated ρ value and A and B parameters (for given net length) in Equation (14).

2.3 | Sensitivity analysis

To understand the impact of errors on density estimates, sensitivity of the model to errors in parameter estimates was examined. Calculations were carried out to determine the range of

FIGURE 5 A nomogram for estimation of $\bar{P}(A_F)$ probability for different net lengths using a given ρ value

$$\bar{P}(A_F) = A \cdot \exp\left(-\frac{\rho}{B}\right)$$

A	B	gill net length, m
0.168	21.318	10
0.201	22.825	15
0.218	25.103	20
0.245	28.364	30
0.252	33.227	40
0.258	38.417	50
0.264	42.855	60
0.268	47.771	70
0.270	52.999	80
0.275	57.641	90
0.278	62.451	100
0.286	74.474	125
0.297	86.478	150
0.309	100.42	175
0.333	121.40	200

fluctuation of density estimates caused by changing parameter values: φ (angle between the ends of upper and lower jaws when the mouth is opened), v (swimming speed), τ (time interval of direct motion) and N_{lim} (the limited number of fish in the net). For the τ parameter, as an example, $N_{D\_\tau-20\%}$ and $N_{D\_\tau+20\%}$ are density estimates for −20% and +20% deviations (20% arbitrarily chosen to illustrate), then sensitivity of density estimates for −20% deviation of τ, $ST_{\tau\_-20\%}$ was

$$ST_{\tau-20\%} = \left(1 - \frac{N_{D\_\tau-20\%}}{N_{D\_\tau\ 0\%}}\right) \cdot 100, \qquad (15)$$

where $N_{D\_\tau-20\%} < N_{D\_\tau\ 0\%}$ (left branch of the curve) $ST_{\tau\pm n\%}$ in Figure 6a; and sensitivity of density estimates for +20% deviation of τ, $ST_{\tau\_+20\%}$ was

$$ST_{\tau+20\%} = \left(\frac{N_{D\_\tau+20\%}}{N_{D\_\tau\ 0\%}} - 1\right) \cdot 100, \qquad (16)$$

where $N_{D\_\tau+20\%} > N_{D\_\tau\ 0\%}$ (right branch of the curve) $ST_{\tau\pm n\%}$ in Figure 6a. These equations defined sensitivity as the percentage change in density that resulted from a specified percentage change in a parameter. Accordingly, $ST_{\tau\_0\%} = 0$ indicated no changes. In general, $ST_{\tau\pm X\%}$ can be either positive or negative, with the sign indicating whether the change made to the parameter was of the same sign as the resulting effect on the density. For example, a negative value of $ST_{\tau-20\%}$ means that the negative (−20%) perturbation led to an increase in the density estimate. This is consistent with sensitivity being defined as the derivative showing the change in density with respect to a change in a parameter. A value greater than 100% is possible and indicates that the density estimate more than doubled in response to the parameter change.

2.4 | Application

We estimate density of two species, including cod *G. morhua*, collected in Kandalaksha Bay, White Sea, Russia, in 2014, and Dolly Varden *S. malma*, collected in Kronotskoe lake in Eastern Kamchatka, Russia, in 2013. Fish were caught with monofilament gillnets of different mesh sizes and a 0.5 hanging ratio. Length of nets was 30 m for cod and 15 m for Dolly Varden and height of nets was 1.5 m for both species. Fishing duration was 12 h (from sunset to dawn) for both species and number of fishing operations was 11 for cod and 9 for Dolly Varden; gillnets were placed on the bottom at a depth of about 5 m. Dolly Varden were caught with gillnets of 22, 25 and 30 mm mesh size (knot to knot) and cod were caught with gillnets of 20, 25 and 30 mm mesh size, fished concurrently. Nets were set in the afternoon and retrieved the following morning. In total, 694 cod and 783 Dolly Varden were caught. Numbers of fish contacting and approaching nets of each mesh size were computed using the method described by Lobyrev and Hoffman (2018) for estimating the number of fish approaching the gillnet (Table 1).

The authors confirm that all methods were carried out in accordance with relevant ethical guidelines and regulations, and approved by the Moscow State University Bioethic Committee, regulated by Russian Committee for Bioethics (bioethics.ru/eng/rucommittee/). The study was carried out in compliance with the ARRIVE guidelines (arriveguidelines.org/).

2.5 | Hydroacoustic surveys

To compare density estimates from this method with estimates obtained by alternative methods, we compared our model-based density estimate to hydroacoustic estimate of cod during early morning,
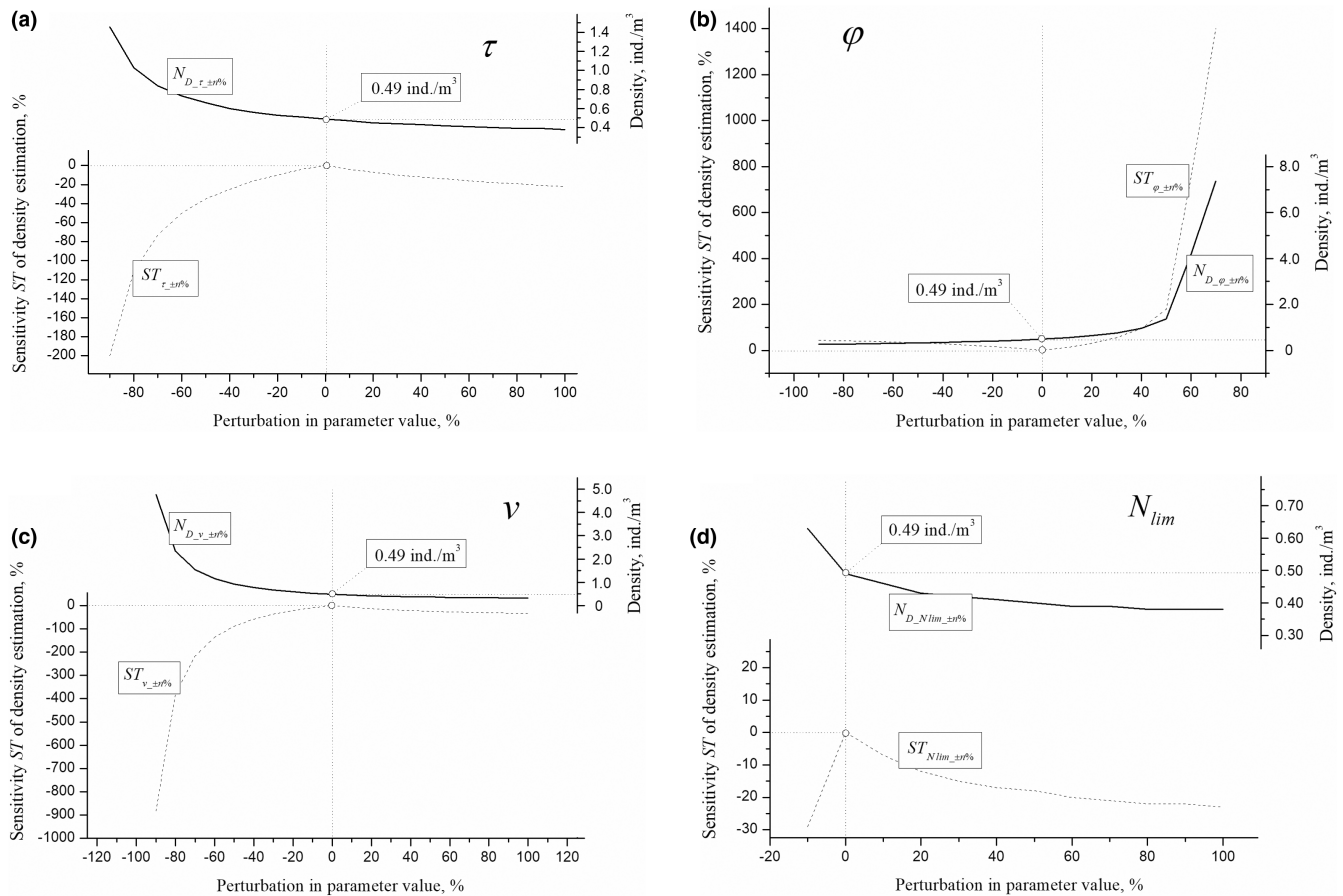
FIGURE 6 Estimated fish density $ST_{X\pm n\%}$ of cod and sensitivity to perturbation $N_{D\_X\pm n\%}$ relation to a range of variation in (a) τ = period of time during which fish moved (sec), (b) φ = angle between ends of upper and lower jaws when the mouth is open, (c) v = swimming speed (body length per sec) and (d) N_{lim} = limited number of fish in the net

July 2–July 25, 2014, over the area of gillnet fishing using a Simrad EY-500 (110 kHz operating frequency, 10° ×4° beam shape, pulse length 0.1 ms, 2–10 pings/s). Eight transects per survey were conducted with a total length of 2.6 km that totally covered the area sampled. Before each survey, the echosounder was calibrated with a standard copper sphere. Average depth in the study area was 5 m. The screen (visualisation of fish distribution by depth) of the Simrad EY-500 allowed estimation of the approximate number of fish in different layers of the water column. Despite the fact that the hydroacoustic assessment of fish at the bottom has an error (Drastic et al., 2017), we assumed that the hydroacoustic gear detected some of these fish targets very close to the bottom because of the shallow depth at the sample location. The hydroacoustic estimate of fish density included all species found in the survey area, so the hydroacoustic estimate of total fish abundance was reduced by assuming the ratio of cod to total catch was the same as in gillnets.

In order to compare the hydroacoustic estimates with the model-based density estimate, the following procedure was followed. First, the average hydroacoustic estimate of density of all species that inhabit the investigated area was computed based on the seven surveys. Next, visualisations of the fish distribution by depth were used to estimate the fraction of fish in the bottom 1.5 m layer (where 1.5

is the height of gillnet). Finally, the hydroacoustic estimate of cod density within the fishing area was obtained using the hypothesis that the fraction of cod in the total catch is the same as in the 1.5 m layer.

3 | RESULTS

3.1 | Density estimates

Density was estimated to be 0.49 cod/m^3 in Kandalaksha Bay, White Sea, Russia, in 2014, and 0.36 Dolly Varden/m^3 in Kronotskoe Lake, Eastern Kamchatka, Russia, in 2013 (Table 2). Density estimates for each length group, computed by Equation (11), used the following parameters: the number $\overline{N}_{AP\_l}^{(t)}$ of fish of length l that approached the net during time t (computed by Equation 12), the probability, $\overline{P}(A_F)$, of a fish approaching the net during time t (Equation 9), and the fishing volume $\overline{V}$ (Equation 3). Average swimming speeds for all length groups, 9.6 cm/s for cod and 23.2 cm/s for Dolly Varden, computed using relative swimming speeds in body length per second (0.4 Bl/s for cod and 0.8 Bl/s for Dolly Varden) and average tracks, ρ, of 20.0 m for cod and 48.2 m for Dolly Varden (Table 2); the average number

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TABLE 1 Length-class distributions of cod and Dolly Varden contacted and approached gillnets computed for averaged catch per unit effort (CPUE), length of gillnet is 30 m for cod and 15 m for Dolly Varden; samples were obtained in 2013 (Dolly Varden, Kronotskoe lake) and in 2014 (cod, White Sea)

	Cod *Gadus morhua*						Dolly Varden *Salvelinus malma*							
	Contacted			Approached			Contacted				Approached			
	Mesh size													
Length group, cm	20	25	30	20	25	30	22	25	30	35	22	25	30	35
14	2			10										
16	8			18			2				4			
18	7	3		14	5		4	9			7	13		
20	6	4		20	9		9	10			16	14		
22	16	13	22	36	34	25	9	6	6		17	10	9	
24	31	27	43	50	58	47	6	7	9		10	13	12	
26	32	20	19	42	38	30	8	11	10	9	13	19	19	13
28	19	8	9	22	15	33	10	5	8	9	14	11	15	13
30	7	5	6	8	8	21	7	7	4	4	9	11	9	6
32		2	3		2	12	2	5	2	2	4	8	5	5
34		3	3		3	9	3	1	1			5	3	4
36								2	2	2		3	3	5
38									1	1			2	2
40									1	1			2	4
42									3	1			3	4

TABLE 2 The number $\overline{N}_{AP\_l}^{(t)}$ of fish of length l that approached the net during time t, probability $\overline{P}(A_F)$ of a fish approaching the net, fishing volume $\overline{V}$ and density N_{D_l} of fish of length l for cod *G. morhua* in Kandalaksha Bay, White Sea, Russia, in 2014 and Dolly Varden *S. malma* in Kronotskoe Lake, Eastern Kamchatka, Russia, in 2013

| Cod *G. morhua* | | | | | Dolly Varden *S. malma* | | | | |
Fish length	$\overline{N}_{AP\_l}^{(t)}$, ind.	$\overline{P}(A_F)$	$\overline{V}$, m³[a]	N_{D_l}, ind./m³	Fish length	$\overline{N}_{AP\_l}^{(t)}$, ind.	$\overline{P}(A_F)$	$\overline{V}$, m³[a]	N_{D_l}, ind./m³
14	10	0.124	3671	0.02	16	4	0.024	13,122	0.01
16	18			0.04	18	10			0.03
18	10			0.02	20	15			0.05
20	15			0.03	22	12			0.04
22	32			0.07	24	12			0.04
24	52			0.11	26	16			0.05
26	37			0.08	28	13			0.04
28	23			0.05	30	9			0.03
30	12			0.03	32	6			0.02
32	7			0.02	34	4			0.01
34	6			0.01	36	4			0.01
					38	2			0.01
					40	3			0.01
					42	4			0.01
				Sum 0.49					Sum 0.36

[a]Average swimming speed (computed using BI/s values): cod — 9.6 cm/s. $SD = 2.7$ cm/s. Dolly Varden — 23.2 cm/s. $SD = 6.7$ cm/s; average track ρ: cod — 20.0 m. $SD = 5.5$ m. Dolly Varden — 48.2 m. $SD = 13.9$ m.

of a given length group from all the fish of that length, $\overline{N}_{AP\_l'}^{(t)}$, ind., that approach every net of a given mesh size, are represented in Table 1.

3.2 | Parameter sensitivity

The sensitivity $ST_{X\pm n\%}$ (where X is parameter) of estimated fish density $N_{D\_X\pm n\%}$ was greater for negative than positive deviations in the number of seconds during which fish moved (τ), swimming speed (v), and number of fish in the net (N_{lim}), but was greater for positive than negative deviations in the angle between ends of upper and lower jaws when the mouth is open (φ) (Figure 6a–d). The sensitivity of estimated fish density was negative for both positive and negative perturbation of v, τ, and N_{lim}, sensitivity of estimated fish density was positive for both positive and negative perturbations of N_{lim}. Overall, estimated fish density was more sensitive to perturbations of φ than to perturbations of v, τ, or N_{lim}, especially for positive perturbations of φ. In contrast, estimated fish density was relatively insensitive to N_{lim}. Thus, when calculating density, overestimating parameters v and τ is more profitable, whereas for parameter φ it is reversed.

3.3 | Hydroacoustic results

Fish density fluctuated between 5022 and 11,278 individuals/ha over seven surveys between July 2 and July 25 with a mean ± 95% of 8196 ± 2191 individuals/ha. On average, 90% of all fish were recorded in the bottom 1.5 m layer. Thus, estimated total fish density in the layer of fishing was (8196/10000)·0.9/1.5 = 0.49 individuals/m^3. This estimate of 0.49 individuals/m^3 was identical to our model-based density estimate of cod density, but the hydroacoustic estimate includes cod and other species found in the survey area. Therefore, the hydroacoustic estimate for cod was reduced by assuming the ratio of cod to total catch was the same as in gillnets. The gillnet catch included 694 cod, 176 navagas *Eleginus navaga*, 171 sculpins *Myoxocephalus scorpius*, and 77 flounders (*Pleuronectes platessa*, *Platichthys flesus*, *Limanda limanda*, *Liopsetta glacialis*) (Lobyrev & Hoffman, 2018), so the ratio of cod to the total catch was 694/(694 + 424) = 0.62, which produced a hydroacoustic estimate of 0.49 cod/m^3·0.62 ≈ 30 cod/m^3.

4 | DISCUSSION

4.1 | Model assumptions

This paper develops a framework for estimating density of fish in a body of water based on gillnet catches. The method extends earlier work for estimating the number of fish approaching a gillnet by modelling fish movement that leads to a gillnet encounter. The method was illustrated using catch data for cod and Dolly Varden to show how the method can be applied in practice. Our density estimates of cod (0.49 ind./m^3) and Dolly Varden (0.36 ind./m^3) were relatively

high because: (1) cod fishing took place in the littoral zone where older age groups were feeding, and (2) Dolly Varden fishing was in the Kronotsky Lake Nature reserve where all fishing was prohibited and few people live, thereby minimising anthropogenic effects and sustaining a lightly fished population.

The proposed method of fish density estimation relies on assumptions required to calculate the number of fish approaching a gillnet during operation (Lobyrev & Hoffman, 2018). Assumptions include: (1) swimming speed and movement did not change during fishing; (2) fish did not migrate vertically or horizontally during fishing; and (3) the gillnet was invisible to fish. To increase accuracy, fishing conditions and equipment could be chosen with these assumptions in mind.

For example, to satisfy assumption (1), fishing should take place during a period of maximum feeding activity of fish (e.g., at morning and evening). The assumption of random movement has generally been confirmed by radio-telemetry studies of swimming activity of many species, including salmonids (Babaluk et al., 2001; Quinn & Groot, 1984; Schmalz et al., 2002; Schulz & Berg, 1992). Therefore, random movement of fish can be described using random walk models developed for movement of living organisms, including fish (Codling et al., 2008; Kim, 2003; Patterson et al., 2008).

The no migration assumption (assumption 2) largely depends on behavioural ecology of target species. For example, Eurasian perch *Perca fuviatilis* within one lake may represent two genetically distinct subpopulations, which suggests the lack of any migrations (Gerlach et al., 2001). Ultrasonic telemetry has shown random movement by other species, such as brown trout *Salmo trutta* (Schulz & Berg, 1992), walleye *Stizostedion vitreum* (McConville & Fossum, 1981), black bass *Micropterus* spp. (Maynard et al., 2017), Arctic char *Salvelinus alpinus* (Dick et al., 2009), and whitefish *Coregonus nasus* (Carter, 2010).

The invisibility of the fishing gear (assumption 3) can be best achieved by using gillnets of appropriate colour and fishing when visibility of fishing gear is low. Gillnets are successful and mechanically selective when fish contact the mesh; so fishers use materials with colours they consider less likely to be seen by fish (Cui et al., 1991; Wardle et al., 1991). Coloured gillnets are favoured, because fishers believe that certain colours reduce the contrast between the net and its background to increase the fishing efficiency (Grimaldo et al., 2019).

Beyond these assumptions, two factors affect accuracy of density estimates: dispersion of fish within the area fished and accuracy of model parameter estimates. When feeding, fish are moving almost constantly, and fish assemblages are highly mobile, non-permanent and patchily distributed. Concerns about fish distribution are best addressed by fishing throughout a water body to ensure all fish in a population are vulnerable to capture.

Our model can also be used to estimate density for fish with rectilinear motion (e.g., migrating). In this case, calculating the probability of a fish approaching the net will be simpler. In accordance with the rectilinear motion (where distance is speed multiplied by time), the probability of approaching the net here will have discrete values: 1 or 0 — that depends on whether a fish of a given size travelled

the distance from a starting point to the net at a given speed during fishing.

4.2 | Accuracy of density estimates

Density of cod using our method (0.49 individuals/m^3) was of a similar order of magnitude as the hydroacoustic estimate (0.30 individuals/m^3). We conclude the model assumptions were reasonable, although the error was still relatively high. Several reasons may explain why model and hydroacoustic estimates differed. First, ratios of fish caught in gillnets are problematic because selectivity and catchability among species, such as sculpins, flounders and cod. Second, other model parameters, such as swimming speed, also differ between the target species, cod, and other non-target species. Third, distribution of fish in the water is likely heterogeneous, which will lead to differences between model–based gillnet and hydroacoustic–based estimates.

4.3 | Parameter accuracy

Assessing accuracy of model parameters is difficult, because they are associated with the behaviour of living organisms that can be influenced by many biotic and abiotic factors. Important parameters include the angle, φ, between the ends of upper and lower jaws when the mouth is opened during ram ventilation (Lobyrev & Hoffman, 2018), the maximum number of fish N_{lim} that can be caught by a particular net, the swimming speed, v, and the period of time, τ, during which fish move directly. Accuracy of these parameters varies. For example, N_{lim} can be estimated more accurately by increasing sampling, whereas parameters v, τ, and φ are difficult to measure accurately even in laboratory experiments. Tank experiments were conducted to estimate φ and τ parameters for cod *G. morhua*, but results for φ were not helpful, because φ is the angle of the mouth opening during ram ventilation, but fish in a tank switch to a different type of gill aeration to reach a natural swimming speed in a small space. Therefore, conditions in the tank were not suitable for estimating φ. Similarly, estimates of v and τ through lab experiments may not correspond to values in natural conditions. This is primarily due to a change in fish behaviour in an artificial environment that cannot imitate true natural conditions. Limits on time and resources may also prohibit realistic experiments.

Numerous studies of swimming speed have shown that the fish swimming speed is ecologically and biologically relevant, and that an optimal swimming speed maximizes the distance travelled per unit energy expenditure (Davison, 1997). The optimal swimming speed, which depends on the size of the fish, optimizes growth and food conversion efficiencies in many species. For example, food conversion efficiency and the deposition of lipids on the digestive tract were maximised at 0.85 BL/s for brook char *Salvelinus fontinalis* (East & Magnan, 1987), growth occurred at swimming speeds of 1.00 BL/s for trout *Salmo gairdneri* (Walker & Emerson, 1978). Thus, proper

assessment of the swimming speed of target species can fluctuate within fairly narrow limits.

When converting published swimming speeds for use in our model, important details need to be considered. In the literature, the swimming speed is typically given as the body length per second, so each size group has its own theoretical swimming speed that differs from other size groups. However, cod and char (and many other fish species) often form groups in natural conditions, which include fish from a range of sizes. Therefore, the swimming speed of all sizes in the swarm must be the same, so we used the mean values of ρ, the $\overline{P}(A_F)$ probability and fishing volume. Density estimation was estimated for the given length ranges of both species, not including fish outside those ranges.

The combined catch of all gillnet mesh sizes often has a range of length classes that does not sample the entire range presented in the full fish population due to high selectivity (Doll et al., 2014; Hamley & Regier, 1973; Holst et al., 1996; Millar & Fryer, 1999; Shoop & Ryswyk, 2016). Several approaches can restore length classes that have not been caught by a net of given mesh size. The first approach is to use a range of mesh sizes that can theoretically cover the entire possible range of length classes to effectively eliminate any non-caught sizes (though research activities often do not set such goals). The second approach is to choose appropriate locations (biotopes) for fishing based on prior knowledge of where juveniles and adults (or different age/size groups) inhabit. Both of the solutions must be used simultaneously, otherwise fish of some sizes would still not be caught. A third approach is data extrapolation. For example, total mortality rates can be estimated from slopes of the right–hand limbs of the catch curves (Baranov, 1948; Ricker, 1975). For instance, if the catch covers the range of length classes, included n age groups of different numbers, then, knowing the population distribution function, for example the function $N_t = N_0 \cdot exp(-Z \cdot t)$ proposed by Baranov (1948), one can estimate the number of missing length classes by extrapolation — provided that proportions of age groups in the catch are representative.

The primary contribution of our article is the development of a theoretical framework for estimating fish density from gillnet catches. Of paramount importance is the investigation of how environmental factors affect the model parameters. In different water bodies, activity of the same species may vary depending on the season and even on the time of day. Changes in weather conditions will also have an impact on the activity of fish, and therefore on the estimated parameters. Most parameters in the model can be estimated using current methods, although some, such as the time a fish swims forward before turning, are more challenging. To understand the effects of errors and uncertainty on the estimates of fish density yielded by the model, we also explored the sensitivity of fish density estimates to perturbations in values of some of the main parameters in the model.

An important area is the study of fish behaviour near the fishing gear and, especially, when contacting with a gillnet, as the influence of environmental factors can change the selectivity and catchability of the net. One of the useful methods to investigate such a

behavioural response could be an approach for directly quantifying selection parameters for fishing gear using a dual underwater video camera apparatus and employing methods to estimate the gillnet retention probability for the target species (Grant et al., 2004). This approach allows observation of fish behaviour around the gillnet and the estimation of the absolute probability of fish encountering, contacting, or being retained by gear.

Particular attention should be paid to the confirmation of density estimates by alternative assessment approaches. Independent methods for estimating fish density would provide a stronger basis for inferring the accuracy and precision of the model-based estimates of fish density. For example, a mark–recapture estimate would be another alternative method that would greatly strengthen the comparison. Ecosystem models, such as "Ecopath with Ecosim" (Christensen & Walters, 2004), also can be used to verify model-based estimates. Fish biomass here can be calculated through a system of mass-balance equations if the population and trophic characteristics of other groups in the trophic chain are known.

CONFLICT OF INTEREST

The authors confirm that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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