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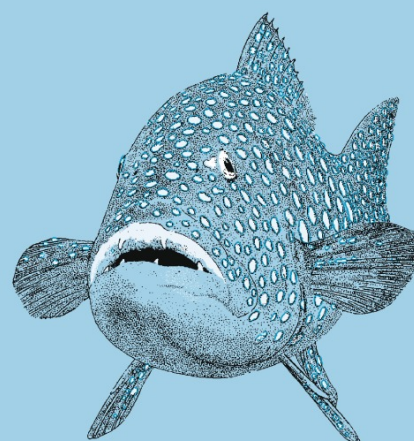
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RESEARCH PAPER

A morphological and geometric method for estimating the selectivity of gill nets

Feodor Lobyrev · Matthew J. Hoffman 

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Abstract We propose a new method for estimating gill net selectivity which estimates the probabilities leading to retention by analyzing both the fish morphology and the mesh geometry. This method estimates the number of fish approaching and contacting gill nets of different mesh sizes as an intermediate step towards computing the selectivity. Instead of assuming an underlying probability distribution as in indirect methods, we split the entire interaction between a fish and the gill net into several stages, each with its own probability. All the necessary parameters to compute these probabilities can be obtained from measurements of the fish, knowledge of the mesh geometry, and catch data from different mesh sizes. The framework offers three pathways for computing the total number of fish contacting the gill nets and has the capability to use both wedged and entangled fish in the analysis. As a proof of concept, the method is

applied to catch data for cod (*G. morhua*) and Dolly Varden (*S. malma*) to estimate the number of fish contacting the gill nets in both cases. By estimating the number of fish contacting the gill net in addition to the selectivity, this method provides an important step towards deriving estimates of fish density in a particular fishery from gill net measurement.

Keywords Gill nets · Mathematical modeling · Selectivity

Introduction

To successfully manage a fishery, one needs to know the properties of the whole fish assemblage: species number, abundance and size distributions. To attain this, representative and reliable fish community samples are needed. Gill nets are widely used both for commercial fisheries and as a research tool to sample the abundance of fish populations, but are highly selective (Doll et al. 2014; Hamley and Regier 1973; Millar and Fryer 1999). A rule of thumb for selectivity states that gill nets catch very few fish whose length differs from the optimum by more than 20% (Baranov 1948). Fish populations are heterogeneous in age, size, sex, condition, behavior, and habitat, so all fish are not equally vulnerable to any given method of fishing (Hamley 1975). Selection refers to any process that

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causes the probability of capture to vary with the characteristics of the fish, and selectivity is a quantitative expression of selection and traditionally means selection by size (Lucas et al. 1960). The act of catching a fish involves several stages: first the ranges of the fish and the fishery must overlap in time and space, then the fish must encounter the nets, and finally be caught and retained by the nets; any stage of this capture process may be selective (Parrish 1963).

The size selectivity of gill nets is important for the management of the fisheries and for understanding the sampling gear's performance. Quantifying this selectivity is crucial, but is challenging due to the many factors involved and the lack of data available to quantify these processes. It was postulated that a fish is caught in a gill net if it enters a mesh beyond the gillcovers but cannot pass completely through and also that selectivity curves for different mesh sizes are congruent (Baranov 1914). These generalizations have remained the basis of most subsequent work. The most important factors that determine gill net selectivity are the mesh size, the elastic stretching of the net, the inelastic stretching of the net (including stretching of the knots), the hanging coefficient of the net, the strength and flexibility of the twine, the visibility of the twine, and the shape of the fish (Clark 1960).

Gill net selectivity curves are typically bell-shaped, though they can sometimes be bimodal. The selectivity curve is described by its mode, width, height, and shape. The mode corresponds to the optimal length of fish caught, the width corresponds to the selection range, the height describes how efficiently the mesh catches fish of the optimum length, and the shape varies according to several characteristics of net and fish (Hamley 1975). There are several definitions of the selection curve: the population-selection curve is the (relative) probability that a fish of length l from the population is captured; the available-selection curve is the (relative) probability that a fish of length l is captured given that it was available to (but possibly avoided) the gear; and the contact-selection curve is the (relative) probability that a fish of length l is captured given that it contacted the gear (Millar and Fryer 1999).

Methods of estimating gill net selectivity can be grouped into five basic types (Regier and Robson 2011). First, selection ranges and, recently, the shapes of selectivity curves have been estimated from girth

measurements by assuming that a fish, upon swimming into a net, is caught if its head girth is smaller than the mesh perimeter but the maximum girth is larger. Second, the size distributions of catches are sometimes reported without further analysis to give a rough estimate of selectivity because the catch depends on both the abundance of each size-class and on selectivity. Next, mortality estimates observe the size distributions of gill net catches over a time sequence while usually assuming that catchability is constant throughout the sampling. They require no assumptions about the nature of the selectivity curves. The most commonly used methods for determining gill net selectivity are direct and indirect methods. Direct estimates compute the length-frequency distributions of the fish population using experiments (such as gill nets, mark-recapture experiments, or video observations) and compare these size distributions with a known standard: the size distribution of the fish population (Borgström 1989; Grant et al. 2004; Yokota et al. 2001). They require no assumptions about the nature of the selectivity curves, and no comparisons of catches by different mesh size. Finally, indirect methods make assumptions about the underlying distributions of the selectivity curves and use catch frequencies from different mesh sizes and statistical software to estimate the parameters (Anderson 1998; Saadet Karakulak et al. 2008; Tanaka 2002). They require no knowledge of the size distribution of the fish population but instead rely on suitable assumptions about the nature of the selectivity curves.

Indirect methods typically require less experimental time and expense than direct methods, so, as a result, indirect methods have been applied to a large range of fisheries (Anderson 1998; Doll et al. 2014; Smith et al. 2017). While indirect methods have proved useful in estimating the shape of selectivity curves, one of the main issues with indirect methods is that the retention and contact curves used in the derivation are normalized to one (Anderson 1998; Hanol et al. 2015; Shoup and Ryswyk 2016). As a result, it is impossible to use the selectivity curves from those methods to estimate the number of fish contacting a gill net of given mesh size.

Another potential deficiency of indirect methods is that fish that are tangled in the gill net are either ignored or are not distinguished from fish caught by wedging (Henderson and Wong 1991). There are two

basic different means of fish capture in a gill net: fish are wedged when they are held tightly by the mesh around their body and are tangled when they are held in the net by teeth or maxillaries without penetrating the mesh (Hansen et al. 1997; Olsen and Tjemsland 1963; Santos et al. 2003). To estimate gill net selectivity, tangled fish are almost always rejected as a nuisance (Amarasinghe and Pushpalatha 1997; Helser et al. 1991; Mahon et al. 2000). This is true even though there are catches which are entirely tangled fish (Hamley and Regier 1973). It has been suggested that tangling is a dependent rather than a random process and from looking at published data (Table 1), it appears that the proportions of tangled fish in the catch are not simply noise but have a trend. This motivates the development of a framework that can incorporate tangled fish.

This paper proposes a framework for estimating gill net selectivity by directly estimating the probabilities leading to retention from the morphology of the fish and the geometry of the gill net instead of from fitting a statistical model. An intermediate step in deriving the selectivity curve through this framework is estimating the number of fish approaching and contacting the gill nets. The framework provides three pathways for estimating the number of fish approaching and contacting the gill nets that use information obtained from either or both wedged and tangled fish, as available. The method is tested by using wedged fish data to estimate the number of cod (*G. morhua*) contacting gill nets in Kandalaksha Bay on the White Sea in Russia and Dolly Varden (*S. malma*) contacting gill

nets in Kronotskoe Lake in Eastern Kamchatka, Russia.

Materials and methods

General methodology

Fish are retained in gill nets through either wedging or tangling and the likelihoods of both capture methods occurring depend on the fish morphology and the mesh parameters. Given a mesh size, wedging will occur for only some size range of fish. Fast-moving fish species have a body shape that minimizes drag, so all moving parts/bones of a skull or/and (bone) fin rays are pressed tightly to the body while moving (Aleev 1963). This allows fish to simply pass through a mesh if the maximum body girth is less than the mesh perimeter. Similarly, if a fish is too large it will not be able to enter the mesh to become wedged.

It has previously been suggested that tangling also depends on the ratio between fish size and mesh size (Grant et al. 2004; Hamley and Regier 1973). Fish become tangled in the mesh when they contact the thread of the gill net with their mouth and the thread catches on their teeth or maxillaries. This happens because many fish swim forward with their mouth open so water will flow across the gills without active pumping by the muscles surrounding the buccal and opercular cavities. This strategy is called ram ventilation, and is used by many active fish species

Table 1 Proportion of tangled fish in catches of different mesh size

Species	Mesh size (mm)	Share of tangled fish	Source
Lake trout <i>S. namaycush</i>	51	0.47	Hansen et al. (1997)
	57	0.47	
	64	0.44	
	70	0.31	
	76	0.18	
Hake <i>M. merluccius</i>	35	0.39	Santos et al. (2003)
	40	0.38	
	45	0.36	
	50	0.43	
Halibut <i>H. hippoglossus</i>	210	0.22	Olsen and Tjemsland (1963)
	241	0.23	
	310	0.24	

including cod and char (Christiansen and Jobling 1990; Randall 2014; Wegner et al. 2010).

For our analysis, we assume that the fish has contacted the plane of the gill net. There are then two possibilities: either the fish contacts the plane of the gill net at an opening (which we will denote O) where it could enter the mesh or it contacts one of the threads of the net (denoted Th). We let $P(O|C)$ be the probability that the fish contacts the net at an opening and $P(Th|C)$ be the probability of contacting a thread of the mesh, where $P(O|C) + P(Th|C) = 1$. Fish that contact the plane of the gill net at an opening will then either enter the mesh with probability $P(E|O)$, or back away from the net with probability $1 - P(E|O)$. Finally, fish that enter the mesh can become wedged—with probability $P(W|E)$ —if their maximum body girth is larger than the mesh perimeter or can pass through the mesh—with $1 - P(W|E)$ probability—if their girth is less than the mesh perimeter. Fish that contact a thread of the mesh, on the other hand, will either become tangled with $P(T|Th)$ probability or will back away from the plane of the net with probability $1 - P(T|Th)$. The pathways that fish can take to become wedged or tangled in a gill net, along with the associated probabilities, are shown in Fig. 1.

We will discuss how to derive each of these probabilities below, but we first note that if these probabilities are known then the number of fish, N_{Total} , that contacted the net can be determined in three ways. Letting N_W be the number of wedged fish in a catch and N_T be the number of tangled fish in the catch, then the three derivations of N_{Total} are:

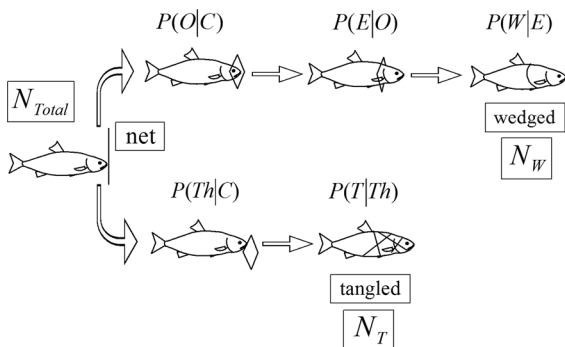


Fig. 1 The different stages of fishing describing their own probabilities. One set of probabilities lead to the fish becoming wedged while the other set leads to the fish becoming tangled

$$N_{Total} = \frac{N_W}{P(E|O) \cdot P(W|E)} + \frac{N_T}{P(T|Th)}, \quad (1)$$

$$N_{Total} = \frac{N_W}{P(O|C) \cdot P(E|O) \cdot P(W|E)}, \quad (2)$$

$$N_{Total} = \frac{N_T}{P(Th|C) \cdot P(T|Th)}. \quad (3)$$

These three equations allow the total number of fish contacting the net to be determined using only the tangled fish in a catch (Eq. 3), only the wedged fish (Eq. 2), or both wedged and tangled fish (Eq. 1).

Derivation and estimation of probabilities

The probabilities in Fig. 1 can be estimated based on the geometry of the mesh and the fish morphology. First we consider the probabilities for the fish contacting the plane of the net at either an opening, $P(O|C)$, or a thread of the mesh, $P(Th|C)$. Because the individual openings of a gill net mesh have a uniform shape throughout the net, these probabilities can be determined by considering a single opening. Let h be the distance between points Q and F on the upper and lower jaws of the fish, respectively (Fig. 2). The line segment QF will then be used to determine when the fish contacts a thread (Fig. 2a). Since the width of the mouth opening is h , there is an interval of height h on either side of the thread within which contact with the plane of the net will result in contact of the fish mouth with a thread (Fig. 2b).

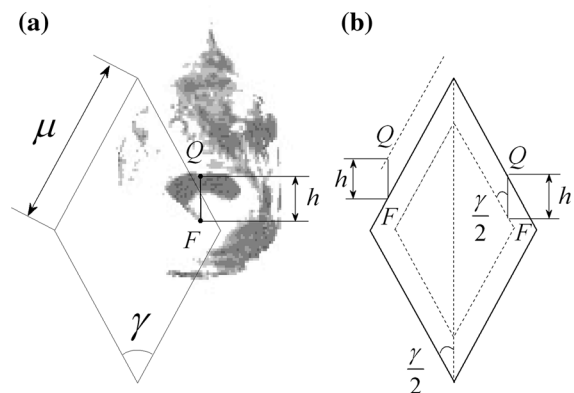


Fig. 2 **a** Contact of fish (shown front-on with mouth open in the background) with net leading to tangling. **b** Parameters determining the $P(Th|C)$ probability

The probability, $P(O|C)$, that a fish contacts the net at an opening where it can enter the mesh without catching a thread in its mouth is then given by the ratio of the area of the mesh opening that is greater than a distance h from any thread divided by the total area of the mesh opening. The probability, $P(Th|C)$, of the fish contacting a thread with its mouth is one minus $P(O|C)$. Using area formulas, these geometric formulas can be written as

$$P(O|C) = \frac{(\cos \frac{\gamma}{2} \mu - h)(\sin \frac{\gamma}{2} \mu - \tan \frac{\gamma}{2} h)}{\cos \frac{\gamma}{2} \cdot \sin \frac{\gamma}{2} \cdot \mu^2}, \quad (4)$$

$$P(Th|C) = 1 - \frac{(\cos \frac{\gamma}{2} \mu - h)(\sin \frac{\gamma}{2} \mu - \tan \frac{\gamma}{2} h)}{\cos \frac{\gamma}{2} \cdot \sin \frac{\gamma}{2} \cdot \mu^2}, \quad (5)$$

where μ is the mesh size, γ is the smaller of the angles between mesh threads as determined by the hanging ratio, and h is the mouth gape (Fig. 2). The mouth gape parameter h can be determined as

$$h = j \times 2 \sin \varphi, \quad (6)$$

where j is the jaw length and φ is angle between the ends of upper and lower jaws when the mouth is opened during ram ventilation. Note that j can be determined by measuring fish in the catch, but φ is difficult to determine experimentally since it is a property of the fish while it is swimming and is significantly smaller than the maximum mouth gape. Because φ is difficult to measure, it is instead estimated by looking at catch data using different mesh sizes. The estimation method is described in the results section.

Both $P(O|C)$ and $P(Th|C)$ change with length class, with the probability of contacting a thread increasing with fish size for a specific mesh size while the corresponding probability of contacting an opening in the mesh decreases with fish size (Fig. 3).

Next we consider what happens after a fish contacts the gill net at a mesh opening. The likelihood that the fish enters the mesh will depend on the size of the fish and the angle at which the fish contacts the plane of the net. We assume that fish always go into the mesh if they encounter the net while moving perpendicular to the plane of the net and the likelihood of entering the net decreases as the angle of incidence decreases. Furthermore, there is some angle, $\alpha_{\text{thres.}} > 0$, where the probability of entering the net becomes zero. Thus no fish enter when encountering the net at an angle

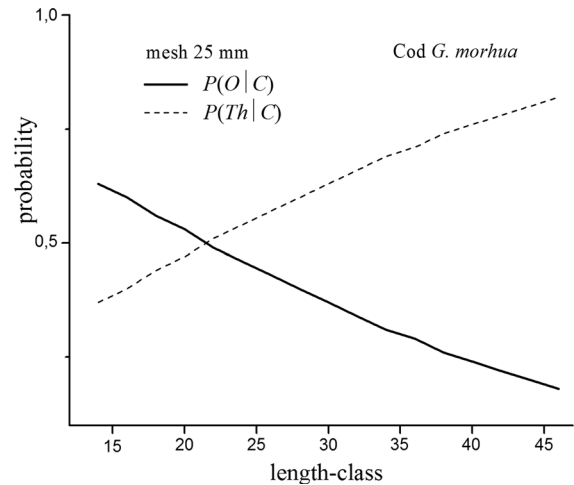


Fig. 3 $P(O|C)$ and $P(Th|C)$ probability curves for different length classes of cod and a mesh size of 25 mm

$\alpha \in [0, \alpha_{\text{thres.}})$ and there is a probability of entering when $\alpha \in [\alpha_{\text{thres.}}, \pi/2]$.

In theory, the probability of being in a certain area is proportional to its square, length or volume (Kendall and Moran 1963). Thus, the probability $P(E|O)$ of entering the mesh after encountering an opening depends on the threshold angle $\alpha_{\text{thres.}}$ as

$$P(E|O) = \frac{\pi/2 - \alpha_{\text{thres.}}}{\pi/2}. \quad (7)$$

The $\alpha_{\text{thres.}}$ value can be estimated by looking at the fish morphology. A fish will enter the mesh if the front of its head (tip of its snout) enters the mesh before the fish contacts a thread of mesh with its gill cover. We note that the movement of a fish tangent to the net does not lead to the fulfillment of this condition. The threshold angle can then be estimated by the fish's location, relative to the gill net, when the fish contacts the mesh with both the tip of the snout and the gill cover, simultaneously (Fig. 4). At that contact, the longitudinal axis of the fish's body forms the threshold angle $\alpha_{\text{thres.}}$ with the gill net.

Using this definition, $\alpha_{\text{thres.}}$ can be determined as

$$\alpha_{\text{thres.}} = \arcsin\left(\frac{d}{\omega}\right), \quad (8)$$

where d is half the fish body thickness at the point of contact of the gill cover with the thread and ω is the distance between opposite mesh knots in the

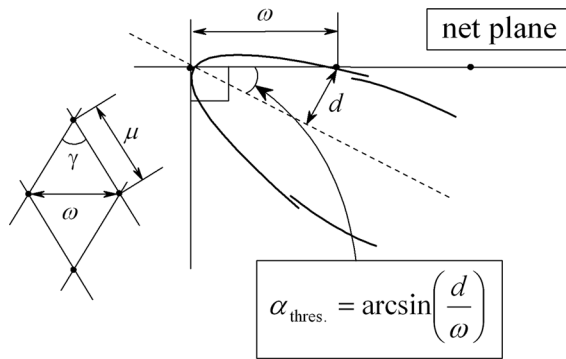


Fig. 4 The pattern of the interaction between the fish and the gill net leading to the $\alpha_{\text{thres.}}$ angle forming

horizontal plane (Fig. 4). Combining Eq. (7) with Eq. (8), the probability $P(E|O)$ for each length class becomes

$$P(E|O) = 1 - \frac{2}{\pi} \cdot \left(\arcsin\left(\frac{d}{\omega}\right) \right), \quad (9)$$

where $\omega = \mu \cdot \sqrt{2 \cdot (1 - \cos \gamma)}$ (Fig. 5).

In practice, Eq. 9 can be well approximated by a linear function whose coefficients can be determined from the catch data. A linear approximation is mathematically valid since the first order Taylor expansion of $\arcsin x$ is $\arcsin x = x$ and graphically it can be seen that the two curves match well (Fig. 6). The smallest length-class of wedged fish has a $P(E|O)$ probability equal to 1, and any fish larger than the biggest length-class of wedged fish has a $P(E|O)$ probability equal to 0. Then function (9) of probability

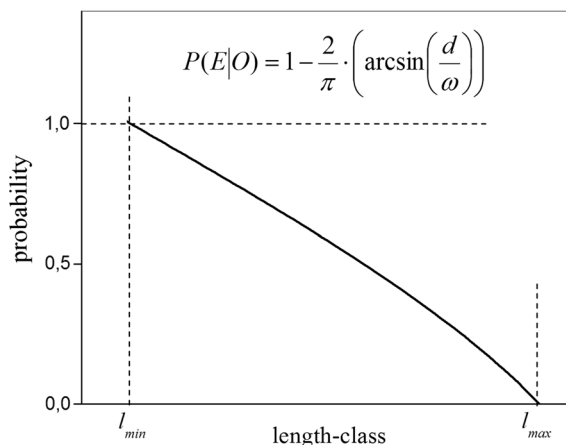


Fig. 5 The $P(E|O)$ probability curve

$P(E|O)$ can be approximated with the linear function: $P(E|O) = a - bx$, where x is the length-class (Fig. 6).

Once a fish enters the mesh, it will become wedged with some probability $P(W|E)$ and the maximum body girth, G_{max} , is what determines fish retention in a mesh (Kawamura 1972). Studies have shown that a fish's body is slightly elastic and can deform when squeezing through a mesh by as much as 14% (Treshev 1974). Thus fish are retained in a given mesh if $G_{\text{max}} \times 1.14$ is greater than the perimeter of the mesh (4μ in Fig. 2) and fish swim through the mesh otherwise. The probability $P(W|E)$ of being wedged for each length-class can then be written as

$$P(W|E) = \frac{N_{G_{\text{max}} \times 1.14 > 4\mu}}{N_{G_{\text{max}} \times 1.14 > 4\mu} + N_{G_{\text{max}} \times 1.14 \leq 4\mu}}, \quad (10)$$

where 4μ is mesh perimeter. It is obvious that $P(W|E) = 1$ for length-class where there are no fish having $G_{\text{max}} \times 1.14 < 4\mu$, and $P(W|E) = 0$ for length-class where no fish have $G_{\text{max}} \times 1.14 \geq 4\mu$.

Now we consider a length class in the catch that has both wedged and tangled fish. It is obvious that wedged fish have $G_{\text{max}} \times 1.14 > 4\mu$ only, whereas among tangled fish there are fish with both $G_{\text{max}} \times 1.14 > 4\mu$ and $G_{\text{max}} \times 1.14 \leq 4\mu$. Then the number of fish N_W^* with $G_{\text{max}} \times 1.14 \leq 4\mu$ that went into the mesh and passed through is proportional to the wedged fish N_W with $G_{\text{max}} \times 1.14 > 4\mu$, and the number of tangled fish N_T with $G_{\text{max}} \times 1.14 \leq 4\mu$ is proportional to a number of tangled fish with $G_{\text{max}} \times 1.14 > 4\mu$:

$$\frac{N_W^*_{G_{\text{max}} \times 1.14 \leq 4\mu}}{N_W_{G_{\text{max}} \times 1.14 > 4\mu}} = \frac{N_T_{G_{\text{max}} \times 1.14 \leq 4\mu}}{N_T_{G_{\text{max}} \times 1.14 > 4\mu}}. \quad (11)$$

Then $P(W|E)$ probability can be written as

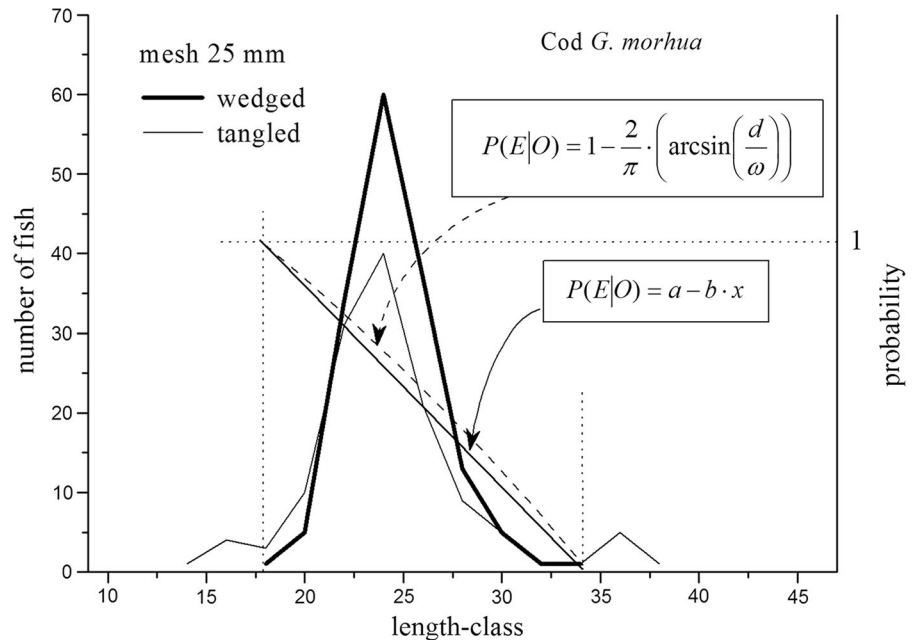
$$P(W|E) = \frac{N_T_{G_{\text{max}} \times 1.14 > 4\mu}}{N_T_{G_{\text{max}} \times 1.14 > 4\mu} + N_W_{G_{\text{max}} \times 1.14 > 4\mu}}, \quad (12)$$

and the number of fish $N_W^*_{G_{\text{max}} \times 1.14 \leq 4\mu}$ that swam through the mesh is

$$N_W^*_{G_{\text{max}} \times 1.14 \leq 4\mu} = \frac{N_W_{G_{\text{max}} \times 1.14 > 4\mu} \times N_T_{G_{\text{max}} \times 1.14 \leq 4\mu}}{N_T_{G_{\text{max}} \times 1.14 > 4\mu}}. \quad (13)$$

Finally, if a fish contacts the plane of the gill net at a thread instead of an opening it will become tangled with some probability $P(T|Th)$. We emphasize that $P(T|Th)$ is more difficult to explicitly estimate based

Fig. 6 The $P(E|O)$ probability distribution for cod, approximated with the linear function and overlaid on the catch totals



on the fish morphology and for this reason we will not use it here in deriving the number of fish contacting gill nets. If further research facilitates the estimation of this probability, however, it can be incorporated into this framework to use the counts of tangled fish.

Saturation

It has been proposed that when gillnets of different mesh size are fished concurrently, approximately the same number of fish contact every net (Baranov 1948) and all indirect methods of estimating gillnet selectivity are implicitly based on the assumption. The more accurate assumption, however, is that approximately the same number of fish *approach* every net because gillnet catchability is affected by saturation (Kennedy 1951; Prchalová et al. 2011; Hansen et al. 1998; Yan et al. 2011). Saturation occurs due to the limited amount of space in a net and an increase in fish avoidance of an occupied net. For example, if the same number of fish approach nets of 20 and 30 mm mesh size and the 20 mm net catches more than the 30 mm net due to selectivity, then the 20 mm net will fill up faster and effectively stop fishing earlier. Thus, in a long enough, fixed period of time the number of fish contacting the 30 mm net will be greater than the number that contacted the 20 mm net. The same number will have approached both nets, but more will

have backed away from the 20 mm net because there were already fish caught in the net.

The number of fish that approach a net of given mesh size during operation can be divided into three groups: (1) those that touched and are retained in the net (Q), (2) those that touched but were not retained due to selectivity (SL), and (3) those that back away from the net due to saturation (B). Let $N_{AP,j}$ be the number of fish approaching a net of mesh size j . Then, for the 20 and 30 mm mesh size examples above, the following is true:

$$N_{AP,20} = Q_{20} + SL_{20} + B_{20}; \quad (14)$$

$$N_{AP,30} = Q_{30} + SL_{30} + B_{30}, \quad (15)$$

where $N_{AP,20} \approx N_{AP,30}$ and $Q + SL = N_{Total}$. Hence, if $Q_{20} > Q_{30}$, then $B_{20} > B_{30}$ and $SL_{20} < SL_{30}$, which means that if more fish were caught by one mesh size net then more fish also backed away during the fishing operation and fewer fish were not retained as a result of selectivity.

Previous studies have shown that the saturation curve of a gill net increases to a certain value and then plateaus (Kennedy 1951; Prchalová et al. 2011; Hansen et al. 1998; Yan et al. 2011). We describe this saturation function as follows. Let the number of fish, Q_t , that have been caught at some time t of net sampling be proportional to the difference $N_{lim} - Q_t$,

where N_{lim} is the maximum number of fish that can be caught by the particular net. Mathematically, the gillnet saturation is then described by the following differential equation:

$$\frac{dQ}{dt} = b \cdot (N_{\text{lim}} - Q); \quad (16)$$

where b is the coefficient of proportionality. The solution to (16) is

$$Q_t = N_{\text{lim}} \cdot (1 - \exp(-b \cdot t)). \quad (17)$$

The coefficient b can be expressed as $1/\tilde{\tau}$, where $\tilde{\tau}$ is the time when the gill net catchability (which is assumed to be proportional to the net area not occupied by fish) is reduced by a factor of e (≈ 2.72) (“Appendix 1”). Hence the catchability of a gill net reduces as fish accumulate in it, as has been observed (Olin et al. 2004).

Let the same number of fish approach the net during fixed time intervals so that the number of fish approaching the net is described by the linear function (Fig. 7):

$$f(x) = kt. \quad (18)$$

Then, the number of fish, B_t , that backed away from the net due to saturation is

$$B_t = N_{AP,t} - Q_t - SL_t, \quad (19)$$

where $N_{AP,t}$ is the number of fish approaching the net during time t and is described by the given function (“Appendix 2”):

$$N_{AP,t} = \left(\frac{N_{\text{lim}} \cdot 1.71 + SL_{\tilde{\tau}}}{\tilde{\tau}} \right) \cdot t. \quad (20)$$

where SL is determined as the difference between N_{Total} and the catch at time t [according to the definition of contact selectivity (Millar and Fryer 1999)]. Hence, the number $SL_{\tilde{\tau}}$ at time $\tilde{\tau}$ is $SL_{\tilde{\tau}} \approx \frac{SL_{\tilde{\tau}} \cdot \tilde{\tau}}{t}$. As one can see, the catch Q_t increases to N_{lim} , SL_t increases to its maximum but then declines to zero at t_{lim} (the time when $Q = N_{\text{lim}}$), and B_t increases constantly during fishing operation (Fig. 7).

In practice N_{lim} can be estimated as follows. Before sampling, each gill net of a given mesh size is fished until totally filled up with fish—that is, there is no vacant net space left at the end of operation. The total number of fish caught then is assumed to be N_{lim} . Then, $\tilde{\tau}$ is:

$$\tilde{\tau} = \frac{t}{-\ln\left(1 - \frac{Q_t}{N_{\text{lim}}}\right)} \quad (21)$$

Data

To evaluate the proposed methodology, we use field data of cod (*G. morhua*) which were collected in Kandalaksha Bay, Russia—which is on the White Sea—in 2014 and Dolly Varden (*S. malma*) collected in Kronotskoe Lake in Eastern Kamchatka, Russia in 2013. Fishing was carried out in both places using identical monofilament gill nets of different mesh sizes with a 0.5 hanging ratio. The length of the nets is 30 m for cod and 15 m for Dolly Varden, the height of the nets is 1.5 m. Duration of fishing operations is 12 h for both species (from sunset to dawn), number of fishing operations are 11 for cod and 9 for Dolly Varden. Dolly Varden were caught with gill nets of 22, 25, 30 and 35 mm mesh size (knot to knot) and cod were caught with gill nets of 20, 25 and 30 mm mesh size. The different mesh size nets were set together and were fished concurrently. In both cases nets were set in the afternoon and retrieved the following morning.

In total, 694 cod and 783 Dolly Varden were caught (Table 2). The weight, length, maximum girth and jaw

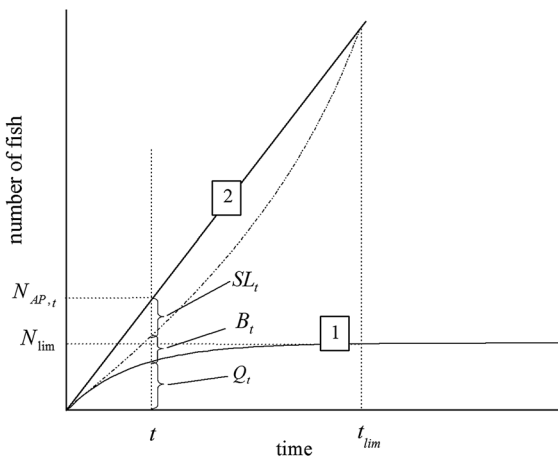


Fig. 7 Number of fish B_t backed away from the net as a difference between the numbers of fish $N_{AP,t}$ approached the net and the sum of catch Q_t and the number SL_t that were not retained due to selectivity at the time t (1—saturation curve, 2—curve of number of fish approaching the net)

Table 2 Catch composition and computed $P(WG)$ Probability for cod *G. Morhua* and Dolly Varden *S. malma*

Length class (cm)	Catch compositions, W —wedged, T —tangled fish												$P(W G)$ Probability															
	Cod <i>G. morhua</i>						Dolly varden <i>S. malma</i>						Cod <i>G. morhua</i>						Dolly varden <i>S. malma</i>									
	Mesh size (mm)																											
	W	T	25	W	T	30	W	T	22	W	T	25	W	T	30	W	T	35	W	T	20	25	30	22	25	30	35	
12																					0.00							
14	2	2			1						4		2	1							0.35	0.00		0.00				
16	20	5			4			2	2		8		6	3							0.69	0.01		0.15	0.00			
18	15	12	1		3			3	5		14		3	15	6						0.81	0.05		0.22	0.05			
20	11	8	5		10			5	29		18		6	11	6						0.88	0.26	0.00	0.70	0.10	0.00		
22	20	18	34	31		2		5	31		18		9	10	2	7					0.98	0.70	0.02	0.90	0.32	0.05		
24	32	24	60	40		8		9	17		9		19	11	5	6					1.00	0.79	0.05	1.00	0.72	0.10	0.00	
26	23	31	37	21		25		11	18		13		31	9	18	11	3	8			1.00	0.88	0.44	1.00	0.90	0.36	0.05	
28	8	19	13	9		15		7	15		16		14	12	15	7	5	7				1.00	1.00	0.70	1.00	0.43	0.10	
30	2	8	5	5		9		5	7		5		13	5	11	6	3	3				1.00	1.00	0.88	1.00	0.82	0.18	
32		2	1			3		6	1		8		7	8	5	6	6	2								1.00	0.70	
34	6	6	1		1	2		2			9		3	5	3	3	2	8					1.00		1.00	1.00	0.86	
36	3	3			5	1		4			5		1	2	3	1	6	3					1.00				1.00	
38	2	2			1			4			3			3	1	3	2	2									1.00	
40		3						1			4		5	1	3	2	6											1.00
42					1						2		4	1	1	1	6											
44											2				1	1	8											
46											4		3		2		1											
48											1																	
50											3																	
52											3				2		2											
54											1				1													
56											2				2													
Total	133	143	157	132	65	64	125	156	106	119	65	82	31	99														

Table 3 Mean jaw length distributions \bar{j} for cod and Dolly Varden

Length class	Mean jaw length, \bar{j}	
	Cod <i>G. morhua</i> $0.81 + 1.16 \cdot x$, $R = 0.99$	Dolly Varden <i>S. malma</i> $- 4.84 + 0.99 \cdot x$, $R = 0.97$
12	–	9.7
14	17.0	10.0
16	19.0	11.8
18	22.0	14.0
20	24.0	15.4
22	26.0	18.5
24	29.0	18.6
26	31.5	18.6
28	33.5	21.2
30	35.5	25.2
32	37.5	27.0
34		29.9
36		25.0
38		–
40		35.0
42		35.9
44		39.6
46		–
48		35.7
50		44.5
52		48.3
54		55.8
56		47.2
58		58.1

length (Table 3) of all captured fish were measured to the nearest gram and millimeter and the method of capture (wedging or tangling) was registered. Together with cod 176 navagas *Eleginus navaga* (141 fish are in the net of 20 mm mesh size, 31 in 25 mm and 5 in 25 mm), 171 sculpins *Myoxocephalus scorpius* (98 fish in 20 mm, 43 in 25 mm and 30 in 25 mm) and 77 flounders (4 species, *Pleuronectes platessa*, *Platichthys flesus*, *Limanda limanda*, *Liopsetta glacialis*—20 fish in 20 mm, 32 in 25 mm and 25 in 25 mm) were caught. In both cases the averaged catches per unit effort (CPUE) were used for analysis.

Results

For both species, we estimate the number of fish contacting the gill net using Eq. (2). This requires computing each of the probabilities as described in the previous section. To estimate the c probability, G_{\max}

was first selected from tangled fish because wedged fish with $G_{\max} \times 1.14 \leq 4\mu$ are absent as a result of escaping through the mesh. For each length class the cod and Dolly Varden were each divided into two groups consisting of $G_{\max} \times 1.14 > 4\mu$ and $G_{\max} \times 1.14 \leq 4\mu$. The $P(W|E)$ probability is then determined for each length class of the given species using Eq. 12 (Table 2).

To calculate the linear approximation of the $P(E|O)$ probability function, the catch compositions are analyzed to find the upper (which corresponds to probability 1 of entering the mesh) and lower (which corresponds to probability 0 of entering the mesh) limits of wedged fish for each mesh size (Table 2). These two points then uniquely determine the linear function (Table 4).

The $P(O|C)$ probability (Eq. 4) has a single unknown parameter—the average angle, φ , between the ends of the upper and lower jaws of the fish when

Table 4 $P(E|O)$ probability function of given mesh size for cod and Dolly Varden

Mesh size (mm)	$P(E O)$ probability
Cod <i>G. morhua</i>	
20	0.100–0.435 ·x
25	1.000–0.056 ·x
30	1.111–0.050 ·x
Dolly Varden <i>S. malma</i>	
22	0.889–0.056 ·x
25	0.900–0.056 ·x
30	1.000–0.045 ·x
35	1.300–0.038 ·x

the mouth is open during ram ventilation. Since this parameter is difficult to determine experimentally, we must estimate it. To estimate φ , we use the assumption that an equal number of fish approach each of the gill nets regardless of mesh size and that φ is independent of mesh size. We then compute the number of fish approaching each of the three gill nets for a range of values of φ and select the value of φ that minimizes the normalized sum of the sample variances between the computed numbers of fish approaching the different mesh size nets in different length classes. For a given length class, l , the estimated number of fish in that class should be the same for all mesh sizes, m . The sample variance for that length class is

$$\sigma_l^2 = \frac{1}{M-1} \sum_{m=1}^M (N_{l,m} - \bar{N}_l)^2 \quad (22)$$

where M is the number of mesh sizes being compared, $N_{l,m}$ is the number of fish estimated to be in length class, l , based on mesh size, m , and \bar{N}_l is the average across mesh sizes of the estimated number of fish in the length class l . We then sum these variances over all of the length classes that have estimates for all mesh sizes and then normalize by dividing by the average total number of fish across these length classes. That is, we minimize the function

$$f(\phi) = \frac{\sum_{l \in L} \sigma_l^2}{\sum_{l \in L} \bar{N}_l} \quad (23)$$

where L is the collection of all length classes that have estimates for all of the mesh sizes being compared. Normalizing is important because otherwise a smaller total variance could be achieved by simply decreasing

the number of fish estimated in each length class. Using the normalization of the total number of fish ensures that multiplying the number of estimated fish by a constant (for example, doubling the estimated number of fish in each length class) will not change the value of φ .

Computed $P(O|C)$ probability distributions for cod and Dolly Varden as a function of φ are given in Table 5. Since different mesh sizes catch different range of length classes, we restrict the comparison to length classes where some fish are caught by every mesh size. In the case of cod, we compare five length classes from 22 to 30 cm and get that φ is 8.7 (Fig. 8) and for Dolly Varden we obtain φ is 6.3 using six length classes ranging from 22 to 32 cm. Although four different mesh sizes were fished for Dolly Varden, we elect to not consider the 35 mm net here. This is done for two reasons. First, it ensures that a larger number of length classes are compared among mesh sizes. In addition, the other mesh sizes appear to capture length classes on sides of the peak of Dolly Varden contacting the net, whereas the 35 mm mesh does not. For both cod and Dolly Varden, the solutions are computed using Excel.

The minimum value of $\varphi = 8.7$ is used to compute the number of cod approaching the gill nets in Fig. 9.

After estimating all of the probabilities and B_i , we can combine them using Eqs. 2, 14 and 20 to derive the number of cod and Dolly Varden contacting and approaching to the gill nets of different mesh size (Table 6). The number of cod approaching the nets was derived taking into account the other species retained together with cod.

Selectivity

The contact-selection curve, $r(l)$, is the probability that a fish of length l that contacts the gear is captured (Millar and Fryer 1999). Since we derived the number of fish contacting the net and we have the number of fish that were captured, we can estimate the selectivity of a gill net of a given mesh size to fish of a length size, l , as the number of fish of length l captured with the given gill net divided by the number of fish of length l that contacted the net. Using this method we can derive the selectivity curves for the experiments described above (Fig. 10).

Selectivity curves from the literature are bell-shaped probability distributions described by normal,

Table 5 Computed $P(O|C)$ probability distributions for cod ($\varphi = 8.7$) and Dolly Varden ($\varphi = 6.3$)

Length class (cm)	Mesh size						
	Cod <i>G. morhua</i>			Dolly Varden <i>S. malma</i>			
	20	25	30	22	25	30	35
	$P(O C)$ probability						
14	0.46	0.58	0.62	0.79	0.82	0.85	0.87
16	0.41	0.54	0.58	0.75	0.78	0.82	0.84
18	0.36	0.50	0.54	0.71	0.74	0.78	0.81
20	0.32	0.46	0.51	0.67	0.71	0.75	0.79
22	0.28	0.42	0.47	0.63	0.67	0.72	0.76
24	0.24	0.39	0.44	0.60	0.64	0.69	0.73
26	0.21	0.35	0.41	0.56	0.61	0.67	0.71
28	0.18	0.32	0.38	0.53	0.57	0.64	0.68
30	0.15	0.29	0.35	0.49	0.54	0.61	0.66
32	0.12	0.26	0.32	0.46	0.51	0.58	0.64
34	0.09	0.23	0.29	0.43	0.48	0.56	0.61
36	0.07	0.21	0.26	0.40	0.45	0.53	0.59
38	0.05	0.18	0.24	0.37	0.43	0.51	0.57
40	0.04	0.16	0.22	0.34	0.40	0.48	0.54
42	0.03	0.14	0.19	0.31	0.37	0.46	0.52
44	0.01	0.12	0.17	0.29	0.35	0.43	0.50
46				0.26	0.32	0.41	0.48

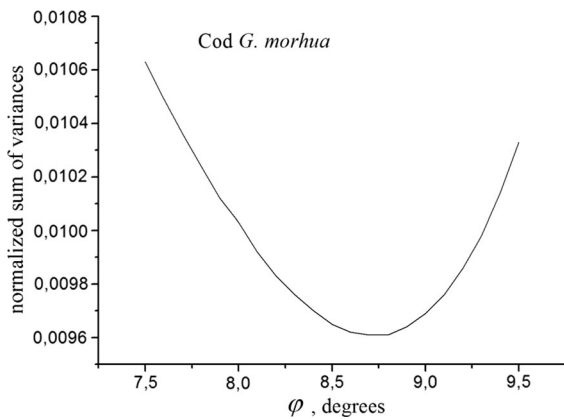


Fig. 8 Normalized sum of variances between the estimated total number of fish approaching the 20, 25 and 30 mm mesh size nets for cod

lognormal, gamma, or other functions (Baranov 1948; Anderson 1998; Hamley and Regier 1973; Millar and Fryer 1999; Tanaka 2002). The selectivity curves derived here also have a bell shape, but are more irregular because the real fish morphometry and gill net parameters are used.

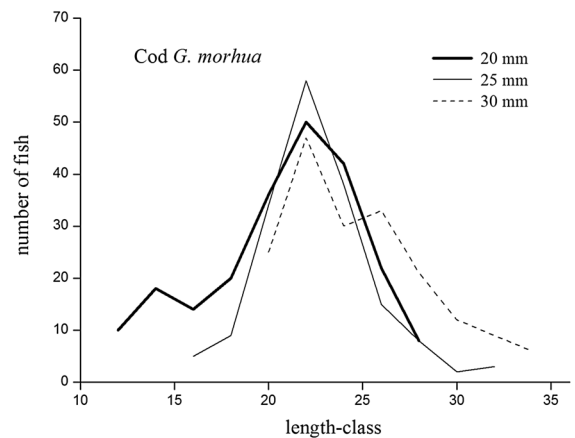


Fig. 9 The computed number of cod of different length classes approaching to the three gill nets for $\varphi = 8.7$

Discussion

Traditional methods of estimating selectivity using normal, log-normal, or gamma functions cannot be used to evaluate the number of fish contacting a gill net. In this paper we introduced a new method that uses the morphology of the fish and the geometry of the mesh to estimate the number of fish that contact a

Table 6 Recovered length-class distributions of cod and Dolly Varden, contacted and approached the gillnets computed for averaged catch per unit effort (CPUE), length of gillnet is 30 m for cod and 15 for Dolly Varden

Length class (cm)	Mesh size															
	Cod <i>G. morhua</i>								Dolly Varden <i>S. malma</i>							
	Contacted				Approached				Contacted				Approached			
	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
N_{lim}					75	55	30						33	28	20	16
$\bar{\tau}$, h					12	11	14						20	18	13	9

gill net. The proposed framework theoretically allows for the derivation to come from either the number of fish caught by wedging or entanglement. Probabilities for each method of entrapment are then broken up into probabilities for several stages of interaction between the fish and the gill net (three steps for wedging, two steps for entanglement) and each of these has its own probability that is described by its own function. Thus, each interaction stage is characterized by its own “selectivity” which defined a proportion of fish that go from the previous interaction to the next one.

The method is tested here on two catches, but can be applied to any fishery. To summarize this method, here is a list of the steps that need to be taken to derive the selectivity.

1. Fish at least 3 separate sizes of gill nets concurrently and remove nets before saturation. To account for saturation effects, also fish a net to saturation to record the amount of time it takes to reach saturation.
2. Record the parameters of the mesh, the size and method of capture of the fish, and measure the jaw length of fish in the catch.
3. Use Eq. 13 to estimate the number of fish that entered the mesh.
4. Derive the linear approximation of the $P(E|O)$ probability (shown in the Fig. 6) using data for the largest and smallest length classes of wedged fish.
5. Compute the total number of fish contacting the gill net, N_{Total} , as a function of the single unknown parameter is φ . This computation is completed using Eq. 2, which relies on Eqs. 4, 5 and 6. We have completed this computation in Excel starting with an arbitrarily chosen φ value (from 4 to 7, for instance). The number N_{Total} must be divided by the number of fishing operations to get an averaged catch per unit effort (CPUE).
6. Using Eq. 20, the number of fish in each length class approaching the net is computed for each gill net.
7. Find the value of φ that minimizes Eq. 23. Here this has been done by trial and error by plugging in different values of φ and recording the output.
8. After determining the correct φ value, the selectivity of the particular net is calculated according to the definition of contact selectivity as the ratio

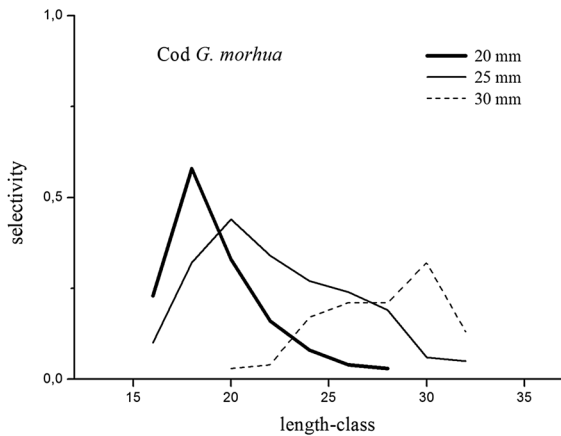


Fig. 10 Derived selectivity curves for the 20, 25 and 30 mm gill net mesh sizes

of the number of fish of the catch to the number of fish that contacted the net.

While we introduce equations that can be used to determine the number of fish contacting a gill net using the number of either tangled or wedged fish, the fact that the probability, $P(T|Th)$, that a fish becomes tangled after it contacts a thread of the net is not well characterized limits the current application of the method to only wedged fish counts. This is a challenging problem, as different species likely have different probabilities of being kept by entangling. For example, it appears that fast-moving fish having teeth, maxillaries and other projections are more likely to become tangled. This indicates that there are additional factors and parameters (e.g. fish speed or shape irregularities) that could be included into the model but are assumed to be negligible in this paper. These and other factors could be included in future work as refinements to this first order model.

There are several places where bias can be introduced to this method due to the fishing practices. One potential source of bias in this calculation arises because of the inaccurate identification of wedged and tangled fish. There are two ways that a fish is kept in the net by tangling. The first—which can be considered “true” entanglement—occurs when the first contact of the fish with the gill net leads to having a thread stuck in the mouth. The second, “false,” way occurs when fish are first wedged and then become tangles while trying to escape gill net. Distinguishing

between these two methods of tangling can be accomplished by pulling the mesh off the fish body.

Other potential important sources of bias are the duration and time of the fishing operation. It is well known that fish activity changes during day time, with freshwater fish species, for example, being most active at sunset and dawn. To reduce bias, it would be ideal to fish during these times when activity has increased and plateaued. In addition, it is crucial that the duration of the fishing operation be less than the time to the complete saturation of the gill nets.

As part of the proposed framework, we propose a method for estimating the average angle, ϕ , between the ends of the upper and lower jaws of the fish when the mouth is open during ram ventilation by minimizing the difference between the derived total number of fish approaching to each of the mesh sizes. The derived values here— $\phi = 6.3$ for Dolly Varden and $\phi = 8.7$ for cod—are reasonable based on the ecology of that species. Dolly Varden is a fast moving species that inhabits cold lakes and rivers that have a high concentration of dissolved oxygen while cod is a saltwater resident where there is a lower oxygen concentration. Cod also has a slower swimming speed. As a result, cod requires more intense aeration of the gill epithelium to meet physiological needs and thus a wider mouth gape and a larger ϕ . There is more work needs to be done, however, to explore whether there are optimal mesh sizes to use in estimating ϕ or whether there is a different analytical solution. Finally, future work could attempt to estimate ϕ experimentally to further refine and validate the estimation of ϕ .

The proposed method is straightforward and requires only a small amount of parameters that can be obtained easily from the total catch distribution analysis and fish measurement. The applicability of the method was demonstrated by estimating the number of two fish species contacting gill nets in lake and marine settings and the results a reasonable. When a group of nets of different mesh size is simultaneously used for fishing, it is expected that approximately the same number of fish approaches every net (Grant et al. 2004). Thus recovered length-class distributions are expected to have a common trend, and this is apparent in the final result.

The fact that this method produces an estimate of the number of fish of different sizes approaching and contacting the gill net in addition to the selectivity curve means that results can be extrapolated to

estimate the fish density in a particular fishery. Estimating the fish density and ultimately the size of the stock of a fishery will be explored in future work. We also note that there will necessarily be uncertainty in these measurements and derived estimates. In order to try to quantify the uncertainty in the selectivity curves, the same nets could be fished in different days and the derived curves could be compared. Taking an average of these curves would also smooth out the selectivity curves.

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Appendix 1

If the saturation curve is described by function (17), the reduction of vacant net area is described by the following function:

$$f(t)^* = \exp\left(-\frac{t}{\tilde{\tau}}\right).$$

Let the number of fish caught by the net be proportional to the net area where fish are retained, and let $t = \tilde{\tau}$. Then, $\exp\left(-\frac{t}{\tilde{\tau}}\right) = \exp(-1) \approx 0.368$. Next, we compare the vacant net area at time $\tilde{\tau}$ (its share is 0.368 from the total space) with the net area at the beginning of fishing where there are no fish in the net (share is 1). Then, $1/0.368 \approx 2.717 \approx e$.

Appendix 2

According to “Appendix 1”, if $t = \tilde{\tau}$, then $N_{AP,\tilde{\tau}} = Q_{\tilde{\tau}} \cdot e + SL_{\tilde{\tau}}$, where $Q_{\tilde{\tau}} \cdot e = Q_{\tilde{\tau}} + B_{\tilde{\tau}}$. Then, for 1 h of fishing $N_{AP,1} = \frac{Q_{\tilde{\tau}} \cdot e + SL_{\tilde{\tau}}}{\tilde{\tau}}$, where $Q_{\tilde{\tau}} = N_{\lim}(1 - \exp(-\frac{\tilde{\tau}}{\tilde{\tau}})) \approx N_{\lim} \cdot 0.63$. Hence, $\frac{N_{\lim} \cdot 0.63 \cdot e + SL_{\tilde{\tau}}}{\tilde{\tau}} \approx \frac{N_{\lim} \cdot 0.63 \cdot 2.72 + SL_{\tilde{\tau}}}{\tilde{\tau}} \approx \frac{N_{\lim} \cdot 1.71 + SL_{\tilde{\tau}}}{\tilde{\tau}}$ —that is the angular coefficient k of $f(t) = kt$ (Eq. 18).

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