A new method of estimating the length-dependency capture modes in gillnets with a case study in the Danish wreck fishery for cod.

Savina Esther[1a], Herrmann Bent[1,2,3], Frandsen P. Rikke[1], Krag A. Ludvig[1]

[1] Technical University of Denmark, Institute for Aquatic Resources, Section for Fisheries Technology, Willemoesvej 2, 9850 Hirtshals, Denmark;

[2] SINTEF Ocean, 9850 Hirtshals, Denmark; and

[3] The Artic University of Norway, 9037 Breivika, Tromsø, Norway.

[a] Corresponding author, esav@aqua.dtu.dk

Keywords: Bottom-set net; Capture mode; Entangling; *Gadus morhua*; Gear efficiency; Gilling; Size selectivity; Snagging; Wedging

Abstract

Gillnets are used world-wide for harvesting groundfish and pelagic species at sea and in freshwater. Little consideration has been given to how fish are caught in gillnets, even though the capture mode provides valuable information with respect to understanding how the fish is caught and retained by the meshes and its effect on gear catchability. This paper describes a new method of estimating the length-dependency capture modes in gillnets. Using this method, we investigated the length-dependency capture modes for cod in commercial monofilament nylon nets. Cod (*Gadhus morhua*) is a target species for several fisheries in the Northern Atlantic. This is the first time that capture mode was formally related to fish size with a direct representation of the experimental observations. The results demonstrated that gillnets are clearly designed for gilling, but capture modes were size dependent, with small fish being caught by the mouth and larger fish by the maxillary. The application of the method is relevant when used by gear technologists to compare different gear characteristics to improve size or species selectivity. Changing the hanging ratio, for instance, or replacing nylon twine by thicker biodegradable material may considerably change the resulting length of maximum probability for a given capture mode.

1. Introduction

A gillnet is a wall of netting hanging vertically in the water column with weights along the bottom and floats along the top that, in principle, fish swim into without noticing (He, 2006). Gillnets are widely used throughout the world for harvesting a variety of groundfish and pelagic species both at sea and in freshwater (He, 2006; Suuronen et al., 2012; Žydelis et al., 2013). Gillnetting is a versatile, fuel-efficient, and flexible fishing method that requires minimal investment and can be conducted from small vessels. It is used in coastal and offshore waters, on soft but also rougher grounds including wrecks and reefs (He, 2006; Suuronen et al., 2012; Žydelis et al., 2013). The name gillnet is given because the largest proportion of fish is caught by gilling , but fish are also caught by other modes of capture, such as by the maxillary (Hamley, 1975; Madsen *et al.*, 1999; Hovgard and Lassen, 2000; Lobyrev and Hoffman, 2018). Four categories are commonly discussed in gillnet literature, i.e., gilling (caught with the mesh behind the gill cover), wedging (caught by the largest part of the body), snagging (caught by the mouth or teeth, or other part of the head region) and entangling (caught by spine, fins or all parts of the body as a result of struggling) (Figure 1).

The capture mode, i.e., how the fish is caught and retained by the meshes, provides valuable information on catchability by understanding how the fish is caught and retained by the meshes. Indeed, an individual retained by a gillnet solely by snagging at mouth has a higher probability of escape from the net, and this can negatively affect catch efficiency (Potter and Pawson, 1991; Grati *et al.*, 2015). Mesh size, hanging ratio, twine diameter, twine construction and material type are well-known factors that affect the catch efficiency and the selectivity of gillnets (He, 2006). The resulting catch modes are therefore a consequence of the specific gillnet design tested. It was previously observed that more cod were caught by gilling and less by the maxillary as mesh size was increased (Hovgård, 1996). The optimal hanging ratio varies by target species, with higher hanging ratio for round fish, and lower hanging ratio for flatfish (He, 2006). When the hanging ratio is reduced the netting becomes slacker and allows for pockets to form, resulting in an increasing number of mainly smaller individuals entangled in the net (Hamley, 1975; Samaranayaka *et al.*, 1997; Hovgard and Lassen, 2000; He, 2006). The thickness of the twine used depends on the target species and the fishing ground where the nets are operated. To increase durability, thicker twine diameters are typically used for nets targeting larger fish, e.g., cod (*Gadhus morhua*) on deeper or rougher fishing grounds, whereas thinner twine is used for smaller species, e.g., sole (*Solea solea*) on smoother substrate. The material properties and thickness of the twine used influence the catchability of the specific net where thicker and therefore stiffer twines are known to reduce the nets ability to catch fish compared to nets with similar mesh sizes made in thinner twine that have a higher tendency for capture by teeth, maxillaries or entangling (Hansen, 1974; Hovgard and Lassen, 2000; Yokota *et al.*, 2001; He, 2006; Grati *et al.*, 2015). Differences in body shape account for some of the differences in the capture mode and catchability. It was observed that bream (*Abramis brama*) are more easily gilled in gillnets with a lower hanging ratio because of the shape of the mesh matching the morphology of the fish, compared to gillnets with a higher hanging ratio where bream is more successful in escaping (Machiels *et al.*, 1994). Protruding anatomical structures also account for some of the differences in the capture mode. Fast-moving fish having teeth, maxillaries and other projections are more likely to become entangled (McCombie and Berst, 1969; Lobyrev and Hoffman, 2018). It was observed that pikeperch (*Stizostedion lucioperca*) are probably not able to escape once wedged due to the spiny dorsal fin (Machiels *et al.*, 1994). Many fish swim forward with their mouth open so water can flow across the gills without active pumping by the muscles surrounding the buccal and opercular cavities, which will make the fish contact the netting with their mouth and get captured by the teeth or maxillaries (Christiansen and Jobling, 1990; Wegner *et al.*, 2010; Randall, 2014; Lobyrev and Hoffman, 2018). Indeed, previous studies on cod showed that most fish were gilled, a smaller proportion caught by the maxillary, and a few were caught by the teeth and otherwise entangled (Hovgård *et al.*, 1999; Wileman *et al.*, 2000; Holst *et al.*, 2002). Capture modes also depend on the fish length and struggling effort. Small fishes were observed to penetrate the mesh by their head and swim through the mesh, becoming snagged (e.g., caught by their mouth or teeth) or gilled, whereas large fish, if not gilled, are mainly enmeshed behind the maxillae or entangled as a result of struggling (Hovgård *et al.*, 1999; Holst *et al.*, 2002; Grant *et al.*, 2004; Rakhmadevi *et al.*, 2008).

The capture mode also provides valuable information with respect to understanding the output and limitations of traditional selectivity models. Gillnet selectivity is usually described by curves, one for each mesh size, that show how the probability of catching a fish changes according to the size of that fish (Hamley and Regier, 1973). Capture mode has been observed to increase the length range of the catch when more fish are entangled than gilled, and in most gillnet selectivity work, selection is therefore assumed to follow a right-skewed distribution or a bi-modal selectivity curve to describe both fish that are gilled and entangled (Hamley, 1975; Samaranayaka *et al.*, 1997; Madsen *et al.*, 1999; Wileman *et al.*, 2000). . Previous studies calculated the proportions caught by the different capture modes for several length classes pooled into given intervals, therefore treating fish length as a categorical variable (Wileman *et al.*, 2000). We argue that, since fish size was shown to have a significant effect on capture mode, fish length should be considered with all lengths classes as a continuous variable instead for a higher sensitivity. Additionally, previous statistical approaches used modelling methodologies developed for indirect estimation of gillnet selection curves based on varying mesh sizes fished simultaneously with equal effort that underestimate confidence limits when averaging over hauls (Millar, 2000; Krag *et al.*, 2014). We suggest instead that the length-dependency of capture modes can be modelled in a catch comparison setup using a double bootstrap approach, which allows estimating the Efron percentile 95% confidence limits for all relevant length values and account for potentially increased uncertainty resulting from model selection (Efron, 1982; Sistiaga *et al.*, 2010; Herrmann *et al.*, 2012; Krag *et al.*, 2014). This study aims at (1) investigating length-dependency of capture modes in the gillnet fisheries while using the double bootstrap approach to obtain confidence bands for each of the capture mode probability curves and (2) drafting guidelines for collection and analysis of selectivity (capture) data in gillnets with respect to capture modes. As a case study, we collected data in the Danish offshore gillnet fishery for cod using commercial monofilament nylon nets onboard a commercial gillnetting vessel. Such dataset pictures the effect of a specific gear design on cod catch efficiency. Changing the hanging ratio, for instance, may considerably change the resulting catch modes. The work is intended to set a methodological framework for further investigating the effect of capture mode on the catchability of different gear designs, i.e., differences in hanging ratio or effect of new netting material such as biodegradable netting.

2. Material and methods

2.1. Experimental design and sea trials

We deployed nylon nets (King Net, Japan) produced by Hvalpsund (Denmark) for the Danish commercial offshore cod fishery. Each gillnet had 75 mm half-mesh size (150 mm full mesh), was made of 0.57mm monofilament nylon twine, 30.5 meshes high, 300 m stretched length (2000 knots x 150 mm mesh size) and green in color. Inside mesh sizes were measured for 20 meshes in the dry state before the sea trial by inserting a steel ruler and using light hand force to stretch the mesh. The netting panel was mounted with a floatline of 10mm polypropylene rope with FL65 floats (65 g buoyancy) every 120 cm, and a leadline no. 4 (11 kg pr. 100 m) with lead in the core with a 6 mm hanging twine. The netting was mounted 3 meshes on 18 cm on the floatline and 3 meshes on 21 cm on the leadline following commercial practices in Skagerrak for cod. A mounted gillnet was about 60 m long and had a hanging ratio of 40%. Individual nets were attached with about 1 m rope between individual nets to form a fleet.

We fished a total of 9 days in August and September 2020 on both rocky grounds (reefs) and wrecks in Skagerrak off the coast of Hirtshals (Figure 2) onboard a Danish gillnetter (vessel length 14 m and engine power 141 kW). When fishing on the reefs, we used four fleets of eight nets. When fishing on the wrecks, we used three to six fleets of two nets. All deployments were done following commercial practices on commercial fishing grounds.

2.2. Data collection including observation of capture modes

Each fleet was hauled onboard using a deep water (Netop, Denmark) net hauler (Figure 3) at about XX. The catch was sorted out on the sorting table as each net was hauled on board the vessel (Figure 2). One individual cod was observed at a time before hauling in additional netting onboard (Figure 2). We registered the capture mode for cod before handling the fish, i.e., the netting section around each fish was carefully unfolded or stretched out to identify the capture mode as the fish was still held in the netting wall to identify the initial capture mode and avoid further or additional entanglement caused by hauling the net onboard or deck handling. The fish total length was measured to the nearest cm below.

Commented [ES1]: Add hauling speed. LUDVIG?

Mechanism of fish capture was classified in one of seven categories (Table 1, Figure 3), adapted from previous work (Hovgård *et al.*, 1999; Hovgard and Lassen, 2000; Wileman *et al.*, 2000; Holst *et al.*, 2002) after observation during a pilot day at sea onboard the commercial vessel prior to the experimental trial. The primary capture mode was defined by the position and tension of the twine, i.e., the tightest meshes indicated the primary mode retaining the fish in the netting, or alternatively the position of the net mark, i.e., a wound on the fish's body caused by mesh chafing (Yokota *et al.*, 2001). A fish was assigned one or several capture modes. Four different researchers participated in the trial, but all trained for identifying the capture modes similarly, and there were always two observers onboard during the entire data collection.

2.3. Assumed primary capture mode in case of several capture modes observed for one individual

In case multiple capture modes were observed, we assumed a primary capture mode according to the following principles. In general, we defined the primary mode based on the principle of likely sequence, i.e., the primary mode is the anatomical part of the fish that touches the netting the last.. We considered unlikely that a fish would be caught by the head after being caught by the mouth, or maxillary, and we therefore assumed that the primary capture mode for the multiple occurrences of "mouth", or "maxillary", and "head" would be "head". In line with this principle, we assumed that a fish cannot be caught by the gill after being caught by the mouth, maxillary, or head, and similarly cannot be caught by the body after being caught by the mouth, or head, or gill (Table 3). We always assumed that entanglement happened after the initial capture, and cases with entanglement were considered with the other capture mode as primary, e.g., maxillary or head or gill (Table 3). All other multiple occurrences, i.e., not possible to decide (mouth and maxillary) or more than 3 capture modes, were treated as "Unclear" in a conservative approach (Table 3).

2.4. *Modelling the length-dependent capture mode probability*

We used the statistical software SELNET (Herrmann *et al.*, 2012) to analyze the capture modes data. We conducted an analysis to determine, conditioned capture, the length-dependent probability for capture with each of the capture modes. We used the numbers and length measurements of fish registered to be caught with each of the modes. We considered all gillnet fleets from a fishing day to constitute a base unit for the analysis. Similarly to commercial deployments, each time a fleet is deployed, the nets may land differently on the sea floor, affecting the catch efficiency and capture modes. Considering fishing day rather than fleet deployment as a base unit for the analysis gives an identical mean estimate, but such approach is more conservative with respect to the additional uncertainty in capture modes due to differences between deployments. The analysis was carried out independently for the capture modes following the description below.

Conditioned capture, the expected probability for the capture mode *q* for fish length *l* will be:

$$CPq_l = \frac{\sum_{j=1}^{h} n_{qlj}}{\sum_{j=1}^{h}\sum_{i=1}^{Q} n_{ilj}} \qquad (1)$$

where n_{qlj} is the number *n* of fish caught per length class *l* with capture mode *q* in haul *j*. Q is the number of capture modes considered. *h* is the total number of fishing days. The functional description of the capture mode probability $CPq(l,\boldsymbol{v})$ expressed by Expression 1 was obtained using maximum likelihood estimation by minimizing the Equation (2):

$$-\sum_{j=1}^{h}\sum_{l}\left\{n_{qlj} \times ln[CPq(l,\boldsymbol{v})] + \left[-n_{qlj} + \sum_{i=1}^{Q} n_{ilj}\right] \times ln[1.0 - CPq(l,\boldsymbol{v})]\right\} \qquad (2)$$

In Equation (2), $\boldsymbol{v}$ represents the parameters describing the capture mode probability curve defined by $CPq(l,\boldsymbol{v})$ that spans the value range [0.0;1.0]. Equation (1) and (2) together are similar in form to what is often used for modelling and estimating the length-dependent catch comparison rate between two fishing gears (Krag *et al.*, 2014). Therefore, we adapted the same approach for modelling $CPq(l,\boldsymbol{v})$ as is often applied for catch comparison studies based on binominal count data (Herrmann *et al.*, 2017):

$$CPq(l,\boldsymbol{v}) = \frac{exp[f(l,v_0,\ldots,v_k)]}{1+exp[f(l,v_0,\ldots,v_k)]} \qquad (3)$$

In Expression (3), *f* is a polynomial of order *k* with coefficients $v_0 - v_k$, such that $\boldsymbol{v} = (v_0, \ldots, v_k)$. The values of the parameters $\boldsymbol{v}$ describing $CPq(l,\boldsymbol{v})$ are estimated by minimizing the Equation (2). We considered *f* of up to an order of 4. Leaving out one or more of the parameters $v_0, \ldots, v_k$, at a time resulted in 31 additional candidate models for the capture mode probability function $CPq(l,\boldsymbol{v})$. Among these models, the capture mode probability was estimated using the multi-model inference to obtain a combined model (Burnham and Anderson, 2002; Herrmann *et al.*, 2017). The ability of the combined model to describe the experimental data was based on the *p*-value, which is calculated based on the model deviance and degrees of freedom (Wileman *et al.*, 1996; Herrmann *et al.*, 2017). Thus, suitable fit statistics for the combined model to describe the experimental data sufficiently well should include a *p*-value >0.05.

We used a double bootstrapping method (1000 bootstrap repetitions) to estimate the 95% confidence intervals for the capture mode probability curve (Lomeli *et al.*, 2019).

We presented the length distribution of the sampled population as the modelled mean number of fish caught for the seven capture modes.

2.5. *Modelling the average (length-integrated) capture mode probability*

Length-integrated average value for the capture mode probability ($CPq_{average}$) was estimated directly from the experimental catch data using the following equation:

$$CPq_{average} = \frac{\sum_l \sum_{j=1}^{h} n_{qlj}}{\sum_l \sum_{j=1}^{h} \sum_{i=1}^{Q} n_{ilj}} \qquad (4)$$

where the outer summations include the size classes in the catch during the experimental fishing period. In contrast to the length-dependent evaluation of the capture mode probability curve $CPq(l, \boldsymbol{v})$, $CPq_{average}$ are specific for the population structure encountered during the experimental trials and cannot be extrapolated to other scenarios in which the size structure of the fish species may be different.

We used the packages dplyr (Wickham *et al.*, 2021) for data formatting and ggplot2 (Wickham, 2016) for graphical output in R statistical software (R Core Team, 2021).

3. Results

3.1. Data collected

Actual measurements of the mesh openings showed that the mesh size (mean ± standard deviation) was 151 ± 0.85 mm.

63 nets in 34 fleets out of a total of 174 nets in 39 fleets caught cod during the experimental period (Table 2). The soak time of the individual fleets varied between 2.02 and 11.7 hours (Table 2). The

fishing depth varied between 36 and 104 meters (Table 2). We registered capture modes for a total of 338 cod in 9 hauls (Figure 2, Table 2).

We could observe a single capture mode for 73% of the fish, mainly captured by the gills, mouth and maxillary (Table 3). For 23% of the fish, we were able to assume a primary mode based on the principle of likely sequence. These multiple occurrences were mostly associated with capture by the gills and mouth, maxillary and head, and gill and body (Table 3). Only 1% of the fish were observed with entanglement as secondary capture mode (Table 3). Other cases treated as unclear, i.e., not possible to decide (mouth and maxillary), or more than 3 capture modes, involved only 3% of the fish observed (Table 3).

With a Minimum Conservation Reference Size of 30 cm for cod in the Skagerrak, there was only one undersized individual caught in the whole catch.

3.2. Length-dependent capture mode probability

The capture mode probability curves described the trend in the experimental data points well (Figure 5). The experimental rates were subject to increasing binomial noise outside the length classes representing the main bulk of the catches, i.e., above 85 cm (Figure 5). The ability of the capture mode probability curves to describe the experimental data was also verified by the fit statistics (Table 4). Indeed, all *p*-value were above 0.05, indicating that the model describes the experimental data sufficiently well.

The main probability of capture was by the mouth for small fish (26-55 cm). However, there were very few individuals caught by the mouth with respect to the number of fish caught, i.e., 34 out of 338 (Figure 5). For fish above 55 cm, the probability of capture by the mouth decreased reaching low value for fish around 70 cm.

There was an indication of a main probability of capture by the maxillary and in a lesser extent by the head for large fish (85-98 cm), but no clear pattern due to wide confidence bands (Figure 5). These two modes caught only a small number of the fish, i.e., less than 5 for each length class (Figure 5).

From size 55 to 85 cm, the main probability of capture was by the gill (Figure 5).

Body, entangled, and unclear (more than 3 capture modes), played no role in capturing cod (Figure 5).

3.3. Average (length-integrated) capture mode probability

The length-integrated average value for the capture mode probability confirmed that the dominant mode of capture was by the gill with up to 67 (54-76) % of the fish observed (Table 4, Figure 6). There was similar and minor contribution of the mouth, maxillary, and head to capture of cod with about 10% probability of capture (Table 4, Figure 6). The length-integrated average value for the capture mode probability corroborated that the body, entangled and unclear capture modes played no role in the capture of cod with less than 5% probability (Table 4, Figure 6).

4. Discussion

We present a new method to collect and analyze capture/selectivity data from gillnets. This is the first time that capture mode was formally related to fish size with a direct representation of the experimental data points. This length-based catch comparison analysis is more informative than previous ways of analyzing and presenting results of capture modes. It offers a precise probability with 95% confidence limits accounting for the uncertainty in the estimation resulting from between-deployment variation as well as uncertainty about the size structure of the catch for the individual deployments due to the double bootstrapping procedure. By incorporating the multi-model inference into each bootstrap iteration, the method also accounts for the uncertainty due to model selection. Collecting information regarding capture mode was easy to execute at sea, providing that it was possible to observe each individual fish still caught in the netting. Providing they had previous experience at sea working with gillnets, the two observers onboard were able to observe capture modes and fish length following standard hauling speed used in commercial conditions. Classification into the different capture modes was relatively easy despite the fact that some individuals had penetrated the netting several times and were well and truly entangled in the netting (Holst *et al.*, 2002). One might consider video observation, but it was not always easy to observe the primary mode of capture without having to disentangle the fish first, and/or turn the fish. Pulling the mesh off the fish body can indeed allow to distinguish between wedged and tangled fish (Lobyrev and Hoffman, 2018). Four categories are commonly discussed in gillnet literature, i.e., gilling, wedging, snagging and entangling. Since we could observe differences between mouth, maxillary, and head capture probability in particular, a refined classification for capture modes may be recommended.

We were able to substantiate gear efficiency and confirmed that gillnets primarily capture fish by the gill, therefore having an appropriate name. It is well known that hanging ratio affects the selectivity of gillnets, the lower the hanging ratio, the broader the length distributions. It is therefore not a surprise that the commercial hanging ratio of 0.4 used in our case study was effective for gilling fish and thus size selective. For a fish to be gilled, it needs to be of a certain size compared to the mesh size of the netting panel. Gillnets are known for good size selectivity, but this study confirmed previous findings that capture modes can increase length range of the catch and therefore reduce size selectivity.

Capture modes were clearly size dependent, with small fish being caught by the mouth and larger fish by the maxillary. Even though about 70% of the catch was gilled, protruding anatomical structures such as the mouth or the maxillary accounted for capture of fish that were too small or too large to be gilled with respect to the fish and mesh geometry. Cod has a slower swimming speed than other species, requiring more intense aeration of the gill epithelium and thus a wider mouth gape which could explain the cases of capture by the mouth (Lobyrev and Hoffman, 2018). Cod in general have a larger head to body ratio than most other fish which could explain the cases of capture by the maxillary. Our observations were not in line with previous statements that no cod were entangled by the teeth without being also enmeshed at the gills or maxillae (Holst *et al.*, 2002).

The work is setting a methodological framework for further investigating the effect of capture mode on the catchability of different gear designs. In order to develop the method, we collected a case study dataset in the Danish offshore gillnet fishery for cod using commercial monofilament nylon nets, which showed good size selectivity with no undersized fish (1 out of 338 individuals). Of course, the application of the method will be much more relevant when used by gear technologists to compare different gear characteristics in order to improve size or species selectivity. Changing the hanging ratio, for instance, or replacing nylon twine by thicker biodegradable material may considerably change the resulting length of maximum probability for a given capture mode. Understanding how the fish is retained by the meshes can provide valuable information with respect to fish damage and quality. Capture by the body involve tight meshes in the filet part of the fish which may damage the product

(Savina *et al.*, 2016), but it was observed for less than 5% of the individuals caught in our case study and might therefore be considered negligible.

The methodology can be used for other species and types of nets, even though one might need to adapt the nomenclature of capture modes when fishing with trammel nets with the addition of a "pocketed" category. This methodology could also be used in other gears such as longlines, where fish are often hooked in different ways (deep hooking, shallow hooking).

Acknowledgements

The authors wish to thank the skipper of the commercial gillnetter and the local fishermen organization in Hirtshals.

Contributors' statement (https://casrai.org/credit/)

E.S.: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft

B.H.: Conceptualization, Software, Validation, Writing – review & editing

R.F.: Investigation, Methodology, Writing – review & editing

L.K.: Conceptualization, Investigation, Methodology, Writing – review & editing

Funding statement

This research was supported by the Danish Fisheries Agency through the European Fisheries Fund (BIOGARN, grant No. 33113-B-19-143) and the Norwegian Research Council (Dsolve, grant No. RCN 300443).

References

Burnham, K., and Anderson, D. 2002. Model selection and multimodel inference - A practical Information-Theoretic Approach. 488 pp.

Christiansen, J. S., and Jobling, M. 1990. The behaviour and the relationship between food intake and growth of juvenile Arctic charr, Salvelinus alpinus L., subjected to sustained exercise. Canadian Journal of Zoology, 68: 2185–2191.

Efron, B. 1982. The Jackknife, the Bootstrap and Other Resampling Plans. Society for Industrial and Applied Mathematics. http://epubs.siam.org/doi/book/10.1137/1.9781611970319 (Accessed 28 May 2019).

Grant, G. C., Radomski, P., and Anderson, C. S. 2004. Using underwater video to directly estimate gear selectivity: The retention probability for walleye (Sander vitreus) in gill nets. Canadian Journal of Fisheries and Aquatic Sciences, 61: 168–174.

Grati, F., Bolognini, L., Domenichetti, F., Fabi, G., Polidori, P., Santelli, A., Scarcella, G., *et al.* 2015. The effect of monofilament thickness on the catches of gillnets for common sole in the Mediterranean small-scale fishery. Fisheries Research, 164: 170–177. https://linkinghub.elsevier.com/retrieve/pii/S0165783614003403.

Hamley, J. 1975. Review of gillnet selectivity. Journal of Fisherise Research Board of Canada, 32: 1943–1969.

Hamley, J. M., and Regier, H. A. 1973. Direct Estimates of Gillnet Selectivity to Walleye (Stizostedion vitreum vitreum) . Journal of the Fisheries Research Board of Canada, 30: 817–830.

Hansen, R. G. 1974. Effect of Different Filament Diameters on the Selective Action of Monofilament Gill Nets. Transactions of the American Fisheries Society, 103: 386–387.

He, P. 2006. Gillnets: Gear design, fishing performance and conservation challenges. Marine Technology Society Journal, 40: 12–19.

Herrmann, B., Sistiaga, M., Nielsen, K. N., and Larsen, R. B. 2012. Understanding the size selectivity of redfish (Sebastes spp.) in North Atlantic trawl codends. Journal of Northwest Atlantic Fishery Science, 44: 1–13.

Herrmann, B., Sistiaga, M., Rindahl, L., and Tatone, I. 2017. Estimation of the effect of gear design changes on catch efficiency: Methodology and a case study for a Spanish longline fishery targeting hake (Merluccius merluccius). Fisheries Research, 185: 153–160. Elsevier B.V. http://dx.doi.org/10.1016/j.fishres.2016.09.013.

Holst, R., Wileman, D., and Madsen, N. 2002. The effect of twine thickness on the size selectivity and fishing power of Baltic cod gill nets. Fisheries Research, 56: 303–312.

Hovgard, H., and Lassen, H. 2000. Manual on estimation of selectivity for gillnet and longline gears in abundance surveys. FAO Fisheries Technical Paper: 84p.

Hovgård, H. 1996. A two-step approach to estimating selectivity and fishing power of research gill nets used in Greenland waters. Canadian Journal of Fisheries and Aquatic Sciences, 53: 1007–1013.

Hovgård, H., Lassen, H., Madsen, N., Poulsen, T. M., and Wileman, D. 1999. Gillnet selectivity for North Sea Atlantic cod (Gadus morhua): Model ambiguity and data quality are related. Canadian Journal of Fisheries and Aquatic Sciences, 56: 1307–1316.

Krag, L. A., Herrmann, B., and Karlsen, J. D. 2014. Inferring fish escape behaviour in trawls based on catch comparison data: Model development and evaluation based on data from Skagerrak, Denmark. PLoS ONE, 9.

Lobyrev, F., and Hoffman, M. J. 2018. A morphological and geometric method for estimating the selectivity of gill nets. Reviews in Fish Biology and Fisheries, 28: 909–924. Springer International Publishing. https://doi.org/10.1007/s11160-018-9534-1.

Lomeli, M. J. M., Wakefield, W. W., and Herrmann, B. 2019. Evaluating off-bottom sweeps of a U.S. West Coast groundfish bottom trawl: Effects on catch efficiency and seafloor interactions. Fisheries Research, 213: 204–211. Elsevier. https://doi.org/10.1016/j.fishres.2019.01.016.

Machiels, M. A. M., Klinge, M., Lanters, R., and van Densen, W. L. T. 1994. Effect of snood length and hanging ratio on efficiency and selectivity of bottom-set gillnets for pikeperch, Stizostedion lucioperca L., and bream, Abramis brama. Fisheries Research, 19: 231–239.

Madsen, N., Holst, R., Wileman, D., and Moth-Poulsen, T. 1999. Size selectivity of sole gill nets fished in the North Sea. Fisheries Research, 44: 59–73.

McCombie, A. M., and Berst, A. H. 1969. Some Effects of Shape and Structure of Fish on Selectivity of Gillnets. Journal of the Fisheries Research Board of Canada, 26: 2681–2689.

Millar, R. B. 2000. Untangling the confusion surrounding the estimation of gillnet selectivity. Canadian Journal of Fisheries and Aquatic Sciences, 57: 507–511.

Potter, E. C. E., and Pawson, M. G. 1991. Gill Netting. Lab. Leafl., MAFF Direct. Fish. Res., Lowestoft, 69: 34 pp. http://www.cefas.co.uk/Publications/lableaflets/lableaflet69.pdf.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rakhmadevi, C. catur, Purbayanto, A., and Sondita, M. F. A. 2008. Studies on Capture Process and Fish Behaviour Towards. Ind. Fish Res.J, 14: 1–6.

Randall, D. 2014. Hughes and Shelton: The fathers of fish respiration. Journal of Experimental Biology, 217: 3191–3192.

Samaranayaka, A., Engås, A., and Jørgensen, T. 1997. Effects of hanging ratio and fishing depth on the catch rates of drifting tuna gillnets in Sri Lankan waters. Fisheries Research, 29: 1–12.

Savina, E., Karlsen, J. D., Frandsen, R. P., Krag, L. A., Kristensen, K., and Madsen, N. 2016. Testing the effect of soak time on catch damage in a coastal gillnetter and the consequences on processed fish quality. Food Control, 70: 310–317. https://linkinghub.elsevier.com/retrieve/pii/S0956713516302870.

Sistiaga, M., Herrmann, B., Grimaldo, E., and Larsen, R. B. 2010. Assessment of dual selection in grid based selectivity systems. Fisheries Research, 105: 187–199. https://linkinghub.elsevier.com/retrieve/pii/S0165783610001098.

Suuronen, P., Chopin, F., Glass, C., Løkkeborg, S., Matsushita, Y., Queirolo, D., and Rihan, D. 2012. Low impact and fuel efficient fishing—Looking beyond the horizon. Fisheries Research, 119–120: 135–146. https://linkinghub.elsevier.com/retrieve/pii/S0165783611003870.

Wegner, N. C., Sepulveda, C. A., Bull, K. B., and Graham, J. B. 2010. Gill morphometrics in relation to gas transfer and ram ventilation in high-energy demand teleosts: Scombrids and billfishes. Journal of Morphology, 271: 36–49.

Wickham, H. 2016. ggplot2 : elegant graphics for data analysis. Springer. 1 Online-Ressource (XVI, 260 Seiten, 232 Illusrati pp.

Wickham, H., François, R., Henry, L., and Müller, K. 2021. dplyr: A Grammar of Data Manipulation. R package version 1.0.7. https://cran.r-project.org/package=dplyr.

Wileman, D., Tschernij, V., Madsen, N., and Holst, R. 2000. Size selectivity and relative fishing power of Baltic cod gillnets. 110–148 pp.

Wileman, D. A., Ferro, R. S. T., Fonteyne, R., and Millar, R. B. 1996. Manual of methods of measuring the selectivity of towed fishing gears. ICES Cooperative Research Report: 1–126. http://www.eurobis.org/imis?module=ref&refid=242792&printversion=1&dropIMIStitle=1.

Yokota, K., Fujimori, Y., Shiode, D., and Tokai, T. 2001. Effect of thin twine on gill net size-selectivity analyzed with the direct estimation method. Fisheries Science, 67: 851–856. http://www.blackwell-synergy.com/links/doi/10.1046%2Fj.1444-2906.2001.00332.x.

Žydelis, R., Small, C., and French, G. 2013. The incidental catch of seabirds in gillnet fisheries: A global review. Biological Conservation, 162: 76–88.

Table 1. Definition of the capture modes.

Capture mode	Description
Mouth	Caught by the mouth or teeth (netting in the mouth)
Maxillary	Caught by the maxillary
Head	Caught by part of the head region other than the maxillary, mouth, or teeth
Gill	Caught with the mesh behind the gill cover (pre-operculum and operculum)
Body	Caught by the largest part of the body
Entangled	Caught by spine, fins, or other parts of the body as a result of struggling
Unclear	Difficult to discriminate the primary mode of capture

Table 2. Type of fishing ground (reef or wreck), depth as mean (min-max) in m, soak time as mean (min-max) in h, total number of fleets and nets that caught fish with total number of fllets and nets deployed in brackets, total number of fish caught in the experimental gillnets with mean (min-max) length in cm for each fishing day (considered as a baseline unit for the analysis), and discard ratio in number for cod.

Date	Ground	Depth (m)	Soak time (h)	Fleets	Nets	Fish	Length (cm)
2020-08-06	Reef	35 (30-39)	9.4 (8.5-10.4)	2 (4)	2 (32)	2	51 (36-65)
2020-08-08	Reef	39 (32-60)	7.8 (6.9-8.7)	3 (4)	5 (32)	5	48 (26-60)
2020-08-12	Reef	38 (34-44)	8.5 (6.9-10.7)	4 (4)	11 (32)	14	66 (61-75)
2020-08-17	Reef	35 (31-38)	8.9 (7.3-10.5)	3 (4)	6 (32)	8	64 (35-72)
2020-08-18	Wreck	73 (66-80)	3.4 (3.1-3.6)	4 (4)	7 (8)	33	69 (57-88)
2020-08-19	Wreck	71 (60-85)	3.7 (2.2-5.4)	6 (6)	11 (12)	106	67 (41-89)
2020-08-20	Wreck	84 (84-85)	2.8 (2.7-2.9)	3 (3)	6 (6)	60	67 (50-90)
2020-09-01	Wreck	87 (59-103)	4.6 (2.0-8.1)	6 (6)	12 (12)	97	72 (32-98)
2020-09-03	Wreck	103 (101-104)	3.3 (2.1-4.3)	3 (4)	3 (8)	13	73 (67-87)

Table 3. Number of fish (in decreasing order) for the observed and assumed primary capture mode(s) in case of the multiple occurrences.

Observed	**Assumed primary**	**Principle**	**Number of fish**
Gill	Gill	Single mode	172
Mouth	Mouth	Single mode	34
Mouth & Gill	Gill	Likely sequence	30
Maxillary	Maxillary	Single mode	24
Maxillary & Head	Head	Likely sequence	13
Gill & Body	Body	Likely sequence	11
Head	Head	Single mode	10
Head & Gill	Gill	Likely sequence	8
Body	Body	Single mode	7
Maxillary & Gill	Gill	Likely sequence	7
Maxillary & Head & Gill	Unclear	Likely sequence	5
Gill & Entangled	Gill	Entangled secondary	2
Mouth & Body	Body	Likely sequence	2
Mouth & Head	Head	Likely sequence	2
Mouth & Maxillary	Unclear	Not possible to decide	2
Gill & Body & Entangled	Unclear	More than 3 occurrences	2
Head& Entangled	Head	Entangled secondary	1
Head & Body	Body	Likely sequence	1
Maxillary & Head & Body & Entangled	Unclear	More than 3 occurrences	1
Maxillary & Entangled	Maxillary	Entangled secondary	1
Mouth & Gill & Body	Unclear	More than 3 occurrences	1
Mouth & Head & Gill	Unclear	More than 3 occurrences	1
Mouth & Maxillary & Gill & Body	Unclear	More than 3 occurrences	1

Table 4. Fit statistics for the length-dependent capture mode probability analysis with p-value, deviance, and degrees of freedom (DOF), and length-integrated average value for the capture mode probability ($CPq_{average}$) as bias-corrected mean with Efron percentile bootstrap 95% confidence limits.

Capture mode	**p-value**	**Deviance**	**DOF**	$\boldsymbol{CPq_{average}}$ **(%)**
Mouth	0.56	44.9	47	11.0 (4.3-17.4)
Maxillary	0.69	41.8	47	7.1 (2.2-12.8)
Head	0.13	57.9	47	12.5 (3.7-21.2)
Gill	0.85	37.0	47	66.8 (53.8-76.0)
Body	1.00	15.7	47	2.7 (1.3-4.9)
Entangled	1.00	0.0	47	0.0 (0.0-0.0)
Unclear	1.00	0.0	47	0.0 (0.0-0.0)

Figure 1. Capture modes. From left to right: mouth and maxillary (top), head and gill (middle), body and entangled (bottom).

Figure 2. Map of the fleets deployed in Skagerrak (ICES area IIIa).

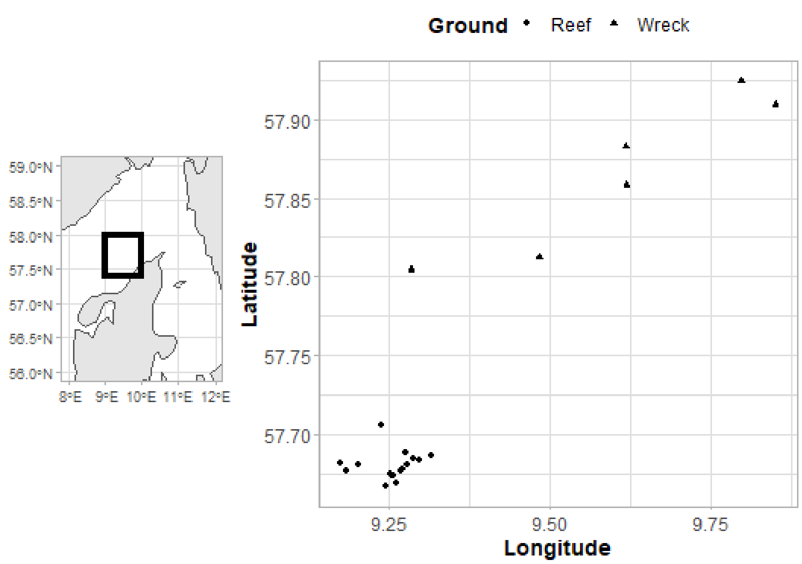

Figure 3. Hauling gillnets (top left) and assessing mode of capture on the sorting table (bottom left and right).

Figure 1. Probability for capture by mode where the curve (solid line) represents the modelled mode probability as bias-corrected mean with Efron percentile bootstrap 95% confidence limits (grey band) fitted to the experimental rate (black dots) (left panel), and length distribution of the sampled population as the modelled mean number of fish caught (right panel) for the seven capture modes (mouth, maxillary, head, gill, body, entangled and unclear, from top to bottom).

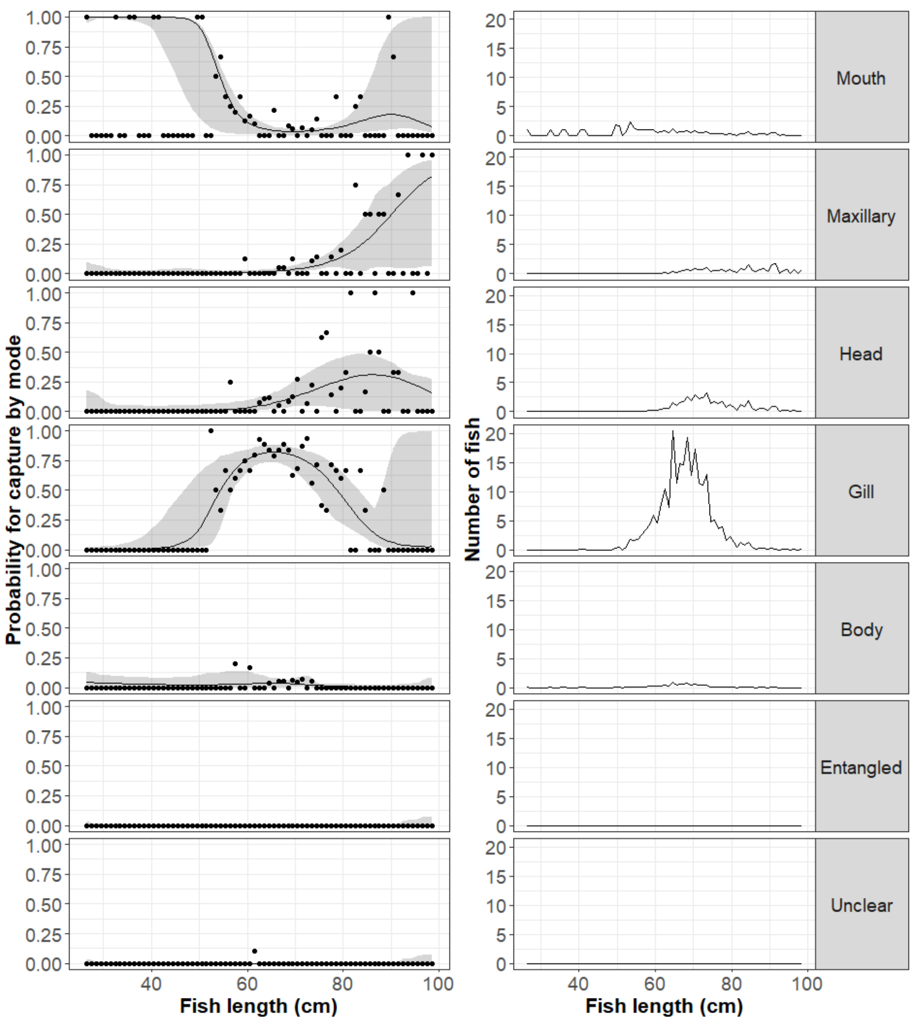

Figure 2. Length-integrated average value in % for the capture mode probability as bias-corrected mean with Efron percentile bootstrap 95% confidence limits.