



Comparison of the efficiency and modes of capture of biodegradable versus nylon gillnets in the Northeast Atlantic cod (*Gadus morhua*) fishery

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ABSTRACT

Modern gillnets are usually made of nylon with high breaking strength, suitable elasticity and durability making them an efficient fishing gear. Lost, abandoned, or discarded gillnets at sea cause plastic pollution and can continue capturing marine animals over long periods of time. Biodegradable materials are being developed to replace nylon in gillnets. However, biodegradable gillnets have shown reduced catch efficiency compared to the nylon gillnets which challenges their acceptance by the fishing sector. This study investigated catch efficiency and modes of capture between biodegradable and nylon gillnets in commercial cod (*Gadus morhua*) fishery. On average, new biodegradable gillnets caught 25% fewer cod compared to new nylon gillnets. The main capture modes were by the gills and by the body in used and new biodegradable gillnets, respectively. Differences in catch efficiency are related to specific modes of capture that may be related to differences in material properties.

1. Introduction

Gillnets, which are efficient and relatively inexpensive, are one of the most commonly used fishing gears in the world (FAO, 2016). Synthetic plastic material (nylon) has high elasticity and breaking strength, and its use as the material for gillnets has increased their fishing capacity and, therefore, the profitability of the industry (He, 2006). However, these same characteristics have a negative effect on the marine environment. Because of the durability of the nylon material, the gear has the potential to continue fishing for years when lost, abandoned and/or discarded at sea (a process known as ghost fishing) (He, 2006). Previous studies have documented large amounts of fish and benthic organisms in lost gillnets upon retrieval (Puente et al., 2001; Humborstad et al., 2003; Good et al., 2010; Beneli et al., 2020). Moreover, nylon does not disappear completely even after long exposure to the conditions at sea. Instead, it is broken down into smaller plastic particles (macro- and microplastics) and toxic substances that continue to impact the marine environment (Moore, 2008). Although gillnets are considered to be a sustainable

fishing gear because of, for example, their limited negative effects on juvenile fish and the benthic environment compared to other fishing methods such as, for instance, bottom trawling, the plastic pollution and potential ghost fishing impact by the lost gear is an increasing concern to the sustainability (FAO, 2016; Standal et al., 2020).

The Northeast Atlantic cod (*Gadus morhua*) fishery is the most economically important single species fishery in Norway. In the coastal gillnet fishery for cod, gillnets account for 21% of the total national allowable catch, which was 331,553 t in 2020 (Norwegian Directorate of Fisheries, 2021). However, incidental losses of fishing gear is relatively high in some of the Norwegian gillnet fisheries (Norwegian Directorate of Fisheries, 2019). Deshpande et al. (2020) estimated the annual loss rates of six types of fishing gear in Norway and identified gillnets as the primary source of lost, abandoned, and/or discarded fishing gears.

The feasibility of using new biodegradable materials to replace nylon in gillnets has been tested in South Korea (Park et al., 2007a, 2007b, 2010; Park and Bae, 2008; Bae et al., 2012; An and Bae, 2013; Kim et al., 2013, 2014a, 2014b, 2016) and Norway (Grimaldo et al., 2018, 2019,

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2020). The aim is for the new biodegradable material to have mechanical properties similar to those of nylon during the operation. However, naturally occurring microorganisms should be able to degrade lost nets into substances that are harmless to the marine environment after a specific amount of time in the water, thereby reducing plastic pollution (Kim et al., 2014a, 2014b) and limiting ghost fishing. However, for the new biodegradable material to be used commercially, the nets should have similar catch efficiency as nylon nets to maintain the profitability of the industry, and, therefore, to be ready to be adopted by the industry.

Previous experimental trials conducted in Norway showed that gillnets made from resin of the biodegradable polymer polybutylene succinate *co*-adipate-*co*-terephthalate (PBSAT) had lower catch efficiency than nylon (polyamide) gillnets (Grimaldo et al., 2018, 2019). Furthermore, the catch efficiency of biodegradable gillnets progressively declined over their lifetime as a consequence of degradation (Grimaldo et al., 2019, 2020). The mechanical properties of the biodegradable material, such as suboptimal tensile strength, elongation at break, and elasticity may explain the differences in catch efficiency between biodegradable and nylon nets as well as the differences between new gillnets and those subjected to repeated use (Grimaldo et al., 2020). Specifically, it was found that the breaking strength decreased more for the biodegradable PBSAT material compared to nylon after 200 h aging test with an initial value that was 23% lower compared to nylon (Grimaldo et al., 2020). Thickness of the twine used and stiffness of the mesh can also affect catch rates (Grimaldo et al., 2020).

To understand how these material properties affect the catch efficiency over time, the underlying mechanisms of how fish are caught in gillnets should be understood. Such information could help identifying the causes of problems regarding the catch efficiency of biodegradable gillnets and, thereby, guide which improvements have to be made regarding the properties of the biodegradable gillnets. Incorporating these modifications would likely increase the use of biodegradable material in commercial gillnet fishery and help to reduce the marine plastic pollution caused by using nylon material in gillnets. Material properties can affect how the fish are caught in the net, with gillnet design parameters expressed as mesh size, hanging ratio, twine thickness, twine construction and material type affecting both catch efficiency and the selectivity of the gear (He, 2006; Sala, 2016; Sala et al., 2018). In the literature, the following capture modes for roundfish have been observed in gillnets: snagging (captured in nets by the mouth, teeth, or maxillae), gilling (captured behind the gill cover by the netting), wedging (stuck in the net by the largest part of the body), or entangling (Hovgard, 2000; He, 2006; Grati et al., 2015). Previous studies reported that the capture mode of fish in gillnets could provide valuable information about how the fish were caught in the netting and how the catch process affected the catchability of the gear (Grati et al., 2015; Savina et al., 2021). The capture mode can also affect whether the fish are retained or released, as some modes of capture are more effective at retaining fish than others (e.g., fish captured by the mouth/maxillae have a greater chance of escaping the netting) (Grati et al., 2015; Savina et al., 2021). Recently, Savina et al. (2021) formally related capture mode to fish size, and the application of this method was relevant to evaluate differences in gear characteristics and to explain catch efficiency.

In the present study, we evaluated whether the assessment of capture modes in gillnets could explain the capture patterns observed for different gillnet materials (PBSAT and nylon) and for the same material over repeated use. We compared the catch efficiency between new and used biodegradable and nylon gillnets used in the cod fishery in northern Norway. We examined whether there were significant differences in

capture modes between the two materials and whether they could explain the differences in catch efficiency between the different gillnets.

2. Materials and methods

2.1. Sea trials and data collection

The fishing performance of 10 new and 10 used nylon and biodegradable gillnets were compared during fishing trials conducted onboard the coastal fishing vessel “Karoline” (10.9 m LOA) under commercial conditions in March 2021 during the most important fishing season for cod. The fishing grounds were located off the coast of Troms (Northern Norway) between 70°21.26–70°21.55 N and 19°40.82–19°42.04 E. The fishing depths varied between 55 and 145 m.

All biodegradable gillnets were made of PBSAT resin (Kim et al., 2017, patent EP3214133). Biodegradable and nylon gillnets were manufactured by S-ENPOL (Gangwon-do, South Korea). Two sets of gillnets were tested in this experiment on separate fleets (Fleet 1 and Fleet 2, respectively):

Fleet 1: New nylon versus new biodegradable gillnets. Both gillnets were made of 0.70 mm monofilament, 210 mm stretched mesh size, and were 30 meshes high and 275 meshes long (stretched length 55 m).

Fleet 2: Used nylon versus used biodegradable gillnets. Nylon and biodegradable gillnets were made of 0.70 and 0.75 mm monofilament, respectively. Both types of nets had 210 mm stretched mesh size and were 30 meshes high and 275 meshes long (stretched length 55 m).

By using this experimental design, we were able to evaluate the effect of catch efficiency from changing from nylon to biodegradable gillnet material for both, new and used gillnets separately. Each fleet consisted of 10 biodegradable and 10 nylon nets that were attached in an alternated order in which two biodegradable net sheets followed two nylon sheets. The distance between individual gillnets was 1 m (Fig. 1). This design provided information that could be used for catch comparison analysis accounting for spatial and temporal variation in the availability of the fish (Herrmann et al., 2017). Here it is important that the two types of gillnets being compared are on average exposed to the same population of fish regarding numbers and size distribution. In order to achieve this, the nets in each fleet was set in a regular pattern. This could in principle be achieved by alternating between the two types of gillnets on the mainline in the following order: B-N-B-N-B-N-B-N-B-N-B-N-B-N. However, for easing of registration of cod in relation to the type of gillnets, the alternation in gillnet types were only applied after each second net sheet following Grimaldo et al. (2019). Therefore, to make conditions as equal as possible between the gillnets, they were arranged as follows: N-BB-NN-BB-NN-BB-NN-BB-NN-BB-N and set 2 as B-NN-BB-NN-BB-NN-BB-NN-B (Fig. 1).

The used nylon and biodegradable nets had been subjected to fishing during the fishing season in 2020 during a total of 12 deployments. Storing of gillnets from one season to the other follow standard procedures; the nets were washed with fresh water, dried, and stored in dry conditions inside a warehouse. The new set of gillnets were new at the start of these trials. The hanging ratio (i.e., ratio of floatline and leadline length to the stretched net length) was similar for all nets and was 0.5. The gillnets were sewn to 26 mm diameter SCANFLYT-800 floatlines with a buoyancy of 150 g m⁻¹ and 16 mm diameter DANLINE line with a weight of 360 g m⁻¹ (lead inside the braided line).

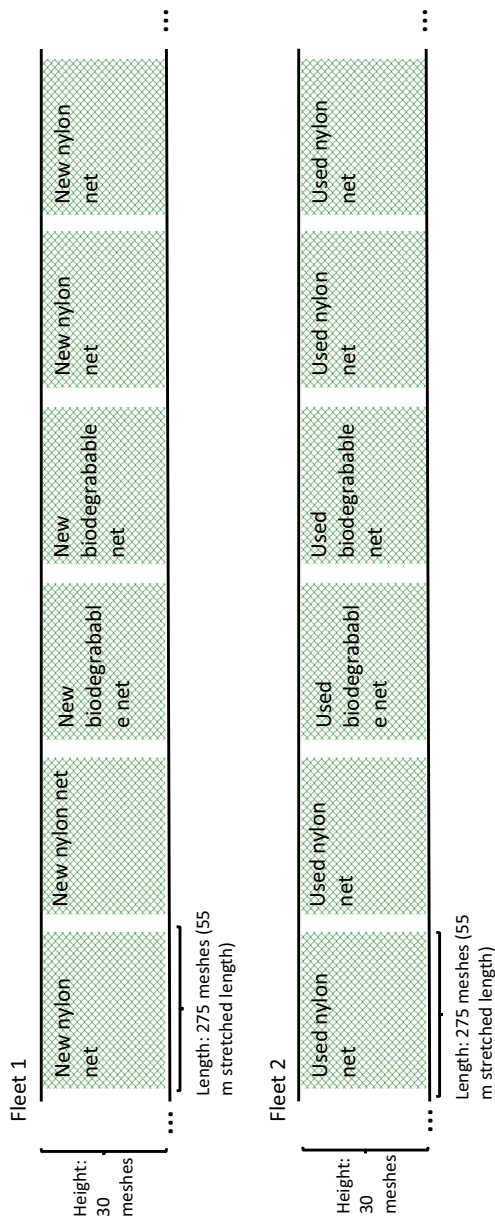


Fig. 1. Experimental setup showing a segment of gillnets used during the fishing trials for each fleet. Fleet 1 contained new nylon and biodegradable gillnets. Fleet 2 contained used nylon and biodegradable gillnets. Fleets were deployed simultaneously and in the same fishing area.

When the nets of Fleet 1 and Fleet 2 were hauled on board, the catch was sorted by type of gillnet. The capture mode of each individual cod was observed and recorded during the hauling operation. We classified the cod into four different modes of capture: tip (mouth and maxillary), gills, largest part of the body, or entangled in the netting. To record capture mode, once onboard each fish was observed one by one, and the mode of capture was determined by the netting tension (i.e., the tightest meshes) around the fish. One or several capture modes was recorded for each individual. In case of multiple modes for an individual cod, we assumed a primary mode according to the principle of likely sequence according to Savina et al. (2021). According to this principle, the primary mode of capture corresponds to the part of the fish that touches the netting last. For example, if a fish was captured by the tip (mouth or maxillary) and gills, the primary capture mode would be recorded as gills. If a fish was captured by the gills and the largest part of the body, the assumed mode of capture would be body (Savina et al., 2021). Finally, the corresponding total length of each cod was measured to the closest cm below. All captured cod were measured for both length and mode of capture.

2.2. Modelling the length-dependent catch efficiency between gillnet types

Comparison of catch efficiency between gillnet types was estimated as the catch comparison rate and catch ratio (Herrmann et al., 2017; Grimaldo et al., 2019, 2020). We analysed relative catch efficiency between nylon and biodegradable gillnets using the statistical software SELNET (Herrmann et al., 2012). Specifically, using the data from Fleet 1 and Fleet 2 (Fig. 1) separately, we were able to quantify the effect on catch efficiency by changing from nylon to biodegradable material for new and used gillnets, respectively. We used the catch information (numbers and lengths of cod caught in each gillnet panel deployment) to determine whether there was a significant difference in the catch efficiency averaged over deployments between nylon and biodegradable gillnets and between used and new gillnets. We also tested whether a potential difference between the gillnet types could be attributed to the size (total length) of the cod. We used the method described in Herrmann et al. (2017) and Grimaldo et al. (2019, 2020) to assess the change in relative length-dependent catch efficiency when changing from a nylon gillnet to a biodegradable gillnet, and we compared the catch data for the two gillnet types. We applied the same method to assess the change in relative length-dependent catch efficiency between used and new gillnets. This method models the length-dependent (l) catch comparison rate ($CC(l, \nu)$) and catch ratio ($CR(l, \nu)$) summed over gillnet deployments for the full deployment period. The functional form for the $CC(l, \nu)$ was obtained using maximum likelihood estimation, where ν represents the parameters describing the catch comparison curve defined by $CC(l, \nu)$. The length-integrated average catch ratio ($CR_{average}$) value was estimated directly from the experimental catch data. Details about the estimation of $CC(l, \nu)$, $CR(l, \nu)$, and $CR_{average}$ are provided in the supplementary material of Grimaldo et al. (2020).

2.3. Modelling the length-dependent capture mode probability

To determine, conditioned capture, the length-dependent probability of capturing fish with each of the four modes of capture, we followed the method outlined in Savina et al. (2021). Specifically, we used numbers of cod that were captured by each of the capture modes and the corresponding length measurements in each of the gillnet types separately. We considered all gillnets of the same material (nylon or biodegradable material) from each fleet deployment to constitute a unit for the analysis. The analysis was carried out for each mode of capture independently. Conditioned capture (the expected probability for the capture mode q for fish length l) is written as (Savina et al., 2021):

$$CPq_l = \frac{\sum_{j=1}^h n_{qlj}}{\sum_{j=1}^h \sum_{i=1}^Q n_{ij}} \tag{1}$$

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; and h is the total number of gillnet deployments. The functional description of the capture mode probability $CPq(l, \mathbf{v})$ was obtained using maximum likelihood estimation by minimizing the Expression (2) (Savina et al., 2021):

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

where \mathbf{v} represents the parameters describing the capture mode probability curve defined by $CPq(l, \mathbf{v})$. Eq. (1) and Expression (2) 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). We adapted the same approach for modelling $CPq(l, \mathbf{v})$ as is often applied for catch comparison studies based on binominal count data (Herrmann et al., 2017):

$$CPq(l, \mathbf{v}) = \frac{\exp[f(l, v_0, \dots, v_k)]}{1 + \exp[f(l, v_0, \dots, v_k)]} \tag{3}$$

In Eq. (3), f is a polynomial of order k with coefficients v_0 to v_k , such that $\mathbf{v} = (v_0, \dots, v_k)$. The values of the parameter \mathbf{v} describing $CPq(l, \mathbf{v})$ are estimated by minimizing the Expression (2). We considered f of up to an order of 4 using multimodel inference (Herrmann et al., 2017). Leaving out one or more of the parameters v_0, \dots, v_4 at a time resulted in 31 additional candidate models for the capture mode probability function $CPq(l, \mathbf{v})$. Among these models, the capture mode probability was estimated using multimodel inference to obtain a combined model (Burnham and Anderson, 2002). The ability of the combined model to describe the experimental data was based on the p -value, which was calculated based on the model deviance and degrees of freedom (DOF) (Wileman et al., 1996). The combined model described the experimental data sufficiently well at $p > 0.05$.

We used a double bootstrapping method with 1000 bootstrap repetitions to estimate 95% confidence intervals (CIs) (Efron, 1982) for the capture mode probability curve (Savina et al., 2021). We presented the length distribution of the sampled population as the modelled mean number of cod caught for the four capture modes.

The length-integrated average value for the capture mode probability ($CPq_{average}$) was directly estimated from the experimental data using the following equation (Savina et al., 2021):

$$CPq_{average} = \frac{\sum_l \sum_{j=1}^h n_{qlj}}{\sum_l \sum_{j=1}^h \sum_{i=1}^Q n_{ij}} \tag{4}$$

where the outer summations include the size classes in the catch during the experimental fishing period. In contrast to the length-dependent

Table 1

Fit statistics, catch comparison results, and number of cod observed. Results for nylon and biodegradable gillnets (comparisons between new (left column) and used (right column) sets of gillnets). Values in parentheses represent 95% CIs.

	New gillnet sets	Used gillnet sets
p -value	0.2349	0.0436
Deviance	48.25	55.29
DOF	42	39
$CR_{average}$	74.53 (54.40–89.91)	56.11 (44.19–71.43)
Number in biodegradable nets	199	156
Number in nylon nets	267	277

evaluation of the capture mode probability $CPq(l, \mathbf{v})$, $CPq_{average}$ is specific for the population structure encountered during the experimental trials. Therefore, this information cannot be extrapolated to other scenarios in which the size structure of the fish species may be different.

2.4. Probability of capture in a specific gillnet type and mode conditioned capture

For each capture mode q separately, we wanted to investigate whether capture efficiency differed for any of the four gillnets compared to all the other gillnets on average. Experimentally we can describe this by the expected probability $CPkq_l$ of being captured in gillnet type k conditioned it is captured with mode q in one of the four gillnets (1 = new biodegradable gillnets, 2 = new nylon gillnets, 3 = used biodegradable gillnets, 4 = used nylon gillnets):

$$CPkq_l = \frac{\sum_{j=1}^h n_{kqlj}}{\sum_{j=1}^h \sum_{i=1}^4 n_{kqlj}} \tag{5}$$

The inner summation in the denominator of Eq. (5) is over the four different gear types. n_{kqlj} represents the number of fish in length class l captured in set j of gear type k with capture mode q .

The functional description $CPkq(l, \mathbf{v})$ for $CPkq_l$ is obtained by minimizing the following expression:

$$-\sum_{j=1}^h \sum_i \left\{ n_{kqlj} \times \ln \left[CPkq(l, \mathbf{v}) \right] + \left[-n_{kqlj} + \sum_{i=1}^4 n_{iqlj} \right] \times \ln [1.0 - CPkq(l, \mathbf{v})] \right\} \tag{6}$$

The model applied for $CPkq(l, \mathbf{v})$ is similar in structure and estimation to that applied for $CPq(l, \mathbf{v})$ (Section 2.3) except from being based on minimizing (6) instead of (2).

If one of the gears for some sizes of cod catches more than the average for the four gears, then $CPkq(l, \mathbf{v})$ would be significantly larger than 0.25. In contrast, a $CPkq(l, \mathbf{v})$ value significantly lower than 0.25 would show that the specific gillnet type captures significantly less cod compared the other gillnets on average regarding capture with mode q .

3. Results

3.1. Catch efficiency of biodegradable versus nylon gillnets

In total, 899 cod were captured and included in the analysis of this study, with 355 and 544 cod captured in biodegradable and nylon gillnets, respectively (Table 1). The fit statistics of the catch comparison analysis showed that the deviation between the experimental data and the modelled data fitted well when new gillnet sets were compared ($p > 0.05$) (Wileman et al., 1996). For used sets of gillnets, the p -value was smaller than 0.05 (p -value = 0.0436) (Table 1). However, the catch comparison curve represented the trends in experimental data well (Fig. 2), therefore, the low p -value was assumed to be due to overdispersion in the data.

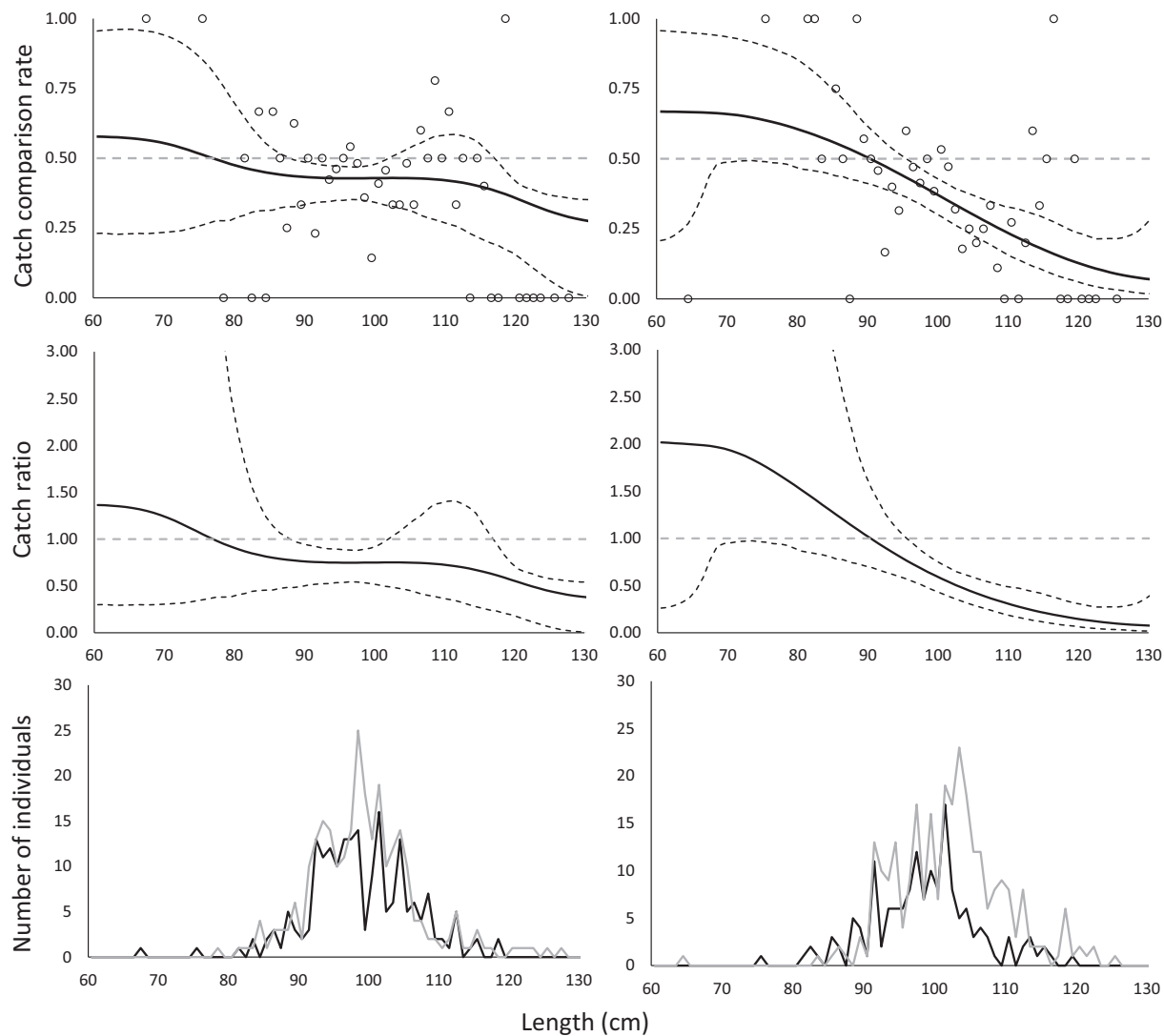


Fig. 2. Catch comparison and catch ratio analysis for biodegradable against nylon gillnets in fishery targeting cod. Left: new biodegradable gillnets versus new nylon gillnets. Right: used biodegradable gillnets versus used nylon gillnets. Upper graph: the modelled catch comparison rate based on all deployments (black curve) with 95% CIs (black stippled curves). Circles represent the experimental catch comparison rate. Middle: the estimated catch ratio curve based on all deployments (black curve) with 95% CIs (black stippled curves). Bottom: the length frequency distribution of cod captured by the biodegradable nets (black line) and nylon nets (grey line). The grey stippled lines at 0.5 and 1.0 represent the baseline at which both types of gillnets fish equally.

Table 2

Fit statistics, catch comparison results, and number of cod observed. Results for used and new biodegradable gillnets (left column) and used and new nylon gillnets (right column).

	Biodegradable gillnets	Nylon gillnets
<i>p</i> -value	0.0223	0.2108
Deviance	52.50	49.07
DOF	34	42
$CR_{average}$	78.39 (61.86–125.00)	103.74 (80.31–159.289)
Number in used nets	156	277
Number in new nets	199	267

Both types of gillnets had a similar tendency of capturing cod between 80 and 125 cm total length. However, for both new and especially for used nets, the biodegradable gillnets had a much clearer length-dependent catch efficiency compared to the nylon gillnets, as they retained significantly fewer cod of larger length classes (Fig. 2). The catch efficiency for fish ≥ 95 cm was significantly lower in the used biodegradable gillnets compared to the used nylon gillnets, and the efficiency continued to decrease with increasing fish length. This trend

was less pronounced when new nets were used. The $CR_{average}$ was 75% (CI: 54.40–89.91) for the comparison between new nylon and biodegradable gillnets and it was further reduced to 56% (CI: 44.19–74.43) for the comparison between used biodegradable and nylon nets (Table 1). Therefore, $CR_{average}$ shows a significant tendency for the biodegradable gillnets to catch fewer cod over time compared to the nylon gillnets.

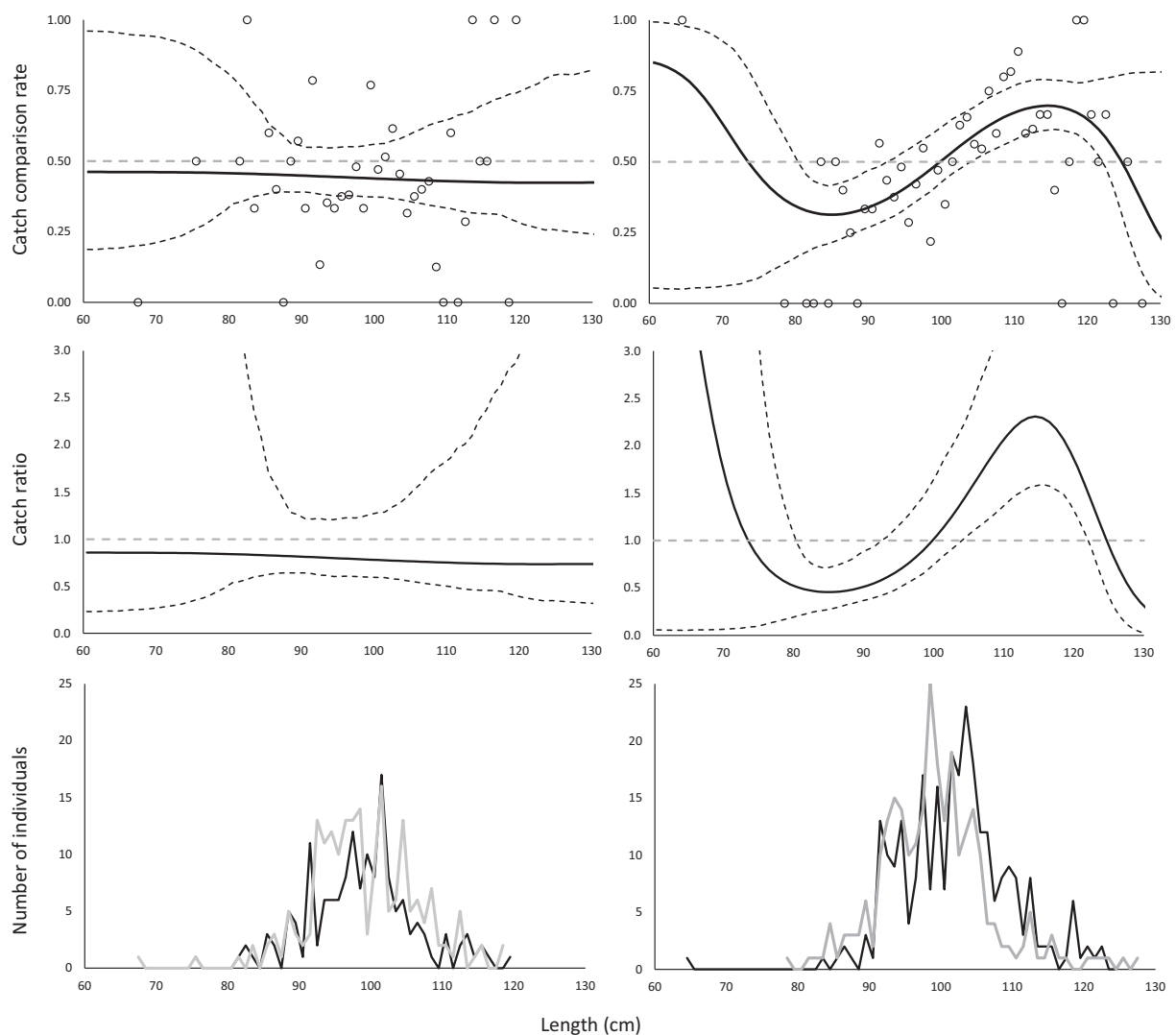


Fig. 3. Catch comparison and catch ratio analysis for used against new gillnets in fishery targeting cod. Left: used biodegradable gillnets versus new biodegradable gillnets. Right: used nylon gillnets versus new nylon gillnets. Upper graph: The modelled catch comparison rate based on all deployments (black curve) with 95% CIs (black stippled curves). Circles represent the experimental catch comparison rate. Middle: the estimated catch ratio curve based on all deployments (black curve) with 95% CIs (black stippled curves). Bottom: the length frequency distribution of cod captured by the used gillnets (black line) and new gillnets (grey line). The grey stippled lines at 0.5 and 1.0 represent the baseline at which both types of gillnets fish equally.

Table 3
Number of cod observed for each capture mode.

Capture mode	New biodegradable	New nylon	Used biodegradable	Used nylon	Total
Tip	36	44	33	59	172
Gills	69	104	83	127	383
Body	74	84	37	84	279
Entangled	20	35	3	7	65
Total	199	267	156	277	899

3.2. Catch efficiency of new versus used gillnets

The comparison of catch efficiency between the two biodegradable and between the two nylon gillnet sets allowed us to estimate the effect of wear on each of the materials. The fit statistics of the catch comparison analysis between new and used nylon gillnets showed that the deviation between the experimental data and the modelled data fitted well ($p > 0.05$) (Table 2). The p -value was 0.0223 (i.e., < 0.05) for the comparison between new and used biodegradable gillnets, so we assessed the deviance and the DOF to determine whether the result was due to structural problems when modelling the experimental data or to overdispersion in the data (Wileman et al., 1996). No clear patterns in

deviations between the experimental rate and modelled rate were observed; therefore, we considered the low p -value to be due to overdispersion in the data.

For biodegradable gillnets, the results indicated a reduction in catch efficiency in used compared to new gillnets.

Compared to new nylon nets, used nylon nets showed a significant reduction in capture of smaller cod between 80 and 95 cm length but a significant increase in captured cod between 105 and 125 cm length (Fig. 3) compared to the new nylon gillnets. In total, the $CR_{average}$ for nylon gillnets showed an equal catch efficiency ($CR_{average} = 103.74$ (CI: 80.31–159.29)).

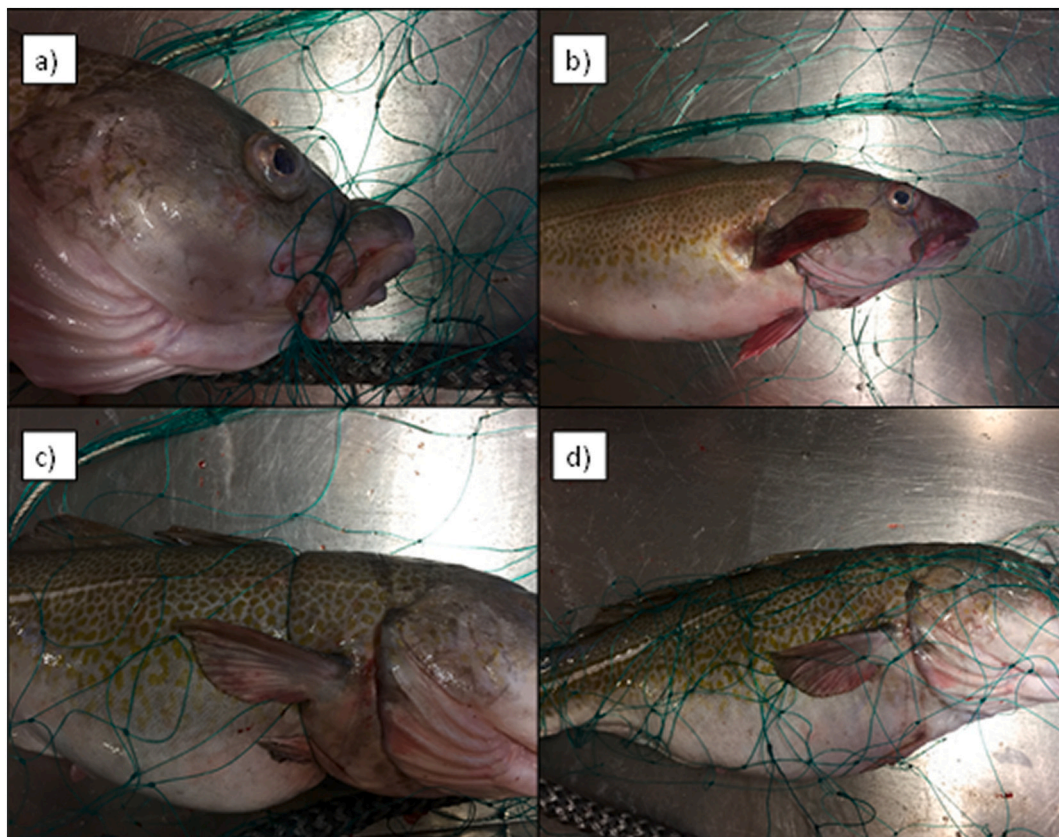


Fig. 4. Examples of capture modes observed. a) Capture by tip (mouth and maxillary); b) gills; c) largest part of the body; d) entangled.

Table 4
Fit statistics for length-dependent capture mode probability: p -value, deviance, degrees of freedom (DOF).

Capture mode	p -Value				Deviance				DOF			
	New biodegradable	New nylon	Used biodegradable	Used nylon	New biodegradable	New nylon	Used biodegradable	Used nylon	New biodegradable	New nylon	Used biodegradable	Used nylon
Tip	0.0856	0.7309	0.1937	0.5151	41.08	32.27	36.45	33.03	30	38	30	34
Gills	0.2758	0.0759	0.2086	0.1025	34.13	51.11	35.98	44.77	30	38	30	34
Body	0.6228	0.9652	0.2533	0.3309	27.01	23.79	34.71	37.03	30	38	30	34
Entangled	0.6228	0.5013	0.9939	0.9723	27.01	37.31	14.12	20.06	30	38	30	34

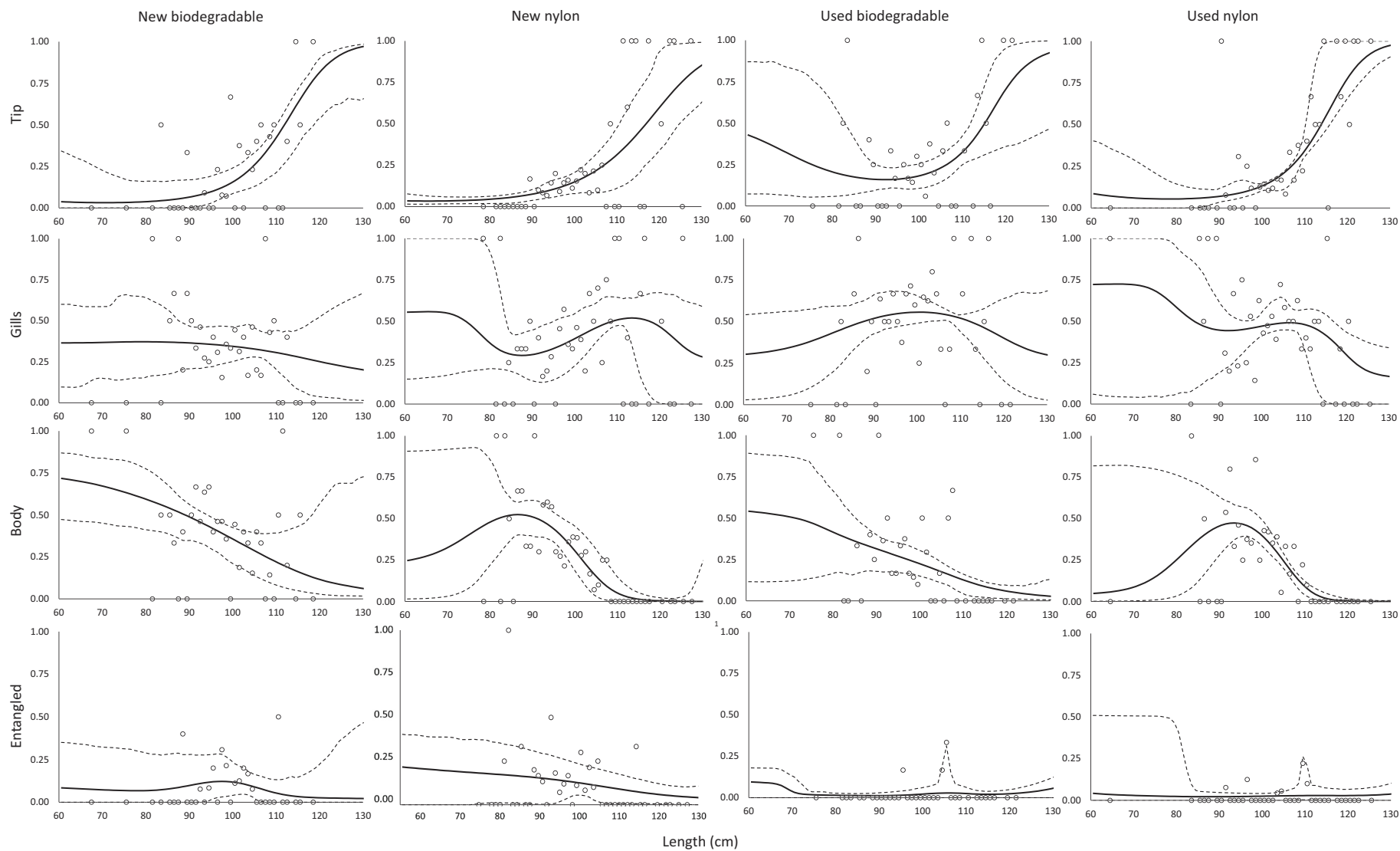


Fig. 5. Probability for capture modes in gillnets (from left to right: new biodegradable, new nylon, used biodegradable and used nylon gillnets). The solid line represents the modelled capture mode probability as bias-corrected mean with Efron percentile bootstrap 95% confidence intervals (stippled lines) fitted to the experimental rate (circle marks).

Table 5
Length-integrated average value for the capture mode probability as bias-corrected means with 95% CIs.

Capture mode	<i>CPq_{average}</i> (%)			
	New biodegradable	New nylon	Used biodegradable	Used nylon
Tip	18.09 (09.55–25.35)	16.60 (08.77–23.58)	21.02 (16.45–25.69)	21.15 (19.81–22.97)
Gills	34.17 (25.41–43.04)	38.49 (25.47–50.75)	53.50 (48.17–60.67)	46.24 (39.08–51.29)
Body	37.19 (25.40–44.37)	31.70 (24.00–40.91)	23.57 (16.00–28.92)	30.11 (26.35–35.35)
Entangled	10.05 (04.00–22.22)	13.21 (03.22–25.95)	01.91 (00.00–04.84)	02.51 (00.76–04.47)

3.3. Length-dependent capture mode probability by gillnet type

The mode of all captured cod was recorded, resulting in 899 capture mode measurements for new and used nylon and biodegradable gillnets distributed over the four modes of fish capture (Table 3; Fig. 4). In most instances, we were able to determine a single mode of capture. For less than 5% of cases (43 cod), we observed more than a single mode of capture. In those cases, a primary mode of capture was determined based on the principle of likely sequence (Savina et al., 2021). Multiple modes of capture were associated mostly with fish being captured by the gills and largest part of the body (33 fish) or tip (mouth or maxillary) and gills (10 fish).

The capture mode probability curves and fit statistics results showed that the model described the experimental data points well. For both biodegradable and nylon gillnets for all four modes of capture, the *p*-value was >0.05 (Table 4; Fig. 5).

In all nets, the main probability of capture of cod was by the gills or the largest part of the body. However, the main probability of capture for the largest fish (> 110 cm total length) was by the tip (mouth or maxillary) (Fig. 5 and Supplementary material 1), whereas individuals under this size were captured by the gills or the largest part of the body. Very few individuals were captured by becoming entangled.

The length-integrated average value for the capture mode probability confirmed that the dominant mode of capture was by the gills in all nets except new biodegradable gillnets (Table 5). The capture mode probability of being caught by the gills was 54% (CI: 48.15–60.67) for used biodegradable nets, 38% (CI: 25.47–50.75) for new nylon nets, and 46% (CI: 39.08–51.29) for used nylon nets (Table 5). For new biodegradable gillnets, the dominant mode of capture was shared between the gills and the largest part of the body (*CPq_{average}* = 37.19% (25.40–44.37) since this probability did not differ significantly from that of capture by the gills because of the overlapping CIs. This was not the case for used biodegradable gillnets, as the main capture mode (gills) in those nets

contained a significantly greater number of cod compared to the body capture mode in the new biodegradable nets (Table 5). The capture by the largest part of the body showed a similar contribution as by the gills in the nylon gillnets as shown by the overlapping confidence intervals (Table 5).

3.4. Probability of being captured in specific gillnets conditioned capture by specific mode

We evaluated capture probability by gillnet type (new or used biodegradable or nylon gillnets, respectively) and examined conditioned capture by a specific mode (tip, gills, body, or entangled) to determine in which fishing gear type the fish had the greatest length-dependent probability of being captured (Table 6). The fit statistics showed that the model described the experimental data points well in all cases except for two. However, for those cases we assumed that the discrepancy was caused by overdispersion in the experimental data.

For the main modes of capture (i.e., gills and body), new nylon gillnets had the greatest probability of retaining fish compared with the other types of gillnets (i.e., 29% (CI: 23.77–33.17) for gills and 31% (CI: 20.94–38.43) for body). Used nylon gillnets had the next highest probability, but the differences were not statistically significant (Table 7).

The probability of capture by the gills for nylon nets was significantly higher than that of used or new biodegradable gillnets. The probability of capture by the largest part of the body in used biodegradable gillnets was significantly lower than that of the other gillnet types, with length-integrated average probability of 13% (CI: 10.41–16.27). Overall, the used biodegradable nets had the lowest length-integrated average probability of capturing fish by all four modes of capture (Fig. 6 and Supplementary material 2). Because only a few individuals were entangled in the nets, it was not possible to draw conclusions about this mode of capture (Fig. 6).

Table 6
Fit statistics for length-dependent probability analysis of being captured in a particular gillnet type conditioned capture by a specific capture mode (tip, gills, body, or entangled). *p*-value, deviance, degrees of freedom (DOF).

Gillnet type	<i>p</i> -value				Deviance				DOF			
	Tip	Gills	Body	Entangled	Tip	Gills	Body	Entangled	Tip	Gills	Body	Entangled
New biodegradable	0.7520	0.0589	0.1772	0.3015	29.93	46.57	34.75	12.88	36	33	28	11
New nylon	0.6478	0.1041	0.5512	0.6422	32.25	43.52	26.40	08.78	36	33	28	11
Used biodegradable	0.1497	0.1699	0.1075	0.4674	44.78	40.62	37.53	10.72	36	33	28	11
Used nylon	0.5659	0.0422	0.1597	0.0444	33.96	40.89	35.36	20.07	36	27	28	11

Table 7
Length-integrated average value for the probability of being captured in a particular gillnet conditioned capture by specific mode (tip, gills, body, or entangled). Data are bias-corrected means with 95% CIs.

Gillnet type	<i>CPq_{average}</i> (%)			
	Tip	Gills	Body	Entangled
New biodegradable	22.11 (15.93–25.13)	18.14 (11.86–21.19)	27.75 (18.55–32.51)	40.00 (23.12–52.99)
New nylon	29.15 (23.88–32.02)	29.30 (23.77–33.17)	30.61 (20.94–38.43)	20.00 (05.58–33.36)
Used biodegradable	17.59 (12.76–23.70)	20.23 (16.56–24.55)	13.47 (10.41–16.27)	12.00 (00.20–35.92)
Used nylon	31.16 (26.67–39.86)	28.16 (22.76–41.34)	28.16 (23.15–40.94)	28.00 (10.44–45.74)

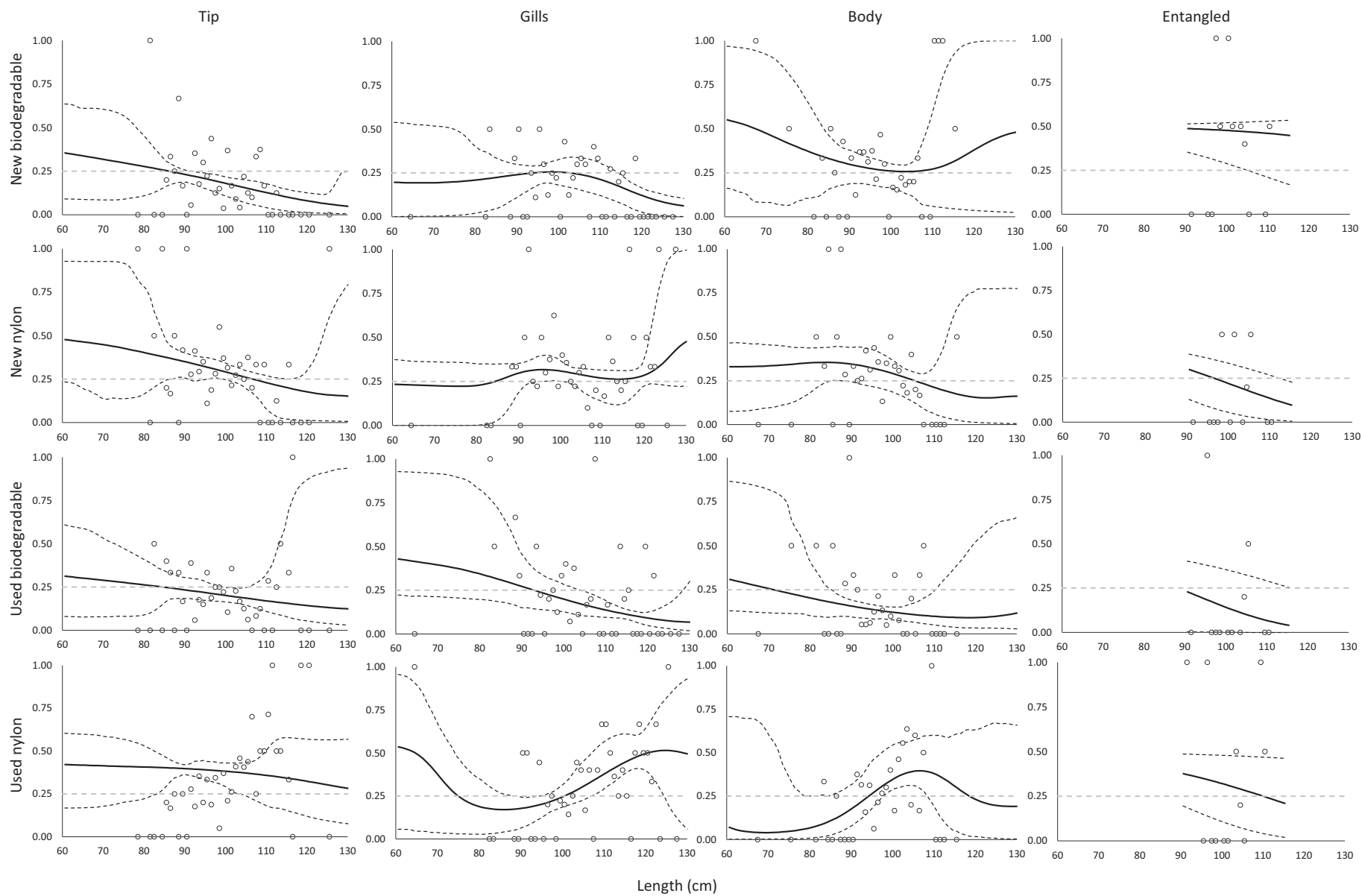


Fig. 6. Probability of capture in a particular gillnet type by a specific capture mode (from left to right: tip, gills, body or entangled). The solid line represents the modelled capture probability as bias-corrected means with Efron percentile bootstrap 95% confidence intervals (stippled lines) fitted to the experimental rate (circle marks). The horizontal grey line represents baseline for no difference in capture efficiency over the gears.

4. Discussion

The results of this study confirmed those demonstrated in earlier trials regarding lower catch efficiency of gillnets made of biodegradable material compared to those made of nylon (Grimaldo et al., 2018, 2019, 2020). We found that on average, new biodegradable gillnets caught 25% fewer cod compared to new nylon gillnets. Similarly, loss of catch efficiency of the biodegradable gillnets after repeated use was indicated, although the difference was not statistically significant: used biodegradable gillnets on average caught 22% fewer cod than used nylon gillnets ($CR_{average} = 78.39$ (CI: 61.86–125.00)).

The observed difference in catch efficiency between biodegradable and nylon gillnets may be due to differences in breaking strength and elasticity affecting when the netting breaks at the point of tension due to the presence of fish caught by the gills or body. Indeed, capture by gills was the most common way of cod being caught in gillnets, but the probability of being retained in biodegradable gillnets for cod captured by the gills was lower compared to that of nylon nets. Since larger fish are more likely to be caught by the gills than the body, this would explain the reduced catch efficiency of larger fish in the biodegradable nets reported by Grimaldo et al. (2019) and observed also in this study.

In this study, we found that the catch efficiency was reduced for used versus new biodegradable nets for cod of the largest length classes (approximately >95 cm length). Grimaldo et al. (2019, 2020) previously documented loss of catch efficiency of biodegradable compared to nylon gillnets. The main mode of capture for new biodegradable gillnets was by the gills, whereas fish caught in used biodegradable nets were mostly captured by the largest part of the body.

Since larger fish are more likely to be caught by the gills than the body, the results of this study helped explaining the reduced catch efficiency of biodegradable gillnets in relation to particular modes of capture where the gillnets lose the capture efficiency for specific capture modes. This loss may be due to changes in different mechanical properties of the netting. Specifically, reduction in elasticity of the material and reduction in the breaking strength can affect the material when the netting is used (Grimaldo et al., 2020). Used nylon nets caught significantly less smaller cod and more larger cod compared to new nylon nets, which we could relate to a higher tendency for capture of large fish by the tip in used compared to new nylon nets, and a higher tendency for entanglement of small fish in new compared to used nylon nets.

Effect of properties such as breaking strength and elasticity require further studies in order to improve the performance (i.e., catch efficiency) of the biodegradable material used in gillnets. Biodegradable gillnets should preferably have catch efficiency similar to that of nylon gillnets in order to be accepted by the industry. Currently, the use of biodegradable material in gillnets is optional in Norway, and it has not been adopted by the commercial fishery because of its lower catch efficiency and higher production costs (Standal et al., 2020).

The results of this study showed that differences in catch efficiency between gillnet types were related to specific capture modes of fish, which in turn may be related to specific differences in material properties. We are the first to use capture mode probability to explain the differences in catch efficiency between biodegradable and nylon gillnets. The differences we observed may be related to different properties of the material. Therefore, systematic studies of the mechanical properties of the biodegradable material and how these properties change with changing mesh size and twine diameter are needed to improve the catch efficiency of future biodegradable gillnets. More catch efficient biodegradable gillnets will gradually lead to the replacement of nylon gillnets and to the reduction of marine plastic pollution and ghost fishing as biodegradable gillnets, compared to nylon, are degraded into substances that do not have any negative effect on the marine environment such as carbon dioxide, methane and water (Kim et al., 2014a, 2014b).

In our study, the modes of capture might depend on the specific gillnet design tested and, specifically, on factors such as hanging ratio, mesh size, monofilament diameters, and material type. However, the use

of capture modes can provide valuable information to explain the catch efficiency for any given hanging ratio, thus this method can be further applied in studies of different gillnet characteristics in order to improve catch efficiency of biodegradable gillnets.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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CRediT authorship contribution statement

Kristine Cerbule: Conceptualization, investigation, formal analysis, visualization, writing – original draft, writing – review and editing.

Bent Herrmann: Conceptualization, software, writing – original draft, writing – review and editing, supervision.

Eduardo Grimaldo: Conceptualization, writing – original draft, supervision.

Roger Larsen: Conceptualization, writing – original draft, supervision.

Esther Savina: Writing – original draft, supervision.

Jørgen Vollstad: Data gathering and investigation.

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