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Bycatch reduction and alternative exploitation patterns in demersal trawl fisheries of the Baltic Sea and the North Sea

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Dedication

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Summary

In the Baltic Sea and North Sea, the sustainability of bottom-trawl fisheries is threatened by many issues, such as the impact of climate change on exploited demersal stocks, long-term overfishing, and the European Landing Obligation for quoted species. This thesis identifies challenges to bycatch and harvesting patterns of targeted species in four relevant Baltic Sea and North Sea bottom-trawl fisheries, and presents six recent research papers that investigate species and size selectivity of fishing gears that can contribute to the mitigation of fishery-specific issues.

The bycatch of flatfish species, such as flounder (*Platichthys flesus*), dab (*Limanda limanda*), and plaice (*Pleuronectes platessa*), is an issue in the Baltic Sea otter-trawl fisheries targeting cod. Paper I investigates if the application of a sorting grid, originally proposed by the fishing industry, can reduce the bycatch of flatfish in these fisheries. The results revealed a large reduction in flatfish bycatch with the added advantage of providing an additional escape possibility for undersized cod without compromising the catchability of marketable sizes.

Paper II evaluates an alternative to the grid system proposed in Paper I: the exploitation of fish behaviour to address the problem of flatfish bycatch in the Baltic cod-directed trawl fisheries. The results demonstrate that a simple flatfish excluder in the lower panel of the extension piece of the trawl can effectively reduce the bycatch of flatfish while maintaining the catches of the targeted cod. Paper II also introduces a novel methodology, based on video recordings, for quantitative evaluation of fish behaviour in relation to selection devices. The method produces behavioural tree diagrams representing and quantifying behavioural patterns in relation to the selection device being assessed. Double bootstrapping is used to account for the uncertainty caused by the limited number of fish observations and natural variation in fish behaviour.

In the frame of the balanced harvesting paradigm, Paper III explores the feasibility of achieving alternative harvesting patterns for Baltic cod. The intended alternative harvesting pattern targets medium-sized cod and avoids catches of juvenile and the largest, most productive cod. Paper III demonstrates experimentally that a bell-shaped retention probability curve, usually associated with gillnet fisheries, can also be achieved in trawl gears by combining standard grid and codend devices.

The current poor status of Baltic cod stocks has led to drastic quota reductions to historical minima. In conformity with the Landing Obligation for quoted species, cod has become a choke species to the emergent flatfish fisheries in the Baltic Sea. Based on the insights obtained in Paper II, Paper IV investigates if the behavioural patterns observed for flatfish and cod in the trawl gear could be used to limit cod catches in flatfish-directed trawl fisheries. Paper IV demonstrates experimentally that a

large reduction in cod catches can be achieved by removing a section of the top panel of the extension piece.

As for Baltic cod, drastic reductions in fishing quotas for North Sea and Kattegat cod have occurred in recent years as a management response to the poor status of these populations. Consequently, cod is a choke species in the North Sea otter-trawl fisheries targeting *Nephrops.* An efficient separation of *Nephrops* from fish species in the trawl could lead to better management of the available quotas. Paper V investigated the potential of square-mesh sieve panels to separate *Nephrops* from fish species. Results from experimentally testing four different sieve panels revealed that most fish species were efficiently separated from *Nephrops*. However, the sieving efficiency (probability to pass through the meshes of the sieve panel) for the largest, most valuable *Nephrops* remained too low. Therefore, the resulting separation rates of fish species and marketable *Nephrops* was found suboptimal and not suitable for commercial fisheries.

Recent shifts in North Sea ecosystems have reduced the abundance of natural fish predators in the fishing grounds of brown shrimp (*Crangon crangon*), making the North Sea beam-trawl fishery the major source of mortality for the targeted shrimp. This new role has also caused concern over the sustainability of the harvesting patterns in this fishery. In the search for optimal harvesting patterns of brown shrimp, Paper VI delivers a predictive framework for codend size selection of brown shrimp. The framework that was created is based on a large selectivity dataset and allows predictions of codend size selection considering the effect of mesh size and mesh orientation. The predictive framework presented in Paper VI could aid fishery modellers to explore population dynamics of brown shrimp under a wide range of predicted exploitation pattern scenarios.

Finally, the work presented in this thesis provides technological advances and a knowledge base that suggests how to reduce the bycatch of unwanted species and generate alternative harvest patterns in different Baltic Sea and North Sea trawl fisheries.

Papers I and III were published in *Fisheries Research*. Paper II was published in the *ICES Journal of Marine Science*. Paper IV is to be published condition revision in *Marine and Coastal Fisheries*. Paper V was published in *Fisheries Management and Ecology*. Paper VI was published in *PLOS One*.

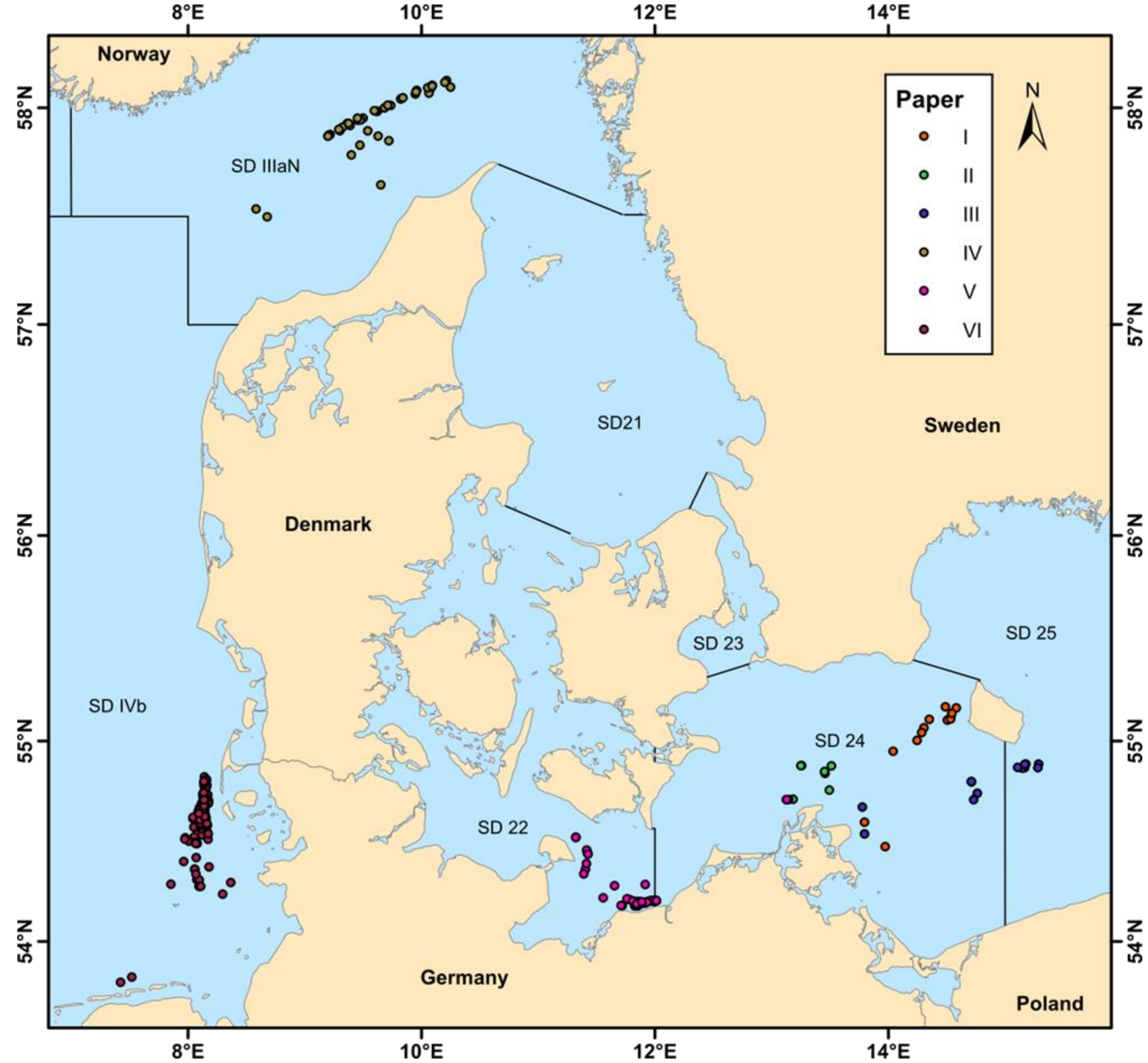

Figure 1. Spatial distribution of the sea trials related to the research of this thesis.

List of papers

Paper I: Santos, J., Herrmann, B., Mieske, B., Stepputtis, D., Krumme, U., Nilsson, H. 2016. Reducing flatfish bycatch in roundfish fisheries. Fisheries Research 184, 64–73.

Paper II: Santos, J., Herrmann, B., Stepputtis, D., Kraak, S.B.M., Gökçe, G., Mieske, B. 2020. Quantifying the performance of selective devices by combining analysis of catch data and fish behaviour observations: methodology and case study on a flatfish excluder. ICES Journal of Marine Science 77, 2840–2856.

Paper III: Stepputtis, D., Santos, J., Herrmann, B., Mieske, B. 2016. Broadening the horizon of size selectivity in trawl gears. Fisheries Research 184, 18–25.

Paper IV: Santos, J., Stepputtis, D., Oesterwind, D., Herrmann, B., Lichtenstein, U., Hammerl, C., Krumme, U. Reducing cod bycatch in flatfish fisheries. Marine and Coastal Fisheries [Published condition revision].

Paper V: Santos, J., Herrmann, B., Mieske, B., Krag, L.A., Haase, S., Stepputtis, D. 2018. The efficiency of sieve panels for bycatch separation in *Nephrops* trawls. Fisheries Management and Ecology 25, 464–473.

Paper VI: Santos, J., Herrmann, B., Stepputtis, D., Günther, C., Limmer, B., Mieske, B., Schultz, S., et al. 2018. Predictive framework for codend size selection of brown shrimp (*Crangon crangon*) in the North Sea beam-trawl fishery. PLOS ONE 13, e0200464.

Thesis structure

The thesis is structured in 10 chapters as follows:

Chapter 1 introduces the specific fisheries studied and identifies challenges to be addressed in the thesis.

Chapter 2 defines the overall objective of the thesis, based on the challenges identified in each of the fisheries described in the previous chapter.

Chapters 3 and 4 review the currently available technologies and methodologies that could be adapted and used to address the thesis objective and the associated challenges to the fisheries.

Chapter 5 formulates the specific research questions to be addressed by the research in the thesis, based on the thesis objective (Chapter 2) and reviews of the currently available technologies and methods (Chapters 3 and 4).

Chapters 6–9 present the research papers and explain how and to what extent the research answers each of the specific research questions (Chapter 5) of the thesis.

Chapter 10 discusses the extent to which the research conducted has fulfilled the overall objective of the thesis.

1 Selected fisheries and related challenges

This section introduces four demersal trawl fisheries from the Baltic Sea and Eastern North Sea, and describes challenges that compromise their current and future sustainability. In the Baltic Sea and North Sea, the synergic effect of overfishing and fishery-extrinsic anthropogenic pressures, such as climate change, are inducing shifts in the oceanographic regimes and marine ecosystems that threaten the productivity of commercially exploited stocks (Eero et al., 2020, 2015, 2014, 2007; Kirby et al., 2009; Lindegren et al., 2010b; Mackenzie et al., 2007; Polte et al., 2021; Reusch et al., 2018; Temming and Hufnagl, 2015). In the Baltic Sea, the perturbations related to anthropogenic pressures and climate change have reached a point that the Baltic is now known as a "time machine" (Reusch et al., 2018), because the example of its decline anticipates the cascade of negative impacts to be expected in other coastal ecosystems and fisheries around the world (Reusch et al., 2018). Because it is unlikely to reverse current climate- and human-induced effects through current ecosystem resource management in the short term (Eero et al., 2015; Kirby et al., 2009), it is important to understand and adapt to new ecological regimes (Kirby et al., 2009), which should also involve adjustments in harvesting patterns of commercial fisheries.

The bycatch of unwanted species and sizes is an ethically unacceptable practice in modern fisheries. It represents an unnecessary waste of natural resources, and it decreases the efficiency of fishing operations and sorting of the catches (Greenstreet et al., 1999; Kaiser and de Groot, 2000). With the main aim of phasing out discarding practices in European fisheries, Article 15 of the reformed EU Common Fisheries Policy (EU 1380/2013) from May 2013 introduced the Landing Obligation (LO), which states: "*all catches of species which are subject to catch limits [...] shall be brought and retained on board the fishing vessels, recorded, landed and, counted against the quotas [...]*." The LO was gradually implemented from 1 January 2015 to 1 January 2019, with the original intention of incentivising more selective fishing in European fisheries (Valentinsson et al., 2019). The LO is a legislative challenge for mixed fisheries, where catches of species with limited quotas can constrain the fishing possibilities available to other (targeted) quoted species. Those species with quotas potentially constraining the fishing possibilities are known as "choke species" (Catchpole, 2017; Eero et al., 2015; Mortensen et al., 2017). Therefore, an ongoing challenge for some of the fisheries selected in this thesis is the presence in catches of potential, perceived, or real choke species.

1.1 Baltic Sea otter-trawl fisheries targeting cod

Atlantic cod (*Gadus morhua*) is a large-bodied, top predator marine fish species inhabiting coastal and shelf areas throughout the North Atlantic, with a key role both in marine ecosystems and fisheries (Link et al., 2009). Cod populations have adapted to the semi-enclosed, brackish and stratified waters of the Baltic Sea (Köster et al., 2005; Lindegren et al., 2010a, 2010b). From a historical perspective, cod is the most important targeted species in the demersal trawl fisheries in the Baltic Sea (Madsen, 2007; Probst et al., 2011; Storr-Paulsen et al., 2012; Bagge et al., 1994). The intensive exploitation of Baltic fish species started with the introduction of demersal otter trawls in the 1940s (Eero et al., 2007; Bagge et al., 1994). After three decades of relative stability, the production of Baltic cod reached a historical peak of spawning-stock biomass (SSB) during the late 1970s and early 1980s (estimated at 700 000–800 000 tons), as a result of favourable reproductive conditions that were driven by frequent oxygenated water inflows from the North Sea (Bagge et al., 1994), and a reallocation of the fishing pressure towards pelagic fisheries (Lablaika et al., 1991). The high productivity of cod during this period reinvigorated the cod-directed trawl fishery, which led to an increase in fishing mortality of the species several times greater than that advised by scientific assessment (Bagge et al., 1994). Coinciding with the renewed interest in the cod fishery, the oceanographic regime in the Baltic Sea started to shift towards a new, unfavourable environmental state for the spawning of cod, characterised by decreasing salinity and oxygen (Köster et al., 2005). The new "cod hostile" environmental state (Cardinale and Svedäng, 2011), combined with the impact of overfishing, led to a rapid decline in the SSB of Baltic cod from its historical peak to < 100 000 tons in the early 1990s (Bagge et al., 1994; Köster et al., 2005). The International Baltic Sea Fishery Commission (IBSFC, management body of shared Baltic Sea fishery resources between 1974 and 2005) reacted to such an alarming situation by setting several resolutions for the recovery of Baltic cod. A key strategy promoted by the IBSFC in response to the decrease in cod biomass was the adjustment of the size selectivity of the fishery in order to protect juvenile cod (Aps and Lassen, 2010; Madsen, 2007). Following the IBSFC resolutions, the period between 1995 and 2010 was characterised by intensive research devoted to developing and testing a countless number of codend modifications with the aim of improving the escape possibilities of juvenile cod (Madsen, 2007). This period was also characterised by a dynamic management, when codends with greater selective properties were progressively implemented in the fishery. As a result, it has been estimated that the length of cod with 50% retention probability (*L50*) increased ~15 cm since the early 1990s (Madsen, 2007; Valentinsson et al., 2019), contributing to a large reduction in juvenile cod bycatch and discards in the fishery (Feekings et al., 2013).

Despite the research and management efforts of previous decades devoted to improving the exploitation patterns of the fishery, currently the Baltic cod-directed trawl fisheries still face two major issues that compromise their immediate and future sustainability. The first persistent problem in the fishery is the high level of bycatch and discarding of flatfish species, especially flounder (*Platichthys flesus*), dab (*Limanda limanda*), and plaice (*Pleuronectes platessa*; ICES, 2020b; Probst et al., 2011; Storr-Paulsen et al., 2012; Wienbeck et al., 2014). Of these three flatfish species, plaice is the only one subject to stock assessment, total allowable catch (TAC), and minimum conservation reference size (MCRS = 25 cm). However, flounder catches are regulated only by minimum landing sizes (23, 21, or 18 cm, depending on the ICES Subdivision), and dab catches are unregulated. The overall TAC for plaice is distributed over four countries: Denmark (72%), Poland (15%), Germany (8%), and Sweden (5%). It has increased steadily during the past decade from 3409 t in 2013 to a peak of 10 122 t in 2019, reflecting the species' improved situation, with a current spawning-stock size above maximum sustainable yield (MSY; ICES, 2021c). Following the European Common Fishery Policy for quoted species, catches of plaice have been subject to the European LO since January 2017. The implementation of the LO for plaice raised concerns about the sustainability of the cod-directed fishery, especially for those riparian countries with limited quotas (Germany, Sweden, and Poland) or zero quotas (Finland, Estonia, Latvia, and Lithuania, where plaice catches are anecdotal; Zimmermann et al., 2015). In such cases, a premature exhaustion of limited national quotas for plaice could affect fishers' ability to fully utilise the fishing possibilities of cod (Wienbeck et al., 2014; Zimmermann et al., 2015). Fishery data obtained in the years after implementation of the LO reveal that the discard of plaice is still an issue, with discards ratios of ~26% and reported "unwanted catch" landings (ICES, 2020b). The poor selectivity of the current mandatory codends for flatfish species (Dahm et al., 2003; Wienbeck et al., 2014) and habitat overlapping (ICES, 2019b; Zimmermann et al., 2015) explain the unsuccessful enforcement of the LO rule for plaice catches in the Baltic Sea. In an attempt to reduce the bycatch of flatfish in the Baltic cod-directed fisheries, Wienbeck et al. (2014) proposed three novel codend designs intended to address the selectivity of the target and bycatch species simultaneously. Experimental results obtained in Wienbeck et al. (2014) revealed, however, very limited success in reducing plaice catches, and considerable losses of marketable cod were observed for some of the designs tested. Therefore, to aid fishers to better manage the available plaice quotas and to reduce discards of other unquoted flatfish species, efficient flatfish bycatch reduction technologies are needed in the cod-directed trawl fisheries.

In the Baltic Sea, it is notable that despite the progressive increase in the selectivity of commercial trawl gears between the 1990s and 2010 (Madsen, 2007) no substantial improvement in the status of cod stocks was achieved (Eero et al., 2020, 2015). On the contrary, the unsustainable harvesting rates and changing environmental conditions have driven Baltic cod into a critical situation (Eero et al., 2020, 2015; ICES, 2021a, 2019a). Since 2003, and based on genetic differences and geographic distributions, the assessment and management bodies recognise two separate populations of Baltic cod (ICES, 2015): the Eastern Baltic cod, the larger Baltic cod stock, widely distributed from the Bornholm basin (ICES Subdivision (SD) 25) to the Gulf of Finland (SD 32); and the smaller Western Baltic cod stock, with a spatial distribution restricted to ICES SD 22–24. Genetic and tagging experiments demonstrate that Eastern and Western stocks mix in the Arkona Basin (SD 24; Nielsen et al., 2013), which presents a challenge to fishery management plans that apply to the individual stocks (Eero et al., 2014). The spawning stock of the Western Baltic cod has remained relatively stable at medium levels over the past decades (Eero et al., 2014), and recruitment has stabilised at low levels since 2015. The Eastern Baltic cod stock started to show signs of recovery in the late 2000s, which has been partially attributed to successful management measures applied over the years (Aps and Lassen, 2010; Cardinale and Svedäng, 2011; Madsen, 2007). However, this positive trend could only be sustained for a few years before a rapid deterioration occurred, driven by negative biological changes in the stock. The current population structure is severely truncated owing to the absence of large individuals (Eero et al., 2020, 2015; ICES, 2020b). The condition and length of the fish, or first maturation, has concurrently decreased in recent years, and it has been estimated that the natural mortality is currently several times higher than fishing mortality (Casini et al., 2016; Köster et al., 2017). Currently, the poor biological condition and productivity make any improvement in Baltic cod stocks unlikely in the mid-term (Eero et al., 2020). Triggered by such an alarming situation, the International Council for the Exploration of the Sea (ICES) assessment has, in recent years, advised zero quotas for Eastern Baltic cod (ICES, 2021a), including fishing areas where Eastern and Western Baltic cod stocks are mixed (ICES, 2019b). Following ICES advice, the European council agreed to close the Eastern Baltic cod fisheries for 2020 and 2021. In 2020, fishers were given with a bycatch quota of 2000 tons to allow them to target other fish species. The 2020 quota was reduced to about 600 tons in 2021 (ICES, 2021a).

Although the disappearance of larger cod in the Baltic Sea is not fully understood (Eero et al., 2015), the continued increase in codend selectivity has been suggested as a plausible explanation for the currently truncated population structures (Svedäng and Hornborg, 2017; Valentinsson et al., 2019). In general, large female individuals are related to greater fecundity and egg production (Figure 2), greater viability of larvae, and longer spawning periods than early spawners (Berkeley et al., 2004; Birkeland and Dayton, 2005; Bobko and Berkeley, 2004). Consequently, it could be hypothesised that the selective removal of large individuals over a long period contributed to the current poor recruitment index of Baltic cod. The selective exploitation of large fish can also trigger evolutionary paths leading to lower stock production, because it favours the survival and reproductive success of early spawners and low-growing individuals (Conover and Munch, 2002; Jørgensen et al., 2009;

Munch et al., 2005; Zhou et al., 2010). Ongoing discussions related to balanced harvesting (Garcia et al., 2012; Jacobsen et al., 2014; Zhou et al., 2010) in the cod-directed trawl fishery should explore alternative exploitation patterns in which the exploitation of individuals is based primarily on their potential productivity rather than their size. From a technical point of view, however, it can be challenging to implement alternative harvest patterns departing from the traditional s-shape selection curve associated to trawl fisheries.

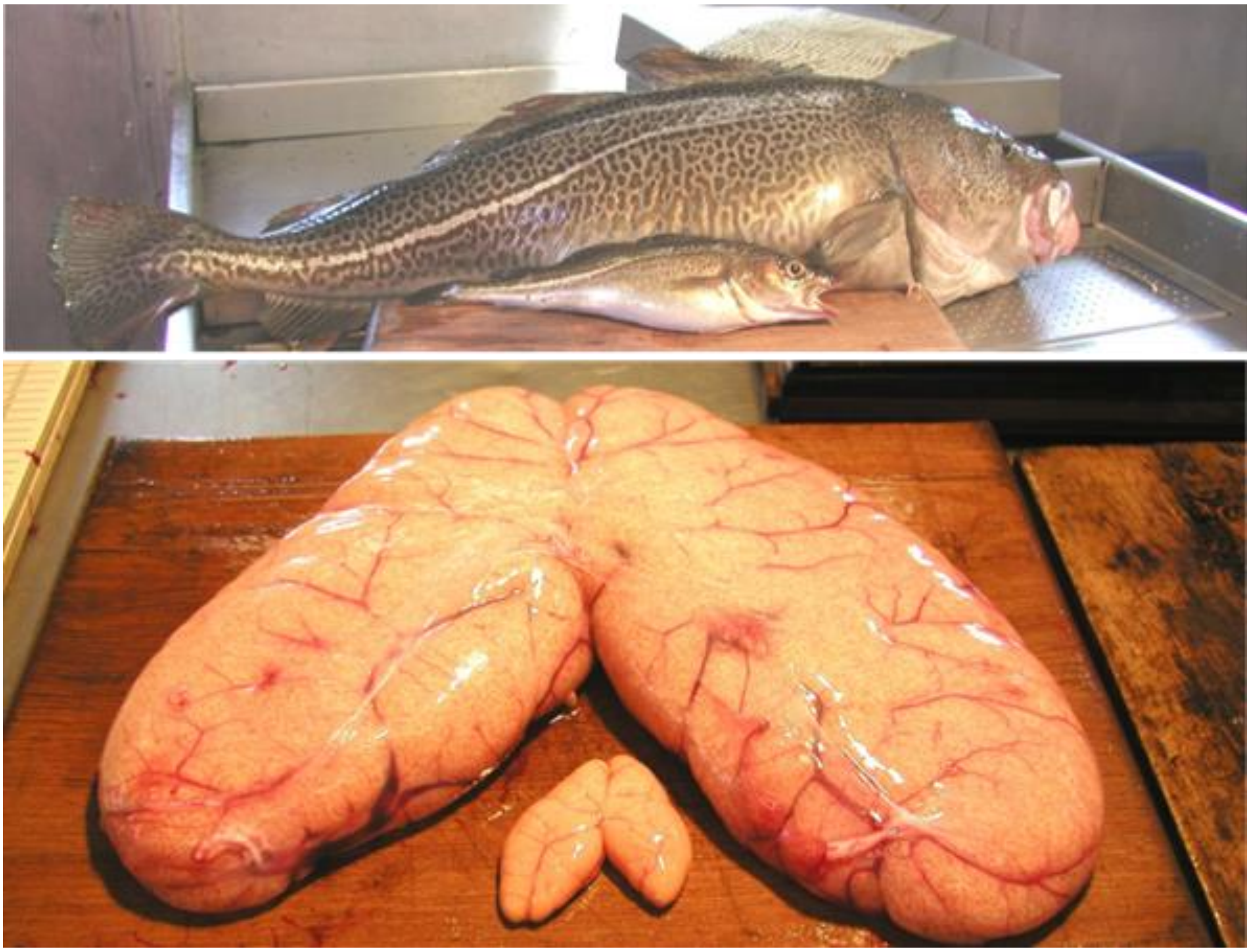

Figure 2. Comparison of body and gonad sizes from small and large Baltic cod spawners (Photo: M. Bleil, TI/OF).

1.2 Baltic Sea otter-trawl fisheries targeting flatfish

In Baltic Sea demersal trawl fisheries, flatfish species can become an important supplement or even a seasonal fishing target. In the Western Baltic Sea (SD 22), a flatfish mixed fishery targeting plaice and dab, in which Danish and German trawlers participate, takes place mostly during the first quarter of the year (ICES, 2020b; Storr-Paulsen et al., 2012; Zimmermann et al., 2015). In the central Baltic Sea (SD 24–25), plaice and especially flounder can be important seasonal catch components in demersal trawl fisheries. Plaice catches in the central Baltic are mostly taken in SD 24 by Danish and German trawlers during the fourth quarter of the year. Flounder landings belong mostly to Polish trawlers (75% in 2018; ICES, 2019b), in a directed trawl fishery occurring particularly in SD 25 during the first quarter of the year (44% in 2018; ICES, 2019b).

The poor status of Baltic cod stocks (ICES, 2021a, 2019a), and the prevailing adverse hydrographic conditions in the Baltic Sea (Köster et al., 2005; Mackenzie et al., 2007; Möllmann et al., 2009), makes any improvement of the cod stocks unlikely in the near future (Eero et al., 2020). To maintain sustainable and economically viable fishing under limited or zero-quota policies to protect cod stocks, vessels that had previously targeted cod will likely shift to targeting flatfish (ICES, 2020b, 2019b). As the habitat distribution of flounder, plaice, and cod overlap in space and time in the central Baltic Sea (SD 24–25), there are no areas or months where flatfish fisheries could be conducted without increasing the risk of cod bycatch (ICES, 2019b; Zimmermann et al., 2015). Following the LO, using trawl gears with high catch efficiency on cod in the area of distribution of Eastern Baltic cod will likely lead to a rapid exhaustion of the bycatch quota allocated to the species, which would constrain the fishing possibilities on healthier flatfish populations. Applying efficient species-selection technologies in fishing gears could help mitigate the problem of cod bycatch in Baltic flatfish trawl fisheries (ICES, 2019b). However, because research efforts have been invested mostly in adjusting codend size selection to protect species juveniles, few technologies to avoid catching cod in the Baltic Sea are available to fishers. One available technology is the species-selective flatfish otter-trawl tested by Madsen et al. (2006). To avoid cod catches, the experimental trawl in Madsen et al. (2006) had a lower entrance height at the mouth than commercial trawls, and applied square-mesh netting between the headline and the first section of the belly. In addition, the groundrope was rigged with tickler chains to increase the catch efficiency of flatfish, a controversial adaptation owing to its potentially greater impact on the seabed (Depestele et al., 2019). Therefore, additional fishing technologies to reduce the bycatch of endangered Baltic cod are needed, especially considering an expected major switch towards flatfish-directed fisheries in the Baltic Sea.

1.3 North Sea otter-trawl fisheries targeting *Nephrops*

Nephrops (*Nephrops norvegicus*) is a highly appreciated decapod species that supports some of the most economically important fisheries in the Northeast Atlantic and Mediterranean Sea (Ungfors et al., 2013). The commercial interest in this small lobster increased sharply between the 1950s and the mid-1980s. Since then, landings have stabilised roughly within a range of 50 000 to 65 000 tons per year (Ungfors et al., 2013). Although creel fisheries target *Nephrops* (Adey, 2007), 95% of the total landings in Europe are caught in otter-trawl fisheries (Briggs, 2010; Ungfors et al., 2013). Catching *Nephrops* efficiently with trawls requires the use of small-mesh codends, a key driver of the high bycatch and discard volumes historically associated with these fisheries (Alverson et al., 1994; Catchpole et al., 2007; Catchpole and Revill, 2008; Kelleher, 2005; Krag et al., 2008). In general, the problem of unwanted bycatch in *Nephrops* fisheries has been addressed by attempting to provide additional escape possibilities for fish species before they enter the codend. Such efforts materialised in a wide variety of trawl modifications (Catchpole and Revill, 2008). Probably the most applied modifications to avoid gadoid catches of all sizes are the Swedish grid (Valentinsson and Ulmestrand, 2008) and the SELTRA codend (Krag et al., 2016), while square mesh panels fitted ahead of the codend are often applied to improve the size selection of those species (Armstrong et al., 1998; Briggs, 1992). Although the aforementioned trawl modifications can reduce bycatch significantly, issues related to bycatch of juvenile fish (Alzorriz, 2018; Frandsen et al., 2009; Lövgren et al., 2016; Nikolic et al., 2015; Valentinsson and Ulmestrand, 2008) and losses of marketable *Nephrops* (Catchpole et al., 2006; Frandsen et al., 2009) must still be resolved.

The condition of cod stocks in the North Sea and Kattegat Sea is alarming, with SSB and recruitment indices at historically low levels (ICES, 2021b, 2020a, 2019c). In this situation, the latest ICES advice offers very restrictive TACs for cod in the North Sea and no quotas in the Kattegat Sea (ICES, 2021b). Consequently, cod can be considered a choke species for *Nephrops* fisheries in these marine regions. Adding new species-selection technologies to the available toolbox could provide fishers involved in the *Nephrops* fisheries of the North Sea, and elsewhere, more alternatives that will help them better adapt to the current situation regarding bycatch of cod and other regulated species.

1.4 North Sea beam-trawl fishery targeting brown shrimp

In the North Sea, the short-lived, small brown shrimp (*Crangon crangon*) sustains a large beam-trawl fishery involving ~550 vessels, mostly from the Netherlands and Germany, and to a lesser extent from Denmark, Belgium, the UK, and France (ICES, 2019d). According to annual landing statistics, brown shrimp is among the most important targeted species in the North Sea (Temming and Hufnagl, 2015), usually surpassing 30 000 tons and gross revenues of €100 million (ICES, 2019d).

Despite its socioeconomic relevance, the brown shrimp stock has never been managed based on scientific advice, implying that the fishery is not subject to quotas or effort restrictions. The historical justification for the fishery's no-management paradigm relied on the assumption that the annual mortality of brown shrimp caused by predation from fish species (mostly cod and whiting (*Merlangus merlangus*) largely exceeded fishing mortality (Welleman and Daan, 2001). However, the steady decline in key predators of brown shrimp, caused by overfishing and climate change, together with the increase in brown shrimp landings over the previous decades, points to a new scenario in which the fishery has become the main source of mortality for adult brown shrimp (total length ≥ 50 mm; Temming and Hufnagl, 2015). Such new ecological and fishery scenarios raise the question of whether or not the no-management paradigm is still a reasonable approach to the brown shrimp fishery (Temming and Hufnagl, 2015). A recent update of the analysis conducted in Welleman and Daan (2001) confirmed that the fishery has taken over as the main source of brown shrimp mortality (Temming and Hufnagl, 2015). Moreover, Temming and Hufnagl (2015) also identified potential growth overfishing (a harvest pattern based on an average size that is smaller than the size that would produce the maximum yield-per-recruit), which could be addressed by reducing the fishing pressure on undersized shrimp via improvements in the size selection of the commercial gears.

Traditionally, efforts to improve gear selectivity in the fishery have focused on reducing the bycatch of fish species. As a result, fishers are obliged to use either sieve nets or grids in their trawls (through EU 2019/1241 and supplementary national regulations), two devices with proven efficiency in reducing the bycatch of age 1+ fish (Graham, 2003; Polet et al., 2004; Revill and Holst, 2004a). Codends traditionally used in the brown shrimp fishery are made of PA netting with inner mesh sizes between 20 and 22 mm (Neudecker and Damm, 2010). The few research studies done on the performance of commercial codends reported high retention rates of undersized shrimp (Polet, 2000; Revill and Holst, 2004b). However, the fishery's lack of science-driven management has downgraded the priority of concerns about the selectivity of commercial codends. In the current state, where the fishery has become the major source of brown shrimp mortality, improving the harvesting patterns has become a priority issue for the sustainability of the fishery. Moreover, in 2015, the Cooperative Fisheries Organisation of the Netherlands, the GbR of Germany, and the Danish Fishermen-Producers Organisation began the process of certifying the fishery for Marine Stewardship Certification (MSC). A key criterion for successful certification is the establishment of a management system that, among other activities, promotes the application of technical measures to reduce discards of undersized brown shrimp. One obvious strategy would be to adjust codend selectivity. However, the few efforts that have been devoted to investigating codend size selection in the fishery do not provide an informed recommendation regarding which codend designs could lead to optimal harvesting patterns for brown shrimp.

2 Objective

Chapter 1 identified and described the challenges faced by each of the four case fisheries described there. The overall objective of this thesis is to identify, develop, and evaluate gear modifications that can reduce bycatch of unwanted species and generate alternative harvest patterns in different Baltic Sea and North Sea trawl fisheries.

3 The selectivity of trawl gears

Trawl gears are broadly defined as cone-shaped nets towed behind one or two boats catching fish through herding and sieving (He et al., 2021). Investigations included in this thesis involve otter-trawl and beam-trawl fisheries. The most conspicuous difference between these two trawl modalities is the technical strategy followed to maintain the horizontal spread of the net during towing. Although otter trawls use a pair of heavy doors to achieve wide spreads (Figure 3), beam trawls use rigid beams that hold the net mouth open (Figure 4; He et al., 2021). The selectivity of trawl gears is defined by processes happening during the fishing operation that cause differences between the catch composition (species and sizes) and the population structure available in the exploited fishing grounds (Millar and Fryer, 1999; Wileman et al., 1996). The selectivity can be adjusted largely by trawl modifications (Bayse and He, 2017; Catchpole and Revill, 2008; Kennelly and Broadhurst, 2021; Madsen, 2007). Such modifications are most often applied at the untapered rear section of the trawl body (Kennelly and Broadhurst, 2021), and more specifically in the codend. The codend, where the catch accumulates and fish most often attempt to escape, is the primary selection device in trawl gears (Glass, 2000). In mixed fisheries, where catches are composed of species of different sizes and morphologies, adjustments in codend selectivity may not solve multispecies selectivity issues. In such cases, the selectivity of the codend is often supplemented with additional selection devices mounted ahead of it. This chapter reviews several trawl gear modifications identified as potential technological solutions to address the objectives of this thesis.

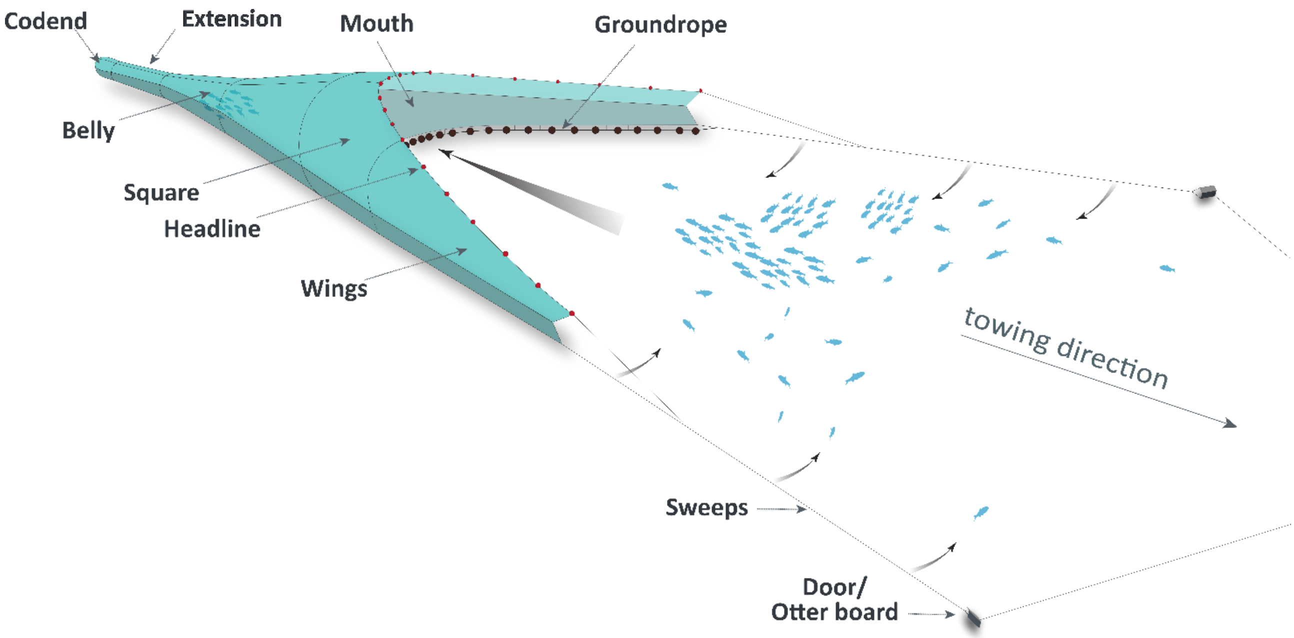

Figure 3. Perspective view of an otter trawl during the capture process.

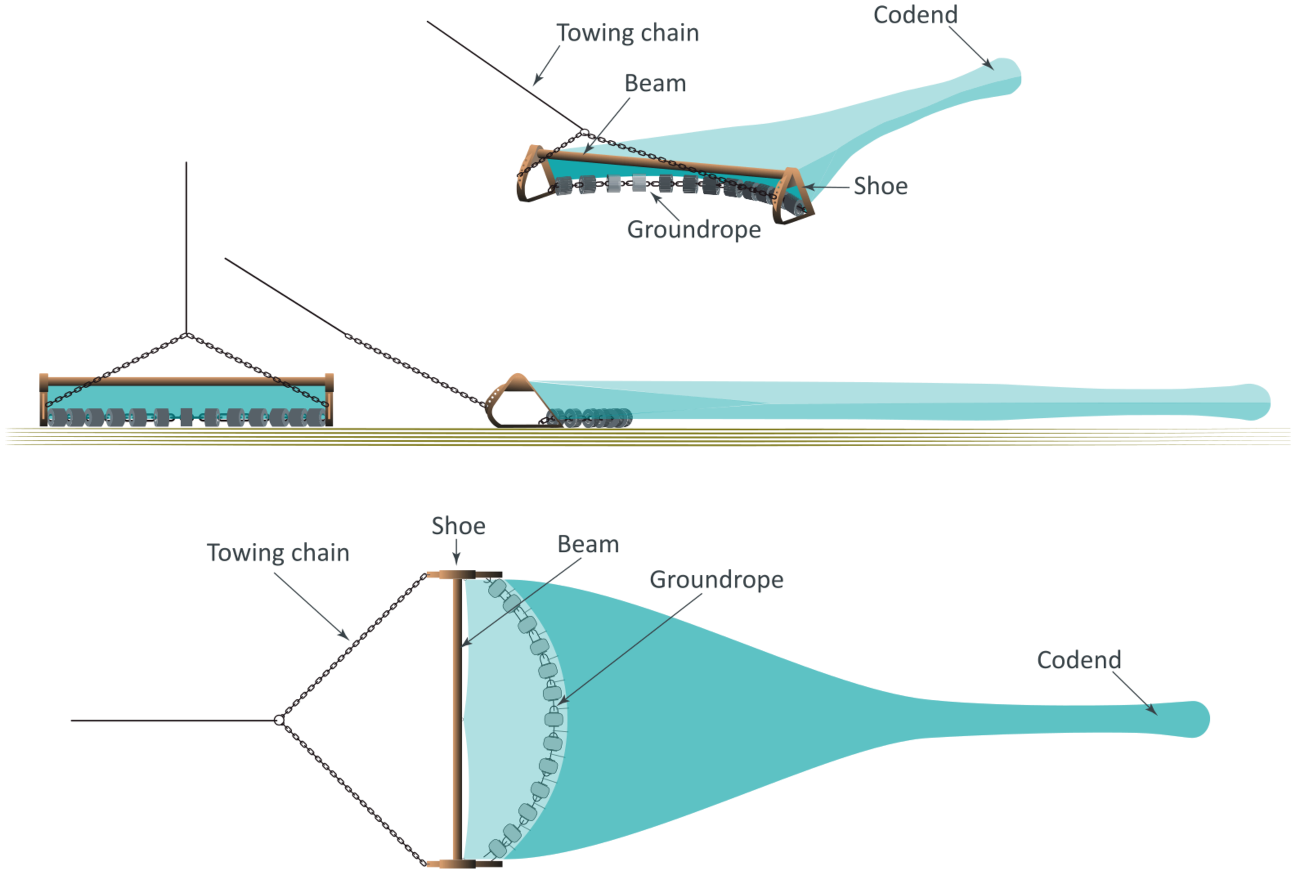

Figure 4. Different views of a beam trawl.

3.1 Codend modifications

Owing to their simplicity and ease of handling on board, codends made of diamond-mesh netting are preferred by commercial fisheries (Herrmann et al., 2013; Wileman et al., 1996). During fishing, opposing forces brought about by the accumulation of the catch and forward towing motion cause the codend to bulge (Herrmann, 2005; Robertson and Stewart, 1988). The opposing forces tend to close the mesh in the forward section of the codend, and only the mesh in the few rows just ahead of the catch bulk stay open and available for size selection (Herrmann, 2005). The mechanical characteristics of the netting make codends imperfect selection devices, often delivering poor and highly variable size selectivity (Robertson and Stewart, 1988; Wienbeck et al., 2011). Adjusting the mesh size is the traditional strategy used to control size selection in codends (Madsen, 2007; Millar and Fryer, 1999; Pope et al., 1975; Wileman et al., 1996); however, owing to the mechanical behaviour of the codend described above, increasing mesh size does not necessarily lead to the desired results in size selection (MacLennan, 1992). Thus, adjustments in mesh size are often combined with other modifications (Kennelly and Broadhurst, 2021) to increase the ratio of open meshes and the openness of individual meshes during towing. Among other options, turning the orientation of the codend netting from the standard T0 configuration (0° turn) can significantly improve the size selection of trawl gears (Robertson and Stewart, 1988; Moderhak, 2000, 1997; Halliday et al., 1999;

Wienbeck et al., 2011). A turn of 45° (T45 configuration; Figure 5) orients the mesh bars parallel and perpendicular to the longitudinal towing force, leading to a square-mesh geometry that keeps the meshes open across the length of the codend. Research on codend size selection for roundfish species has demonstrated that square-mesh codends can deliver significantly larger *L50* and sharper selection curves than diamond-mesh codends (Fonteyne and M´Rabet, 1992; Halliday et al., 1999; Robertson and Stewart, 1988). However, T45 codends are more difficult to handle and more liable to break with very large catches (Madsen, 2007). Such issues led to investigations with a wider turn of 90° (Herrmann et al., 2013; Moderhak, 2000, 1997; Wienbeck et al., 2011). In T90 codends (Figure 5), the wider axis of the knots are oriented perpendicular to the towing force, which tends to keep the mesh more open than in the standard T0 configuration. In a comparison of the selectivity of T90 and T0 codends made of the same netting on Baltic cod, Wienbeck et al. (2011) found that T90 codends significantly increased the *L50* by ~6.5% and ~11% (depending on the number of meshes in circumference), and reduced both the selection range (SR, range of lengths between lengths with 75% and 25% retention) and the between-haul variation obtained with T0 codends. Although it is widely recognised that T45 and T90 codends can significantly increase the selectivity of T0 codends for roundfish species (Kennelly and Broadhurst, 2021), the effect of turning the meshes is less evident for animals with other body morphologies. This is the case with flatfish species, whose flat morphology fits better to the diamond-shape opening of the traditional T0 codends (Bayse et al., 2016a; Tokac et al., 2014). Turning the meshes of traditional codends can therefore have a neutral or even opposite effect on flatfish species, explaining the high retention rates of flatfish species in fisheries where turned-mesh codends are used to improve escape possibilities for roundfish species, as in the Baltic Sea cod-directed trawl fisheries (Dahm et al., 2003; Madsen, 2007). Turned-mesh codends have also demonstrated better selectivity performance than T0 codends in crustacean fisheries (Thorsteinsson, 1992; Campos et al., 2002; Broadhurst et al., 2004; Guijarro and Massuti, 2006; Deval et al., 2016). Thus, adjusting the mesh size and turning the codend meshes are codend modifications that, either alone or combined, could be used in the search for sustainable harvesting patterns in the North Sea beam-trawl fishery targeting brown shrimp.

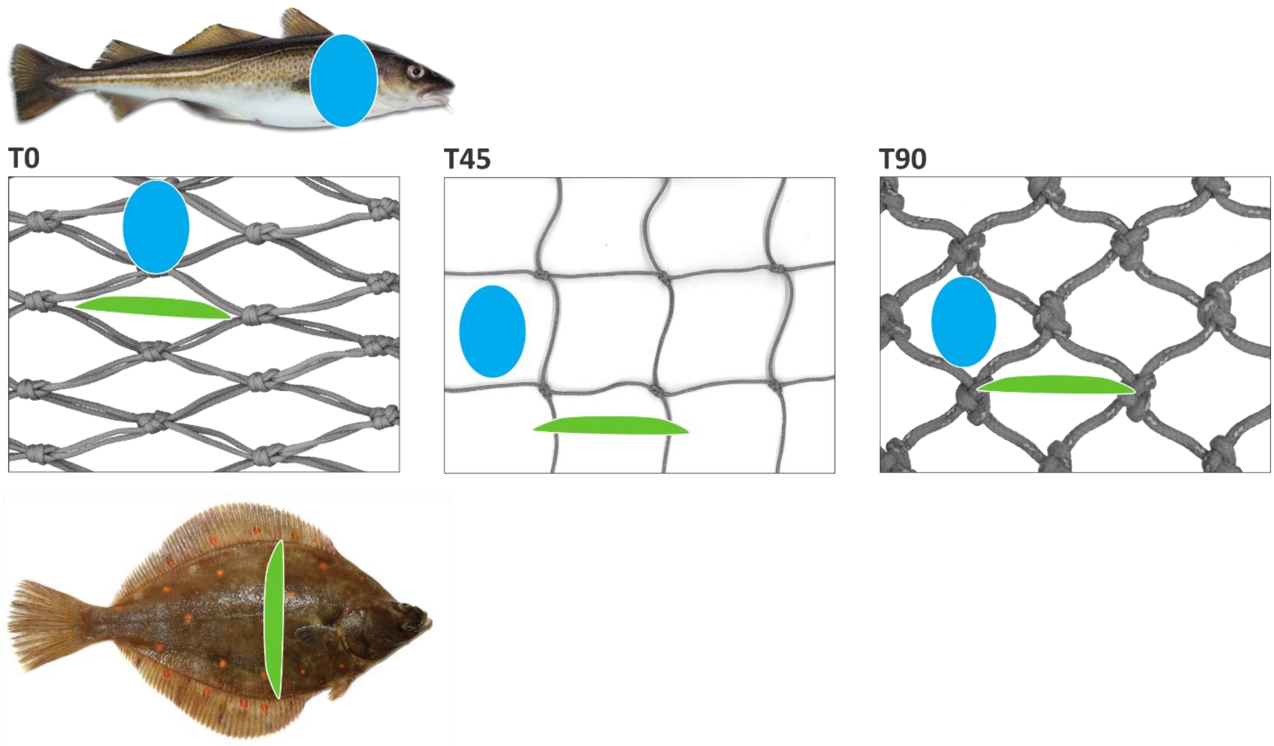

Figure 5. Nominal geometries of traditional T0 netting orientation, netting turned 45° (T45), and netting turned 90° (T90). The cross sections of roundfish (cod, blue) and flatfish (plaice, green) illustrate the potentially opposite selectivity properties of the different netting configuration for these species.

3.2 Sorting grids

Sorting grids were originally developed in Norwegian shrimp fisheries where the bycatch of fish species is still a problem (Isaksen et al., 1992). The traditional sorting grids in shrimp fisheries (hereafter referred to as Nordmøre grids; Figure 6) are usually mounted with an inclination in the range of 35–45° (Graham, 2003; Larsen et al., 2019; Valentinsson and Ulmestrand, 2008) in the non-tapered section of the trawl, and with the bars oriented vertically, blocking the free passage to the codend. For a marine animal to be able to pass through the grid towards the codend, two conditions need to be met: (a) the individual must contact the grid with the correct body orientation, and (b) the size and morphology of the individual must fit through the space between the bars. When crustacean grid systems such as the Nordmøre grid are applied, individuals not meeting any of these conditions are guided towards an outlet usually positioned at the top panel of the net. Thus, the conceptual functioning of sorting grids involves (a) a behavioural component that determines the probability of contacting the grid; and (b) a mechanical size-selection component, defined by the relationship between the morphology and size of the subject being selected, and the space between the grid bars. It has been widely demonstrated that Nordmøre grids can effectively reduce fish bycatch in crustacean fisheries such as the northern shrimp (Larsen et al., 2019, 2017a, 2017b), brown shrimp (Graham, 2003; Graham et al., 2004), and *Nephrops* fisheries (Catchpole and Revill, 2008; Valentinsson and Ulmestrand, 2008). A suboptimal choice of the bar spacing, however, can lead to a poor balance between bycatch reduction and the passage of targeted species and sizes to the codend (Graham and Fryer, 2006; Isaksen et al., 1992). The inclination of the grid (Grimaldo, 2006; Larsen et al., 2019) and the use of guiding devices in front of the grid (Frandsen et al., 2009; Larsen et al., 2017b) are other design characteristics that can substantially influence their performance. In general, sorting grids are less effective at excluding the smallest fish that can pass through the grid (Graham, 2003; Lövgren et al., 2016). However, medium and small fish that can pass through the grid can subsequently be released through the codend meshes. Lövgren et al. (2016) demonstrated in a Swedish *Nephrops* fishery that the partial selectivity of a Nordmøre grid followed by the partial selectivity of a codend can result in a combined bell-shaped selectivity pattern in which the largest and the smallest lengths available in the population are excluded by, respectively, the selectivity of the grid and the codend. The results obtained by Lövgren et al. (2016) suggest that combining a Nordmøre-type grid with a selective codend could be used to explore alternative exploitation patterns in the Baltic cod-directed trawl fishery, which is relevant considering the critical situation of cod stocks.

In trawl fisheries where fish species are targeted, a variety of sorting grid designs have been developed in the past three decades to address specific selectivity issues. In the Northeast Atlantic gadoid fisheries, the Sort-X, Sort-V, and Flexigrid (Grimaldo et al., 2015; Jørgensen, 2006; Larsen and Isaksen, 1993; Larsen et al., 2018c; Sistiaga et al., 2016a, 2010) are mandatory grid systems used to supplement the selectivity of diamond-mesh codends. In a Faroese coastal flatfish-directed trawl fishery, the large morphological differences in flatfish and roundfish species inspired a grid system with the inner bars horizontally arranged to separate the targeted lemon sole from bycatch species (ICES, 1997). Based on the original Faroese flatfish grid, Valentinsson and Ulmestrand (2008) developed and tested a similar horizontal grid concept in the Swedish *Nephrops* fishery, with the aim of catching plaice and avoiding cod. However, such designs greatly reduced *Nephrops* catches (−26%) without improving the catchability of flatfish. In the US West Coast groundfish trawl fishery, Lomeli et al. (2017) developed and tested a flexible sorting grid system made of two vertical panels, with slot-like openings 4.4 cm high and 21.6 cm long. This configuration is meant to exploit differences in size and morphology of the targeted flatfish species and the bycatch species, mostly roundfish and Halibut. Lomeli et al. (2017) reported a bycatch reduction of > 80% for shelf rockfish, sablefish, and Pacific Halibut while most of the targeted flatfish (85.6%) were retained in the codend. Studies conducted in the Faroese flatfish fishery and US North Pacific groundfish fisheries demonstrate that grids with horizontally arranged bars or slots can efficiently separate targeted flatfish from bycatch roundfish species. Linked to those experiences, it would be relevant to investigate if a grid system with horizontally arranged bars could be an efficient technical solution to reduce the bycatch of flatfish species in the cod-directed trawl fishery in the Baltic.

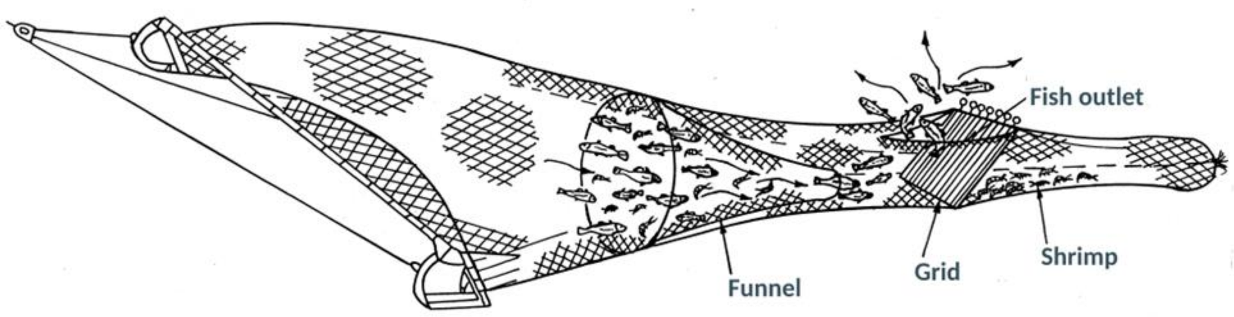

Figure 6. Illustration of a Nordmøre grid adapted to a beam trawl used in the North Sea brown shrimp fishery. A net funnel installed in a forward section directs marine animals to the lower side of the grid (Illustration: W. Rehme, TI/OF).

3.3 Square mesh panels

Square mesh panels (SMPs) are simple selective devices usually applied in demersal trawl fisheries where codend selectivity alone is not sufficient to prevent catches of unintended species or sizes (Brčić et al., 2016; Briggs, 1992; Broadhurst, 2018; Catchpole and Revill, 2008; Cuende et al., 2020; Revill et al., 2007; Revill and Jennings, 2005). SMPs exploit the escape behaviour of bycatch species and facilitate escape by maintaining an open mesh geometry in a certain area of the gear (Briggs, 1992). The conceptual simplicity and effectiveness demonstrated for some gadoid species (Briggs, 1992) make SMPs one of the most tested and applied selection devices in *Nephrops* fisheries in the past decades, either to reduce the bycatch of juvenile fish (Armstrong et al., 1998; Briggs, 1992; Drewery, 2010; Krag et al., 2008) or the bycatch of species regardless of their size (Krag et al., 2016). For SMPs to work efficiently, fish intended to escape the gear should identify the SMP as a potential escape zone and alter their normal swimming behaviour to contact the open meshes. The search for optimal functioning of these devices has led to countless investigations of ways to improve SMP efficiency, e.g., different panel dimensions (Cuende et al., 2020; Graham and Kynoch, 2001; Herrmann et al., 2015), different positions along the trawl (Herrmann et al., 2015; O'Neill et al., 2006), applying multiple SMPs (Revill et al., 2007), or applying devices to stimulate escape reactions (Grimaldo et al., 2018; Herrmann et al., 2015). Despite the many variants tested, inserting SMPs in the upper panel of the trawl (Figure 7) is the mainstream configuration (Armstrong et al., 1998; Briggs, 1992; Bullough et al., 2007; Frandsen et al., 2009; O'Neill et al., 2006; Zuur et al., 2001).

The effectiveness of top-positioned SMPs relies on the fishes' ability to identify and actively alter their swimming direction upwards to encounter the SMP, a sequence of behavioural events that conflicts with the natural behaviour of many fish species to stay clear of the netting while falling back towards the codend (Glass, 2000). Such natural behaviour can explain the poor escape efficiency of cod observed in the North Sea N*ephrops* fisheries, where a top-positioned SMP usually does not substantially change the bycatch of undersized individuals (Briggs, 1992; Frandsen et al., 2009). Using on-board-observer data, Nikolic et al. (2015) also estimated poor performance of top-positioned SMPs in a French *Nephrops* fishery on European hake (*Merluccius merluccius*). The findings of Nikolic et al. (2015) were supported by experimental research conducted in an equivalent Basque *Nephrops* fishery operating in the same area, which estimated that only < 1% of hake entering the gear could make contact with the standard SMP (Alzorriz, 2018). Further, the poor performance obtained with top-positioned SMPs in different European *Nephrops* fisheries should lead to an evaluation of alternative applications of SMPs in these fisheries.

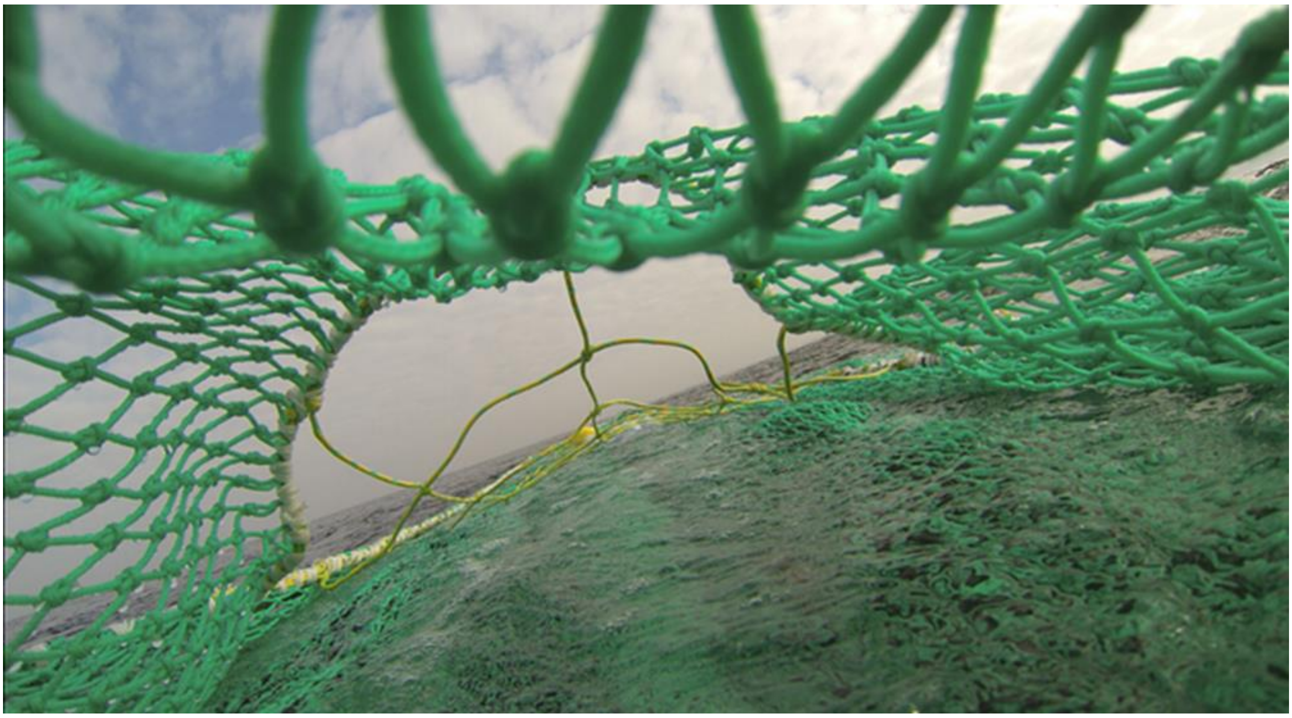

Figure 7. View of a SMP fitted to the top panel of the trawl.

3.4 Sieve panels

Sieve panels share the same selective purpose and functional principle as Nordmøre grids, being the preferred option, for a number of reasons, in several European brown shrimp fisheries where the bycatch of fish species is an issue (Polet et al., 2004; Revill and Holst, 2004a; van Marlen et al., 2001). In general, sieve panels are less expensive and easier to produce than sorting grids. The soft nature of sieve panels is another advantage, because it removes the practical inconveniences often associated with the use of rigid grids (Catchpole and Revill, 2008; Graham, 2003), while providing greater design freedom (which can improve performance). In North Sea beam-trawl fisheries targeting brown shrimp, fishers are obliged to use either sieve nets or Nordmøre grids (through EU 2019/1241 and supplementary national regulations). Sieve nets in these fisheries are made of two diamond-mesh panels of 60–70 mm inner mesh size, sewn to each other longitudinally, forming a tapered funnel (Figure 8). The front edge of the funnel is sewed to the full circumference of the trawl belly, gradually tapering off towards an outlet often located in the rear bottom panel of the trawl belly. Sieve nets are designed to direct those species and sizes too large to pass through the meshes towards the outlet, whereas shrimp of all sizes can pass the sieve net towards the codend. Evaluations of the performance of sieve nets in the UK and Belgian brown shrimp fisheries have demonstrated their effectiveness in avoiding bycatch of large fish while maintaining the catchability of marketable shrimp ≥ 85%, although slight variations in the design of the sieve net or seasonal change in the bycatch composition can lead to greater losses of shrimp catch (Polet et al., 2004; Revill and Holst, 2004a). As with Nordmøre grids, sieve nets also perform poorly at separating juvenile fish of sizes similar to the targeted shrimp, and consequently the use of sieve nets has mostly limited the impact on the bycatch of age-0 (< 10 cm) fish in the brown shrimp fisheries (Polet et al., 2004; Revill and Holst, 2004a). The good performance of sieve nets in some of the shrimp fisheries mentioned in this section, and the need for alternative applications of SMPs in *Nephrops* fisheries raised in the previous section, suggests that applying SMPs as sieve panels in the *Nephrops* otter-trawl fisheries might be effective in separating bycatch and targeted species.

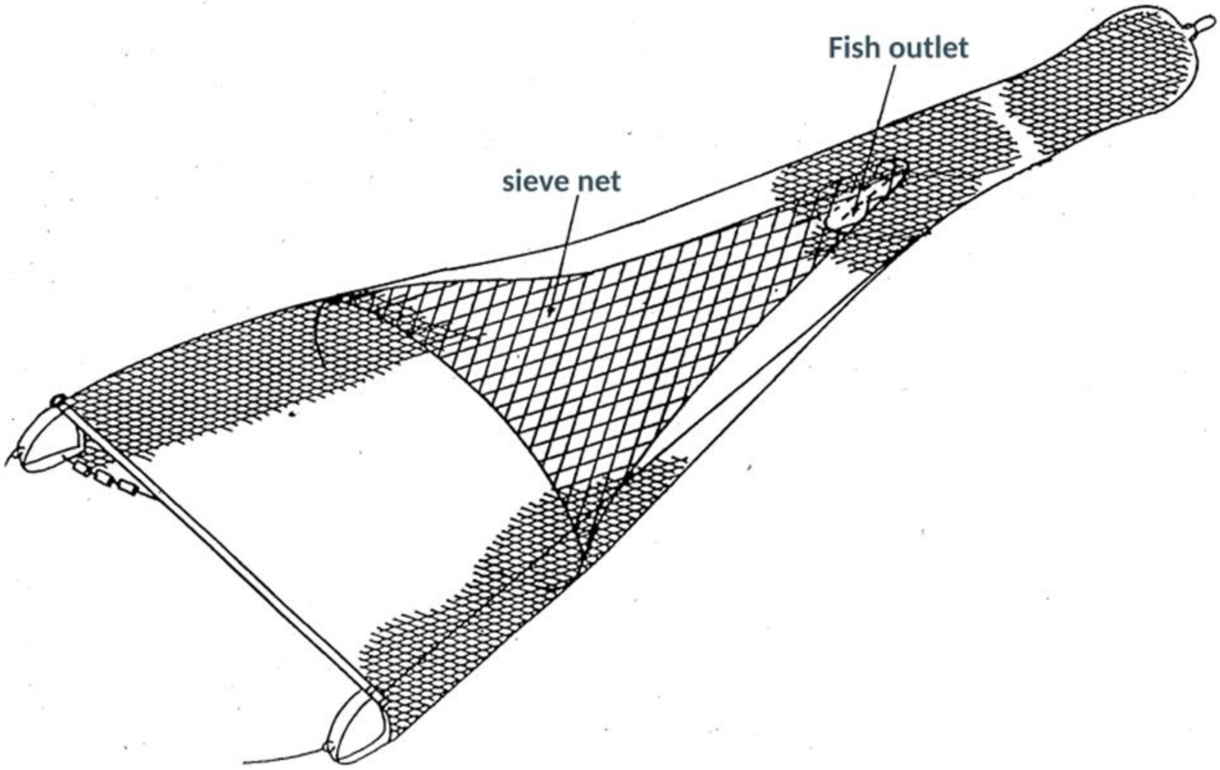

Figure 8. Sieve net design commonly applied in North Sea brown shrimp beam trawl fisheries (Illustration: W. Rehme, TI/OF).

3.5 Behaviour selection devices

Fish react to stimulus generated during the catch process according to their natural anti-predatory behaviour, and such reactions can substantially affect the efficiency of mechanical selection devices such as grids and SMPs (Glass, 2000). Conversely, species-specific behavioural responses during the catch process can be exploited to adjust the selectivity in trawls (Bayse and He, 2017; Bublitz, 1996; Glass and Wardle, 1995; He et al., 2008; Jones et al., 2004; Ryer, 2008). In the Baltic Sea, Herrmann et al. (2015) applied floating ropes beneath an SMP to stimulate upwards escape behaviour of cod, resulting in a significant increase in the escape efficiency of the baseline SMP. In the Barents Sea, Grimaldo et al. (2018) tested the ability of floating ropes to improve the escape efficiency of cod and haddock (*Melanogrammus aeglefinus*) through the meshes of a square-mesh section installed ahead of the codend. In this study, applying floating ropes significantly improved the escape efficiency of haddock; however, cod did not react significantly to the presence of the stimulators. Melli et al. (2018a) found that a counter-herding device mounted in the herding zone ahead of the trawl mouth significantly reduced the bycatch of fish species in *Nephrops* fisheries (Figure 9), especially in the cases of haddock and whiting. The vertical swimming preferences along the trawl have been exploited extensively to separate different species and direct them into separate codends, for example, by applying horizontal separator panels in the fore- or mid-section of the trawl (Ferro et al., 2007; Fryer et al., 2017; Main and Sangster, 1985). Applying a separator panel raised 75 cm from the groundrope in a Scottish *Nephrops* mixed fishery, Main and Sangster (1985) reported high separation rates of haddock and whiting (mostly found in the upper codend) from *Nephrops*, cod, and flatfish (mostly found in the lower codend). Contrary to other gadoid species, several studies have reported cod's preference for swimming low when entering the trawl (Beutel et al., 2008; Main and Sangster, 1985), through the trawl body (Ferro et al., 2007), and even in the aft end of the trawl (Krag et al., 2009a, 2009b; Melli et al., 2019). In a meta-analysis assessing the separation rates using horizontal panels at different heights and positions in relation to the trawl mouth, Fryer et al. (2017) found that the proportion of cod moving to the upper compartment increases as the distance of the separator panel from the mouth of the trawl increases. Flatfish species tend to swim close to the bottom during initial phases of the catch process in the fore part of the gear (Bublitz, 1996; Ryer, 2008), and this preference for the lower layer is also maintained in the aft of the trawl (Karlsen et al., 2019; Krag et al., 2009a). Exploiting observed differences in the vertical preference of cod and flatfish species in the trawl could, therefore, be an efficient strategy for reducing species bycatch in Baltic Sea otter-trawl fisheries.

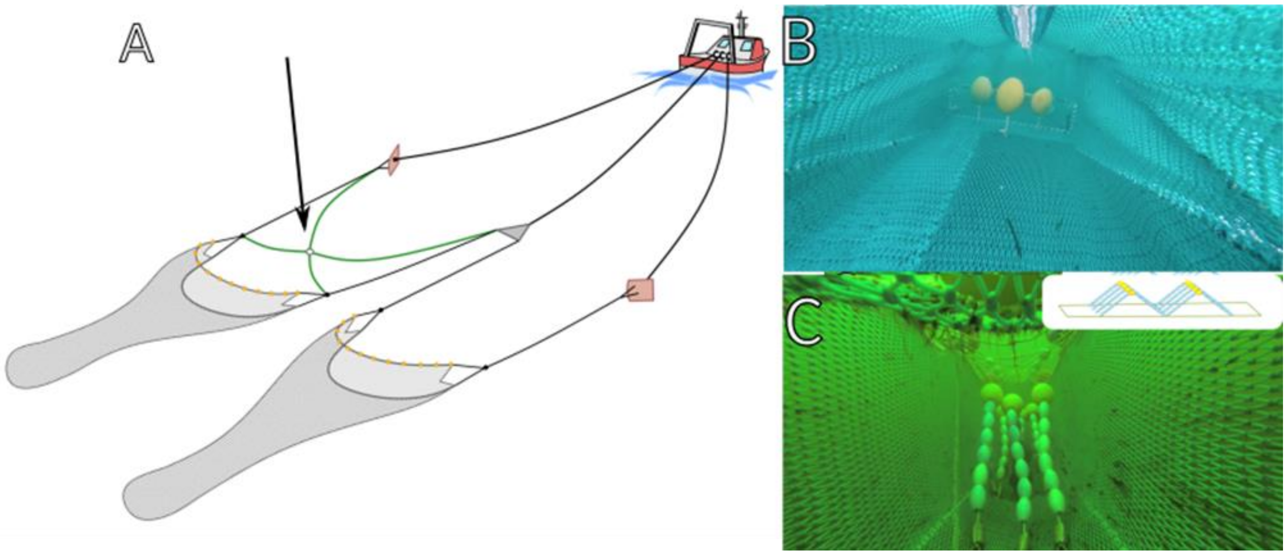

Figure 9. (A) FLEXSELECT device (green lines) designed to deter roundfish species from entering the trawl. Trawl with the FLEXSELECT device is compared with a standard trawl in Melli et al. (2018a). (B) Inside view of a trawl with separated codends. Three stimulation devices are placed in front of the separation zone to stimulate upwards reactions of roundfish. (C) Floating ropes designed to improve the efficiency of SMPs.

4 Overview of current methodologies to assess trawl selectivity

4.1 Methods for collecting selectivity data

This section provides a brief overview of the most commonly applied experimental methods for collecting selectivity data at sea (Wileman et al., 1996). The alternatives are divided in three categories: (a) methods providing direct information about the fish escaping from the selective device being assessed (direct methods), (b) methods in which the selectivity performance of the selection device is evaluated by assessing differences in catches from different catch compartments (indirect methods), and (c) methods to compare the selectivity properties of two (or more) selective gears (catch comparison).

4.1.1 Direct methods

In direct methods, fish escaping the trawl through the selection device being studied are retained in small-mesh netting covers. This methodology was first introduced and is widely applied in codend-selectivity studies, where a large cover made of small mesh surrounds the entire codend to collect the fish escaping through the codend meshes (Bahamon et al., 2006; He, 2007; Madsen et al., 1998; Madsen and Holst, 2002; Pope et al., 1975; Tokac et al., 2014; Tschernij and Holst, 1999; Wienbeck et al., 2014, 2011; Wileman et al., 1996). The main benefits of the cover-codend method (Figure 10) are the simplicity of the tools required to analyse the collected data, and the precision of the resulting estimates, often achieved with relatively low sampling effort (Herrmann et al., 2016; Millar, 2010; Sistiaga et al., 2009). The cover-codend method requires a carefully designed cover, adapted to the specific characteristics of the vessel used and/or the fishery (Tschernij and Holst, 1999; Wienbeck et al., 2014). One risk is that the cover masks the codend meshes, which could produce biased size-selection estimates (Madsen and Holst, 2002; O'Neill and Kynoch, 1996; Pope et al., 1975). To prevent this, codend covers are often made of materials with neutral or slightly positive buoyancy material (Wileman et al., 1996) and rigged with elements specifically designed to maintain a sufficient and stable space between the cover and the codend. A traditional strategy to keep the cover netting clear of the codend meshes is the use of large hoops, which can be difficult to handle in practice (Herrmann et al., 2015; Madsen et al., 1998; Tokac et al., 2014; Wienbeck et al., 2014, 2011). Attaching kites around the cover generates hydrodynamic forces that keep the cover clear of the codend (He, 2007; Madsen et al., 2001), making this technique a simpler and handier alternative to hoops.

In many cases, codend selectivity is supplemented by installing selection devices such as grids and SMPs at the trawl's extension piece (Catchpole and Revill, 2008; Kennelly and Broadhurst, 2021).

Direct information related to the performance of such selection devices is often obtained by using top covers (Brčić et al., 2016; Cuende et al., 2020; Larsen and Isaksen, 1993; Sistiaga et al., 2016a, 2010; Zuur et al., 2001). Top covers are often designed following the guidelines provided in Wileman et al. (1996), and rigged with floats to prevent the masking of the device's escape area. Applying individual covers to the device installed at the extension piece and the codend (Figure 11) allows partial and combined assessment of the selectivity properties of both devices (Sistiaga et al., 2010; Wileman et al., 1996).

A strategy to improve the selectivity of trawl gears in multispecies fisheries sometimes involves separating species into divided codends before size selection (Ferro et al., 2007; Karlsen et al., 2019; Krag et al., 2009a; Melli et al., 2019, 2018b). A method commonly applied to obtain direct information about the separation rates achieved is to use small-mesh codends or catch compartments with limited selectivity for the species being studied. This technique prevents any confounding of the separation rates at length and a subsequent size selection at the specific catch compartments. Therefore, differences in catches across compartments can be attributed only to the sorting efficiency of the testing device.

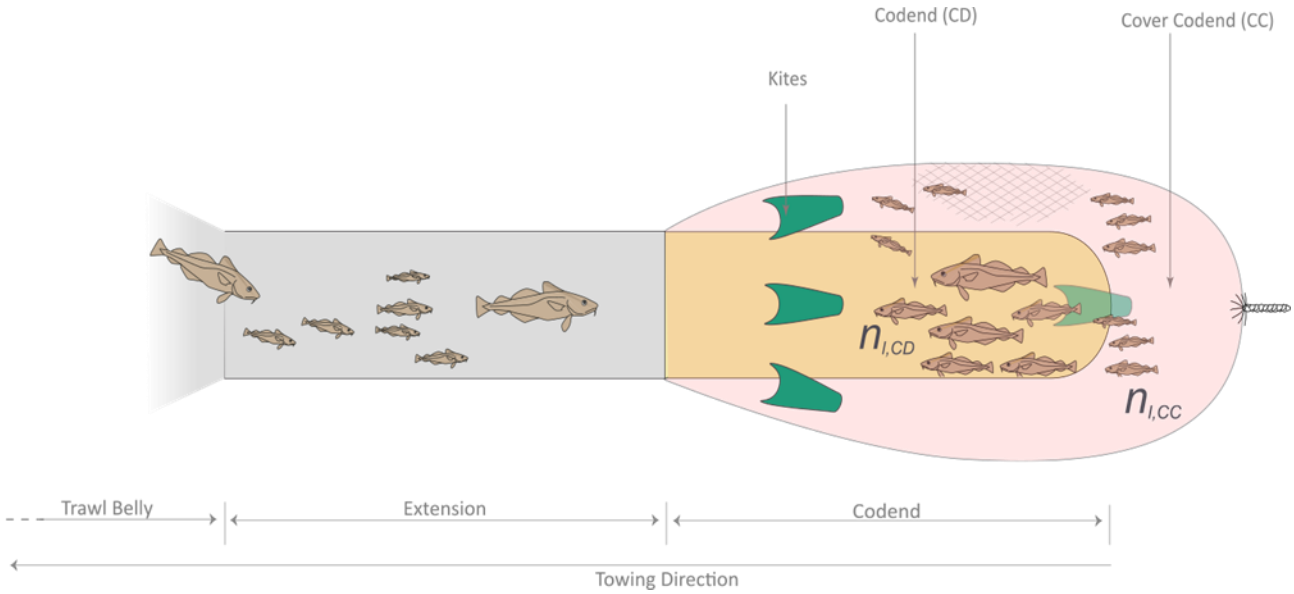

Figure 10. Cover codend method. Fish able to escape through the codend (CD) meshes are retained in the cover codend (CC).

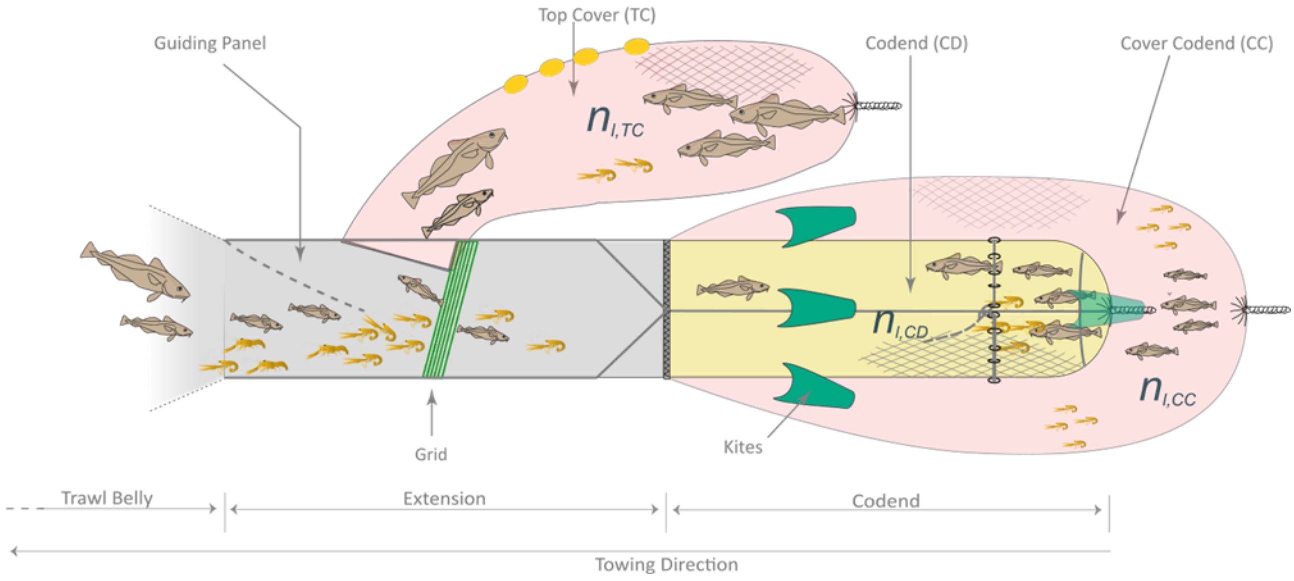

Figure 11. Dual cover method. Fish not passing the grid are retained in the top cover (TC). Fish passing the grid and able to escape through the codend (CD) meshes are retained in the cover codend (CC).

4.1.2 Indirect methods

This category encompasses methodologies that allow the quantification of the device's selective properties without directly observing the fish that have actually escaped the device. Instead, the device's selectivity is evaluated by comparing differences in catches taken by the gear with the selection device (test gear) with catches from a non-selective gear (control gear). Usually, it is assumed that the only escape possibility available to the fish entering the test or control gears is the selection device mounted in the test gear (Millar and Walsh, 1992). Indirect methods in which the test and reference gears are used simultaneously are referred to as paired-gear methods. Paired-gear methods (Figure 12) often use trouser trawls (Cadigan et al., 1996; Grimaldo et al., 2007; Millar and Walsh, 1992), twin trawls (Graham, 2003; Jørgensen et al., 2006; Madsen et al., 1998), or two vessels of similar characteristics fishing in parallel (Holst and Revill, 2009). When paired-gear facilities are not available, the test and reference gears are used alternately (Browne et al., 2021; Mous et al., 2002; Perez-Comas et al., 1998). Owing to variation between hauls not related to the selection process, alternate hauls deliver poorer selectivity estimates than paired-gear methods. A way to reduce such uncontrolled variation is to conduct pairs of test and control hauls close together spatially and temporally (Wileman et al., 1996). There are, however, practical circumstances that can force a collection of unpaired test and control data (Ingólfsson et al., 2021; Sistiaga et al., 2016b).

Indirect methods have the advantage of testing the selection device without any modification (e.g., use of covers) that could bias its performance. The relative simplicity of indirect methods makes them preferable for tests conducted in commercial conditions. The disadvantages of indirect methods are the need for more complex statistical tools to analyse the resulting data (Millar and Walsh, 1992; Wileman et al., 1996), and the lower precision of the selectivity estimates compared with those obtained from direct methods (Herrmann et al., 2016).

4.1.3 Catch comparison methods

Catch comparison methods are preferred when the aim is to directly compare the performance of two or more selective gears (Armstrong et al., 1998; Briggs, 1992; Holst and Revill, 2009; Krag et al., 2014). A common catch comparison setup involves fishing simultaneously or alternately with a test and a reference gear. The test gear is often a potential candidate for implementation in the fishery, while the reference gear is often the compulsory gear. Analysis of catches from two selective gears provides direct information regarding the cost and benefit derived from the use of the test gear compared with the reference gear, and consequently the results obtained can be easier to communicate to industry and management bodies. Another advantage of this method is that it does not require experimental rigging of the gears; therefore, it is easy to apply in commercial fishing vessels. In contrast, the main disadvantage is that the selectivity of the individual selection devices tested is not accessible from the data; therefore, the assessment is restricted to the specific comparison conducted in the study.

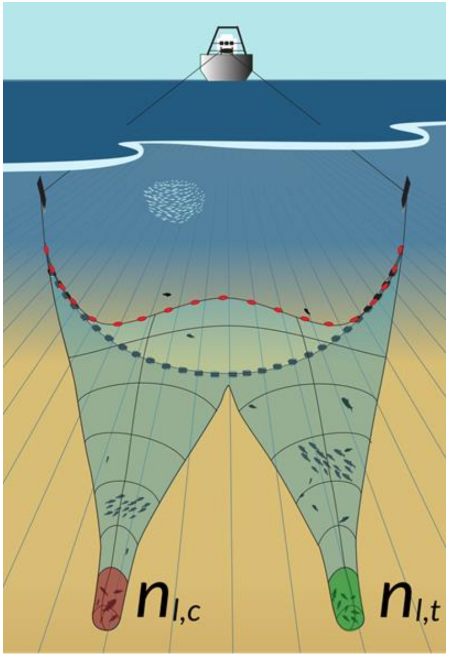

Figure 12. An example of indirect method: paired-gear using a double-belly trawl (i.e., trouser trawl).

4.2 Structural modelling

This section describes several models sharing the same modelling philosophy, for which the individual parameters defining the model structure contain usable information regarding the selection process being analysed through the experimental data. Structural modelling is usually applied when the length-dependent component of the selection process investigated has a mechanical nature (e.g., codend selectivity).

4.2.1 Models for selectivity data collected by direct experimental methods

In codend-selectivity analysis, it is assumed that (a) the proportion of the fish retained in the codend is determined by the ability of the fish to pass through the codend meshes, and that (b) such ability is determined mostly by the size of the fish and the meshes' size and geometry. These basic assumptions allow modelling the codend retention probability *r(l)* by simple mathematical functions with parametric structures leading to non-decreasing, s-shaped selectivity curves (Figure 13) asymptotically restricted to values between [0, 1] (Millar and Fryer, 1999; Wileman et al., 1996). The most often applied selectivity function is the *logit* function:

$$r(l, L50, SR) = \frac{exp(\frac{ln(9)}{SR} \times (l - L50))}{1.0 + exp(\frac{ln(9)}{SR} \times (l - L50))} \qquad (1)$$

where the parameter *L50* represents the length size with 50% probability of being retained in the codend. Therefore, the parameter *L50* determines the position of the selectivity curve relative to the range of fish lengths evaluated. The *SR* is the range between lengths with 75% and 25% retention probability, determining the slope of the selection curve. Other selectivity functions used to describe the selectivity properties of a codend are the *probit* (Equation 2), *Gompertz* (Equation 3), and *Richards* (Equation 4):

$$r(l, L50, SR) \approx \Phi\left(1.349 \times \frac{(l - L50)}{SR}\right) \qquad (2)$$

$$r(l, L50, SR) \approx exp\left(-exp\left(1.573 \times \frac{(l - L50)}{SR} - 0.366\right)\right) \qquad (3)$$

$$r(l, L50, SR, \delta) = \left(\frac{exp\left(logit(0.5^{\delta}) + \left(\frac{logit(0.75^{\delta}) - logit(0.25^{\delta})}{SR}\right) \times (l - L50)\right)}{1 + exp\left(logit(0.5^{\delta}) + \left(\frac{logit(0.75^{\delta}) - logit(0.25^{\delta})}{SR}\right) \times (l - L50)\right)}\right)^{\frac{1}{\delta}} \qquad (4)$$

the term Φ in the *probit* function (Equation 2) refers to the cumulative distribution function of a standard normal distribution (Wileman et al., 1996). The *logit* and *probit* functions provide very similar fits resulting in symmetry curves (mirrored functional form towards left and right of the curve), although some differences can be detected in the tails. In contrast, the selection curves delivered by the *Gompertz* (Equation 3) and *Richards* (Equation 4) functions can be asymmetrical. In the *Richard*s function, the degree of asymmetry of the curve is controlled by the parameter δ, which is estimated together with the other parameters describing the curve.

In cover-codend experiments, where retained and escaped fish are collected in the codend (*CD*) and the cover (*CC*), respectively, the expected number of fish obtained in both catch compartments can be directly related to the total number of fish entering the codend n_l and the retention probability:

$$\begin{aligned} n_{l,cd} &= n_l \times r(l, L50, SR) \\ n_{l,cc} &= n_l \times (1.0 - r(l, L50, SR)) \end{aligned} \qquad (5)$$

therefore, the expected proportion of fish with length *l* retained in the codend is:

$$r_l = \frac{n_{l,cd}}{n_{l,cd} + n_{l,cc}} \qquad (6)$$

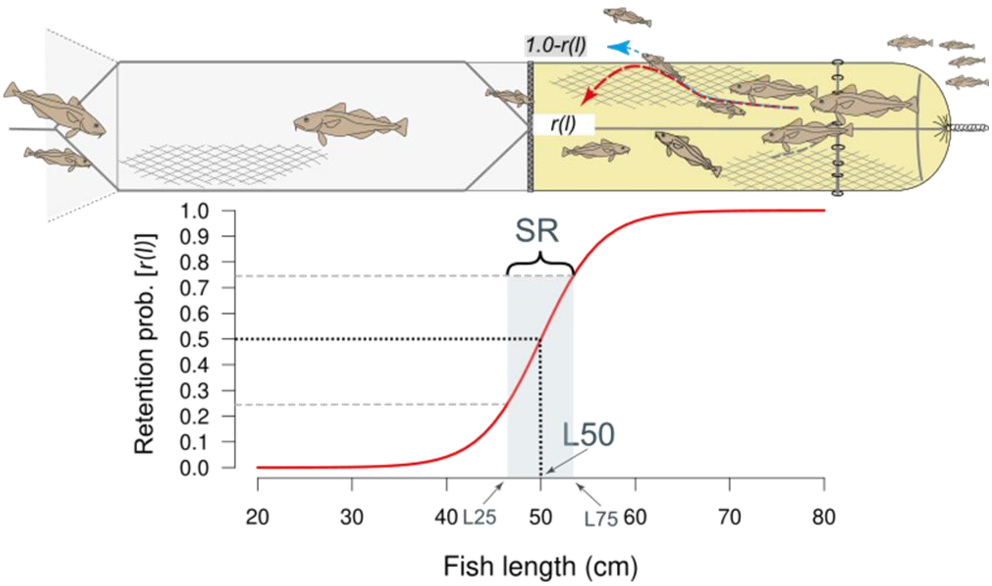

Figure 13. Top: representation of a size-selection process in the codend. Bottom: example of a retention curve describing codend retention probability, with associated parameters L50 and SR. The notation referred to retention curve r(l) in the figure is an abbreviation of r(l,L50,SR) in text.

The performance of size-selection devices such as sorting grids can be determined largely by the way fish react to their presence. Often, a fraction of fish entering the gear will not contact the device, and consequently it will not be subject to a size-selection process. To cope with this situation, size-selection models often introduce an additional parameter that quantifies the fraction of the fish entering the gear that actually comes into contact with the device and becomes available for size selection (Figure 14). The sequence of these two probabilistic events defines the length-dependent contact retention of the grid (Millar and Fryer, 1999; Sistiaga et al., 2010):

$$r_{cgrid}(l) = C_{grid} \times r_{grid}(l, L50, SR) \qquad (7)$$

where C_{grid} quantifies the fraction of the fish that contacted the grid, and $r_{grid}(l,L50,SR)$ is the length-dependent function (usually the *logit* function described in Equation 1) that expresses the available size selectivity of the grid. Likewise, the probability that a fish of length *l* will pass through the spaces between bars towards the codend (passage probability) can be expressed as:

$$p_{grid}(l, L50, SR) = C_{grid} \times (1.0 - r_{grid}(l, L50, SR)) \qquad (8)$$

in experiments where the escape opening of the grid is covered by a top cover (*TC*), those fish passing to the codend (assumed to be non-selective for simplification) and those not passing to the codend are collected in the *TC* and the codend (*CD*), respectively. As for the codend cover method, the expected number of fish obtained in both catch compartments can be directly related to the total number of fish entering the grid zone (n_l) and the retention probabilities in Equations 7 and 8:

$$n_{l,tc} = n_l \times (r_{cgrid}(l, L50, SR) + (1.0 - C_{grid}))$$
$$n_{l,cd} = n_l \times p_{grid}(l, L50, SR) \qquad (9)$$

consequently, the expected proportion of fish of length *l* that passed the grid is,

$$p_{l,grid} = \frac{n_{l,cd}}{n_{l,cd} + n_{l,tc}} \qquad (10)$$

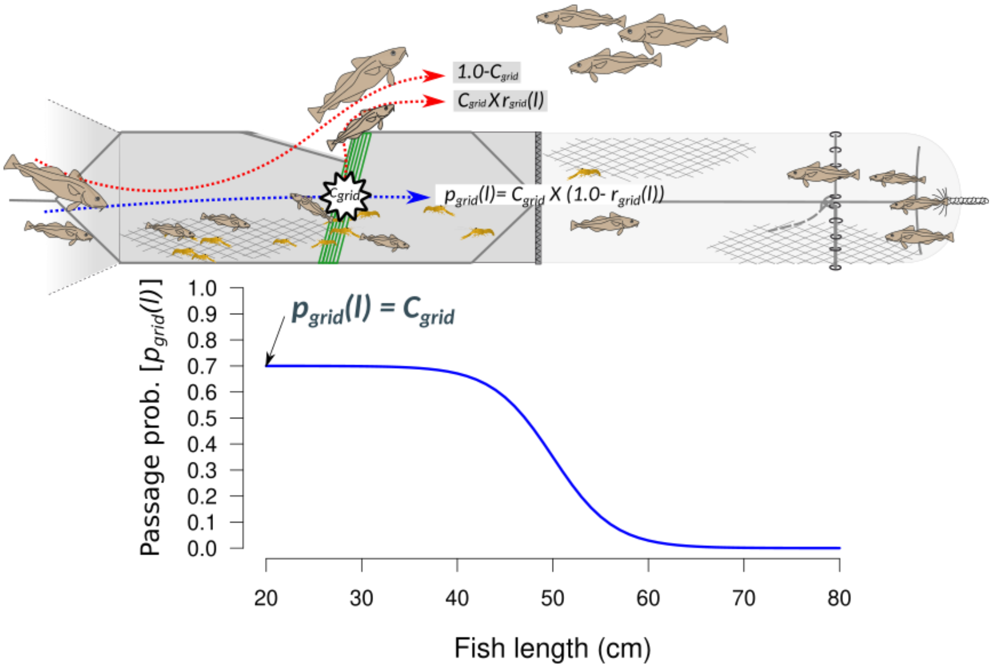

Figure 14. Top: representation of a selection process associated with grid systems. Bottom: example of a length-dependent curve describing passage probability through the grid. The notations $r_{grid}(l)$ and $p_{grid}(l)$ in the figure are abbreviations of respectively $r_{grid}(l,L50,SR)$ and $p_{grid}(l,L50,SR)$ in text. Note that at $r_{grid}(l) = 0$, $p_{grid}(l) = C_{grid}$.

4.2.2 Models for selectivity data collected by indirect experimental methods

In the simple case of a codend-selectivity study applying the paired-gear method in a twin trawl configuration, the size selection of the codend is evaluated by assessing the differences in catches of the test trawl with the selective codend and the control trawl with a non-selective codend. Assuming that the only escape possibility for fish entering either the test or control trawl is the test codend, the probability for a fish of length *l* to be found in the test trawl is determined by a sequence of two fishing events. The first event is controlled by the probability that a fish entering the gear did it to the test trawl, which is mathematically expressed as the length-independent "split" parameter (*SP*; Millar and Walsh, 1992; Wileman et al., 1996). Equal probability of entering both the test and control trawls is expressed with a value of *SP* = 0.5. A value of *SP* > 0.5 implies that the test trawl has a higher fishing power (Wileman et al., 1996) than the control trawl, whereas the opposite happens when *SP* < 0.5. The split parameter only can take values in the range [0.1], and it is assumed to be length-independent. If the fish entered the test trawl, the second fishing event is the length-dependent retention probability of the test codend, usually defined by the *logit* function. With the two sequential fishing events taking place during a paired-gear experiment, the conditional probability that a fish of length *l* entering the gear will be caught in the test and control codends are:

$$P(test|caught) = SP \times r(l, L50, SR)$$
$$P(control|caught) = 1.0 - SP \qquad (11)$$

this can be used to model the share of the total catch obtained in the test codend:

$$\phi(l, SP, L50, SR) = \frac{SP \times r(l, L50, SR)}{(1.0 - SP) + SP \times r(l, L50, SR))} \qquad (12)$$

the expected number of fish of length *l* caught in test and control codends can be directly related to the total number of fish entering the paired-gear n_l and the catch share probability in Equation 12:

$$n_{l,t} = n_l \times \phi(l, SP, L50, SR)$$
$$n_{l,c} = n_l \times (1.0 - \phi(l, SP, L50, SR)) \qquad (13)$$

having the expected catch numbers in the test and control gears, the expected catch share at length *l* in the test trawl is:

$$\phi_l = \frac{n_{l,t}}{n_{l,t} + n_{l,c}} \qquad (14)$$

4.3 Empirical modelling

The models introduced in the previous section are the preferred to analyse selectivity data with length-dependencies generated mostly by mechanical size-selection processes. However, these models are not suitable for a wide range of situations where (a) the size selection of individual selection devices cannot be accessed (either directly or indirectly) from the available data, or when (b) the mechanical size-selection component is confounded with other length-dependent components (e.g., length-dependent behaviours), or when (c) the size-selection process being studied has no mechanical component. An alternative modelling approach to deal with such types of data incorporates flexible functions where functional forms are solely defined by the data being analysed. Often, the parameters of empirical models do not contain any usable information regarding the selectivity process studied.

Flexible empirical models are usually (but not exclusively) applied to analyse catch comparison data, where the catch efficiency of a specific test gear is compared with the efficiency of the reference/baseline gear. One example is,

$$CC(l, \mathbf{v}) = \frac{exp(f(l, \mathbf{v}))}{1.0 + exp(f(l, \mathbf{v}))} \qquad (15)$$

where *CC(l,**v**)* is often referred to as catch a comparison curve, which quantifies the catch share in the test gear relative to the reference. The term *f(l,**v**)* is an unknown flexible function to model the potential length dependence in the relative catch efficiency of the test gear, for example, a 4-order polynomial basis with parameters ***v*** *= (v0, v1, v2, v3, v4)*. The expected number of fish of length *l* caught in test and reference codends can be directly related to the total number of fish caught and the catch share probability in Equation 15:

$$\begin{aligned} n_{l,test} &= n_l \times CC(l, \mathbf{v}) \\ n_{l,ref} &= n_l \times (1.0 - CC(l, \mathbf{v})) \end{aligned} \qquad (16)$$

having the expected catch numbers in the test and control gear, the expected catch share in the test trawl is:

$$CC_l = \frac{n_{l,test}}{n_{l,test} + n_{l,ref}} \qquad (17)$$

leaving one or more of the parameters out of the vector ***v*** = *(v0, v1, v2, v3, v4)* defining the functional form of *f(l,**v**)* (Equation 15) leads to additional simpler models, which are also considered potential candidates for modelling the catch comparison data. The competing models are then ranked by decreasing AIC values (Akaike, 1974). At this point two optional procedures are available (Symonds and Moussalli, 2011): (a) model selection: Pick only the top ranked model for further analysis; (b) model averaging: Estimate an average model combining all ranked models, weighted by increases in AIC relative to the first candidate model.

To facilitate model interpretation, an additional curve named catch ratio curve, *CR(l,**v**)*, is derived from the comparison curve *CC(l,**v**)*:

$$CR(l, \mathbf{v}) = \frac{CC(l, \mathbf{v})}{1.0 - CC(l, \mathbf{v})} \qquad (18)$$

the resulting *CR(l,**v**)* curve directly relates the catch efficiency of the test trawl to the catch efficiency of the reference trawl and, therefore, it is better suited to quantitatively assess the relative catch efficiency of the test gear. For example, values of *CR(l,**v**)* close to 1.0 would imply similar catch efficiency of the test and reference gears. Conversely, low *CR(l,**v**)* values would express low relative catch efficiency of the test gear. For example, a value of *CR(l,**v**)* = 0.2 would imply that the test gear only has 20% of the catch efficiency of the reference gear at length *l*.

4.4 Model estimation

This section describes the traditional method applied to estimate the selectivity of codends with codend cover data. The same method is adapted and applied to data collected with other methods described in the previous sections (e.g. paired-gear method). In the analysis of cover codend data, it is assumed that the fate of the fish entering the codend is independent from each other, and that the number of fish of length *l* retained in the codend is determined by a binomial process,

$$n_{l,cd} \sim Binom(n_{l,cd} + n_{l,cc}, r(l, L50, SR)) \qquad (19)$$

where the values of the parameters *L50* and *SR* are unknown and need to be estimated. In traditional selectivity analysis, the estimation of the selectivity parameters is done by Maximum Likelihood (Fisher, 1912; Millar, 2011), a general-purpose toolbox commonly applied for estimation and inference of statistical models. The basic idea is to find the combination of *L50* and *SR* parameters that most likely produced the observed selectivity data. Maximum likelihood estimation is done by computer-based optimization tools, usually by minimizing the negative of the log-likelihood of the probability mass function derived from Equation 19:

$$- \sum_l (n_{l,cd} \times log(r(l, L50, SR)) + n_{l,cc} \times log(1.0 - r(l, L50, SR)) \quad (20)$$

where $n_{l,cd}$ and $n_{l,cc}$ represent the catches from a single haul. Maximum Likelihood estimations present many good properties, including asymptotic normality, especially when the dataset is sufficiently large. Such property provides well-established procedures for statistical inference and hypothesis testing, including the estimation of uncertainties and confidence intervals associated to the estimated parameters (Millar, 2011).

Evaluation of the ability of the fitted model to describe the data sufficiently well is usually done following the recommendations stated in Wileman et al. (1996). One fit statistic widely applied is Pearson's statistic. The *p*-value obtained assuming a Chi-squared distribution of the statistic expresses the likelihood for by coincidence obtaining at least as large a discrepancy between the fitted model and the observed experimental data. This *p*-value is based on testing the null hypothesis, that the modelled retention probability and the observed experimental data belongs to the same length-dependent distribution. Therefore, this *p*-value should not be <0.05 for the fitted model to be a candidate to model the size selection data.

4.4.1 Dealing with subsampled data

Often, only a fraction of the fish caught during the fishing trials can be measured. In that case, the subsample factor (q) is calculated for each catch compartment separately, as the ratio of the weight/counts of the measured fish to the total weight/counts of the catch. Being q_{cd} the subsample factor of the codend, and q_{cc} the subsample factor of the cover, the total number of fish of length l caught in each compartment can be estimated respectively as $\hat{n}_{l,cd} = \frac{n_{l,cd}}{q_{cd}}$ and $\hat{n}_{l,cc} = \frac{n_{l,cc}}{q_{cc}}$
Using the raised data instead of the measured data in Equation 20, however, would result in a biased estimation of the uncertainty in the model, as it would not account for the uncertainty introduced by the subsampling factor. A way to account for the subsample factors requires a general reformulation of the objective function in Equation 20:

$$- \sum_l (n_{l,cd} \times log(\frac{r(l,L50,SR)q_{cd}}{r(l,L50,SR)q_{cd}+(1.0-r(l,L50,SR))q_{cc}}) + n_{l,cc} \times log(1.0 - \frac{r(l,L50,SR)q_{cd}}{r(l,L50,SR)q_{cd}+(1.0-r(l,L50,SR))q_{cc}}))$$
(21)

4.4.2 Modelling variability in replicate haul experiments

The performance of selective devices varies randomly from haul to haul, even if the hauls are deployed successively under the same fishing conditions and keeping the design of the studied selection device unaltered (Fryer, 1991). To account for this random between-haul variation, selectivity trials are normally designed as repeated measurements experiments, in which the selection device is tested for a number of fishing hauls, ideally under the same fishing conditions (Fryer, 1991; Millar and Fryer, 1999). Often, the aim of the research is to experimentally assess the effect of a given design modification on the selectivity delivered by the device investigated. In the case of codend research, for example, it is often of interest to assess the effect of increasing the mesh size (Fryer et al., 2016), mesh orientation (Herrmann et al., 2013; Tokac et al., 2014; Wienbeck et al., 2011), or twine thickness (Herrmann et al., 2013; O'Neill et al., 2016; Sala et al., 2007). Additionally, it is of interest to isolate and quantify the effect of physical measurable variables related to the catch or fishing operations, such as total catch size (Fryer et al., 2016; Herrmann, 2005; Herrmann et al., 2013; Wienbeck et al., 2011) and state of the sea (O'Neill et al., 2003). The effect of controlled changes in gear characteristics and physical measurable variables are usually referred as fixed effects. Therefore, when the research objective is to assess how a set of fixed effects of interest affects the selectivity of the device under study, modelling tools able to discern and quantify the variability caused by the random variation between hauls and the fixed effects evaluated are required. One method available was introduced in Fryer (1991). The following description of such method (hereafter referred as Fryer method) consider the specific example of a covered cod-end experiment with a set of $H=h_{i=1},\dots,h_m$ hauls. The Fryer method assumes that the selectivity parameters estimated at haul level, $\hat{\mathbf{v}}_i = (L50_i, SR_i)^T$ are drawn from a multivariate normal distribution of the form:

$$\hat{\mathbf{v}}_i \sim N(\mathbf{X}_i\boldsymbol{\beta}, \mathbf{R}_i + \mathbf{D}) \qquad (22)$$

where $\mathbf{X}_i$ are $2xp$ model matrices that establish a linear relationship between the average selectivity parameters of haul i and p observed and measured covariates taken as fixed effects. The covariates in $\mathbf{X}_i$ can be numeric representing categories (for example identifiers of gear design associated to haul i) or measured quantities (e.g. catch volume). Coefficients associated to the fixed effects in $\mathbf{X}_i$ are contained in the vector $\boldsymbol{\beta} = \beta_0, \dots, \beta_p$, being β_0 the coefficient associated to the intersect. The variance in Equation 22 is composed by $\mathbf{R}_i$, a 2x2 covariance-variance matrix (in case of two-parameter estimation) which quantifies the uncertainty in the estimation of the selectivity at haul level. This within-haul uncertainty is often related to the binomial sampling variability, affected by the experimental method applied, the size structure of the catches relative to the size selectivity of the codend, and/or the number of fish measured relative to the total catch obtained in each of the experimental compartments (Herrmann et al., 2016; Millar, 2010; Sistiaga et al., 2009). The term **D** in Equation 22 refers to the variance-covariance matrix accounting for the random between-haul variation in the data. The Fryer model takes the selectivity parameters of individual hauls $\hat{\mathbf{v}}_i = (L50_i, SR_i)^T$ and related variance-covariance matrix $\mathbf{R}_i$ as input data to estimate the parameters $\boldsymbol{\beta} = \beta_0, \ldots, \beta_p$ and the between-haul variation matrix **D,** under the assumption stated in Equation 22. This is done either via Maximum Likelihood or Restricted Maximum Likelihood, and requires the use of iterative tools such as the EM algorithm (Dempster et al., 1977). The Fryer method can be applied with small adjustments to other experimental methods such as the paired-gear method. More mathematically detailed information regarding this method can be obtained in (Fryer, 1991).

4.4.3 *Estimation of average selectivity*

The method described in the previous subsection is used to find (linear) relationships between the selectivity observed at haul level and a set of measured covariates. However, fishery researchers and managers are interested mostly in the average selective performance of a given selection device, often used to represent the exploitation patterns for stock assessment purposes. Average estimates of selective performance are often obtained via Maximum Likelihood (Equation 20) by pooling the experimental data over hauls:

$$-\sum_{i=1}^{m}\sum_{l}(n_{il,cd} \times log(r(l, L50, SR) + n_{il,cc} \times log(1.0 - log(r(l, L50, SR)) \qquad (23)$$

which introduces the summation over hauls $h \in \{i=1,\ldots,m\}$, being $n_{il,cd}$ and $n_{il,cc}$ the fish sampled in haul *i*. Thus, assuming that the *m* experimental hauls were randomly drawn from all possible hauls that could be conducted in the fishery, Equation 23 returns an estimate of the expected average selectivity in the fishery. It is known that the selectivity of a device is affected by a wide range of uncontrolled factors that yield between-haul variation around the selectivity it delivers. One disadvantage in the average selectivity estimation is the removal of the explicit variation in selectivity between hauls (Fryer, 1991); therefore, uncertainties derived from the likelihood framework would not properly represent the actual variation contained in the data. A valid method widely applied to account simultaneously for the within- and between-haul variations in an average selectivity estimate is the bootstrap (Efron, 1979; Efron and Tibshirani, 1993; Manly, 2018). The central idea of bootstrapping is to quantify the variability of a target population directly from the sample data, without any other consideration or parametric assumption. Because it is not feasible to access the true variability of the targeted population, the bootstrap technique estimates the variability of the population from B artificial resamples generated by applying resampling methods to the original sampled data. Therefore, to obtain valid bootstrap variance estimates (and subproducts such as confidence intervals), it is fundamental to apply a resampling scheme that properly captures the main sources of variability in the original sampled data. The resampling scheme applied to multi-haul selectivity data was first implemented by Millar (1993) to estimate confidence intervals of nonparametric selectivity curves, and later applied in a wide range of selectivity models (Krag et al., 2014; Melli et al., 2020; Millar 1993; Revill and Holst, 2004a; Sistiaga et al., 2010). The bootstrap resampling scheme is plugged into the empirical data as follows:

(a) Based on the observed hauls, $H = h_{i=1},\ldots,h_m$, a random sample of hauls $H^* = h_{i=1^*},\ldots,h_{m^*}$ is artificially generated by nonparametric resampling. In other words, after selecting haul i, this is replaced in the original sample so that it can be chosen again. This outer resampling scheme emulates the between-haul variation in the population from which the data was generated.

(b) A second, inner resampling scheme is applied to the length distribution of the measured fish, separately for each haul drawn in Step (a) and catch compartment within the haul. Following the example of cover-codend data, this step generates artificial distributions of lengths of measured fish in codend ($n^*_{il,cd}$) and cover ($n^*_{il,cc}$). Once this step is concluded, a new sample $H^{**} = h_{i=1^{**}},\ldots,h_{m^{**}}$ is artificially generated from the original data.

(c) Obtain selectivity estimates from the artificial data generated in the two previous steps, by using, for example, the Maximum Likelihood procedure in Equation 20, resulting in a selectivity curve estimated from the artificial data, $r^*(l)$.

(d) Repeat Steps (a)–(c) B times (often B = 1000), so that an artificial population of selectivity curves $r^{*b}(l)$, $b=1,\ldots,B$, is generated.

(e) The distribution of the asymptotic selectivity estimates is approximated by the histogram based on the population of B selectivity curves $r^{*b}(l)$ generated in Step (d).

(f) Bootstrap confidence intervals of the average selectivity curve are obtained from the histogram obtained in Step (e) using, for example, the percentile method.

4.5 Selectivity indicators

The size-selection estimates obtained with the models described in Sections 4.2–4.3 are independent of the structure of the exploited populations. To better communicate to the industry and managers about the potential usability of a given selection device, it is relevant to provide information regarding expected catches that considers the specific population structure fished. Selectivity indicators (Brčić et al., 2016; Sala et al., 2016; Wienbeck et al., 2014) can provide a deeper insight into the cost–benefit trade-off associated with the use of a given selection device to specific population structures. Their simplicity and intuitive meaning make usability indicators an interesting tool for communicating experimental results with managers and fishers. Selectivity indicators are often estimated as the ratio of catches from two or more catch compartments. For example, in catch comparison experiments:

$$
\begin{aligned}
nE &= 100 \times \left(1.0 - \frac{\sum_{i=1}^{m}\left\{\sum_{l} n_{il,test}\right\}}{\sum_{i=1}^{m}\left\{\sum_{l} n_{il,ref}\right\}}\right)\\
nE_{-} &= 100 \times \left(1.0 - \frac{\sum_{i=1}^{m}\left\{\sum_{l<rs} n_{il,test}\right\}}{\sum_{i=1}^{m}\left\{\sum_{l<rs} n_{il,ref}\right\}}\right)\\
nE_{+} &= 100 \times \left(1.0 - \frac{\sum_{i=1}^{m}\left\{\sum_{l\geq rs} n_{il,test}\right\}}{\sum_{i=1}^{m}\left\{\sum_{l\geq rs} n_{il,ref}\right\}}\right)
\end{aligned} \qquad (24)
$$

selectivity indicators in Equation 24 are estimated for each of the species studied independently. The indicator *nE* is the escape efficiency provided by a test gear relative to a reference gear, estimated as the theoretical ratio associated with equal catch efficiency in the test and reference gear (1.0), minus the experimental ratio of the observed catches in a test gear ($n_{il,test}$) to the observed catches in a reference gear ($n_{il,ref}$). The indicator nE_{-} represents the escape efficiency estimated for the catch fraction below a predefined reference size (*rs*); nE_{+} is the escape efficiency for the catch fraction ≥ *rs*. In mixed fisheries, the use of selection devices to reduce the bycatch of unwanted species often leads to catch losses of the target ones, compromising the devices' adoption by commercial fisheries (Suuronen and Sarda, 2007; Suuronen et al., 2007). In this scenario, and especially in fisheries subject to the LO, it is of interest to quantify the trade-off between catch losses of targeted species per unit of effort and the additional fishing opportunities derived from a reduction in the bycatch of a potential choke species. Key questions to be answered could be: (a) How much must the fishing effort be increased to compensate for potential catch losses of targeted species owing to the use of a given selection device? (b) To what extent would the reduction in the bycatch of the most limiting (potential) choke species improve fishing opportunities for the target species? Combined with traditional selectivity analysis, these indicators could provide a wider picture of cost–benefit trade-offs related to the use of a given selection device, thus pointing to the best technical solution for individual fishing and management scenarios.

4.6 Assessment of selectivity based on video recordings

Traditionally, the effectiveness of selective devices in trawl gears has been evaluated based on catch data alone, following well-established methodologies for data collection and subsequent statistical analysis (Wileman et al., 1996). However, in most cases, these quantitative methods based on catch data do not provide detailed information on the contribution of the different components of the device to its overall performance, or about the sequences of behavioural events occurring when the fish interacts with the selection device. This lack of detailed information limits the understanding of the functioning of the device and, therefore, the ability to optimise its performance.

The general development in camera technology in the past decade has led to the availability of low-cost cameras with high image quality for making underwater video recordings. Therefore, these cameras have become an affordable method to assess fish behaviour in selectivity studies (Bayse and He, 2017). Video observations are often used by fishery technologists to obtain a qualitative picture of how fish interact with a selection device (Larsen et al., 2018a, 2018b; Lövgren et al., 2016; Queirolo et al., 2010). A review of recent literature suggests, however, a growing interest in more detailed descriptions of fish behaviour based on quantitative analysis (Bayse et al., 2016b, 2014; Chosid et al., 2012; Hannah and Jones, 2012; He et al., 2008; Krag et al., 2009a; Queirolo et al., 2019; Yanase et al., 2009). The methodology applied in quantitative behavioural studies often involves tracking observed fish from their first detection to their final fate (capture or escape). During this time lapse, the occurrence of behavioural events categorised at different stages of the selection process are identified and counted. Although it is reasonable to assume that the fate of the fish can be related to sequences of behavioural events occurring throughout each of the selection stages, with few exceptions (Hannah and Jones, 2012; Yanase et al., 2009) the stage-wise nature of the behavioural data is usually ignored. Instead, events from different stages are analysed together as predictors in regression models (Bayse et al., 2016b; Underwood et al., 2015) or separately in contingency tables (Bayse et al., 2014; He et al., 2008; Krag et al., 2009a; Queirolo et al., 2019) and are therefore treated independently of events recorded in previous and subsequent stages. Behavioural responses to selection devices can be influenced by factors intrinsically related to the individual being selected, and by extrinsic factors such as fishing conditions varying during and/or between hauls. Therefore, estimating uncertainties associated with observed behaviours can be relevant information in the assessment and development of selection devices. However, no selectivity study based on fish behaviour provides such information.

Ignoring the stage-wise nature of the behavioural events and the uncertainty of occurrence preclude answering all of the following questions. (a) How often does a given event happen? (b) How precise is the estimated probability of occurrence of a given behavioural event? (c) Does the occurrence of an event condition the events happening next? At the same time, this can lead to more general questions. (d) What are the connections between different events being observed before, during, and after the fish contacts the selection device. (e) Could the observed sequences of events be related to the fate of the fish in relation to the selection process?

Therefore, to benefit fully from incorporating the use of underwater recordings into the process of studying, developing, and optimising the performance of selective devices in fishing gears, it is necessary to develop and apply a method that provides quantitative answers with uncertainties to the previous questions. Such method could help to achieve the overall objective of this thesis.

5 Research questions

Following the review in Chapter 3 on trawl gear modifications that could address the objectives of this thesis, and the overview in Chapter 4 on quantitative methods to assess trawl selectivity, the specific research questions were formulated:

1. Can grid systems reduce the bycatch of flatfish species in the Baltic Sea otter-trawl fisheries while maintaining capture efficiency of targeted cod?

2. Can differences in species behaviour be utilised to reduce the bycatch of flatfish species in the Baltic Sea otter-trawl fisheries while maintaining capture efficiency of targeted cod?

3. How can the behavioural information of fish species from underwater video recordings be quantified to study, develop, and optimise the performance of selection devices?

4. Can a combination of grid and codend technologies generate harvesting patterns for Baltic cod that are alternatives to those traditionally delivered by trawl gears?

5. Can differences in species behaviour be utilised to reduce the bycatch of cod in the Baltic Sea otter-trawl fisheries while maintaining capture efficiency of targeted flatfish species?

6. Can sieve panels be used to efficiently separate *Nephrops* from fish species?

7. How can optimal harvesting patterns for brown shrimp be identified considering the combined effect of altering the codend mesh size and mesh orientation?

6 Baltic Sea otter-trawl fisheries targeting cod

6.1 Reduction in flatfish bycatch using sorting grid technologies (Paper I)

One unsolved problem in the Baltic cod-directed trawl fisheries is the high bycatch and discard rates of flatfish species (ICES, 2020b; Probst et al., 2011; Storr-Paulsen et al., 2012; Zimmermann et al., 2015). Paper I addresses Research Question 1 in Chapter 5 by reporting on the development and testing of a grid system that aims to provide an escape possibility for flatfish ahead of the codend. The initial concept was proposed by the fishing industry and consisted of four 600 x 500 mm stainless-steel grids fitted to the sides of the rearmost tapered section of the trawl. Further collaboration by German and Swedish researchers resulted in the so-called FRESWIND (Flatfish Rigid EScape WINDow) device (Figure 15). FRESWIND consists of two rigid windows mounted on each side of a four-panel extension piece. The windows are constructed as grid-like sections with horizontal steel bars to facilitate the passage of flatfish species (ICES, 1997; Lomeli et al., 2017; Rillahan and He, 2021; Valentinsson and Ulmestrand, 2008). The space between the bars was based on previous experiences with grid devices in *Nephrops* fisheries, where the use of 35 mm bar spacing has been associated with a value of $L50_{grid}$ = 38 cm for cod (Lövgren et al., 2016). This matched the species minimum landing size (MLS) in the Baltic Sea until January 2015 (With the introduction of the LO for cod, the 38-cm MLS regulation was replaced by an MCRS of 35 cm). A V-shaped guiding device (860 mm high and 200 mm wing long) was mounted ahead of the windows to direct fish from the central path of the extension towards the windows. Paper I:

- Evaluates the efficiency of FRESWIND in reducing bycatch of flatfish species while maintaining the catchability of commercial-sized cod.
- Evaluates the potential of FRESWIND to supplement codend size selection by reducing the bycatch of undersized cod.
- Evaluates the size-selection properties of FRESWIND on target and bycatch species.
- Quantifies the probability that target and bycatch species will make efficient contact with the escape windows.

The efficiency of FRESWIND was tested in commercial conditions on board a German twin trawler seasonally engaged in the cod-directed trawl fishery. The experiment was conducted as a catch comparison in which one of the trawls mounted FRESWIND (test) and the other maintained its commercial configuration (reference). Both the test and reference trawls mounted the same

BACOMA codends (EU 2019/1241). Sea trials with the twin trawl configuration were conducted in the central southern Baltic Sea (SD 24), during the major cod-fishing period (March 2013). Twelve hauls were successfully conducted, resulting in abundant catches of cod, plaice, and flounder. FRESWIND's performance was evaluated by comparing catches in the test and reference gears by species. In Paper I, the catch comparison analysis used two competing approaches. The first approach modelled the catch share between the test and reference trawls using an empirical flexible model based on the model described in section 4.3. The second approach used a model with a parametric structure that accounted for the selectivity properties of FRESWIND, and the length-independent probability for the different species analysed to contact the rigid escape windows (see section 4.2 on structural modelling for further details). Consequently, in addition to a catch comparison curve, the second modelling approach also provided estimates of the selectivity parameters of FRESWIND (*L50, SR*) and the contact probability parameter (C_{grid}). The catch comparison curves fitted by the two competing modelling approaches demonstrated high goodness-of-fit to the experimental data in both cases. However, a considerable gain in inference power was achieved with the structural model. Another gain derived from the use of the structural model was the information provided about the selectivity properties of FRESWIND. For cod, the average length at 50% retention ($L50_{grid}$ = 38.9 cm) and contact probability parameter (C_{grid} = 0.4) were consistent with the average values estimated in Lövgren et al. (2016; $L50_{grid}$ = 38.1 cm and C_{grid} = 0.4). The contact probabilities estimated for the flatfish species were higher than for cod (C_{grid} = 1.0 and 0.7 for plaice and flounder, respectively). This methodological comparison demonstrated the benefit of using structural models in catch comparison studies, when applicable.

Paper I reports ∼68% flatfish bycatch reduction in the test trawl owing to the effect of FRESWIND. In addition, the catch of undersized cod was reduced ∼30%, and losses of marketable cod were relatively minor (∼7%). Furthermore, selectivity indicators, estimated by incorporating the catch composition of the fleet obtained by the German fishery observer programme, predicted a reduction of at least 50% in flatfish catches if FRESWIND was adopted in the fishery. The results obtained in Paper I demonstrate that grid systems can effectively reduce the bycatch of flatfish species in the Baltic Sea, while reducing the bycatch of juvenile cod with minor catch losses of targeted sizes. The identification of the potential of grid technologies to mitigate the problem of flatfish bycatch in the cod-directed fishery, and subsequent development and testing of FRESWIND, are examples of collaborative work between Baltic fishers and researchers, which aligns with the original intention of the LO in EU waters.

The FRESWIND concept and its proof of efficiency attracted the attention of the German media, helping to raise social awareness of the problem of flatfish bycatch in the Baltic Sea. The concept was awarded a runner-up prize at the 2014 WWF-International Smart Gear Competition (https://www.worldwildlife.org/initiatives/international-smart-gear-competition). A video presenting FRESWIND to the 2014 Smart Gear Competition can be found at https://www.thuenen.de/de/infothek/videothek/freswind-ein-netz-lernt-unterscheiden.

The FRESWIND concept might be of interest to any other roundfish fishery where the bycatch of flatfish, or any flat-body species, poses a problem. This is the case on the Northeast Atlantic coast of the United States in a fishery targeting haddock, where the FRESWIND concept has been successfully adapted to specific needs (Rillahan and He, 2021).

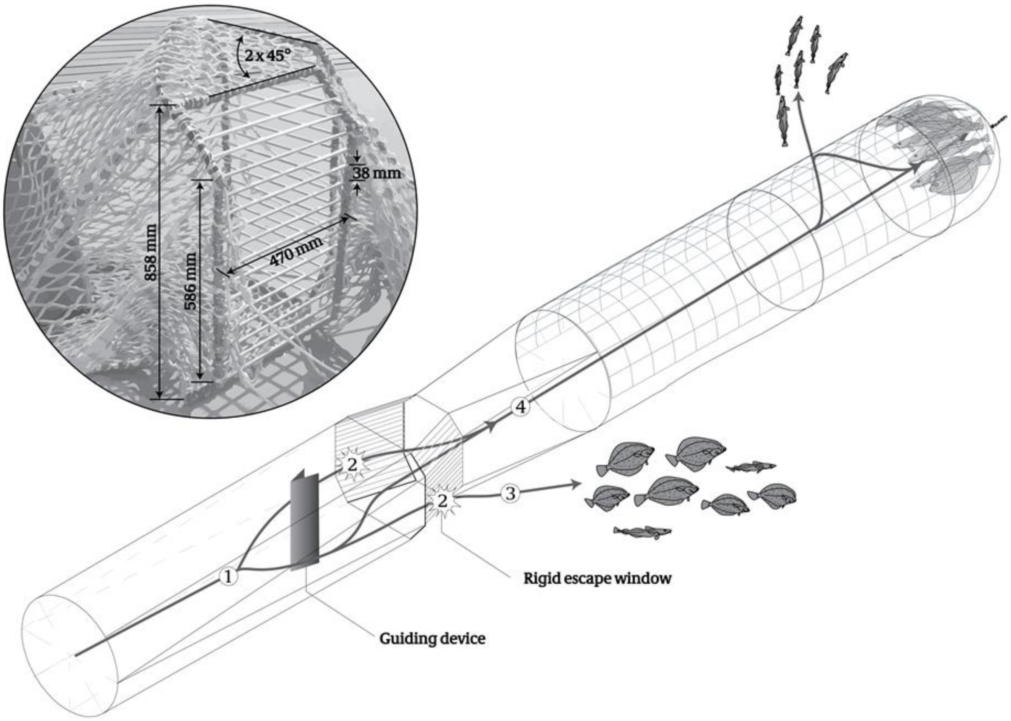

Figure 15. Bottom: isometric view of the experimental setup in Paper I, combining the FRESWIND device and the mandatory BACOMA codend. The FRESWIND device involves inserting a guiding device intended to divert fish sideways towards the rigid grids. Top: technical details of the rigid grids.

6.2 Reduction in flatfish bycatch using behaviour selection technologies (Paper II)

Under certain circumstances, grid systems such as the FRESWIND concept, developed and tested in Paper I, can be difficult to handle under commercial conditions (Catchpole and Revill, 2008), especially for small trawlers with limited space on deck. Another concern brought by the fishing industry regarding FRESWIND's usability was the limited adaptability of the device to situations in which the flatfish bycatch could be of commercial interest. Considering this feedback, the need was identified for an alternative to FRESWIND's flatfish bycatch reduction device. An ideal alternative should be free of rigid elements, with selective properties easy to install and remove, providing adaptive control of the trawl's species selectivity, preferably from haul to haul. This feature should help fishers adapt their harvesting patterns to changing fishing conditions and let them manage the available quotas according to their own preferences.

Utilising differences in species behaviour can be an efficient strategy in reducing the bycatch of unwanted species (Bayse et al., 2016b; Beutel et al., 2008; Lomeli et al., 2018; Melli et al., 2018a). Observed differences in flatfish and cod behaviour at the extension piece of trawl gears inspired the following question: Could a simple escape opening installed at the bottom panel of the extension piece of the trawl be an efficient modification to reduce flatfish bycatch in the Baltic cod-directed trawl fisheries? The case study presented in Paper II addresses Research Question 2 in Chapter 5, by reporting on the development and testing of a simple and adaptive FLatfish EXcluder device (FLEX; Figure 16).

FLEX consists of half an oval-shaped outlet placed in the lower panel of the extension piece of the trawl, with the major axis formed by a 90 cm long fibreglass rod. The bow of the outlet is oriented downwards and defined by an elastic wire connected to the forward edge of the net cut. A 1.5 m lead rope is connected to the vertex of the bow, running lengthwise through the forward section of the extension to create a furrow on the floor of the net to direct flatfish swimming in close contact with the bottom towards the outlet. Further, a 90 × 20 cm rectangular net shield with small floats on top was connected to the fibreglass rod. This net shield with fluttering floats on top should stimulate avoidance reactions in cod swimming close to the lower panel of the trawl, reducing the probability of encountering the outlet (Figure 16).

The performance of FLEX was tested on experimental fishing trials on board the RV "Solea," using the paired-gear methodology described in Chapter 4. A double-belly trawl was used. Both sides of the trawl mounted the same non-selective extension pieces and codends. FLEX was mounted in one of the sides, making it the only escape possibility for fish entering the trawl. Results obtained by comparing catches from the sides with and without FLEX installed revealed an escape efficiency > 73% for the flatfish species studied (plaice, flounder, and dab). Catch losses of marketable cod averaged ~8%, a value comparable to the losses estimated for FRESWIND (Paper I). The evaluation of the catch data obtained with FLEX demonstrated that exploiting differences in fish behaviour during the travel across the trawl net effectively reduces the bycatch of flatfish species in the cod-directed trawl fishery. The conceptual simplicity of FLEX can be easily adapted to other demersal fisheries where excessive flatfish bycatch can be a problem.

Research Questions 2 and 5 formulated in Chapter 5 suggested addressing bycatch issues in the Baltic Sea by exploiting differences in species behaviour. However, although the region has one of the longest and most productive traditions in size-selection research, the potential of exploiting fish behaviour to reduce bycatch remains largely unexplored. Consequently, at the time the research contained in this thesis started, little information was available regarding the behaviour of the local species in relation to selection devices. To properly address Research Questions 2 and 5, a method to quantitatively evaluate fish behaviour in relation to selection devices based on video recordings was needed. Paper II addresses Research Question 3 in Chapter 5 by introducing a method that (a) quantifies the probability that an observed behavioural event occurs during the selection process; (b) quantifies the probability that a given behavioural event will occur, conditioned to the occurrence of events observed previously; and (c) establishes behavioural tree diagrams, formed by all sequences of events displayed by the observed fish towards their final fate in the catch process. Moreover, the method accounts for uncertainties derived from the limited number of fish observations and the natural variation in fish behaviour that can influence the between- and within-haul variation in performance of selection devices (Fryer, 1991). Adding uncertainties to quantitative behavioural estimates, therefore, should help in discerning strong behavioural patterns from behaviours that could be observed by chance. This is done by adapting and incorporating the bootstrap procedure traditionally applied to the analysis of catch data (Millar, 1993). In addition to presenting results from FLEX, Paper II also pursues the following objectives:

- Demonstrate the applicability of the quantitative behavioural method using FLEX as a case study.
- Demonstrate how a quantitative behavioural method can complement traditional assessment of performance of selection devices based on catch data, to improve understanding of the functioning of the device and identify opportunities for further development.
- Increase the knowledge of the behaviour of Baltic demersal species interacting with selection devices at the extension piece of the trawl.

The application of the method involved collecting behavioural data across five hauls. Altogether, the behaviour of 89 flatfish and 150 roundfish was recorded and analysed according to an ethogram made of a stepwise succession of predefined behavioural events (Figure 16). The collected behavioural data were used to successfully generate behavioural trees for flatfish and cod. The behavioural trees were composed of all individual sequences of behavioural events performed by the observed fish in their travel along the extension piece where FLEX was installed. The body orientation of the observed individuals, fate (escaped using FLEX or continued towards the codend), and the duration of the selection process since first visual contact were recorded. The behavioural analysis produced values of escape efficiency comparable to those obtained in the catch analysis, validating the representativeness of the collected observations. Evaluation of the resulting behavioural trees revealed that ~80% of the observed flatfish individuals passed calmly through the excluder, whereas most of the observed roundfish displayed avoidance-swimming reactions in the presence of FLEX. The results for flatfish behaviour presented in Paper II are consistent with other studies on flatfish behaviour conducted in other regions.

The methodology presented in Paper II for quantitative analysis of fish behaviour has been adapted and successfully applied in two published studies related to passive gears (Chladek et al., 2021a, 2021b). The application of the method in Paper II, Chladek et al. (2021a) and Chladek et al. (2021b) successfully addresses Research Question 3.

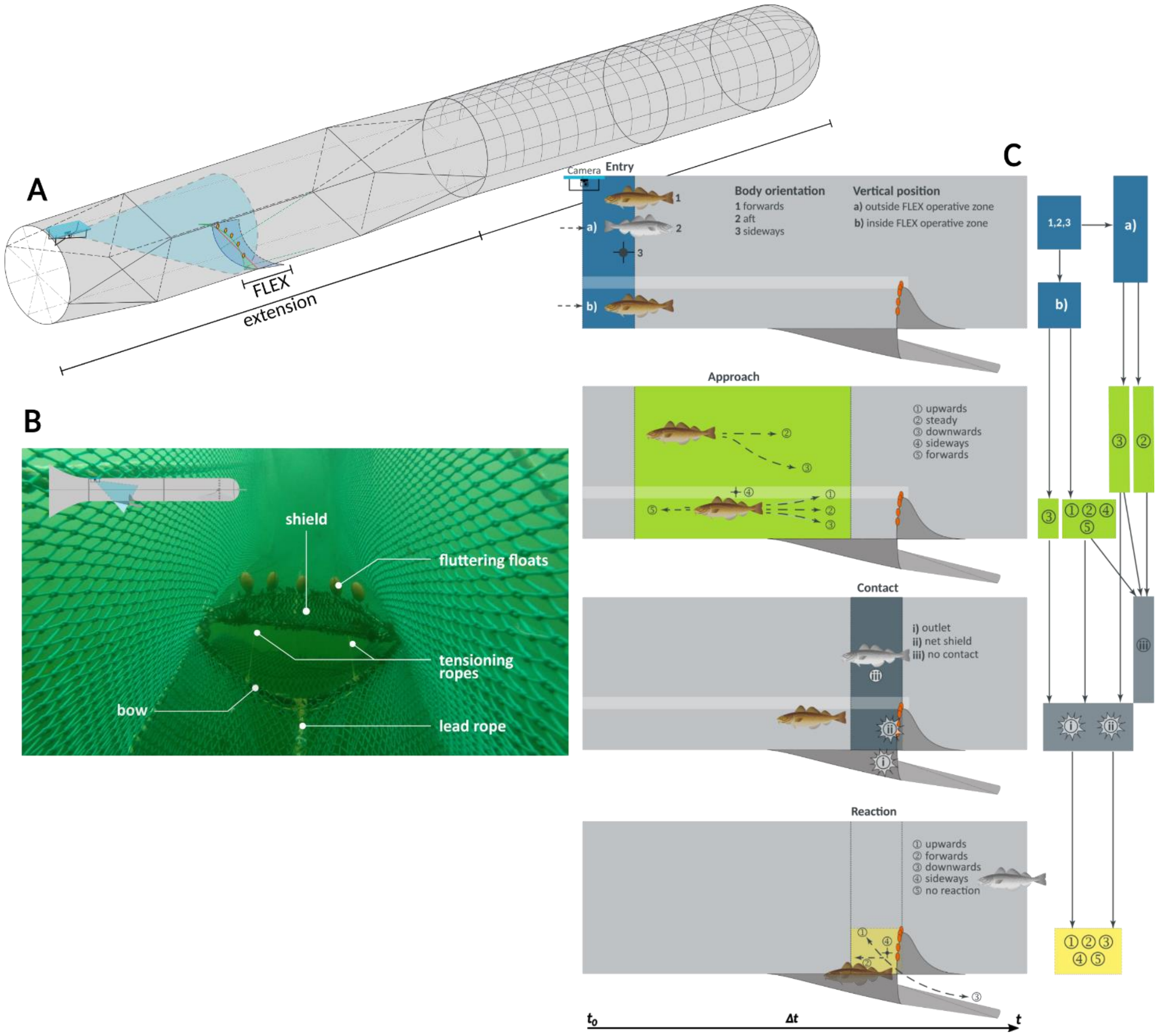

Figure 16. (A) Perspective view of the flatfish excluder (FLEX) fitted in the extension piece of the trawl. (B) Front view of the device (underwater picture taken from the camera position shown in (A). (C) Graphical representation of predefined behavioural events used to characterise the behaviour of fish observed in video recordings in four different behavioural stages: (1) entry, (2) approach, (3) contact, and (4) reaction.

6.3 Exploring alternative harvesting patterns for Baltic cod by combining grid and codend technologies (Paper III)

Decades of continuous adjustments to harvesting patterns in the demersal trawl fishery in the Baltic Sea have not resulted in concurrent improvements of Baltic cod stocks (Eero et al., 2020). In the current situation, it would be relevant to investigate alternative fishing patterns for which cod is harvested, primarily considering potential individual productivity rather than individual size. However, discussions related to balanced harvesting (Garcia et al., 2012; Jacobsen et al., 2014; Zhou et al., 2010) in trawl fisheries are often constrained by the technical limitations to recreating alternative harvesting patterns by departing from the traditional s-shaped selection curves of trawl gears. For example, although it has been recognised that through harvest patterns associated with passive gears, such as gillnets and longlines (He et al., 2021), fisheries can improve the sustainability and productivity of exploited fish stocks (Jørgensen et al., 2009; Svedäng and Hornborg, 2017), it is not clear how the traditional bell-shaped selection pattern of gillnets could be achieved in trawl gears. Therefore, Paper III addresses Research Question 4 by pursuing the following objectives:

- Demonstrate the feasibility of alternative selectivity patterns for trawl, specifically by achieving a bell-shaped selection curve traditionally associated with gillnets.
- Demonstrate that alternative selectivity patterns can be achieved in practice by combining and adjusting well-known selective devices commonly applied in trawl fisheries around the world.
- Stimulate further discussion between fishery scientists and managers to broaden the scope of feasible harvesting patterns in trawl fisheries.

In Paper III, a trawl design used commercially in the Baltic Sea was adapted by inserting a Nordmøre grid in the extension piece ahead of the codend. The grid was made of steel, mounted with the bars arranged vertically and with a nominal angle of ~75°. A triangular outlet was cut in the upper panel in front of the grid to provide an outlet for fish not passing through the grid. Two additional elements were applied to encourage fish contacting the grid: (a) a guiding panel to direct fish towards the lower section of the grid, and (b) a piece of net masking the outlet (so-called MEO) to avoid early escape prior to size selection. The grid's purpose was to exclude large fish before entering the codend, while letting small- and medium-sized fish pass. Small- and medium-sized fish passing through the grid were subsequently selected by a T90 codend. It was expected that the sequential combination of the passage probability of the grid and the retention probability of the codend would lead to a bell-shaped selectivity curve of the experimental trawl.

To define the bar spacing of the grid and the mesh size of the codend, prior information on the population structure of cod in the exploited fishing grounds was used. The survey data provided by Baltic International Trawl Survey (ICES, SD 24, first quarter 2014), revealed a very low abundance of large cod (> 50 cm). Considering the expected population structure, computer-based simulations using theoretical selectivity patterns for different bar spacings (grid component) and mesh sizes (codend component) indicated that a combination of a grid with 50 mm bar spacing and a T90 codend with a nominal stretched inner mesh size of 110 mm (Fonteyne, 2007) would maximise the probability of achieving an experimental bell-shaped selection curve.

The experiment was conducted on a research vessel using the dual-covered method as in Sistiaga et al. (2010; Figure 17). Fish escaping from the outlet associated with the grid were retained in a top cover, and fish escaping through the codend meshes were retained in the codend cover. The direct observations of fish collected in the three-compartment configuration (top cover, codend, and cover codend) allowed fitting a structural model to the catch data, which accounted for the selectivity of the grid and the codend separately. Moreover, the structural model applied also accounted for the length-independent probability that a fish efficiently contacts the grid (C_{grid}). Sixteen models differing in the selectivity functions (*logit*, *probit*, *Gompertz*, and *Richards*), applied to describe the selectivity of the grid and the codend, were fitted. The best candidate model was chosen by AIC. A double bootstrap method was used to estimate the Efron percentile confidence intervals for both the estimated parameters and associated curves. Based on the experimental catch data collected in eight hauls, the estimated $L50_{grid}$ = 47.93 cm and $L50_{codend}$ = 29.70 cm were in agreement with the expected values previously obtained in the computer simulations. Despite the technical elements applied to maximise the probability of cod contacting the grid, the resulting model estimated a contact value of C_{grid} = 0.73, which implies that the resulting bell-shaped selection curve did not reach the full catchability (retention probability) at the targeted mid-sized length classes. Nevertheless, the overall gear selectivity curve clearly demonstrates the possibility of obtaining bell-shaped size selectivity in trawls using combinations of well-known selectivity devices already available. Therefore, the first two aims of Paper III, and consequently Research Question 4, were successfully addressed. Results reported in Paper III were disseminated among German fishery modellers and managers involved in the management of Baltic cod. The study was presented by the author of this thesis at international conferences, such as the 144th Annual Meeting of the American Fisheries Society (2014) within a thematic session related to balanced harvesting, and by publishing Paper III in a special issue on selective fishing and balanced harvesting in *Fisheries Research*.

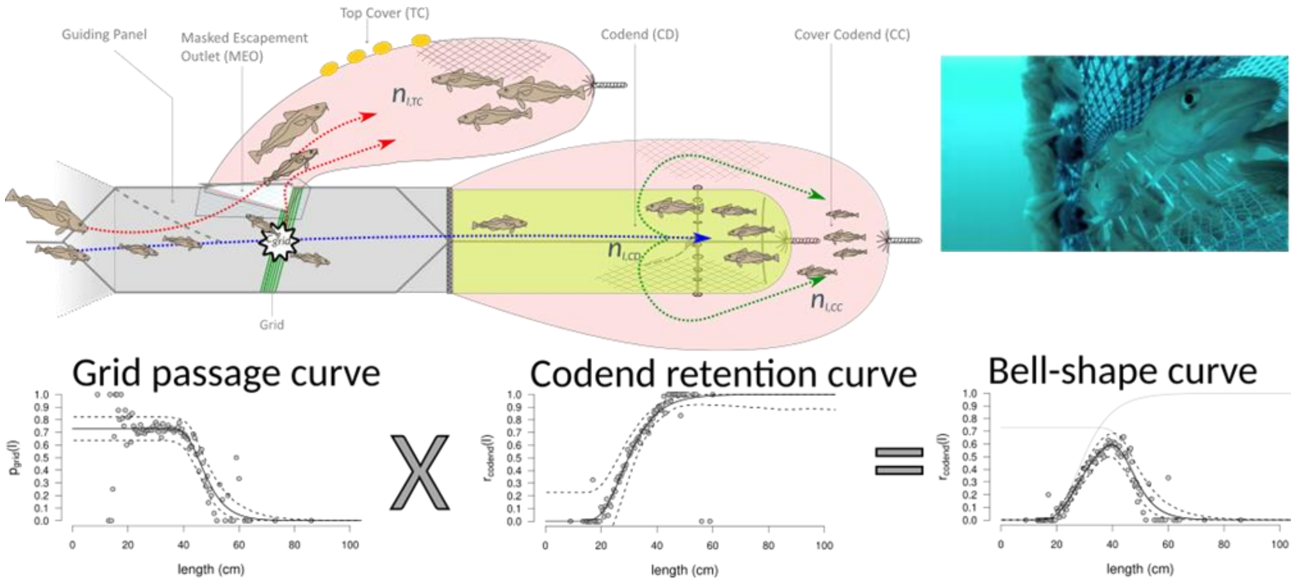

Figure 17. Top: schematic side view of the test gear combining a sorting grid and a selective codend, and the experimental setup known as dual cover. Bottom: partial selection curves obtained for the grid (left) and codend (centre), and the bell-shaped curve resulting from the combination of the partial curves (right).

7 Baltic Sea otter-trawl fisheries targeting flatfish

7.1 Reduction in cod bycatch using behaviour selection technologies (Paper IV)

The current poor status of Baltic cod stocks, and the prevailing "cod hostile" oceanographic conditions in the Baltic Sea (Eero et al., 2015; Köster et al., 2005; Mackenzie et al., 2007; Möllmann et al., 2009) jeopardise the viability of the cod-directed trawl fishery. Therefore, vessels traditionally involved in the cod-directed fishery are shifting the target towards flatfish species (ICES, 2020b, 2019b). To maintain sustainable fishing in this emerging flatfish fishery, fishing technologies that reduce the bycatch of cod are needed. Otherwise, access to targeted flatfish populations can be heavily constrained. Therefore, Paper IV addresses Research Question 5 by reporting on the development and testing of a behavioural selection device designed to reduce the bycatch of cod in flatfish fisheries.

Sea trials with the FLEX device presented in Paper II (case study) demonstrated the potential of utilising differences in cod and flatfish behaviour to reduce flatfish bycatch. Following the same principle, Paper IV evaluates if removing a net section from the upper panel of the extension piece of the trawl could reduce cod bycatch without affecting the catches of targeted flatfish. The roofless concept was achieved by removing a 14.5 meshes long (~175 cm) rectangular net section of the top panel at the extension piece (Figure 18). Two modifications of the baseline design thought to further stimulate cod escape behaviour were also developed and tested. The first modification involved doubling the length of the roofless section from ~175 cm to ~330 cm, and the second modification applied float ropes blocking the free path along the extension piece, according to Herrmann et al. (2015). Tests on the performance of the three roofless designs were done following the catch comparison methodology during two different research cruises. The first cruise took place in ICES SD 22 and 24 on board RV "Clupea." The vessel was rigged with a twin trawl, which allowed evaluation of the fishing efficiency of the trawl with the roofless device (test gear) relative to the trawl with the top panel unaltered (reference gear). Both the test and reference gears used identical mandatory T90 codends (EU 2019/1241). The second cruise took place in ICES SD 24 on board RV "Solea," using the same experimental design as in the previous cruise, except that the test and reference gears were paired using a double-belly trawl. Catches of cod, plaice, and flounder in the test and reference gears were analysed using empirical flexible models (Krag et al., 2014). The modelling results were supplemented with traditional selectivity indicators for single species. In addition, Paper IV introduced two new usability indicators to answer relevant questions such as: (a) How much should fishing effort be increased to compensate for potential catch losses of targeted flatfish when using the selection device? and (b) What are the cost–benefit trade-offs related to potential reductions in cod bycatch and catch losses of target flatfish species?

Analysis of the resulting catch data revealed that applying the baseline roofless design consistently reduced cod bycatch by ~75%. Catches of the target species plaice and flounder were reduced 15%; however, we estimated that catch losses of the two flatfish species could be balanced by increasing fishing effort to ~8% and ~12%, respectively. Under a fishing scenario where cod catches choke a flatfish fishery, it has been estimated that the use of the roofless concept could increase the flatfish catch by > 300%. Consistently with the results obtained in Paper II, the evaluation of the roofless concept demonstrated that exploiting differences in fish behaviour can be an effective strategy to reduce the bycatch of cod in flatfish-directed trawl fisheries of the Baltic Sea.

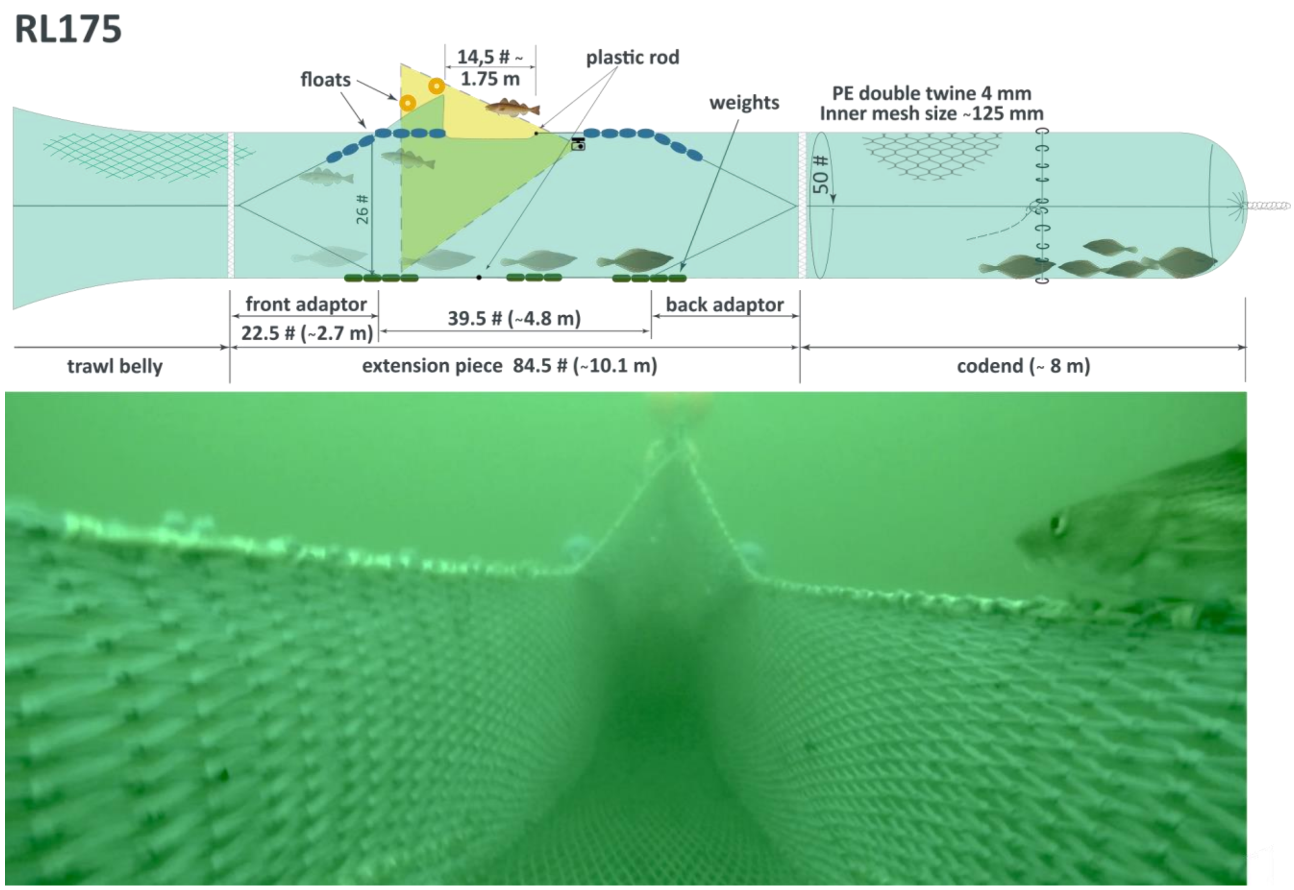

Figure 18. Top: technical characteristics and conceptual functioning of the roofless device. Bottom: underwater picture taken from the rear end of the roofless section, showing a cod escaping the trawl.

8 North Sea otter-trawl fishery targeting *Nephrops*

8.1 Investigating the bycatch separation properties of sieve nets (Paper V)

Paper V addresses Research Question 6 by testing the effectiveness of different sieve net designs to sort *Nephrops* and fish species into separate codends (Figure 19). The concept can be described as a long (~10 m) SMP mounted in the extension piece of the trawl with a low inclination upwards (~2.5°). The sieve panel divides the extension piece into upper and lower compartments, ending in separate codends made of 50 mm nominal mesh size, which is considered non-selective for the study's species and sizes of interest. The considerable length of the sieve nets and the low upwards inclination are meant to exploit assumed differences in *Nephrops* and fish behaviour. Information already collected from video observations of *Nephrops* indicates that the species has limited swimming activity and tends to roll over the lower panel of the trawl (Briggs and Robertson, 1993; Main and Sangster, 1985), whereas fish tend to stay clear of the surrounding net (Glass and Wardle, 1995). Therefore, it was expected that the open square meshes, low inclination, and length of the sieve net should result in high sieving rates for *Nephrops* rolling over its surface, while fish would be guided towards the upper codend regardless of the species. Four different sieve net designs were tested. Design 1 was made of knotless PA netting with 45.2 mm bar length and 2.5 mm nominal twine thickness. Design 2 used knotless PE netting with 60.9 mm bar length and 5 mm twine thickness. Design 4's construction was similar to Designs 1 and 2, but used PE standard netting with 94.3 mm mesh bar length and 3 mm twine thickness. Design 3 used the same sieve panel as Design 2, but the monotonous inclination was altered by inserting six floating lines, arranged in two groups of three and attached at two different positions on the panel's lower side. Further technical information regarding the different sieve net designs is provided in Paper V.

The four sieve nets were tested in Danish fishing grounds in Skagerrak (ICES Division IIIa), on board the RV "Solea." Sieving efficiency was successfully analysed for *Nephrops* (n = 7559), American plaice (*Hippoglossoides platessoides, n* = 45 363), blue whiting (*Micromesistius poutassou, n* = 13 677), cod (*n* = 7804), and witch flounder (*Glyptocephalus cynoglossus, n* = 5471). Owing to the confounding effect of behavioural and size-selection components detected in the catch data, a flexible empirical model often applied in catch comparison studies was applied to model the sieving efficiency of the four different designs.

The sieving efficiency obtained for *Nephrops* with Design 1 was poor (~17%), but improved progressively as mesh size was increased in successive designs, achieving an efficiency of 71% with Design 4. Designs 1 and 2 guided most cod sizes towards the upper codend; however, increased mesh size (Designs 3 and 4) reduced the guiding effect, resulting in more small cod in the lower codend. The guiding effect of the sieve panels was very strong for blue whiting, regardless of the design tested. The sieving efficiency for flatfish showed a strong mechanical size-selection signature, which can be related to the preference of these species to swim close to the lower panel in the gear.

In conclusion, sieving efficiency for the largest, most valuable *Nephrops* remained too low even with considerable increases in mesh size. Therefore, further improvements to the sieve-panel concept presented in Paper V are needed before it can be considered for commercial *Nephrops* fisheries.

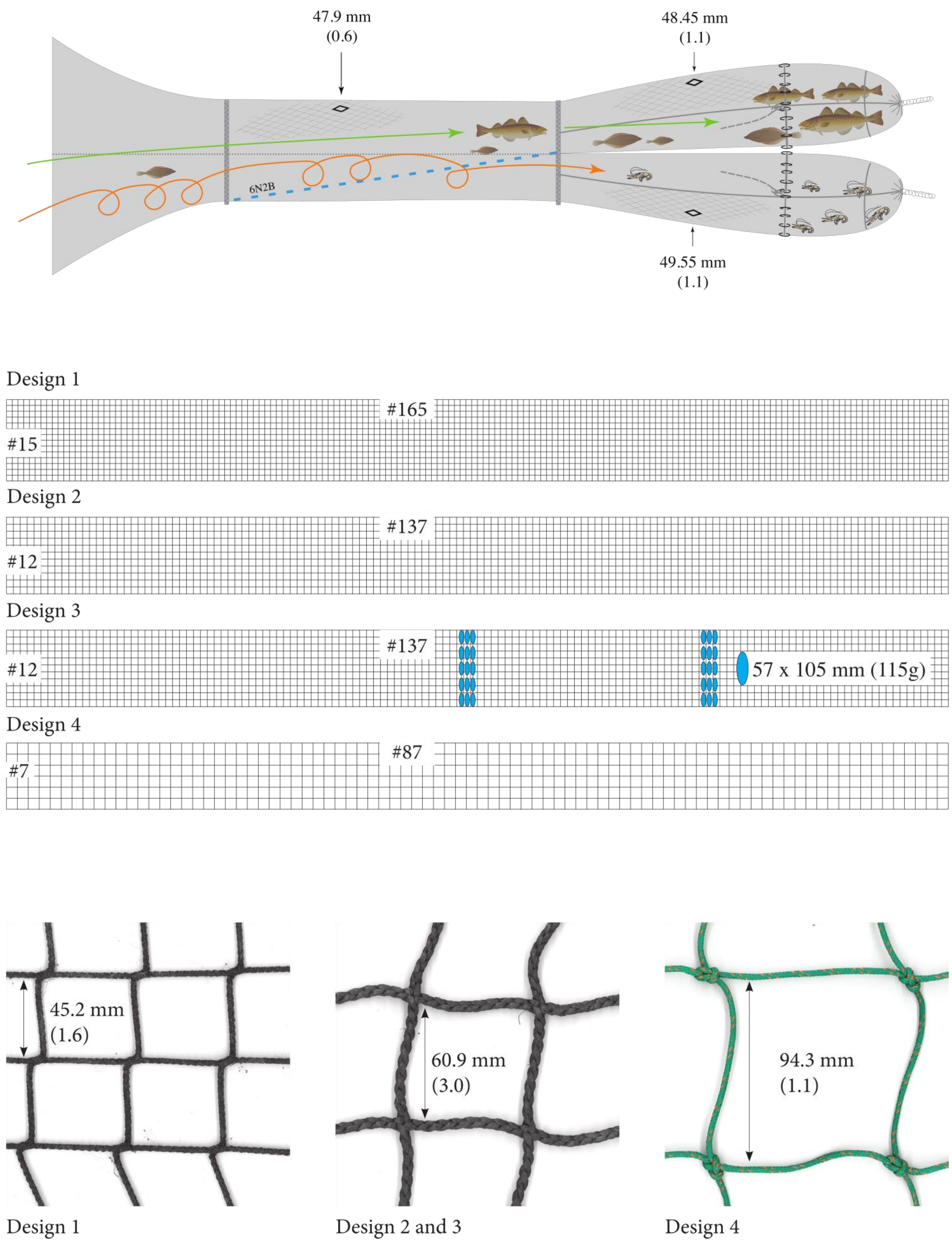

Figure 19. Side view of the experimental gear with the general design of a sieve panel (blue stippled line) mounted ahead of the double codend setup. Middle: Schematic representation of the four-sieve panel designs. Bottom: Netting used in the different designs and the measured mesh bar length of each (s.d. in parentheses).

9 North Sea beam-trawl fishery targeting brown shrimp

9.1 Predictive framework for the size selection of brown shrimp in the codend (Paper VI)

Shifts in the distribution and abundance of natural predators and the steady increase in landings have made the North Sea beam-trawl fishery the principal source of mortality for brown shrimp (Temming and Hufnagl, 2015). Thus, unsustainable harvesting patterns, caused primarily by poor selectivity of the commercial codends used in the fishery, have become an issue of concern (Polet, 2000; Revill and Holst, 2004b). However, the lack of knowledge of how to adjust the size selection in commercial trawls prevents the identification of alternative codend designs that could lead to optimal harvesting patterns for brown shrimp. Paper VI addresses Research Question 7 by providing a predictive framework for codend size selection of brown shrimp intended to:

- Fill the gap in knowledge of brown shrimp codend selectivity in the North Sea beam-trawl fishery.
- Provide a quantitative tool that could aid fishery modellers in the search for optimal exploitation patterns.
- Aid fishery managers in decision-making.

The predictive framework was developed using experimental selectivity data collected during four research cruises, in which the selective properties of 33 different codend designs were tested. The collection of the size-selection data used in Paper VI was based on the paired-gear method described in section 4.1.2, using two identical beam trawls. One trawl mounted a non-selective control codend of 11 mm stretched inner mesh size (Fonteyne, 2007), and the other mounted one of the 33 test codends. In all, 89, 51, and 68 hauls tested T0, T45, and T90 codends, respectively (Figure 20) of different mesh sizes in the range of 17–36 mm. Subsamples of brown shrimp catches in test and reference trawls were landed and length-measured using digital technologies. Altogether, > 350 000 brown shrimp were length-measured and used for analysis in Paper VI.

The predictive framework involved two sequential analytical stages. The first stage involved the analysis of individual haul data using the structural model for paired-gear data (Millar and Walsh, 1992; Wileman et al., 1996) described in section 4.2.2. The resulting *L50* and *SR* and *SP* parameters were used as input data in the second analytical stage based on the so-called Fryer method (Fryer, 1991). Predictions obtained in the second step were subsequently used to simulate expected harvesting patterns, considering the size-selection properties predicted for T0, T45, and T90 codends within the range of mesh sizes experimentally tested during the sea trials. The expected harvesting patterns were presented as isolines of retention probabilities (5%–95% in steps of 5%) at length, considering the available population structure for brown shrimp.

The results in Paper VI confirmed previous concerns regarding the exploitation pattern in the fishery, as it estimated that T0 codends made of 20–22 mm retain up to 95% of the undersized shrimp entering the codend. The study also demonstrated that modifying codend mesh size and/or mesh geometry influences the size selection of brown shrimp and, therefore, both design strategies could be combined to alter the exploitation patterns in the fishery according to specific management purposes. For example, the framework predicts that increasing the mesh size of T0 codends from 21 mm to 29 mm mesh size would reduce the bycatch of undersized shrimp by ~50%, while maintaining the catchability of commercial sizes over 70%. A similar result would be achieved using either a T45 codend of 25 mm mesh size, or a T90 codend of 27 mm mesh size.

The research effort and results summarised in Paper VI expand the set of tools supporting the evaluation of strategies on how to harvest brown shrimp sustainably and efficiently. Paper VI allowed an informed management decision to increase the codend mesh size 2 mm every two years since 2016, until reaching a minimum mesh size of 26 mm in 2020. The predictive framework provided in Paper VI was also applied successfully to simulate brown shrimp fishery and population scenarios derived from the use of different codend designs in the fishery (Günther et al., 2021). Finally, the research effort and results obtained in Paper VI played a significant role in the fishery's recent MSC certification:

https://fisheries.msc.org/en/fisheries/north-sea-brown-shrimp/

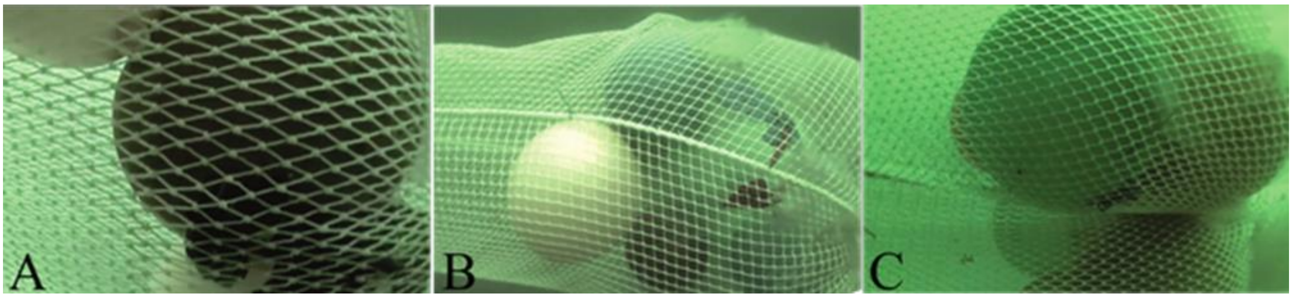

Figure 20. Working geometries of (A) T0, (B) T45, and (C) T90 codends using simulated catches.

10 Discussion

Chapter 1 introduced four demersal trawl fisheries in the Baltic Sea and the North Sea, and identified challenges that compromise their sustainability related to (a) bycatch of unwanted species, or quoted species perceived as potential choke species in the view of the current European Common Fisheries Policy; and (b) unsustainable harvesting patterns of targeted species considering new environmental states caused by the effect of climate change. Chapter 2 formulated the main objective of the thesis. Chapter 3 looked at existing fishing technologies that could be adapted and applied to sustainability challenges of the fisheries being studied. Chapter 4 provided an overview of existing methods to collect and analyse selectivity data, and identified limitations in the current methodological toolbox. Chapter 5 formulated several practical and methodological research questions that guided the research efforts of the thesis. Finally, Chapters 6–9 presented the research papers addressing the overall objective of this thesis.

With Baltic cod populations on the path to full recovery (Eero et al., 2012), the high incidence of bycatch for flatfish species was one of the most concerning challenges faced by the Baltic cod-directed trawl fisheries at the beginning of the past decade. The bycatch of plaice was particularly concerning, because this species was perceived by some riparian countries as a potential choke species for the cod-directed fishery (Zimmermann et al., 2015). To address this challenge, Papers I and II identified, adjusted, and evaluated trawl modifications that can reduce the bycatch of flatfish species in the cod-directed trawl fisheries, either by exploiting differences in morphology (Paper I) or differences in behaviour of bycatch and targeted species (Paper II). Paper I evaluated the first research question formulated in this thesis, *Can grid systems reduce the bycatch of flatfish species in the Baltic Sea otter-trawl fisheries while maintaining capture efficiency of cod?* Based on the experimental results obtained with the FRESWIND concept, it can be concluded that grid systems positioned in the lateral sides of the trawl with the bars arranged horizontally can largely solve the bycatch of flatfish in the cod-directed trawl fishery of the Baltic Sea. FRESWIND also had the advantage of providing additional escape possibilities for juvenile cod before entering the codend, without compromising the catches of targeted sizes.

A simpler alternative to FRESWIND (Paper I) proved to be a desirable feature for the German trawl fleet, which is composed of small vessels with no ramp facilities and reduced fishing decks. In the search for simpler species-selection concepts than the grid system presented in Paper I, Paper II evaluated Research Question 2, *Can differences in species behaviour be utilised to reduce the bycatch of flatfish species in the Baltic Sea otter-trawl fisheries while maintaining capture efficiency of cod?* By testing the release efficiency of a flatfish excluder mounted in the bottom panel of the trawl, Paper II demonstrated that (a) the different vertical swimming preferences of flatfish and cod at the extension piece of the trawl, and (b) the different behavioural reactions, in relation to the presence of a selection device in their path towards the codend, can be exploited to reduce flatfish bycatch as much as the bycatch reduction obtained with the grid system evaluated in Paper I. Overall, this thesis has demonstrated that exploiting differences in flatfish and cod morphology or behaviour can effectively reduce the bycatch of flatfish species. These results provided Baltic fishers with timely information on two ways of reducing the bycatch of flatfish species without significantly compromising the catches of marketable cod.

This thesis has identified limitations in the current methodological toolbox available for quantifying species behaviour in relation to selection devices. By developing a quantitative method based on video observations, Paper II also addressed the third research question in this thesis, *How can the behavioural information of fish species from underwater video recordings be quantified to study, develop, and optimise the performance of selection devices?* The proposed method estimates probabilities that a given behavioural event will happen and establishes behavioural tree diagrams representing and quantifying behavioural patterns in relation to the selection device under assessment. Further, the method incorporates uncertainties to the observed behavioural paths by adapting and implementing the double bootstrap method traditionally applied in the analysis of catch data. The method presented in Paper II has been adopted rapidly and adjusted to other research (Chladek et al., 2021a, 2021b), highlighting the need for broadening the current catalogue of quantitative methods to assess fish behaviour in relation to selection devices.

Following the positive trend estimated for cod stocks in the early 2010s (Eero et al., 2012), a rapid deterioration of several biological cod indicators was detected, e.g., very low abundance of large cod in commercial catches and scientific surveys since 2013–2014. Such an alarming situation of the targeted species has downgraded the priority of concerns about bycatch of flatfish species in the fishery, prompting discussions among fishery scientists about the suitability of the traditional harvesting patterns for Baltic cod based on targeting large fish, and the feasibility of alternative harvesting patterns aligned to the balanced harvesting paradigm. Aiming to identify, adapt, and evaluate trawl modifications that can generate alternative harvesting patterns for Baltic cod, Paper III addresses the research question *Can a combination of grid and codend technologies generate harvesting patterns for Baltic cod that are alternatives to those traditionally delivered by trawl gears?* In so doing, it demonstrates experimentally that bell-shaped retention curves can be achieved in trawl fisheries by combining already available and simple selectivity technologies. Thus, the experimental demonstration in Paper III removes assumed technical restrictions that often limit discussions between fishery modellers, fishing managers, and other stakeholders regarding what other feasible harvesting pattern could be implemented to better manage exploited stocks in distress. Therefore, Paper III fulfils the objective of *identifying, adapting, and evaluating trawl modifications that can generate alternative harvesting patterns for Baltic cod.*

In recent years, the Eastern Baltic cod stock had deteriorated to such a level that fisheries directed at this stock had to be banned in 2020 (ICES, 2021a). Although cod-directed fisheries are still allowed in the Western Baltic, current assessments of the Western stock suggest that it is following a declining path similar to the Eastern stock (ICES, 2019a). The magnitude of the changes in the cod stocks in a relatively short period (Eero et al., 2020) has reversed the priority associated with bycatch challenges in the Baltic demersal trawl fisheries. In the early 2010s, the most concerning issue was the bycatch of flatfish in cod-directed fisheries. Ten years later, however, cod has become a choke species for the flatfish-directed trawl fishery and other fisheries (ICES, 2019b). With the aim of identifying, adjusting, and evaluating trawl modifications that can reduce the bycatch of Baltic cod in flatfish-directed fisheries, Paper IV addresses the research question, *Can differences in species behaviour be utilised to reduce the bycatch of cod in the Baltic Sea otter-trawl fisheries, while maintaining capture efficiency of flatfish species?* From the experimental results obtained in Paper IV, it can be concluded that the bycatch of cod in the flatfish-directed fisheries of the Baltic Sea can be largely reduced by exploiting species-specific behaviours in the trawl. The roofless device developed and tested in Paper IV has been proposed to EU member states involved in flatfish-directed trawl fisheries in the Baltic Sea as a technical solution to address the urgent demand by the EU Commission to find strategies to avoid cod bycatch (ICES, 2019b). During the writing of this thesis, the member states agreed to develop a joint recommendation to legally implement the roofless device in the Baltic Sea.

Overall, it can be concluded that the results obtained in Papers I, II and IV fulfil the objective of *identifying, adapting, and evaluating trawl modifications that can reduce bycatch of unwanted species in Baltic Sea fisheries*

Paper V addresses the research question *Can sieve panels be efficient at separating Nephrops from fish species?* by evaluating experimentally whether SMPs could be applied efficiently as sieve panels to separate the targeted *Nephrops* from fish species. Experimental testing of four sieve panels varying in mesh sizes revealed that most fish species and sizes were efficiently guided towards the upper codend. However, the sieving efficiency for the largest, most valuable *Nephrops* remained too low, and a considerable number of large *Nephrops* were found in the upper codend. Therefore, the sieve-panel concept tested in Paper V should be improved before being considered a functional option for the commercial fishing fleet. Norwegian deep-water shrimp fisheries compared the performance of the Nordmøre grid with a sieve panel made of square-mesh netting (144 mm mesh size) and an inclination of ~9° (Larsen et al., 2018b). The comparative assessment in Larsen et al. (2018b) revealed that the sieve panel was more effective at avoiding the bycatch of small roundfish and flatfish of all sizes than the Nordmøre grid. However, as with the results in Paper V, the panel showed relatively low sieving efficiency on marketable shrimp, (37–56% catch losses). The poor results in Paper V and in Larsen et al. (2018b) regarding sieving efficiency for the targeted species can be caused by a limited understanding of how crustaceans interact with the sieve panel. In the development of the sieve-panel concept tested in Paper V, it was assumed that *Nephrops* would travel towards the codends by rolling over the panel and hit the meshes in different body positions until the individuals are sieved towards the lower codend. However, the few video recordings obtained during the sea trials showed a much more active and controlled behaviour of *Nephrops* than was initially expected. Therefore, it can be concluded that the limited success obtained with the sieve-panel concept tested in Paper V was partly the result of unexpected behaviour of the target species when interacting with the panel. This conclusion highlights the importance of having quantitative information on animal behaviour in the process of developing new selection device concepts.

To answer the research question *How can optimal harvesting patterns for brown shrimp be identified considering the combined effect of altering the codend mesh size and mesh orientation?*, Paper VI provides a predictive framework that uses a large size-selection dataset from 33 different codend designs varying in mesh size and mesh orientation, tested during four experimental fishing cruises. Contrary to traditional research procedures in which a small set of codends with specific characteristics are tested at a time, the research summarised in Paper VI adopted an ambitious alternative strategy that aimed at filling the knowledge gap regarding codend selectivity for brown shrimp within a short yet intensive experimental period. Consequently, Paper V has fulfilled the objective of *identifying, adapting, and evaluating trawl modifications that can generate alternative harvesting patterns for brown shrimp in the North Sea beam-trawl fisheries.*

10.1 Final remarks

Prior to the writing of this thesis, selectivity research on Baltic demersal trawl fisheries focused on adjusting the size selection of the codend to reduce the bycatch of undersized cod (Madsen, 2007), and more recently, to improve the size selection of both flatfish species taken as bycatch and cod (Madsen et al., 2021; Wienbeck et al., 2014). Influenced by the introduction of the European LO (EU 1380/2013), the focus of this thesis has evolved in the direction of identifying, adapting, and testing technologies that might improve species selectivity in Baltic Sea trawl fisheries. In particular, the work in this thesis demonstrates that selection devices mounted ahead of the codend and designed to exploit differences in species morphology or differences in species behaviour can effectively reduce the bycatch of flatfish species in cod-directed fisheries (Papers I and II) or the bycatch of cod in flatfish-directed fisheries (Paper IV). Considering the long tradition of codend-selectivity research done from the perspective of a single species, applying selection devices to supplement the selectivity of the codend from a multispecies perspective is a novel approach in the region. This thesis also demonstrates the potential of combining selection devices to achieve completely different harvesting patterns for targeted species (Paper III). This demonstration is relevant and should be considered in discussions about alternative management strategies aimed at preventing the collapse of exploited stocks affected by irreversible changes in marine ecosystems, driven by ongoing climate change or any other human-induced pressure.

Contrary to the case of Baltic Sea demersal trawl fisheries, the traditional focus in the North Sea beam-trawl fishery targeting brown shrimp has been on reducing the bycatch of fish species (Graham, 2003; Polet, 2002; Revill and Holst, 2004a). In contrast, the observed high discard rates of undersized brown shrimp, a consequence of the poor size selectivity of commercial codends (Polet, 2000), was historically downgraded to an issue of low priority. This thesis has filled the knowledge gap about codend selectivity in the brown shrimp fishery by developing a framework for predicting codend size selectivity for different mesh sizes and mesh types (Paper VI). The predictive framework has been applied successfully to improve decision-making about fishery harvesting patterns (Günther et al., 2021).

From a methodological perspective, this thesis applied a guide range of procedures and methods for the development and testing of the selectivity technologies presented. The proposed selectivity concepts have been conceived in collaborative work involving the industry and fishing technologists (Papers I and VI), fishery modellers and fishing technologist (Paper III), or exclusively by fishing technologist (Papers II, IV, and V). Sea trials were conducted in commercial vessels (Paper I) or research vessels (Papers II–VI). For the collection of selectivity data, direct methods—dual cover method (Paper III) and blind codends method (Papers V)— indirect methods—the paired-gear method (Papers II and VI) — or catch comparison methods (Paper I, IV) were applied. The analysis of selectivity data applied structural modelling (Papers I, III, VI) and/or empirical modelling (Papers I, II, IV, V). The modelling analysis was supplemented with selectivity indicators in Papers I, II, IV, and VI. By developing and applying the quantitative method to describe fish behaviour in relation to selection devices based on video recordings (Paper II), this thesis has increased the toolbox of methodologies available for trawl selectivity and passive-gear selectivity (Chladek et al., 2021a, 2021b) research. Other methodological contributions included in this thesis are i) the comparison of performance of empirical and structural models in Paper I, which highlighted the benefits of applying structural modelling (when possible) over more flexible empirical methods, and ii) the introduction of dual species and fishing effort selectivity indicators in Paper IV, which will be used as contributions to the topic group on selectivity indicators established from 2022 onwards at the ICES-FAO Working Group of Fishing Technology and Fish Behaviour.

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Papers I-VI

Paper I

"Reducing flatfish bycatch in roundfish fisheries"

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Reducing flatfish bycatch in roundfish fisheries

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ABSTRACT

Flatfish bycatch is a concern in many demersal trawl fisheries around the world, especially for fisheries operating under discard-ban regulations. We introduce and assess the performance of FRESWIND (Flatfish Rigid EScape WINDows), a concept for a selection device that reduces flatfish bycatch in roundfish-directed fisheries. The new concept was tested for the first time in the Baltic cod-directed fishery, using a commercial twin trawler. The vessel was rigged with two trawls; one standard trawl gear and one incorporating the experimental FRESWIND. Comparison of the catches from both trawls exhibited up to ~68% reduction in flatfish bycatch for the trawl with FRESWIND mounted. In addition, the catch of undersized cod was reduced by ~30%, whereas losses of marketable cod were relatively minor (~7%). Further simulations predicted that, in the commercial fishery, a reduction of more than 50% in flatfish bycatch could be achieved if FRESWIND were adopted. Given these promising results, FRESWIND may also provide a method that significantly reduces flatfish bycatch in other fisheries.

1. Introduction

Discarding is an ethically and ecologically undesirable fishing practice of global concern. It wastes natural resources and severely challenges the sustainability of fisheries (Hall et al., 2000). It decreases the efficiency of fishing operations and changes the trophic flows in foodwebs and entire ecosystems (Catchpole et al., 2005; Greenstreet et al., 1999).

Societal interest groups have discussed the consequences of discarding and potential solutions intensively for decades (Catchpole et al., 2005; Alverson and Hughes, 1996). To date, different strategies have been implemented around the world to reduce or avoid unwanted catches (Condie et al., 2014). For example, one of the main aims of the upcoming European Commission Common Fisheries Policy reform (EU regulation 1380/2013) is to phase out discards by obliging fishermen to keep all catches of species with quota on board, land them, and count them against their quotas. The new policy is controversial because it puts the economic viability of the industry at risk, especially fleets engaged in mixed fisheries, where the bycatch of species with low quota can alter or even stop the normal fishing activities focused on species with less constraining quotas (STECF, 2014). It is a fishing industry priority to reduce and/or avoid the catch of such choke species (those species that can prematurely close a mixed fishery due to the exhaustion of their limited quotas).

Flatfish bycatch contributes substantially to the volume of discards in many demersal trawl fisheries around the world (Storr-Paulsen et al., 2012; Anon, 2011; Branch, 2006; Borges et al., 2005). This is often the result of a mismatch between the selectivity properties of the gear and the specific characteristics of flatfish morphology. For example, flatfish bycatch often occurs in fisheries targeting roundfish species (Wienbeck et al., 2014; Milliken and DeAlteris, 2004). Attempts to improve the selectivity in these fisheries often involve codend modifications in order to improve the size selectivity of the target species. These modifications include strategies like increasing codend mesh size or using meshes with square geometry (Guijarro and Massutí, 2006; Ordines et al., 2006; Fonteyne and M'Rabet 1992). Square mesh geometry facilitates escapement for roundfish species, while the effect on flatfish selectivity is unclear or negative (Guijarro and Massutí, 2006; Fonteyne and M'Rabet, 1992; Robertson and Stewart, 1988). These obser-

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vations indicate that alternative technological methods should be applied to reduce flatfish bycatch in roundfish fisheries.

This paper introduces a new concept for a selection device specifically developed for flatfish species. The FRESWIND (Flatfish Rigid EScape WINDows) uses the special morphology of flatfish to optimize selectivity (i.e., to largely avoid flatfish catches) without compromising the catchability of marketable sizes of the roundfish target species. FRESWIND is designed to be mounted ahead of the codend, to create a sequential selection process in which flatfish selection is achieved mainly by FRESWIND and roundfish size selection is achieved in the codend.

FRESWIND was tested for the first time in the western-Baltic-cod-directed trawl fishery, with catches composed primarily of the target species (*Gadus morhua*), with a mix of flatfish species taken as bycatch. To date, most research efforts in Baltic Sea trawl fisheries have concentrated on improving the size selectivity of cod through codend modifications (Madsen, 2007). As a result, two cod-selective codends are mandatory in the area (T90 and BACOMA; EU 686/2010). Although these codends present good size-selective properties for cod, flatfish selectivity is an increasing concern in the fishery, because species with limited quotas, such as plaice (*Pleuronectes platessa*), can disrupt normal fishing strategies due to the landing obligation rules stated in the new European policy (STECF, 2014; Wienbeck et al., 2014).

This study assesses the performance of a FRESWIND design, developed specifically for the Baltic cod-directed fishery, on the targeted cod and two common flatfish species in the area, plaice and flounder (*Platichthys flesus*). Plaice is the most valuable flatfish bycatch, regulated by total allowable catches (TACs) and a minimum landing size (MLS) of 25 cm. Estimates from the German catch sampling program in commercial fisheries yielded discard ratios ranging from10% to 100% between trips, with mean values from 10% to 40% in the cod directed-trawl fishery. Flounder is the most widely distributed flatfish species in the Baltic Sea, regulated by a MLS of 23 cm (ICES Subdivisions 22–25). It is mainly a bycatch species (ICES, 2012), and the German catch sampling program estimates discard ratios with high variation between trips (0–100%) and mean discard values between 5 and 40%.

This paper will investigate the performance of FRESWIND in the Baltic cod-directed trawl fishery. Further, we predict the consequences of the commercial fishery adopting FRESWIND.

2. Material and methods

2.1. The FRESWIND concept

The FRESWIND concept relies on the differences in flatfish and roundfish species morphology to optimize species selectivity. It was proposed originally by Swedish fisherman Vilnis Ulups, and further developed into the device presented here. The experimental gear design consists of rigid windows mounted on each side of a four-panel extension piece connected forward to the codend. The windows are constructed as grid-like sections with horizontal bars of steel to ensure well defined escape outlets, allowing the body shape of flatfish to pass in natural swimming orientation (Fig. 1). The windows were made of bars 10 mm in diameter with 38 mm barspacing. For this barspacing, the FISHSELECT method (Herrmann et al., 2009) predicted escapement possibilities for a wide range of flatfish sizes, while enabling only escapements for undersized cods (below Minimum Landing Size, MLS = 38 cm). The extension piece where the FRESWIND was mounted was cut in a way that induced ∼45° angle of attack of the windows in relation to the towing direction. By using this specific design, it is intended to produce a tapering zone, which should enhance the probability for a fish to come into contact (attempt made by the fish to escape (Sistiaga et al., 2010)) with the side windows when swimming or drifting towards the codend. The extension piece was made with four net panels of 4 mm double twine and diamond mesh netting. The mesh size was 120 mm, and the number of meshes around was 4 × 25. A V-shape guiding device 860 mm high and 200 mm wing length, was mounted in the centerline of the extension piece ahead of the windows, with the aim of directing fish from the central path of the extension towards the windows. Wires were inserted into the vertical edges of the guiding device to increase its stiffness.

The codend used after the extension piece was the mandatory BACOMA codend (EU 686/2010) provided by the fishers. With this combination of FRESWIND and the codend, a stepwise selection process along the gear is intended, in which flatfish selection is achieved mainly by FRESWIND and cod size selectivity is achieved by the codend.

2.2. Sea trials

Sea trials were carried out on the German commercial twin trawler FV “Crampas” (18 m, 219 kW) during daytime. The cruise was conducted in the western Baltic, west of the island of Bornholm (ICES Subdivision 24), 15–25 March 2013, during the major cod fishing period. The skipper chose the fishing ground and fishing tracks based on his normal fishing strategies, to ensure the fish populations available for the gears were representative of the commercial trips. Two trawls model *ballontrawl 260*, constructed with 120 mm diamond mesh size netting, and with 260–144 meshes in circumference (from the square to the last section of the belly) were provided by the vessel. The groundrope of the trawls were equipped with rubber discs, and the doors used were Thyborön Type 11, weighting 451 kg. The trawls were equipped with the mandatory BACOMA codend and extension pieces. The extension pieces were identical, except that one included the FRESWIND device. The combination of the FRESWIND device and the BACOMA codend is denoted hereafter as the *test* selection system; the setup with the simpler extension piece (without FRESWIND) and the BACOMA codend is denoted as the *reference* selection system. The trials were conducted as a catch comparison experiment (Krag et al., 2014). The test and reference gear were twin trawled for each haul, and the position of each gear were swapped after completing half of the planned experimental hauls, to remove effects from side. Catches from each experimental haul were weighted by species, and the total length of all fish was measured with electronic measuring boards (0.5 cm below).

2.3. Data analysis

2.3.1. Estimation of catch comparison (CC) curves

The number of individuals of each length class caught in each of the trawls was used to evaluate the length-dependent relative catching efficiency of the two trawls for each species separately. For each of the species considered, the proportion of catches in the test system to the total in a haul *i* was given as:

$$CC_{il} = \frac{nt_{il}}{nt_{il} + nr_{il}} \tag{1}$$

where, nt_{il} is the number of fish of length class l caught by the test system in haul i, and nr_{il} represents the same number for the reference system. The experimental CC_{il} data are commonly used in catch-comparison analyses to estimate the gain/loss of catchability of the test gear, assuming that the observed trend is caused by the introduction of a selection device in the reference gear (Krag et al., 2014). In catch comparison studies, it is of main interest to assess any potential length dependency on the observed catch proportions. This assessment is carried out by estimating the most likely functional form of the catch comparison curve $CC(l)$.

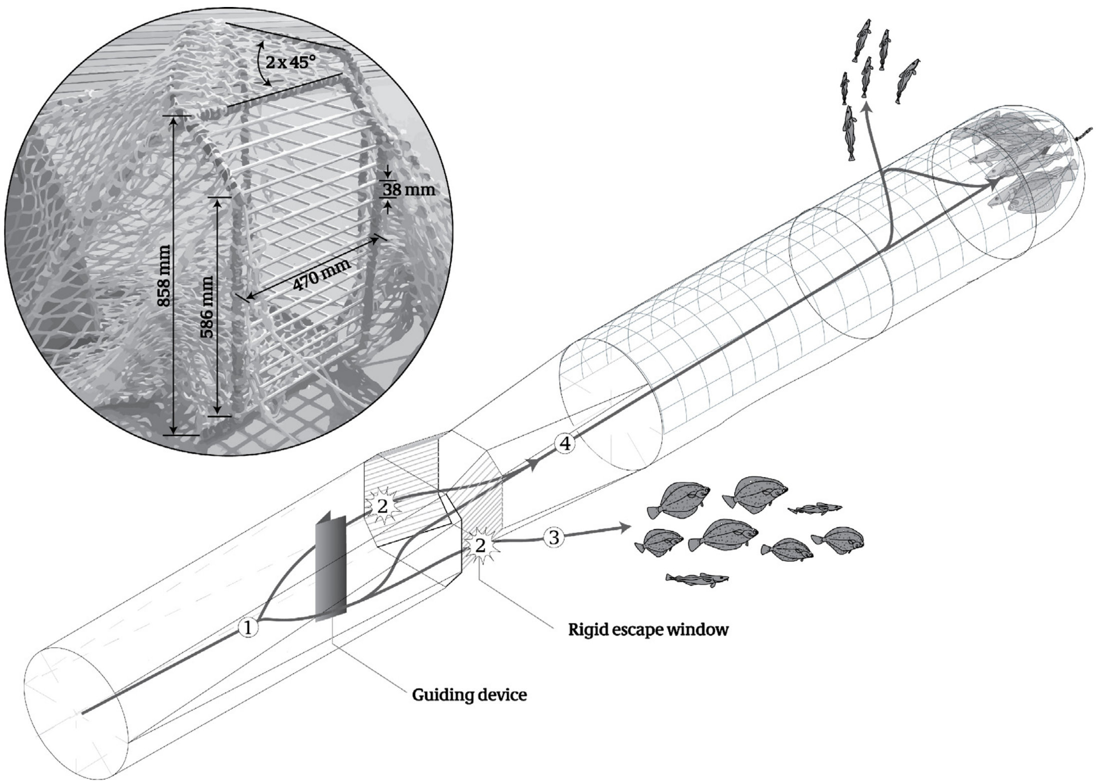

Fig. 1. Sequential selection system with FRESWIND mounted in front of the BACOMA codend. The numbers represent the different events occurring when fish swim into the FRESWIND enclosure. Fish entering the extension piece are guided sideways by the V-shaped canvas device (1). Fish escapements (3) after contacting the windows (2) depend on FRESWIND size selection, which is defined by the bar spacing. Fish not contacting the windows, or not able to escape through the rigid windows because of inefficient contact or size selection, retake the path towards the codend (4), where a successive, cod-directed selection process takes place. Steps 2 and 3 are parametrized in the alternative structural equation model (see Eqs. (3) and (4)). Topleft: FRESWIND picture showing design details of the windows.

Assuming that the performance of the tested device over the hauls conducted during the experiment, is a representative sample of how it would perform under commercial fishery, estimation of the averaged *CC(l)* curve would provide information on the consequences for the catching efficiency by adopting the device in the fishery (Millar, 1993; Sistiaga et al., 2010). The averaged catch comparison of hauls is estimated by pooling the data from the different hauls. A parametric model for *CC(l)* is defined by *CC(l,v),* where v is a vector consisting of the parameters of the model. The catch-comparison analysis is therefore reduced to a regression problem to estimate the values of the parameters v, which make the observed experimental data averaged over hauls most likely, assuming that the model is able to describe the data sufficiently well. Thus, the maximum likelihood function for binomial data (Eq. (2)) is minimized with respect to v, which is equivalent to maximizing the probability for the observed data.

$$-\Sigma\Sigma\{nt_{il} \times \ln(CC(l,v)) + nr_{il} \times \ln(1.0 - CC(l,v))\} \quad (2)$$

where the sums are for hauls i and length classes l. Evaluation of a model's ability to describe the data sufficiently well using Eq. (2) was based on the calculation of the corresponding p-value together with the visual inspection of residuals distribution. See Wileman et al. (1996) for details on how to apply these fit statistics.

It is necessary to identify the appropriate models for *CC(l,v)* to be able to apply Eq. (2) to the evaluation of the catch-comparison rate for the gear with FRESWIND compared with the reference gear. The two models considered are described in the following subsections.

2.3.1.1. Polynomial model. In catch comparison analysis, the *CC(l,v)* is often modelled using the following equation:

$$CC(l,v) = \frac{\exp(f(l, q_0, \ldots, q_j))}{1 + \exp(f(l, q_0, \ldots, q_j))} \quad (3)$$

where, *CC*(l,v)) expresses the probability of finding a fish length class l in the codend of the test gear, given that it was found in one of the two codends. A value of $CC = 0.5$ would mean a balanced probability of finding the fish in one of the two codends, implying no FRESWIND effect on catch efficiency. The term f in Eq. (3) refers to a polynomial of order j with coefficients q_0–q_j, such that $v = (q_0,\ldots,q_j)$. We considered f up to an order of 4 with parameters q_0, q_1, q_2, q_3, and q_4. Leaving out one or more of the parameters $q_0q_0,\ldots,q_jq_4$ led to 31 additional models that were also considered potential candidates for the catch-comparison function *CC(l,v)*. Selection of the best model for *CC(l,v)* among the 32 competing models was based on a comparison of their respective Akaike information criterion (AIC) values (Akaike, 1974). The model with the lowest AIC value was selected as the best model used to describe the experimental catch-proportion data.

2.3.1.2. Structural model. The structural model had the following form:

$$CC(l, \mathrm{C}, \mathrm{L50}, \mathrm{SR}, \mathrm{SP}) = \frac{\mathrm{SP} \times C\mathrm{Logit}(\mathrm{C}, \mathrm{L50}, \mathrm{SR})}{\mathrm{SP} \times C\mathrm{Logit}(\mathrm{C}, \mathrm{L50}, \mathrm{SR}) + 1 - \mathrm{SP}} \quad (4)$$

With:

$$C\mathrm{Logit}(l, C, \mathrm{L50}, \mathrm{SR}) = 1 - C \times \left(1 - \frac{\exp\left(\ln(9) \times \frac{(\mathrm{l}-\mathrm{L50})}{\mathrm{SR}}\right)}{1 + \exp\left(\ln(9) \times \frac{(\mathrm{l}-\mathrm{L50})}{\mathrm{SR}}\right)}\right) \quad (5)$$

Table 1
Length class range and catch abundance by minimum landing size (MLS; N_{-}= numbers below MLS; N_{+}= numbers equal to or above MLS) and haul observed in test and reference gears for the three species under study (length classes pooled to the centimeter below).

		Cod			Plaice			Flounder		
Haul no.	Gear	Length range (cm)	N_{-}	N_{+}	Length range (cm)	N_{-}	N_{+}	Length range (cm)	N_{-}	N_{+}
1	Ref	40–40	0	1	24–37	1	6	12–42	230	135
	Test	42–57	0	2	36–36	0	1	15–27	69	34
2	Ref	40–50	0	4	24–25	1	1	15–28	203	96
	Test	–	0	0	33–33	0	1	17–26	55	29
3	Ref	28–65	27	266	20–42	79	301	17–42	57	742
	Test	28–68	8	210	20–42	24	109	18–40	15	275
4	Ref	26–62	20	63	21–45	18	251	20–37	14	97
	Test	27–52	8	37	22–38	7	50	21–37	3	67
5	Ref	27–56	41	177	22–43	53	204	20–41	33	236
	Test	26–57	50	176	23–37	15	89	19–40	17	96
6	Ref	27–59	8	66	22–42	30	115	18–37	25	277
	Test	27–62	29	77	22–43	14	54	20–37	14	103
7	Ref	25–62	65	238	22–38	27	102	18–44	37	186
	Test	25–64	77	222	22–38	6	50	21–39	4	72
8	Ref	24–57	67	83	20–37	53	234	18–40	91	419
	Test	24–58	36	59	22–46	15	170	19–35	39	196
9	Ref	21–70	22	51	22–39	39	276	18–38	25	149
	Test	29–56	8	68	21–46	11	103	20–37	5	74
10	Ref	26–66	18	69	21–46	15	176	21–42	8	112
	Test	31–56	5	42	22–40	12	98	22–40	1	63
11	Ref	26–100	78	309	22–38	30	206	18–38	23	134
	Test	27–74	28	361	22–39	15	111	20–47	10	64
12	Ref	25–56	31	120	22–37	14	122	19–42	14	94
	Test	35–70	6	93	22–40	5	73	20–32	5	23
Pooled	Ref	21–100	377	1447	20–46.5	360	1994	12.5–44.5	760	2677
	Test	24–74	255	1347	20–42	124	909	15–47.5	237	1073

where *SP* is the assumed length independent split parameter, which quantifies the probability of a fish entering the extension piece of the test gear, given that it enters one of the two extension pieces. Because the two trawls are identical in design and rigging, except in the section just ahead of the codend, an average *SP* of ≈0.5 is expected, implying equal probability for a fish to enter one of the extension pieces. Therefore, for the analysis, *SP* is assumed to be a constant with a value of 0.5. The justification for considering Eq. (4) with Eq. (5) as a candidate to model the catch comparison performed in this study is that the *C*Logit given by Eq. (5) could account for the reduced probability for fish entering the codend with FRESWIND installed in the extension piece. The parameter *C* can be interpreted as the fraction of fish entering the FRESWIND zone that actually make contact with the FRESWIND windows on their way toward the codend. *L50* (fish length with 50% retention probability) and SR (Selection Range: range between lengths with expected 25 and 75% retention probability) can be interpreted as the selection parameters for fish making contact with the FRESWIND windows (see Herrmann et al., 2013 for further details on model (5)). To validate the use of this modelling alternative on the current experimental data, it is necessary to compare its performance with that of the polynomial-based model (3). The diagnosis of the usability of model (5) is done by (i) plotting together the curves estimated by both methods to inspect if model (4)–(5) provides a description of the experimental catch-proportion data similar to the polynomial model (3), and (ii) checking and comparing the pattern of Pearson residuals from both models (Wileman et al., 1996). In case it is concluded that Eqs. (4) with (5) can be applied equally as well to the experimental data as Eq. (3), the structural model will be used for further analysis. This type of model allows better extrapolations outside the range of available length classes from the experimental dataset than the empirically based type given by Eq. (3), because it is bounded in the nature of the Eqs. (4) and (5) (Fryer and Shepherd, 1996). The catch comparison analyses described above were performed using the statistical analysis software SELNET (Herrmann et al., 2012).

2.3.2. Estimation of catch ratio curves

Catch comparison curves cannot directly express the rate of fish of length *l* that would be retained in the codend when using the FRESWIND, relative to the standard gear. Experimentally, such a question can be answered by the catch ratio (*CR*):

$$CR_l = \frac{nt_l}{nr_l} \tag{6}$$

where, data were pooled for hauls, therefore skipping the subscript for individuals. Combining Eq. (1) for the experimental catch-comparison rate with Eq. (6) leads to:

$$CR_l = \frac{CC_l}{1 - CC_l} \tag{7}$$

Thus, if the catch comparison curve *CC(l,v)* has been estimated at a specific length, the catch ratio derived in Eq. (7) can also be estimated. If a functional description of the catch-comparison rate is established, based on the procedure described in the preceding sections, the functional form for the catch ratio *CR(l,v)* can be estimated by:

$$CR(l, v) = \frac{CC(l, v)}{1 - CC(l, v)} \tag{8}$$

Eq. (8) is used to assess the length-specific benefit of using the test selective system (FRESWIND + BACOMA) compared with the reference selective system (BACOMA codend alone). For the marketable sizes of target species (sizes above MLS), the value of *CR(l,v)* should preferably be close to 1.0. In contrast, *CR(l,v)* values closer to 0 are desirable for length classes below MLS and for non-target species. For example, a value of *CR(l,v)* = 0.4 implies that the test gear presents a catch efficiency of 40% for length class *l*, compared with the reference gear, which represents a reduction in the catch by 60%.

2.3.3. Estimation of usability indicators

To evaluate the usability of FRESWIND in conjunction with the size-selective codend for the specific fishery, three different indicators were estimated each for cod, plaice, and flounder separately.

Contrary to the catch ratio curve, the indicators defined in this section consider the size structure of the population caught. The following indicators are used:

$$nP_{-} = 100 \times \frac{\sum_i \left\{ \sum_{l<MLS} nt_{il} \right\}}{\sum_i \left\{ \sum_{l<MLS} nr_{il} \right\}}$$
$$nP_{+} = 100 \times \frac{\sum_i \left\{ \sum_{l\geq MLS} nt_{il} \right\}}{\sum_i \left\{ \sum_{l\geq MLS} nr_{il} \right\}} \quad (9)$$
$$nP = 100 \times \frac{\sum_i \left\{ \sum_{l} nt_{il} \right\}}{\sum_i \left\{ \sum_{l} nr_{il} \right\}}$$

where, the sum of i is for hauls and l is for length classes. nP_{-} and nP_{+} estimate the ratio of catches below and above MLS, for the test selection system to the reference system, while considering the size structure of the population caught in the reference gear. nP_{-} and nP_{+} are specifically useful for species under discard practices highly conditioned to MLS, allowing a combined assessment on how much and in what sense the catches from the reference system is altered by the effect of FRESWIND. For a good performance for species on which MLS has a strong influence on discard patterns, nP_{-} should be low whereas nP_{+} values should be kept high (close to 100), i.e., that the use of FRESWIND does not lead to considerable loss of individuals greater than MLS, compared with the codend alone. The indicator denoted as nP provides the ratio of catches in the test gear to the catches in the reference gear greater than the available length range; nP represents an indicator of the global change in catch profile resulting from the FRESWIND effect. This indicator is particularly noteworthy for bycatch species, such as flounder in the Baltic Sea, where MLS is not the main factor affecting discard behavior.

2.3.4. Assessment of confidence intervals

The confidence intervals (CI) for the averaged catch comparison curve $CC(l,v)$ based on Eq. (2), were estimated using a double bootstrap approach, accounting both for uncertainty at haul level and between haul variation. 2000 bootstrap iterations were applied to estimate the Efron percentile 95% confidence limits (Efron, 1982) for all relevant length classes. This approach, which avoided underestimating confidence limits when averaging over hauls, is identical with the one described in Sistiaga et al. (2010) and Herrmann et al. (2012). Traditionally, the CI for a curve and for the parameter values describing this curve are estimated without accounting for potentially increased uncertainty resulting from uncertainty in the selection of the model used to describe the curve (Katsanevakis, 2006). In this study, we accounted for this additional uncertainty of the catch comparison curve, when this was based on the polynomial model (3) (see Section 2.3.1.1) by incorporating an automatic model selection based on which of the 32 models produced the lowest AIC for each of the 2000 bootstrap iterations. It was not necessary to account for such increased uncertainty in the structural-based model (4) and (5) because this has a fixed functional form (see Section 2.3.1.2).

The uncertainty of $CR(l,v)$, nP_{-}, nP_{+}, and nP was also assessed by including these parameters estimations into the same bootstrap scheme used for $CC(l,v)$.

2.4. Predicting the effect of adopting FRESWIND in the commercial fishery

The effect of adopting the FRESWIND device in the commercial fishery can be predicted based on applying the estimated catch ratio curves to catch data from the target fishery (fishing with the BACOMA codend without FRESWIND). The catch data was collected by German observers sampling the target fishery in 2012, within the scope of the EU data collection framework. To ensure that the datasets remained representative of the experimental conditions, only trawl datasets from ICES Subdivision 24, with cod as target species and BACOMA codends, were used. The use of species length-class structure from the fishery catch data, and the species $CR(l,v)$ estimated in (8) (Section 2.3.2), allow prediction of the effect on the fishery catch profile if the FRESWIND were installed ahead of the codend. The usability indicators described in Section 2.3.3 were also estimated for the commercial catch data. This simulation used the parametric simulation facilities in the software tool SELNET.

3. Results

3.1. Description of sea trial conditions and catches

In all, 12 hauls were carried out during the commercial cruise in the Arkona basin at depths ranging from ~15 to ~48 m. Haul duration was between 2 and 3 h, and the towing speed ranged from 2.8 to 3.4 knots. The FRESWIND design did not cause any extra handling effort on the test gear, and the crew reported no problems when storing the test gear on the net drum. The catches obtained during the cruise were considered by the crew as representative of commercial catch sizes. Cod, flounder, and plaice accounted for 98.7% of the total catch in weight (test + reference gears). Hereafter, the catches from these three species are denoted as major catch. Cod, flounder, and plaice contributed 61.2, 17.5, and 21.2%, respectively, to the major catch weight. In particular, the major catch observed in the test gear was 1740.2 kg, 30.8% lower than in the reference gear (2514.5 kg). The difference in catch weights was mainly the result of fewer plaice (57.8%) and flounder (56.4%) in the test codend; cod catch was only reduced 9.5%. The total number of cod caught in test gear was 1602 individuals, ~12.2% less than in the reference gear (1824 individuals; Table 1). Greater differences in catches were observed for the flatfish species. A total of 1033 plaice and 1310 flounder were caught in the test gear, ~56.1% (2354 individuals) and ~61.9% (3437 individuals) less than in the reference gear respectively (Table 1).

3.2. Experimental catch data

All hauls and observed length classes were used in the catch-comparison analysis (Sections 2.3.1.1 and 2.3.1.2). The Pearson residual distributions of the polynomial and structural models demonstrated that both models described the experimental catch-comparison rates equally well, without any systematic trends in the deviations for any of the three species. The mean curves estimated by the two models overlapped along the most abundant length classes, but differences arose for cod and flounder on the tails (Fig. 2), where shortest and longest lengths were not well represented because of their scarcity in catches (Table 1). The predictions for the polynomial-based model (3) for the longest cod and flounder lengths tended to $CC(l,v) = 0$, whereas for the same species and lengths, the structural model exhibited a non-decreasing tendency reaching equal catch probability ($CC(l,v) = 0.5$). The differences in model predictions were not significant, however, because their CIs overlapped. The CIs for the polynomial-based model were exceptionally wide in the tails, resulting in an overall hourglass shape, in contrast with the narrow band observed for the structural model. The narrower CIs for the structural model suggested a gain in inference power in the tails, resulting in greater length ranges where the differences in catch proportions were significant between the test and reference systems (Fig. 2).

For cod, the equal catch efficiency reference line (0.5) fell within the polynomial-based model CI, i.e., there was no significant difference in catchability between the reference and test gear, whereas

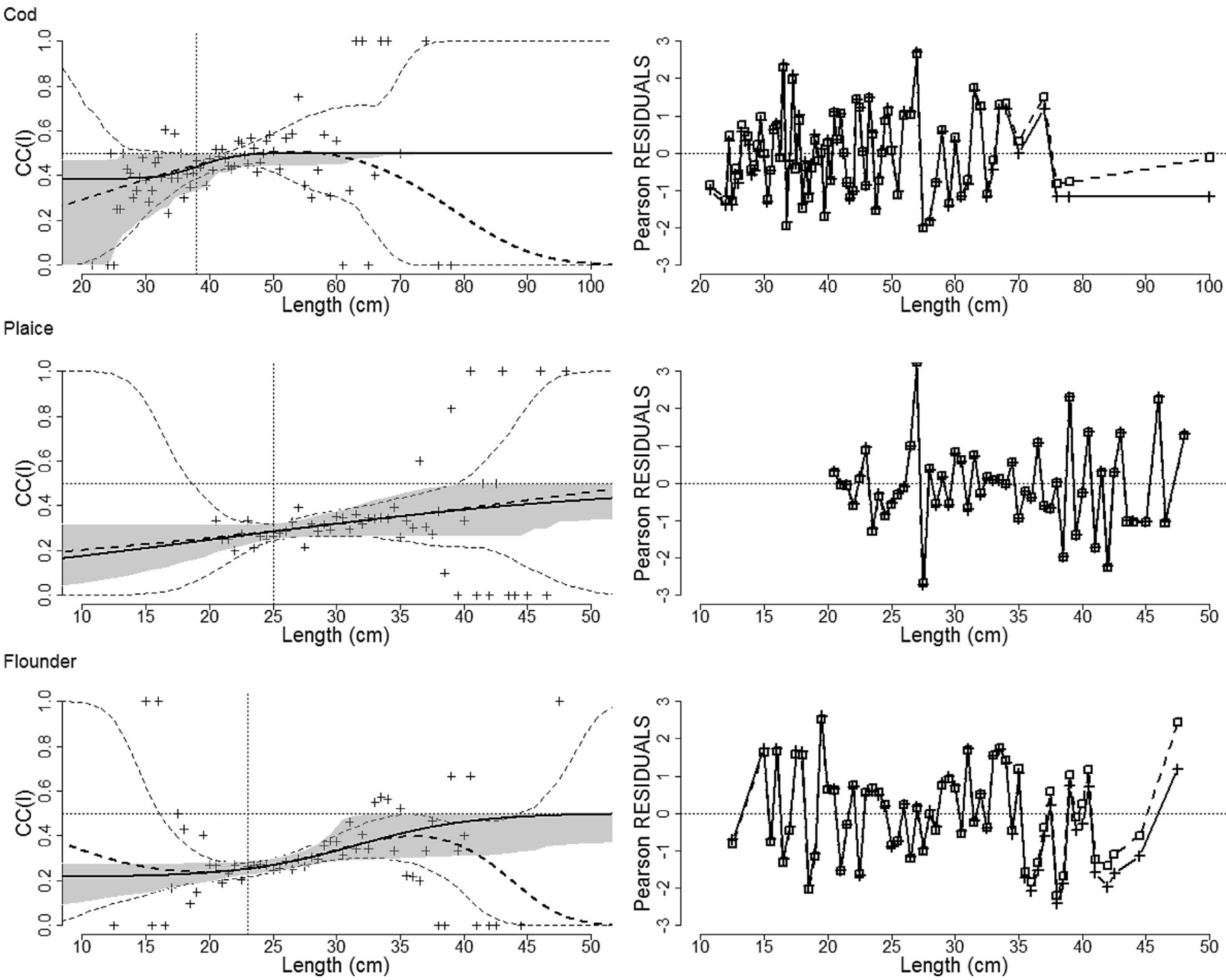

Fig. 2. Catch comparison curves with confidence intervals estimated for the polynomial model (dashed lines) and the structural model (solid line, shaded CI), horizontal dotted baselines at *CC*(l) = 0.5 represent equal catch efficiency, vertical dotted lines represent species MLS (left). Pearson residuals of the two models (right).

the structural modelling demonstrated a significant catch reduction in the test gear for length classes shorter than 27 cm (Fig. 2). For plaice, both models found a significant catch reduction for length classes shorter than ~39 cm, although the polynomial-based model estimated equal catchability for length shorter than ~19 cm, an unexpected result not supported by the structural model. Similar results were found for flounder: a significantly lower catch proportion was found by the polynomial-based model for the length range 16–35 cm, whereas the structural model curve extended the significant area to the length range shorter than ~33 cm.

For cod, the structural model estimated a contact probability of $C = 0.4$ (0.1–1.0). This value can be interpreted as ~40% of cod entering the test gear contacted the rigid windows, although it must be noted that the CI of this parameter covered nearly the full range of probabilities (Table 2). Cod *L50* was, with 38.9 cm (20.4–62.5), estimated to be 1 cm above the MLS, and *SR* was 6.7 (0.1–29.2). Higher contact probability was estimated for flatfish species. For plaice, a value of $C = 1.0$ (0.5–1.0) was achieved, and $C = 0.7$ (0.8–1.0) was estimated for flounder. The CIs from both estimates were narrower than for cod, but they overlapped each other. The estimated *L50* were also similar to both flatfish species (plaice *L50* = 32.1 (26.7–55.8); flounder *L50* = 33.6 (28.2–46.3)), but *SR* differed considerably (but not significantly), with *SR* of 36.8 (0.1–94.6) for plaice and *SR* = 9.9 (0.1–65.2) for flounder (Table 2). As an equal split at 0.5 was assumed (see Section 2.3.1.2), this parameter is presented with no uncertainty (Table 2).

Table 2
Parameter values and fit statistics for the structural model and the values for the usability indicators from the experimental fishing. 95% confidence intervals are in brackets.

Parameter	Cod	Plaice	Flounder
C	0.4 (0.1–1.0)	1.0 (0.5–1.0)	0.7 (0.6–1.0)
L50	38.9 (20.4–62.5)	32.1 (26.7–55.8)	33.6 (28.2–46.3)
SR	6.7 (0.1–29.2)	36.8 (0.1–94.6)	9.9 (0.1–65.2)
SP	0.5	0.5	0.5
p-value	0.1503	0.0827	0.0068
Deviance	86.6	63.3	84.3
d.o.f	74	49	55
nP_-	67.6 (36.9–104.7)	34.4 (25.9–46.9)	31.9 (24.4–39.6)
nP_+	93.3 (77.6–107.6)	45.6 (35.5–57.0)	39.8 (35.0–45.7)
nP	87.8 (71.8–101.1)	43.9 (36.0–53.0)	38.8 (33.7–44.1)

The value of the usability indicators (9) obtained from the experimental sea trials (Table 2) suggests that using FRESWIND reduced the catches of juvenile cod compared to the reference gear by 32.4% ($nP_- = 67.6\%$) on average, although the wide CI associated with the estimate (crossing the 100% boundary) indicated no statistical significance. On the other hand, a significant reduction of 65.6% and 68.1% was found for the number of plaice and flounder, respectively. The estimation of cod nP_+ indicated a small, non-significant catch reduction of 6.7% caused by FRESWIND, whereas the nP_+ values for plaice and flounder indicated significant catch reductions of 54.4% and 60.2%, respectively. Considering the species full length range,

Table 3
Estimated values for the usability indicators from adapting FRESWIND to the commercial fishery. 95% confidence limits based on the confidence limits for the catch ratio curves are in brackets.

Parameter	Cod	Plaice	Flounder
nP_-	70.5 (40.9–100.0)	36.1 (27.8–47.2)	31.8 (26.4–39.6)
nP_+	91.9 (70.6–100.0)	44.4 (35.1–57.5)	44.5 (34.9–59.4)
nP	90.5 (68.4–100.0)	42.3 (33.3–54.9)	41.8 (33.0–55.1)

the catch reductions caused by FRESWIND were 56.1 for plaice and 61.2% for flounder.

The assessment of the catch ratio curves (*CR(l,v)*) was based on the catch comparison curves from the structural model (Fig. 3). The estimated *CR(l,v)* for cod indicates that catch efficiency on lengths shorter than 35 cm was reduced by ~30–38% as a result of FRESWIND, whereas equal catch efficiency was reached for length classes longer than 52 cm. Considering the upper confidence limit of the estimate, the loss of catch efficiency for cod would only be significant for length classes shorter than 27 cm, with values not lower than ~10% from the reference gear efficiency. Plaice *CR(l,v)* exhibited a reduction in catch efficiency over the available length classes as a result of FRESWIND. The loss in catch efficiency was ~60% at 25 cm MLS, reaching values of ~75% for length classes of ~15 cm. The upper confidence limit demonstrated that the reduction could only be considered significant for length classes shorter than ~39 cm, and the loss of catch efficiency on MLS length class was at least 52%. The flounder *CR(l,v)* curve was steeper than the plaice *CR(l,v)* curve. The estimated loss in catch efficiency for the species at MLS was ~67%, reaching the same catch efficiency as the reference gear on length classes ~50 cm. The upper confidence limit demonstrated that the reduction can only be considered significant for length classes of flounder shorter than 33 cm, and the loss of catch efficiency on MLS length class was at least 60%.

3.3. Adopting FRESWIND in the commercial fishery

In all, 21 hauls sampled during 14 commercial fishing trips were selected from the German catch sampling program. The total catch abundances by length class for cod, plaice, and flounder were pooled over the selected hauls and used as input data for the assessment of adopting FRESWIND in the commercial fishery (Table 3). The expected flatfish catches considering FRESWIND adoption is substantially lower compared to the observed catch profile, while differences in cod catches are less evident (Fig. 4). The values of the usability indicators obtained from the commercial fishery data were similar to those estimated for the experimental fishing data. For cod, the mean value for nP_- was 70.5%, i.e., a 29.5% catch reduction for cod below MLS as a result of the FRESWIND, whereas marketable cod losses were estimated to be 8.1% ($nP_+ = 91.9$), and the CI reached the 100% boundary. Therefore, catch reductions were considered non-significant for cod. For plaice, the effect of introducing FRESWIND in the commercial fishery would imply a significant reduction in undersized plaice and flounder catches of ~63.9% and ~68.2%, respectively, whereas ~55% significant reduction was estimated for the catch fractions above MLS for both flatfish species (Table 3; Fig. 4). Considering the full length range for the species in the area, the estimated FRESWIND-induced catch reduction in the fishery would be 57.7% for plaice and 58.2% for flounder.

4. Discussion

This paper introduces a new concept for a species selection device—FRESWIND—designed to reduce flatfish bycatch in roundfish-directed fisheries. In general, species-selection devices intend to reduce unwanted catches by exploiting differences in behavior or morphology between the targeted species and the species taken as bycatch (Glass, 2000). The FRESWIND concept exploits the differences in body shape between roundfish and flatfish. The strategy is exemplified by the design of the rigid windows and the horizontal bars with spacing that matches the cross-sectional shape of flatfish. At the same time, the FRESWIND concept improves the probability that fish will interact with the escape windows. A simple guiding device made of canvas directs the natural swimming path sideways, and its effect is enhanced by the angle at which the windows are mounted in the net.

The new concept was adapted and tested for the first time in the Baltic cod-directed trawl fishery, and the results demonstrate that fishing with FRESWIND mounted ahead of the codend significantly reduced flatfish catches over the available length range. The reduction in catch of undersized plaice was 65.6% ($nP_- = 34.4\%$), whereas the reduction in catch above MLS was 54.4% ($nP_+ = 45.6\%$). Although it is desirable for a new selection device to improve the escape rates of undersized individuals, the loss of fish above MLS may compromise its adoption by the industry. This is not the case for plaice in Baltic cod directed fishery, since ~90% of the discarded plaice are above species MLS (Anon, 2013). In fact, partially low national TACs for plaice may limit the use of the cod quota and choke the trawl fisheries on cod, if the catchability of flatfish is not reduced in coming years. The estimated catch reduction for flounder was similar to the reduction achieved for plaice. Both species have similar morphology, and their populations have similar length-class structure in the fishery, but it is unknown if these species have similar swimming behavior and vertical preference when drifting toward the codend. The similarity in the performance of FRESWIND for these flatfish species supports the use of fish morphology as a sorting strategy over other strategies, and also indicates that the concept can be adapted and used for other flatfish species, considering their morphological characteristics. FRESWIND also induced a substantial but not significant 32.4% reduction in undersized cod catches. These results indicate that, in addition to the reduction in flatfish catches, FRESWIND also supplemented cod size selection occurring in the codend. On the other hand, only a small and not significant loss of 6.7% marketable cod was estimated.

The usability indicators estimated using the experimental catch information can only be extrapolated to the specific experimental conditions. By using commercial fishing data from the German catch sampling program and simulations, we predicted the effect of introducing FRESWIND into the commercial fishery in Baltic Sea. The simulations predicted flatfish catch-reduction rates similar to those estimated in the experimental fishery, demonstrating at the same time that FRESWIND can reduce undersized cod catches in the fishery, but with an estimated loss in marketable cod at ~9%.

Wienbeck et al. (2014) addressed the problem of flatfish bycatch in the Baltic cod fishery by proposing and testing three different modifications of the mandatory BACOMA codend. However, none of the new codends was found to improve the selectivity for plaice below MLS, compared with the mandatory T90 codend. As a result, lower catches of marketable cod were observed for the alternative codends, compared with the catches in the standard BACOMA, implying potential economic losses and thus rendering its use in the commercial fishery unlikely. The results obtained by Wienbeck et al. (2014) demonstrate the challenge of using codend modifications to reduce flatfish bycatch while maintaining roundfish catchability. Milliken and DeAlteris (2004) attempted to reduce flatfish bycatch in the New England silver hake fishery by placing large mesh panels in the lower part of the belly. Four different panels were investigated, and the best setup achieved significant flatfish bycatch reduction with non-significant, ~25% target species losses. The concept relies on exploiting behavioral differences between flatfish and roundfish while in the fishing gear, assuming that roundfish tend to rise upon entering the mouth of

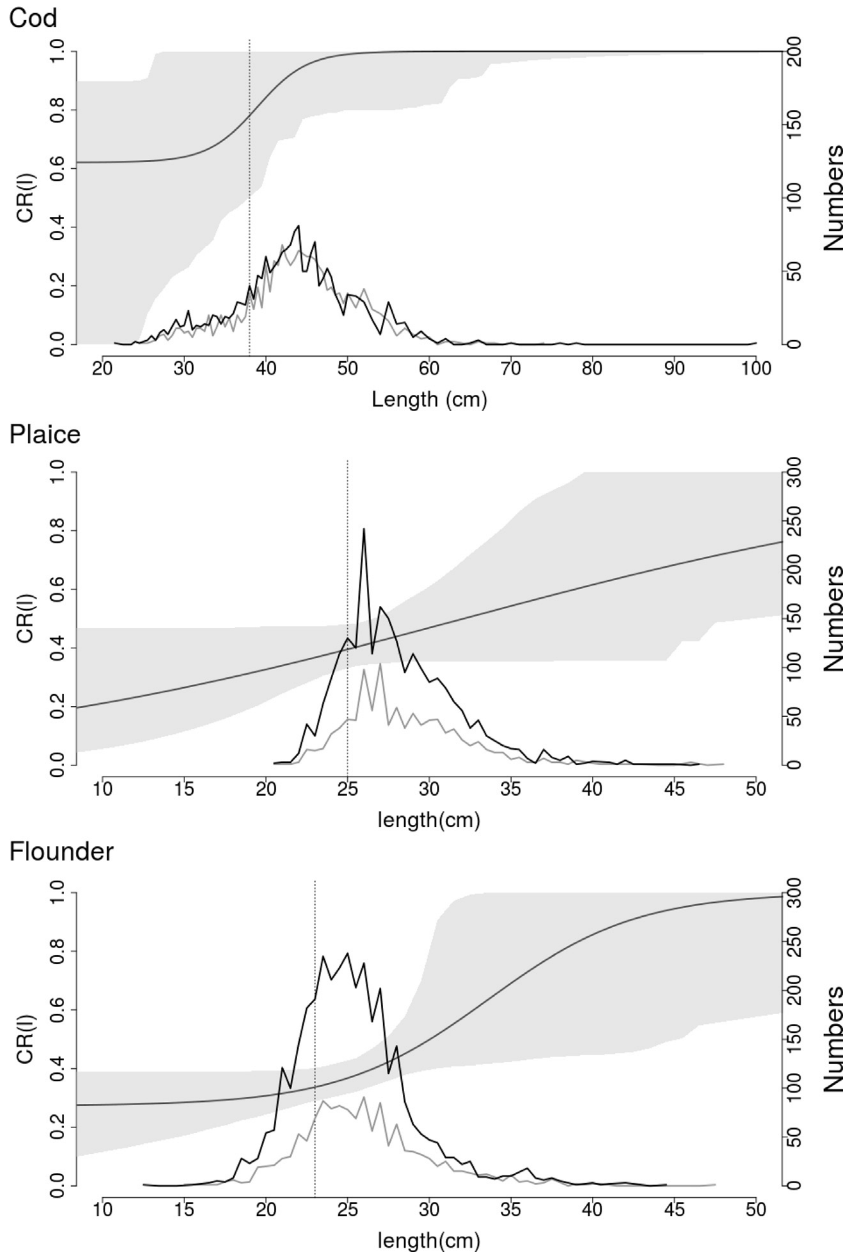

Fig. 3. Estimated catch ratio curves with confidence intervals for cod, plaice, and flounder. Bottom lines represent the length class distribution obtained by the reference (black line) and test (grey line) selection systems (numbers pooled over hauls). Vertical dotted lines represent species MLS.

the gear, whereas flatfish tend to remain close to the seabed. This species separation criteria can be generalized but it may not be applicable within specific fisheries and/or conditions. For example, it is known that cod also tend to stay near the bottom at the first stage of the fishing process (Beutel et al., 2008) in a way similar to the natural response of flatfish (Bublitz, 1996). In contrast, we consider the FRESWIND concept to have a wider application, because it uses inherent differences in morphology that define both groups of species to be separated.

Our sea trial was based on a direct catch comparison between the test and reference selective systems fished simultaneously. The advantage of using such an experimental setup is the easy and practical implementation on commercial twin trawlers, because it does not require extra rigging or the use of small mesh covers that might alter normal fishing behavior. By testing the new system on a commercial vessel, it was possible to collect valuable feedback from the fishermen about operational differences between gears. According to the fishermen involved in the experimental cruise, the FRESWIND did not alter significantly the normal shooting/haul-back manoeuvres, and the test gear was stored on the drum without difficulties. In addition, with the lateral position of the FRESWIND windows, no clogging of the escapement outlets were observed even for hauls with high catches, and no blocking events were experienced in the extension piece, a common problem when large objects collide with grids in fishing gears (Catchpole and Revill, 2008).

With the structural model used in this study, we were able to estimate the FRESWIND selection parameters for cod, plaice, and flounder. This facilitates a better understanding of the selection process occurring in the FRESWIND compared to what can be obtained from the polynomial model. The structural model estimated a high contact probability for the flatfish species with the FRESWIND rigid windows, whereas less than half of the cod was estimated to do so. Further investigation based on underwa-

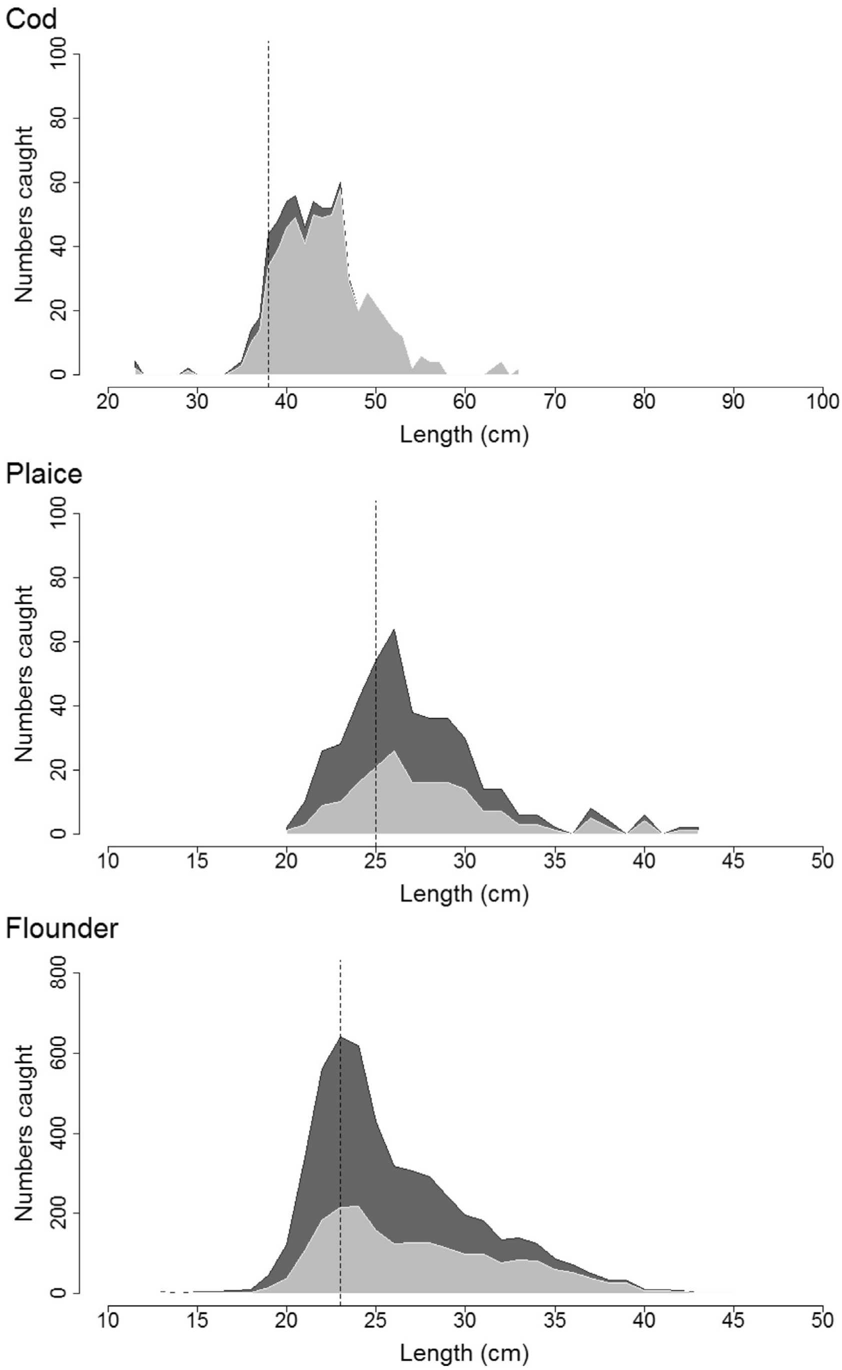

Fig. 4. Catch profile obtained from the German commercial catch sampling program in the same fishing ground as the experimental sea trials (SD24) in 2012, and the same reference selection system (BACOMA; dark grey polygon); expected catch profile after adding the effect of FRESWIND (test system: FRESWIND + BACOMA) to the catch sampling data (light grey polygon).

ter observations would be of interest, clarifying how flatfish and roundfish interact with the guiding device and when they approach the FRESWIND windows.

For size selection, cod *L50* was only 1 cm greater than MLS, whereas for flounder and plaice, the estimated *L50* was far greater than their respective MLSs. Such results comply with the objectives. However, a better understanding of the rigid windows' mechanical sorting would be useful in adapting the bar spacing to specific requirements of the commercial fishery.

The positive results obtained in the case study demonstrate the potential of the FRESWIND to reduce flatfish bycatch in the commercial fishery. Based on these results, it is likely that the concept can also be adapted to other roundfish fisheries with similar flatfish bycatch problems.

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Paper II

"Quantifying the performance of selective devices by combining analysis of catch data and fish behaviour observations: methodology and case study on a flatfish excluder"

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Quantifying the performance of selective devices by combining analysis of catch data and fish behaviour observations: methodology and case study on a flatfish excluder

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This article describes a method for the quantitative analysis of fish behaviour relative to selection devices in trawl gears. Based on video observations, the method estimates probabilities for a given event to happen and establishes behavioural tree diagrams representing and quantifying behavioural patterns in relation to the selection device under assessment. Double bootstrapping is used to account for the uncertainty originating from a limited number of fish observations and the natural variation in fish behaviour. The method is used here to supplement standard analysis of catch data for the performance assessment of a flatfish excluder (FLEX). The Baltic Sea trawl fishery targeting cod (*Gadus morhua*) provides the pilot case. Results obtained by comparing catches with and without FLEX installed revealed that >75% of bycaught flatfish individuals escaped through the device, while no evidence was found that catches of cod in the targeted sizes were reduced. The behavioural analysis produced values of escape efficiency comparable to those obtained in the catch analysis. Furthermore, it revealed that ~80% of the flatfish went calmly into the excluder, while most of the roundfish displayed avoidance swimming reactions. The method provides quantitative information of fish behaviour that can be relevant for developing and optimizing selection devices.

Keywords: behavioural trees, bycatch, flatfish, FLEX, quantitative analysis, selection devices

Introduction

Flatfish are common bycatch species in bottom-trawl fisheries targeting crustaceans or roundfish species (Beutel *et al.*, 2008; Ulleweit *et al.*, 2010; Storr-Paulsen *et al.*, 2012; Lescrauwaet *et al.*, 2013). Often, unintended flatfish catches are of low commercial value for the fishers, being partially or totally discarded (Borges *et al.*, 2006; Lescrauwaet *et al.*, 2013). In fisheries subjected to catch-restricted legislation, bycatch of flatfish with limited quota can represent a challenge for fisheries targeting other species. For example, in US Georges Bank, healthy roundfish stocks are largely under-exploited due to the abundance of flatfish species with limited quota (Beutel *et al.*, 2008; ICES, 2018).

Catches of unintended species often occur due to a mismatch between the selective properties of the trawl and specific morphological characteristics and somatic growth of captured species (Catchpole and Reville, 2008; Wienbeck *et al.*, 2014). In such cases, a common strategy to reduce bycatch is to mount selection devices in the fishing gear able to provide additional escapement possibilities to those non-targeted species that enter the gear (Milliken and DeAlteris, 2004; Catchpole and Reville, 2008).

Traditionally, the effectiveness of selective devices in trawl gears is evaluated based on catch data alone, following well-established methodologies for data collection and for the subsequent statistical analysis (Wileman *et al.*, 1996). However, in most cases, these quantitative methods based on catch data do not provide any detailed information on the contribution of the different components of the device to its overall performance, or about the sequences of behavioural events occurring when the fish interacts with the selection device. This lack of detailed information limits the understanding of the functioning of the device, and therefore, the ability to optimize its performance.

The general development in camera technology that occurred in the last decade has led to the availability of low-cost cameras with high image quality for underwater video recordings, which are therefore becoming an affordable method to assess fish behaviour in selectivity studies (Bayse and He, 2017). Video observations are often used by fisheries technologists to obtain a qualitative picture on how fish interact with a selection device (Queirolo *et al.*, 2010; Chosid *et al.*, 2012; Lövgren *et al.*, 2016; Grimaldo *et al.*, 2018; Larsen *et al.*, 2018). A review of recent literature suggests, however, a growing interest in more detailed descriptions of fish behaviour based on quantitative analysis (He *et al.*, 2008; Krag *et al.*, 2009a; Yanase *et al.*, 2009; Chosid *et al.*, 2012; Hannah and Jones, 2012; Bayse *et al.*, 2014, 2016; Underwood *et al.*, 2015; Queirolo *et al.*, 2019). The methodology applied in quantitative behavioural studies often involves tracking observed fish from their first detection to the final fate (capture or escape), during which the occurrence of behavioural events categorized at different stages of the selection process is identified and counted. While it is reasonable to assume that the fate of the fish can be related to sequences of behavioural events occurring throughout each of the selection stages, with few exceptions (Yanase *et al.*, 2009; Hannah and Jones, 2012), the stage-wise nature of the behavioural data is usually ignored. Instead, events from different stages are analysed together as predictors in regression models (Underwood *et al.*, 2015; Bayse *et al.*, 2016) or separately in contingency tables (He *et al.*, 2008; Krag *et al.*, 2009a; Bayse *et al.*, 2014; Queirolo *et al.*, 2019) and are therefore treated independently to events recorded in previous and subsequent stages. Behavioural responses to selection devices can be influenced by factors intrinsically related to the individual being selected and by extrinsic factors such as fishing conditions varying within and/or between hauls (Winger *et al.*, 2010). Therefore, estimating uncertainties associated to observed behaviours can be relevant information in the assessment and development of selection devices. However, to the best of our knowledge, no selectivity study based on fish behaviour provides such information.

Ignoring the stage-wise nature of the behavioural events and the uncertainty of occurrence preclude answering all the following questions: (i) how often does a given event happen?; (ii) how precise is the estimated probability of occurrence of a given behavioural event?; (iii) does the occurrence of an event condition the events happening next?, which at the same time can lead to more general questions like: (iv) what are the connections between different events being observed before, during, and after the fish contacts the selection device; and (v) could the observed sequences of events be related to the fate of the fish in relation to the selection process?. Therefore, to fully benefit from incorporating the use of underwater recordings in the process of studying, developing, and optimizing the performance of selective devices in fishing gears, it is necessary to be able to provide quantitative answers with uncertainties to the former questions.

This study introduces and applies a new method to quantitatively analyse fish behaviour in relation to selection devices. The method enables (i) quantifying the probability for a observed behavioural event to happen, (ii) quantifying the probability for a given behavioural event to happen, conditioned to the occurrence of events observed in previous behavioural stages, and (iii) establishing behavioural tree diagrams, formed by all the sequences of events displayed by the observed fish towards their final fate in the catch process. Moreover, the method accounts for uncertainties derived from the limited number of fish observations, and the natural variation in fish behaviour (Winger *et al.*, 2010) that potentially influences the between- and within-haul variations in the performance of selection devices (Fryer, 1991).

Applicability of the method is demonstrated here using a flatfish excluder as a case study. The device was conceived in the Baltic Sea, where large amounts of flatfish bycatch such as plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*), and dab (*Limanda limanda*) frequently occur in cod-directed trawl fisheries (ICES, 2017). Therefore, the present study develops, tests, and assesses the efficiency of such device using the standard analyses of catch data, supplemented with the proposed method for the quantitative analysis of fish behaviour based on video observations.

Material and methods

Development of a simple flatfish excluder for trawls

The design strategy for FLEX (a simple FLatfish EXcluder for trawls) exploits behavioural differences between fish species. According to several studies, cod tend to enter the trawl swimming downwards, after which it starts to redistribute up in the water column as it approaches the gear's aft (Holst *et al.*, 2009; Fryer *et al.*, 2017; Karlsen *et al.*, 2019). At this point in the trawl, the vertical distribution of cod might be length dependent, with small cod more likely to swim closer to the bottom net panel than larger ones (Melli *et al.*, 2019). Flatfish are commonly observed swimming near the floor of the trawl (Bublitz, 1996; Ryer, 2008; Fryer *et al.*, 2017). Based on these behavioural patterns, establishing an outlet in the bottom panel of the extension piece of the trawl could be an efficient strategy to reduce the bycatch of flatfish and undersized cod. This selection concept was adopted as the basis for the development of a simple and adaptive FLEX design that could be activated or deactivated with simple modifications at haul level, therefore providing fishermen with flexibility to switch their fishing strategies and targets in the short term.

The initial version of FLEX was developed on board the German research vessel RV CLUPEA during sea trials in October 2014. The earliest design consisted of an outlet established by a simple cut in the netting of the bottom panel of a four-selvedge extension piece. The cut was made at the mid-length of the 6-m-long extension. Stepwise improvements were achieved during the cruise based on video observations of fish responses near the outlet. Such observations revealed, for example events in which flatfish individuals turned back to the gear after passing through the outlet and losing contact with the bottom panel, or avoidance reactions due to the excessive waving of the net around the outlet. The behavioural information collected guided the development of the concept into the final design (Figure 1). FLEX consists of a

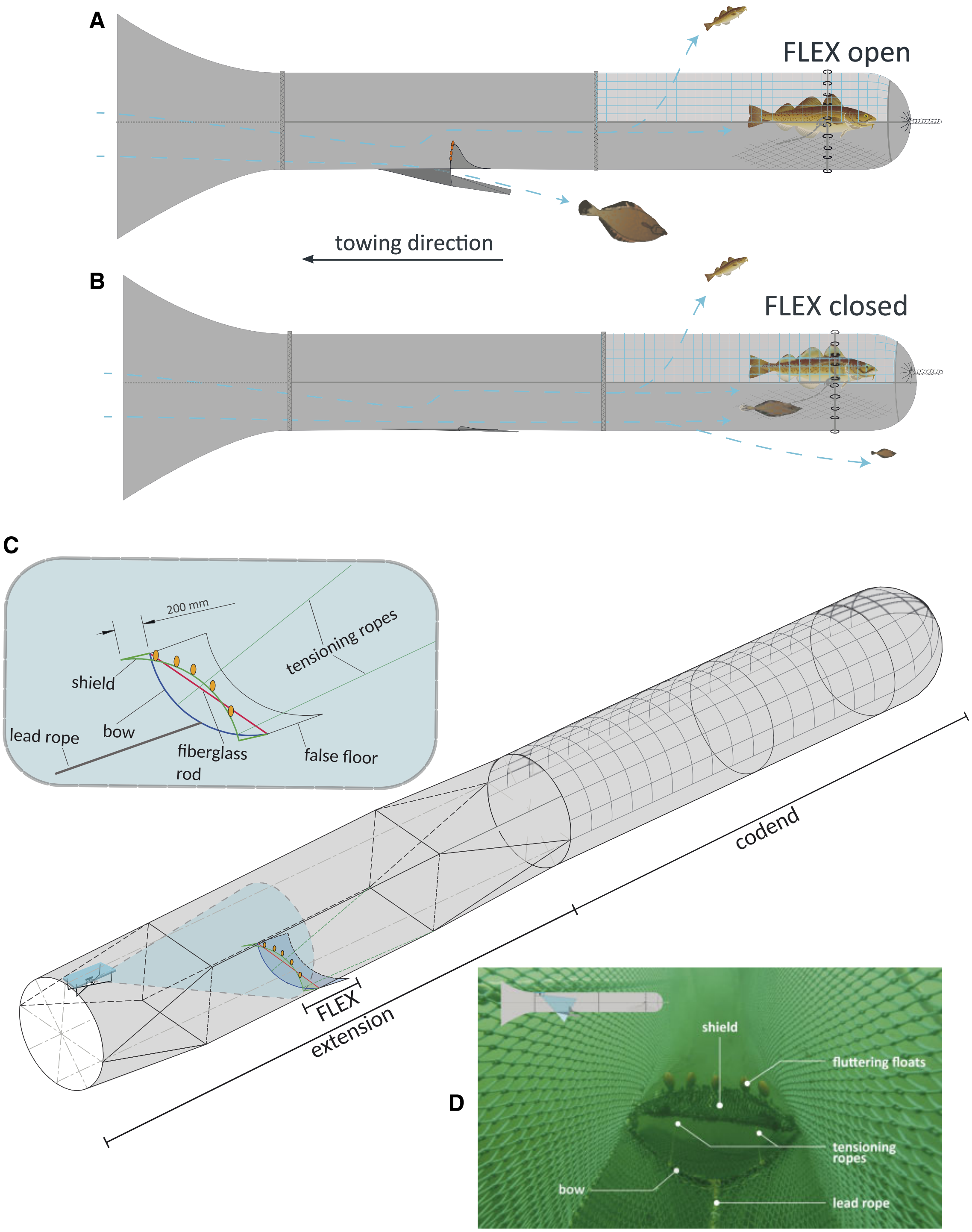

Figure 1. Design and working principle of the FLEX as it is intended for a commercial fishery (a and b). Blue arrows represent the expected swimming paths of roundfish and flatfish. (a) With FLEX open, flatfish escape before entering the codend, while roundfish selectivity occurs in the codend. (The BACOMA codend used in the Baltic Sea is included here only for illustration purposes. It was not used in this study.) (b) FLEX can be closed easily between hauls; with FLEX closed, all fish entering the trawl are size selected in the codend. (c) Construction details and placement of FLEX in the extension piece. (d) Front view of the device [underwater picture taken from the camera position shown in (C)].

half oval-shaped outlet, with the major axis formed by a 90-cm-long, straight fibreglass rod, connected to the rear edge of the net cut, and the tips fixed to the lower selvedges of the extension. The bow of the outlet is oriented downwards and defined by an elastic dentex wire connected to the forward edge of the net cut. A 1.5-m lead rope was connected to the vertex of the bow, running lengthwise through the forward section of the extension to create a furrow on the floor of the net. The furrow should guide the flatfish towards the outlet. Furthermore, a 90 cm × 20 cm rectangular net shield with small floats on top was connected to the fibreglass rod as a deterrent device for cod. In particular, the presence of a net shield with fluttering floats on top should stimulate avoidance reactions in cod swimming close to the floor (Herrmann *et al.*, 2015), reducing the probability of encountering the outlet. In the final design, we also connected a piece of netting to the outside of the bow (a false floor), aiming to guide flatfish further out of the gear. Such device could also create an optical illusion for the fish that the outlet is blocked. This visual effect could motivate the approaching cod to choose the clearer path towards the codend (Figure 1).

Collection and analysis of catch data

Experimental fishing was conducted 12–20 November 2014 on board the 42.40-m, 1780-kW German research vessel RV SOLEA. The experimental design applied was a paired catch comparison set-up (Krag *et al.*, 2015), with two identical four-panel extensions made of 60-mm nominal mesh length (Wileman *et al.*, 1996) on each side of a Double Belly Trawl (DBT; Supplementary Figure S1). The DBT was specifically designed to conduct paired-gear experiments on vessels with no twin-trawl facilities and has no application in commercial Baltic fisheries. FLEX was installed on one side of the DBT, referred to here as the test gear, and the other side remained as control, referred to here as the control gear (Figure 2).

A two-selvedge codend made of the same netting material as the extensions was connected to each gear. To ensure that fish entering the DBT would have an average equal probability of entering either gear, they were switched between sides during the cruise. Catches from the test and control gears were kept separate and sampled one after another at the end of each haul. The catch in each codend was sorted by species before each individual was length-measured to the half centimetre below (total length), using electronic measuring boards.

Estimate of FLEX's escape efficiency

Analysis of the catch data was conducted by species, following the procedure described in this section to estimate the efficiency of FLEX as an excluding device. The mesh length of the codends (60 mm) might not be small enough to retain all individuals from the smallest length classes. Therefore, only fish longer than 15 cm were considered for the analysis. The limit at 15 cm was set based on comparing fish morphology with the codend meshes for samples of fish of different species based on the mesh fall-through method described in Wienbeck *et al.* (2011). Fifteen centimetres was judged by this method to be a safe size limit that guaranteed that none of the species investigated would have been subjected to codend size selection, which potentially could have biased results in case of differences in codend size selection between the two gears used. Such differences in codend size selection could be caused by differences in catch size (O'Neill and Kynoch, 1996) due to the effect of mounting FLEX in the test gear. Furthermore, hauls with fewer than 20 individuals of the specific species studied were not included in the analysis.

In this section, we develop a model and method for quantifying length-dependent escape efficiency based on catch data. The method compares the catches obtained with the two gears (test and control) and relates the observed proportions of the catches to the efficiency of FLEX as an excluding device, $e_{flex}(l)$ (Figure 2). Because both gears fished simultaneously, the collected catch data were treated as paired catch comparison data (Krag *et al.*, 2015).

Based on Herrmann *et al.* (2018), the size selection processes in the two gears can be considered as sequential processes, first with a size selection $r_{front}(l)$ in the part of the trawl ahead of the extension, followed by the size selection in the extension piece $r_{ext}(l)$, and finally the selection process in the codend $r_{codend}(l)$. The only difference between the two gears is that the test gear has FLEX installed in the extension piece. This leads to an additional selection process, which can be expressed as $r_{flex}(l) = 1.0 - e_{flex}(l)$, where $e_{flex}(l)$ is the length-dependent escape probability (escape efficiency) through FLEX for a fish entering the extension. Based on these sequential selectivity processes, the total selectivity for the test gear with FLEX $r_t(l)$ and the control gear $r_c(l)$ can be modelled as:

$$\begin{aligned} r_t(l) &= r_{front}(l) \times r_{ext}(l) \times \left(1.0 - e_{flex}(l)\right) \times r_{codend}(l) \\ r_c(l) &= r_{front}(l) \times r_{ext}(l) \times r_{codend}(l) \end{aligned} \quad (1)$$

Based on the group of valid hauls h, we can quantify the experimental average catch comparison rate CC_l (Herrmann *et al.*, 2017) as follows:

$$CC_l = \frac{\sum_{i=1}^{h} nT_{il}}{\sum_{i=1}^{h} (nC_{il} + nT_{il})} \quad (2)$$

where nT_{il} and nC_{il} are the numbers of fish in length class l caught in haul i in the codend of the test gear and the codend of the control gear, respectively. The next step is to express the relationship between the catch comparison rate CC_l and the size selection processes (retention probability) for the test gear with FLEX $r_t(l)$, and the control gear $r_c(l)$. First, the total number of fish n_l in length class l entering the DBT is separated into the test or the control gears (Figure 2). The split parameter (SP) accounts for this initial catch separation by quantifying the proportion of fish entering the test gear compared with the total entering the DBT. SP is assumed to be length independent; therefore, the expected values for $\sum_{i=1}^{h} nT_{il}$ and $\sum_{i=1}^{h} nC_{il}$ are:

$$\begin{aligned} \sum_{i=1}^{h} nT_{il} &= n_l \times SP \times r_t(l) \\ \sum_{i=1}^{h} nC_{il} &= n_l \times (1 - SP) \times r_c(l) \end{aligned} \quad (3)$$

Based on (1)–(3) and Figure 2, the theoretical catch comparison rate CC(l) becomes:

$$\begin{aligned} CC(l) &= \frac{n_l \times SP \times r_{front}(l) \times r_{ext}(l) \times \left(1.0 - e_{flex}(l)\right) \times r_{codend}(l)}{\left(\begin{array}{c} n_l \times SP \times r_{front}(l) \times r_{ext}(l) \times \left(1.0 - e_{flex}(l)\right) \times r_{codend}(l) \\ + n_l \times (1 - SP) \times r_{front}(l) \times r_{ext}(l) \times r_{codend}(l) \end{array}\right)} \\ &= \frac{SP \times \left(1.0 - e_{flex}(l)\right)}{1.0 - SP \times e_{flex}(l)} \end{aligned} \quad (4)$$

Equation (4) establishes a direct relationship between the escape probability through FLEX $e_{flex}(l)$ and the catch comparison rate CC(l). Therefore, FLEX's length-dependent escape efficiency can be assessed by estimating the catch comparison rate as formulated in (4). The expected equal catch efficiency of both sides of

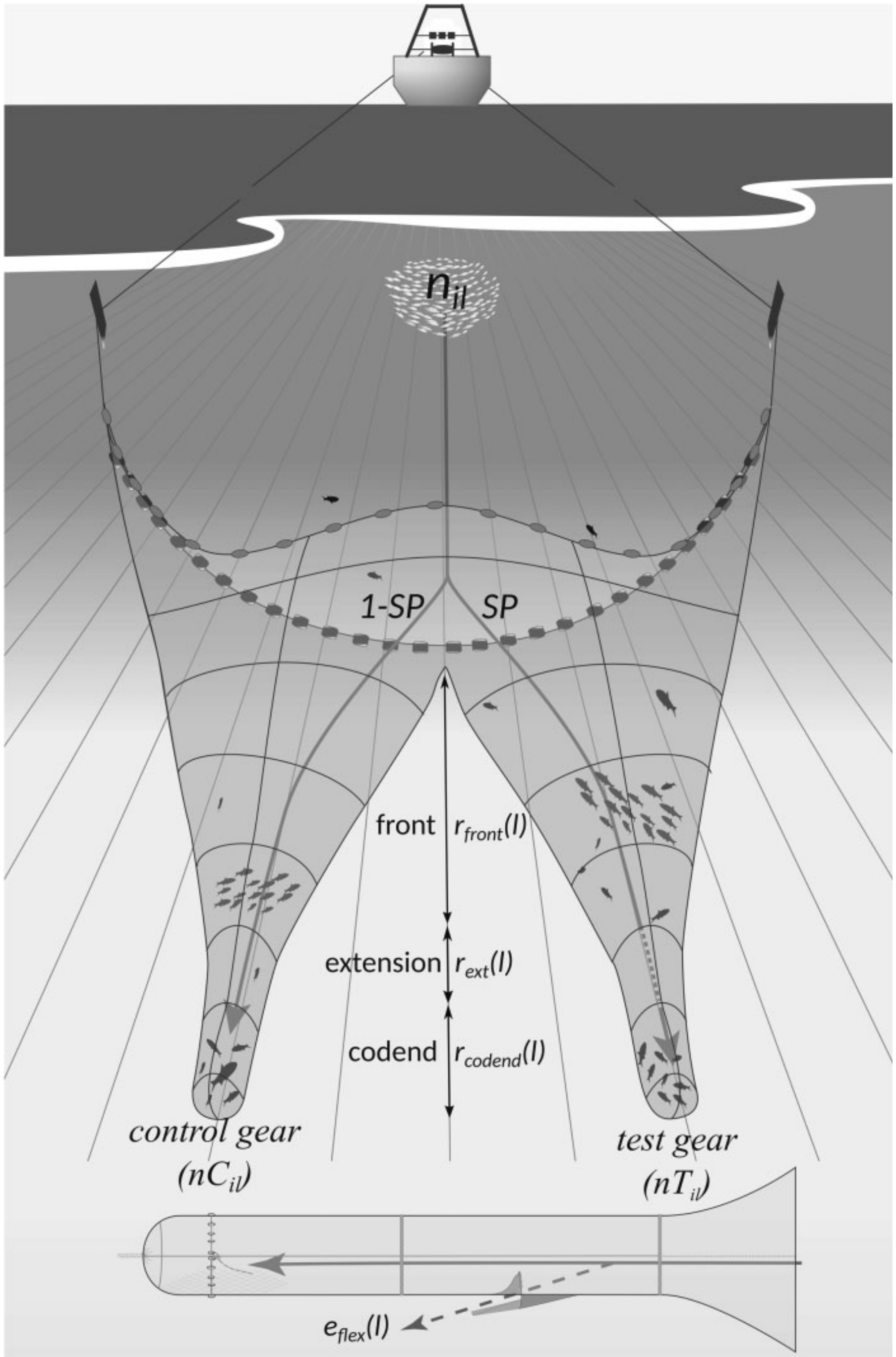

Figure 2. Experimental design applied during the sea trials with RV SOLEA. Test (FLEX) and control gears were mounted on different sides of the DBT. Numbers of fish by length l caught at haul i in the test codend (nT_{il}) and in the control codend (nC_{il}) were used for subsequent analysis. Description of the other mathematical notations showed in the figure can be found in the 'Collection and analysis of catch data' section.

the DBT and the swapping of the test gear between sides during the experiment led to the assumption that fish entering the trawl would have an average equal probability of entering either the test or the control gear; therefore, the parameter SP in (4) was fixed to a value of 0.5.

The escape efficiency of FLEX might depend on species-specific behaviour and length-dependent swimming ability. Therefore, to be able to model $e_{flex}(l)$ for the different species investigated, we used a highly flexible function often used in catch comparison studies (Krag *et al.*, 2015, 2014; Herrmann *et al.*, 2017, 2018):

$$e_{flex}(l, v) = \frac{\exp(f(l, \boldsymbol{v}))}{1.0 + \exp(f(l, \boldsymbol{v}))}, \tag{5}$$

where $f(l,\boldsymbol{v})$ is a polynomial of order 4 with parameters $\boldsymbol{v} = (v_0, v_1, v_2, v_3, v_4)$ (Krag *et al.*, 2015). Therefore, the estimation of the catch comparison rate in (4) is conducted by minimizing the following maximum likelihood equation with respect to the parameters $\boldsymbol{v}$ describing $CC(l,\boldsymbol{v})$:

$$-\sum_i \sum_l \{nT_{il} \times \ln(CC(l,\boldsymbol{v})) + nC_{il} \times \ln(1.0 - CC(l,\boldsymbol{v}))\}. \quad (6)$$

Leaving out one or more of the parameters v_0–v_4 in (5) led to 31 additional simpler models, which were also considered potential candidates for modelling FLEX escape efficiency and therefore also estimated by (6). The model with the lowest AIC (Akaike, 1974) was selected from among the candidates. Following the guidelines in Wileman *et al.* (1996), the ability of the selected model for $CC(l,\boldsymbol{v})$ to describe the data sufficiently well was based on the calculation of the *P*-value associated with the Pearson's Chi-squared statistic, together with the visual inspection of residual length-dependent patterns. The *p*-value expresses the likelihood of obtaining at least as big a discrepancy between the fitted model and the observed experimental data by coincidence. Therefore, this *p*-value should not be <0.05 for the fitted model to be a good candidate to describe the observed length-dependent escape efficiency.

Efron confidence intervals (95%) of the curves predicted by (4) and (5) were obtained using the same double bootstrap procedure (1000 replications) as in Santos *et al.* (2016). This includes accounting for between-haul variation in FLEX's escape efficiency and the uncertainty in individual hauls related to the finite number of fish caught. In addition, the bootstrap method accounts for uncertainty in model selection to describe $e_{flex}(l,\boldsymbol{v})$ by incorporating in each of the bootstrap iterations an automatic model selection based on which of the 32 models produced the lowest AIC. The analysis of FLEX's escape efficiency described above was carried out using the software tool SELNET (Herrmann *et al.*, 2013; Santos *et al.*, 2016).

Indicators of escape efficiency

To further evaluate the efficiency of FLEX by accounting for the length structure of the population fished, three different escape efficiency indicators were estimated:

$$\begin{aligned} nE_- &= 100 \times \left(1.0 - \frac{\sum_i\{\sum_{l<ref} nT_{il}\}}{\sum_i\{\sum_{l<ref} nC_{il}\}}\right), \\ nE_+ &= 100 \times \left(1.0 - \frac{\sum_i\{\sum_{l\geq ref} nT_{il}\}}{\sum_i\{\sum_{l\geq ref} nC_{il}\}}\right), \\ nE &= 100 \times \left(1.0 - \frac{\sum_i\{\sum_l nT_{il}\}}{\sum_i\{\sum_l nC_{il}\}}\right), \end{aligned} \quad (7)$$

where the summation of *i* is over hauls and *l* is over length classes. The escape efficiency indicators in (7) are calculated as one minus the ratio of catches from each of the species studied in FLEX gear (nT) to the catches in the control gear (nC). This is done for the total catch (nE), and for the fractions below (nE_-) and above (nE_+) a given reference fish size (ref). If available, the reference length used was the species Minimum Conservation Reference Size (MCRS), length used for management purposes that replaced the Minimum Landing Size in European fisheries. In general, high values of the three indicators for flatfish and low values for roundfish would indicate that the intended species selection was achieved. Any length dependency in the escape efficiency would be expressed by differences in the values of nE_- and nE_+. If this is the case, high values of nE_- and low values for nE_+ would be the preferred results for cod, indicating FLEX to potentially contribute in the reduction of bycatch of undersized cod without producing losses of marketable sizes. Confidence intervals associated to these indicators were obtained by including the calculations in (7) into the same bootstrap scheme used to obtain the confidence intervals associated to the curves predicted by (4) and (5).

Assessment of fish behaviour based on video observations

Video recordings were collected during selected hauls with a GoPro camera mounted in a protective structure on the upper panel of the extension, in front of FLEX. The camera focused on the selection device, with sufficient depth of field to visually follow the observed fish in the vicinity of FLEX (Figure 1). Only the video footage that provided a clear view of FLEX and surroundings during towing were used in the assessment. Estimation of fish length was not possible due to the limitations of the recording methodology, which only provided a front perspective of the selection device and surroundings. The behaviour of each fish observed was assessed within four different behavioural stages: entry (1), approach (2), contact (3), and reaction (4) stages (Figure 3). At the entry stage, we assessed two different behavioural categories, body orientation and vertical position of the observed fish immediately after entering in the field of view of the camera. Body orientation was categorized with three mutually exclusive possibilities; facing forwards in the direction of towing, facing aft towards the codend, or sideways. Vertical position at entry was assessed relative to a horizontal plane projected from the top of the fluttering floats of FLEX. Fish entering inside the field of view below the projected plane were considered "in" the operative zone of the device; individuals swimming above the projected plane were considered "out" of the operative zone. The path followed by the observed fish from its first detection until it reaches the zone where FLEX was mounted was categorized within the approach stage. Predefined main reactions were "upwards", "steady", "downwards", "sideways", and "forwards". The paths followed by fish "in" the operative zone of FLEX that did not display any evident attempt to avoid contacting the device were categorized as "steady". Paths followed by fish out of the operative zone of FLEX other than downwards were not relevant for this study and therefore also categorized as "steady". More complex approaching paths were also considered by combining two or more of the defined main paths. Infrequent approaching paths (less than five observations) were aggregated into category "others". At the contact stage, it was evaluated to which component of the device the fish made first contact. Three mutually exclusive possibilities were predefined: "outlet", "net shield", and "no contact". The first reaction after contacting FLEX was evaluated at the reaction stage. Predefined main reactions were "upwards", "forwards", "downwards", "sideways", and "no reaction". As in the approach stage, more complex reactions were also categorized by combining two or more of the defined main reactions, and infrequent reactions (less than five observations) were aggregated into category "others". Those individuals that did not contact the device at all were categorized with "no reaction". Finally, the fate of the observed fish (selection outcome, escaped or caught) was recorded once the individual went out of

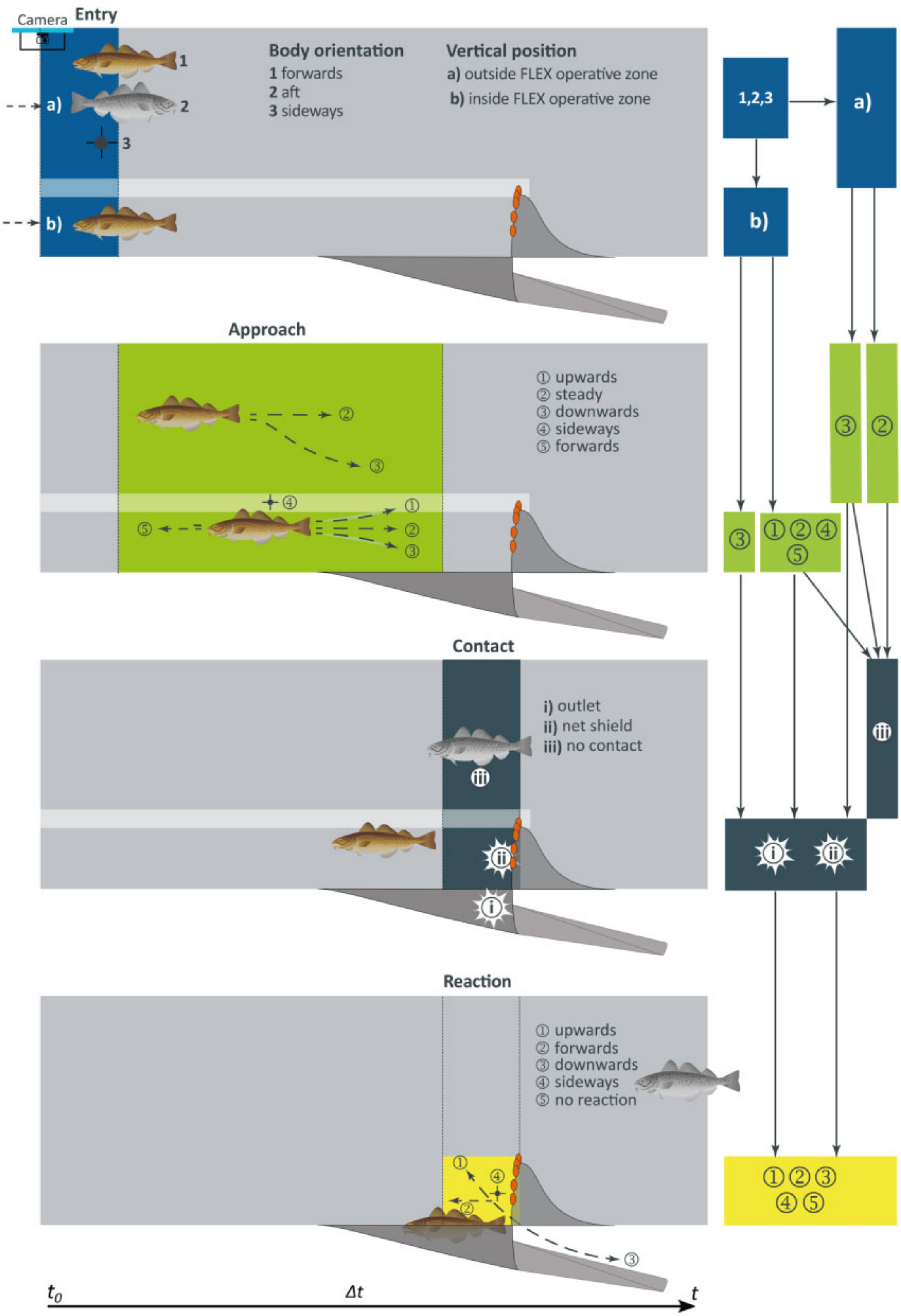

Figure 3. Graphical representation of the methodology applied in the analysis of video recordings for the assessment of fish behaviour in relation to FLEX. The plots illustrate the side view of the fore part of the extension piece where FLEX is mounted. Each plot shows a given behavioural stage highlighted by a coloured rectangle (blue = entry, green = approach, dark grey = contact and yellow = reaction). The behavioural events considered within behavioural stages are represented as items (possibilities) or broken arrows (paths). Horizontal pale band represents the projection of the horizontal plane used to determine if the observed fish enters the field of view "in" or "out" the operative zone of FLEX. Such band is visually projected by the observer from the point of view of the camera. Right margin: flow chart representing all possible connections among behavioural events from successive behavioural stages.

the camera focus. The duration of the selection process in seconds (Δt), from the first detection of the observed fish (t_0) until the moment when the selection outcome occurred (t) was also recorded (Figure 3).

The recorded events (either a possibility or path) displayed in the different behavioural stages characterize a specific behavioural sequence that could be related to the final fate of the observed fish.

Behavioural assessment was conducted following a systematic sampling procedure, whereby the first 30 roundfish and 30 flatfish that entered the field of view of the camera during towing were sampled. The information collected from each fish observed (including the behavioural sequence displayed and the resulting selection outcome) was pooled within and between hauls. The pooled data were arranged in a tree-like structure, departing from a root that represents the total number of individuals observed. The root is connected to behavioural nodes ($N_{Z,j}, j \in \{1, \ldots, J\}$), each counting the number of times a specific behavioural event j from stage $Z \in \{1, 2, 3, 4\}$ was observed. The nodes were arranged in four levels related to the four observation stages, with the branches of the tree representing the observed connections among nodes from successive levels. The leaves at the bottom of the tree contain the number of observed fish retained or escaped after following a given behavioural sequence of events.

Using the behavioural tree described above, we calculated two different statistics associated to each of the behavioural events recorded. First, the marginal probability (MP) for a given behavioural event j from behavioural stage Z to happen was calculated as:

$$\mathrm{MP}_{Z,j} = P(N_{Z,j}) = \frac{N_{Z,j}}{\mathrm{Root}}. \qquad (8)$$

In (8), $N_{Z,j}$ is the node representing the total number of fish that displayed the behavioural event j in behavioural stage Z, while Root is the total number of fish observed. Similarly, the conditional probability (CP) that event j from behavioural stage $B \in \{2, 3, 4\}$ could happen, given that the parent attribute k from behavioural stage $B - 1$ happened was calculated as:

$$\mathrm{CP}_{B,j} = P\left(N_{B,j} | N_{B-1,k}\right) = \frac{N_{B,j}}{N_{B-1,k}}. \qquad (9)$$

The total numbers of observed fish retained and escaped were also used to calculate an escape efficiency indicator based on video recordings:

$$nE^* = 100 \times \left(\frac{\sum_{i=1}^{h} nEscaped_i^*}{\sum_{i=1}^{h} \left(nEscaped_i^* + nRetained_i^* \right)} \right), \qquad (10)$$

where the sum of h is for hauls used for video observation. For a given group of species studied, the indicator nE^* accounts for the rate of observed individuals that escaped through FLEX, to the total individuals observed. Therefore, values of nE^* are equivalent to nE (7) and can be compared to assess the consistency of escape efficiency indicators obtained with the current video analysis and the analysis based on catch data.

The uncertainty derived from the limited number of fish observed by haul and the natural variation in fish behaviour occurring between hauls were accounted in (8)–(10) using the same bootstrap scheme applied in the previous section. In particular, the double bootstrap technique produced a total of 1000 artificial trees from which it was possible to estimate Efron confidence intervals (95%) associated to probabilities MP, CP, the indicator nE^*, and the average duration of the selection process, Δt.

The video sequences were observed using BORIS (Friard and Gamba, 2016), a free software specifically developed to investigate animal behaviour. Subsequent analyses were conducted using R (R Core Team, 2018), with data.tree (Glur, 2018) and DiagrammeR (Iannone, 2019) packages.

Results

Description of fishing operations and catch data

Altogether, 33 valid hauls were conducted during nine fishing days on two different fishing grounds, in the western Baltic Sea, respectively in ICES Subdivisions 22 and 24. The average haul duration was 84 min [standard deviation (SD) = 30.4] and the towing speed averaged 3.1 (SD = 0.42) knots (Table 1). In total, 15 hauls were conducted with the test gear mounted on the starboard side and 18 hauls were conducted with the test gear mounted on the port side. Catches consisted mostly of dab, cod, whiting, flounder, and plaice, together making up ∼90% (in weight) of the total catch. These species were used in the data analysis. Dab was the most frequently occurring species in the catches with 10 339 individuals. However, hauls 20 and 26 were not used in the subsequent analysis for dab owing to problems with the sampling of dab lengths. The second most frequent species was cod with 8848 individuals caught, followed by whiting (*Merlangius merlangius*) with 3219 individuals, flounder with 2718 individuals, and plaice with 410 individuals.

Catch-data analysis

After excluding the hauls with fewer than 20 individuals for specific species, a total of 8, 17, and 21 hauls were used to analyse three flatfish species, plaice, flounder, and dab, respectively. The model estimated by (4)–(6) described well the length-dependent catch comparison rate between the test and control gears for the three species (Figure 4). The models yielded p-values >0.05, implying that the model fitted the experimental data sufficiently well (Table 2). The experimental catch comparison rates reveal that the catches of dab and flounder (the two most abundant flatfish species) were mostly caught in the control codend. The catch comparison curves (4) are significantly below 0.5 (the value expressing equal catch sharing probability) throughout the available length classes (Figure 4). This demonstrates the escape of flounder and dab through FLEX. Both curves exhibit similar patterns, with a slight and positive trend in the range of the most abundant lengths, dropping down across the largest, less abundant length classes. The catch comparison curve for plaice had higher uncertainty as a result of the smaller catches obtained for this species. For flounder and dab, FLEX's escape efficiency was estimated to be >75% for all lengths caught during the trials (Figure 4). For example, the escape efficiency for flounder at its MCRS (23 cm) was significantly >80%, a value slightly higher than for dab at the same length (78%). For plaice, the escape efficiency at MCRS (25 cm) was estimated at 66%, however, with high uncertainty because the 95% confidence band spanned >1–94%.

Altogether, 16 and 21 hauls were used to estimate FLEX's escape efficiency for cod and whiting, respectively. Visual

Table 1. Operational information of the hauls conducted during the experimental trials, and fish caught per species (in numbers) by each gear (test = *nT*, control = *nC*).

Date	Haul	Time (CET)	Duration (min)	Latitude	Longitude	Speed (knots)	Side	Cod		Whiting		Plaice		Dab		Flounder	
								nT	*nC*	*nT*	*nC*	*nT*	*nC*	*nT*	*nC*	*nT*	*nC*
12 November 2014	1	9:53	120	54°12N	011°58E	2.6	Starboard	0	0	0	0	0	0	0	2	0	0
12 November 2014	2	12:44	30	54°12N	011°45E	2.4	Starboard	0	0	2	6	0	0	0	4	1	5
12 November 2014	3	14:06	30	54°11N	011°50E	2.7	Starboard	1	0	0	0	0	0	0	1	2	0
12 November 2014	4	16:01	60	54°11N	011°56E	2.8	Starboard	1	1	0	0	0	0	1	1	0	0
13 November 2014	5	7:132	60	54°26N	011°25E	2.7	Starboard	15	2	68	16	4	9	261	589	22	176
13 November 2014	6	9:11	120	54°26N	011°25E	3.2	Starboard	9	10	69	52	7	30	349	1 534	83	483
13 November 2014	7	12:43	120	54°21N	011°24E	3.3	Starboard	5	5	35	39	7	27	269	1 377	55	325
13 November 2014	8	15:22	60	54°27N	011°25E	3	Starboard	4	1	40	27	3	9	218	696	26	126
14 November 2014	9	7:09	60	54°10N	011°49E	3.6	Portside	549	646	131	127	10	48	33	170	34	150
14 November 2014	10*	9:12	90	54°11N	011°50E	2.9	Portside	46	117	31	193	2	3	3	20	7	34
14 November 2014	11*	12:07	90	54°10N	011°51E	3.5	Portside	47	28	13	23	0	0	4	4	3	8
14 November 2014	12	14:07	90	54°10N	011°43E	2.6	Portside	128	181	25	25	7	31	39	172	18	74
15 November 2014	13	7:08	90	54°42N	013°08E	2.8	Starboard	60	86	1	4	0	3	0	5	4	24
15 November 2014	14	9:42	119	54°42N	013°07E	3.2	Starboard	169	153	1	1	0	3	0	0	2	8
15 November 2014	15	12:40	120	54°42N	013°07E	3.2	Starboard	76	80	1	3	0	3	1	0	4	9
16 November 2014	16	7:07	60	54°13N	011°33E	3.1	Starboard	0	0	3	11	2	1	0	1	0	1
16 November 2014	17	8:57	90	54°10N	011°428E	3.4	Starboard	6	2	28	33	0	1	2	20	1	17
16 November 2014	18	11:13	120	54°12N	011°48E	3.5	Starboard	2	1	3	1	0	0	3	4	0	4
16 November 2014	19	14:26	8	54°17N	011°55E	3.1	Starboard	0	0	2	4	0	0	10	61	0	0
17 November 2014	20	14:07	60	54°26N	011°25E	3.4	Portside	5	3	42	23	3	4	0	588	15	97
17 November 2014	21	15:47	60	54°23N	011°24E	3.1	Portside	1	15	12	53	3	5	47	169	11	26
18 November 2014	22	7:35	90	54°16N	011°39E	3.6	Portside	8	19	35	44	1	6	34	83	3	21
18 November 2014	23	10:11	113	54°20N	011°23E	2.1	Portside	12	11	93	106	1	30	150	1 213	31	357
18 November 2014	24	13:15	60	54°31N	011°19E	3.6	Portside	5	4	44	65	2	37	102	777	25	132
18 November 2014	25	15:05	60	54°31N	011°196E	3.8	Portside	7	2	44	53	25	5	163	661	22	92
19 November 2014	26	7:04	120	54°12N	012°00E	4	Portside	270	435	143	224	0	17	5	66	4	24
19 November 2014	27*	9:41	120	54°11N	011°51E	3.2	Portside	589	1 237	128	165	4	27	20	165	12	85
19 November 2014	28*	13:19	90	54°12N	012°00E	3.3	Portside	382	274	82	29	1	1	2	24	1	4
19 November 2014	29	15:25	75	54°11N	011°53E	3.5	Portside	689	692	239	334	0	3	16	23	0	7
20 November 2014	30	7:03	90	54°12N	012°00E	2.9	Portside	84	212	19	4	1	9	3	41	3	11
20 November 2014	31	9:21	120	54°11N	011°50E	2.9	Portside	773	170	138	52	3	4	7	59	5	15
20 November 2014	32	12:41	90	54°12N	012°00E	2.7	Portside	44	257	2	9	1	4	2	30	0	3
20 November 2014	33*	14:48	90	54°11N	011°53E	3.1	Portside	185	32	6	13	2	1	8	27	2	4
							Total	4 172	4 676	1 480	1 739	89	321	1 752	8 587	396	2 322

The column named "side" provides information about the side of the trawl the test gear was used. Towing speed averaged over continuous measurements automatically taken by the vessel. Videos collected from hauls with (*) were used for the behavioural analysis.

inspection of the catch comparison curves provided a good description of the length-dependent trend in the experimental rates for both species (Figure 5). However, the *P*-value obtained for whiting was <0.05 and, therefore, required a deeper investigation of the model fit. No systematic pattern was found in the length-dependent distribution of residuals around the predicted curve; therefore, the *p*-value of <0.05 was attributed to overdispersion. Because overdispersion does not affect the predictive capability of the model, we found it valid to describe the experimental catch comparison data for whiting by the model. With average values between 0.4 and 0.5, the catch comparison curves predicted for cod and whiting exhibit nearly equal catch shares between both gears (Figure 5). For cod, the average catch comparison curve dropped below CC = 0.5 for sizes smaller than 46 cm, whereas the curve estimated for whiting dropped below CC = 0.5 within the range of lengths between ∼15 and ∼30 cm. However, there was no statistical evidence of escape through FLEX of any sizes for both roundfish species, because 0.0 escape (CC = 0.5) was within the 95% confidence bands for all length classes (Figure 5).

The values of the escape efficiency indicators obtained from the catch data are consistent with the estimated catch comparison curves. The reference lengths used to calculate nE_{-} and nE_{+} were the species MCRS, except for dab. For this species, we used the same reference length as for flounder (Table 3). The highest values were obtained for flounder, with escape efficiencies ∼85% regardless of the indicator considered. Lower values were obtained for dab, especially considering the nE_{+} indicator, ∼5 percentage points lower than the species nE_{-}, however, attending to the wide overlapping of the indicator's confidence intervals, such difference cannot be considered significant. The indicators for plaice resulted in the lowest and least accurate values for the three flatfish species studied. The *nE* indicator for the roundfish species was very similar and below 15%. The average values of nE_{-} obtained for both species (∼18%) was higher than the nE_{+} for cod (∼9%) and whiting (∼5%), indicating higher, but not significant escape efficiency for small roundfish.

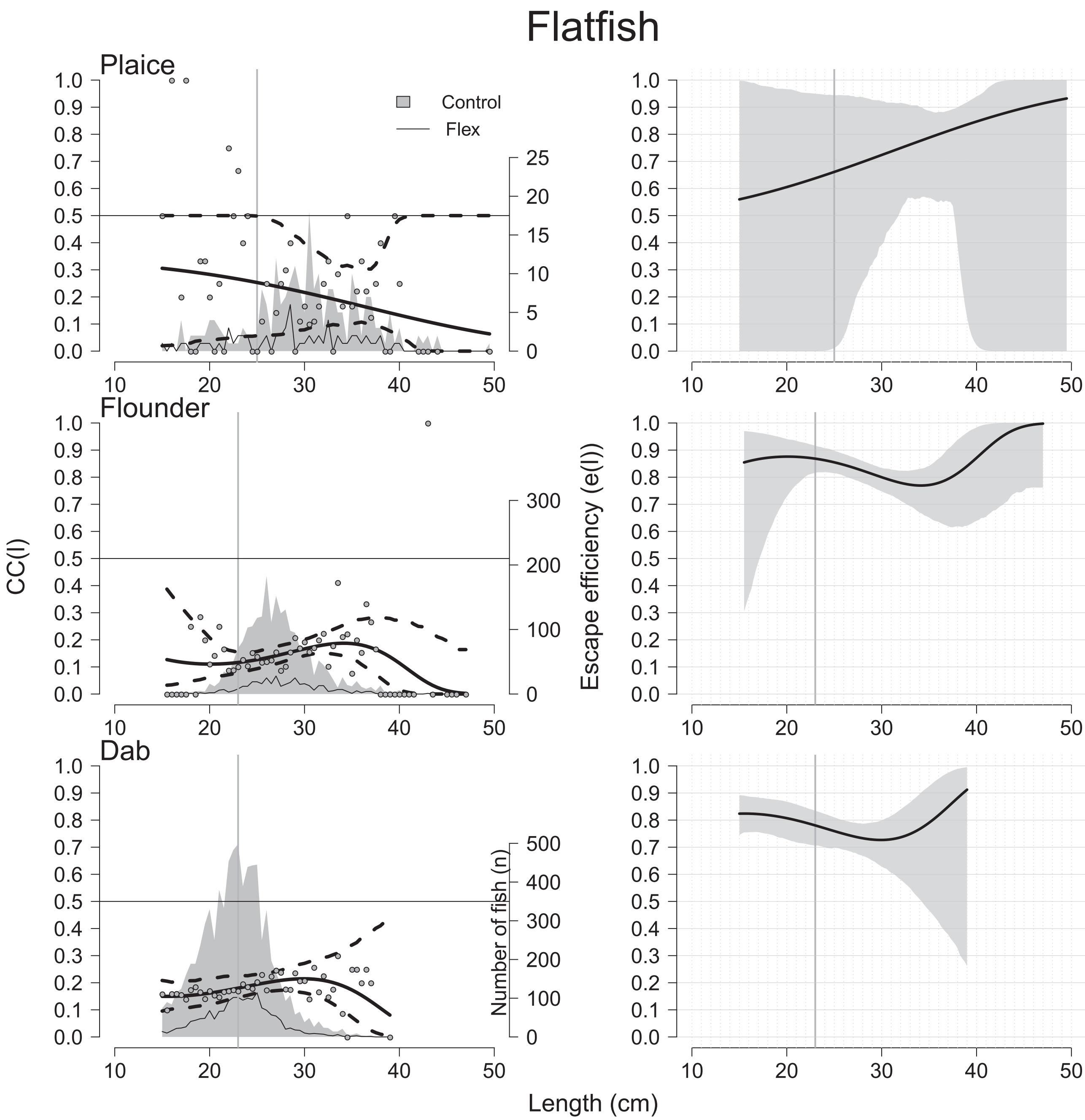

Figure 4. Experimental catches and model results for the three flatfish species analysed [plaice (top), flounder (middle), and dab (bottom)]. The left column shows the catch comparison plots. Grey-filled circles represent experimental catch comparison rates per length class (CC_l) (2). The solid thick line represents the estimated catch comparison curve ($CC(l)$) (4–6); dashed lines represent their respective 95% confidence intervals. Total numbers of fish caught per length class in the test gear (solid thin line) and control gear (grey area) are plotted in the background. The right column shows the predicted escape efficiency curves of FLEX ($e_{flex}(l)$, solid line) and associated 95% confidence intervals (grey band). Vertical grey lines represent species MCRS.

Assessment of fish behaviour based on video observations

A total of 11 hauls had the camera mounted in the position shown in Figure 1. Clear images were obtained in hard-bottom fishing grounds. However, towing on soft bottoms—where most of the flatfish catches occurred—led to dense clouds of sediments, which drastically reduced the visibility and sharpness of the video footage. Therefore, only hauls 10, 11, 27, 28, and 33 (Table 1) could be used for simultaneous assessment of flatfish and roundfish behaviour. Four out of these five hauls had a towing duration of 90 min, while haul 27 had a towing duration of 120 min (Table 1). Turbidity associated to soft grounds impeded reaching the predefined number of 30 flatfish observations per haul and the observations of 12, 8, 30, 5, and 24 individuals respectively were obtained throughout the entire tows. Observations on roundfish reached the predefined number of 30 individuals per

Table 2. Fit statistics for the escape efficiency models for the three flatfish species and the two roundfish species analysed (d.o.f = model degrees of freedom, *n* hauls = number of hauls included in the analysis).

Species	*p*-Value	Deviance	d.o.f	*n* hauls
Plaice	0.60	51.79	55	8
Flounder	0.69	53.12	59	17
Dab	0.96	29.86	45	21
Cod	0.49	101.64	102	16
Whiting	<0.01	85.20	54	21

haul and were all collected during the first 50 min of towing. The images obtained were not sufficiently clear to identify fish species accurately; therefore, the assessment was conducted considering two groups of species: flatfish and roundfish. Altogether, 79 flatfish and 150 roundfish were successfully observed, of which 67 [$nE^* = 84.8\%$ (95% confidence interval: 64.3–94.0%)] and six [$nE^* = 4.0\%$ (1.3–8.0%)] individuals escaped through FLEX, respectively. Most of the observed selection processes (Δt) lasted for <2 s, being 35% faster for flatfish than for roundfish (Table 3). Most of the observed flatfish (62 individuals, ~78.5% of the total observed) entered the field of view facing aft towards

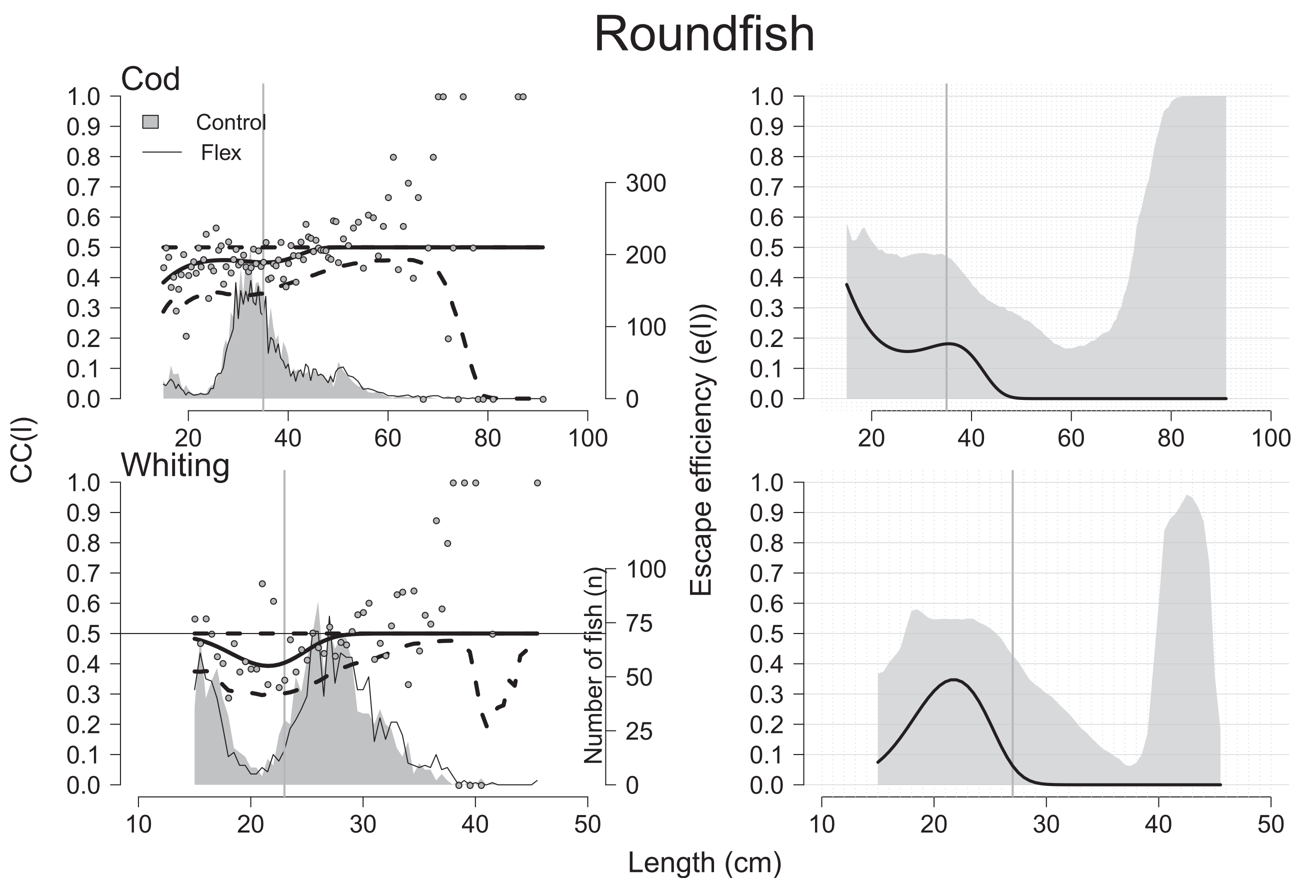

Figure 5. Experimental catches and model results for the two roundfish species analysed [cod (top) and whiting (bottom)]. The left column shows the catch comparison plots. Points represent experimental catch comparison rates per length class (CC_l) (2). Solid thick lines represent the estimated catch comparison curve ($CC(l)$) (4–6); dashed lines represent their respective 95% confidence intervals. Total numbers of fish caught per length class in the test gear (solid thin line) and control gear (grey area) are plotted in the background. The right column shows the predicted escape efficiency curves of FLEX ($e_{flex}(l)$, solid line) and associated 95% confidence intervals (grey band). Vertical grey lines represent species MCRS.

Table 3. Indicators for escape efficiency of FLEX for the different species studied.

Species	Ref length (cm)	nE_-	nE_+	nE	nE^*	Δt
Dab	23	80.66 (72.96 − 86.09)	75.64 (70.51 − 80.14)	78.09 (71.74 − 82.96)	84.81 (64.28 − 93.96)	1.24 (0.88 − 2.24)
Flounder	23	84.97 (77.16 − 91.59)	83.11 (79.13 − 86.17)	83.27 (79.49 − 86.45)		
Plaice	25	62.26 (0 − 91.67)	76.80 (54.46 − 88.43)	73.50 (41.57 − 88.28)		
Cod	35	17.70 (0 − 46.24)	8.84 (0 − 35.59)	14.11 (0 − 41.65)	4.00 (1.31 − 8.00)	1.97 (1.54− 2.53)
Whiting	27	18.37 (0 − 43.99)	4.45 (0 − 37.54)	13.35 (0 − 42.17)		

The three first indicators, nE_-, nE_+, and nE, were calculated by applying (7). The fifth and sixth columns of the table contains the escape indicators obtained from the video observations (nE^*), and the average duration of the observed selection processes (Δt) in seconds. Efron confidence intervals (95%) in brackets.

the codend, while 11 and 6 individuals entered facing forwards and sideways, respectively. Contrary, most roundfish (109 individuals, ~73% of the total observed) entered the field of view facing forwards, while 25 and 16 individuals entered heading aft and sideways, respectively. Altogether, 37 fish (2 flatfish and 35 roundfish) entered the field of view swimming outside the operative zone of FLEX. From these, only two roundfish and one flatfish interacted with FLEX, and all of them were finally retained in the codend. The behaviour of these fish was considered of minor interest in the assessment of FLEX efficiency and therefore the related branches were removed from the resulting trees. To further reduce the dimensions of the trees and therefore to improve their readability, information relative to fish body orientation was also removed (Figures 6 and 7). Raw trees for flatfish and roundfish containing the information of fish orientation and counts of fish outside FLEX active zone are found in Supplementary Figure S2 and S3.

Only 10 out of the 77 flatfish individuals swimming in the operative zone of FLEX ended in the codend. On the other hand, three quarters of the total flatfish observed (59 individuals) approached the device with no evident avoidance behaviour, contacted the device directly at the outlet, and escaped with no evident reaction after contact [MP = 74.7% (57.9–86.5%)] (Figure 6). Seven individuals that steadily approached and contacted the outlet, reacted to the contact actively, and, as a result, four of them ended in the codend. Six individuals that entered in the operative zone of FLEX approached the device swimming upwards [CP = 7.8 (0.0–19.4%)], but none of them avoided contacting the device; four out of the six contacted the net shield [CP = 66.7% (0.0–100.0%)], but such contact did not stimulate a downwards reaction; therefore, all ended up in the codend. The remaining two contacted the outlet [CP = 33.3% (0.0–83.3%)], and one of them escaped. Three flatfish within the active zone approached the device swimming sideways and one did it swimming downwards. These four fish were aggregated into the node "others" at the approach stage [MP = 5.2% (0.0–14.0%)]. All these four fish escaped through FLEX.

The behavioural tree for roundfish resulted leafier than the flatfish tree, indicating more behavioural variation in relation to the selection device. Three quarters of the observed roundfish (115 individuals) entered the field of view of the camera swimming in the operative zone of FLEX. Half of these fish approached FLEX swimming upwards [55 fish, CP = 47.8% (35.1–62.7%)] or other less frequent approaching paths categorized as "others" [3 fish, CP = 2.6% (0.0–6.3%)]. All of these fish ended in the codend, having contacted or not the device. The other 57 individuals steadily approached the device and 34 of them contacted the net shield. Such contact prompted an upwards reaction in 25 of them directing the fish towards the codend [MP = 16.7% (8.7–25.3%)]. Five out of the six observed roundfish escapees occurred when fish steadily approached and contacted the outlet, displaying infrequent reactions after contact categorized as "others" [MP = 1.3% (0.0–5.3%)] or no reacting at all [MP = 2.0% (0.0–4.7%)]. Of those 57 fish that approached FLEX steadily, 22 contacted the outlet and 17 of them avoided passing through it by performing upwards [MP = 7.3% (2.7–12.7%)] or forwards–upwards [MP = 4.0% (0.0–9.3%)] reactions.

Due to the impossibility to obtain escape efficiency indicators by species from the video observations, the comparison with the indicators calculated from the catch data only could be done relatively and by groups of species (Table 3). For flatfish, the average

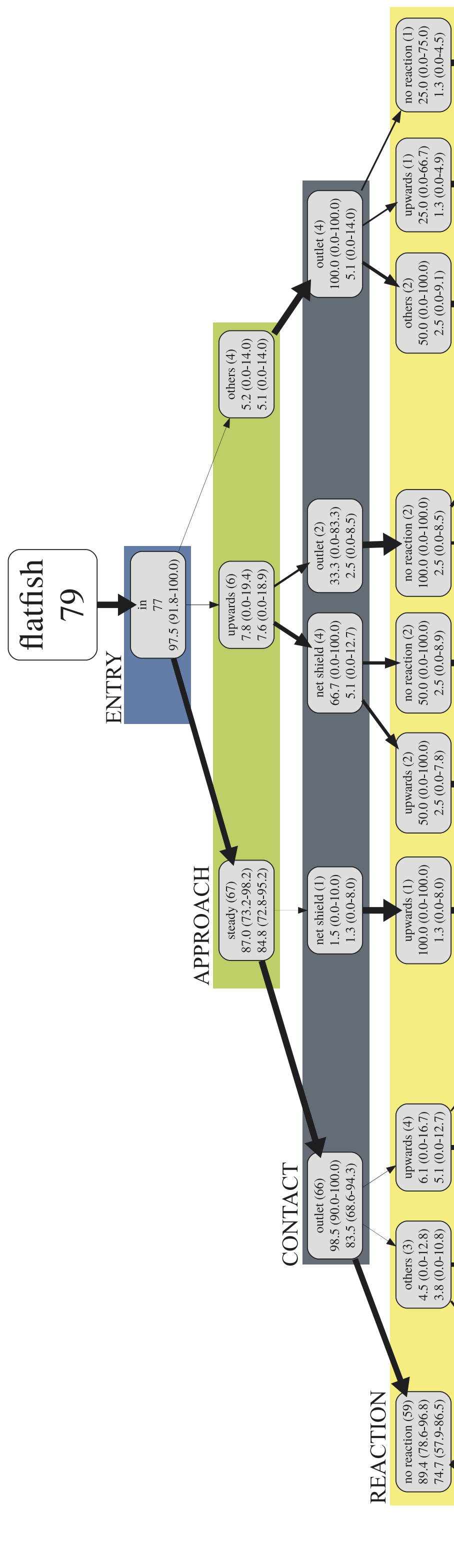

Figure 6. Behavioural trees resulting from the analysis of flatfish video observations. White box represents the root of the tree showing the total number of fish observed. Behavioural events are represented as grey nodes and organized in four different levels related to the behavioural stages. Red boxes represent leafs with counts of fish caught after following a specific sequence of behavioural events, while green boxes represent leafs with counts of fish that escaped through FLEX. The first text line within each node/leaf contains the label of the event plotted and the number of fish observed performing such event (in brackets). The second and third lines show the CP and MP with 95% confidence intervals (in brackets).

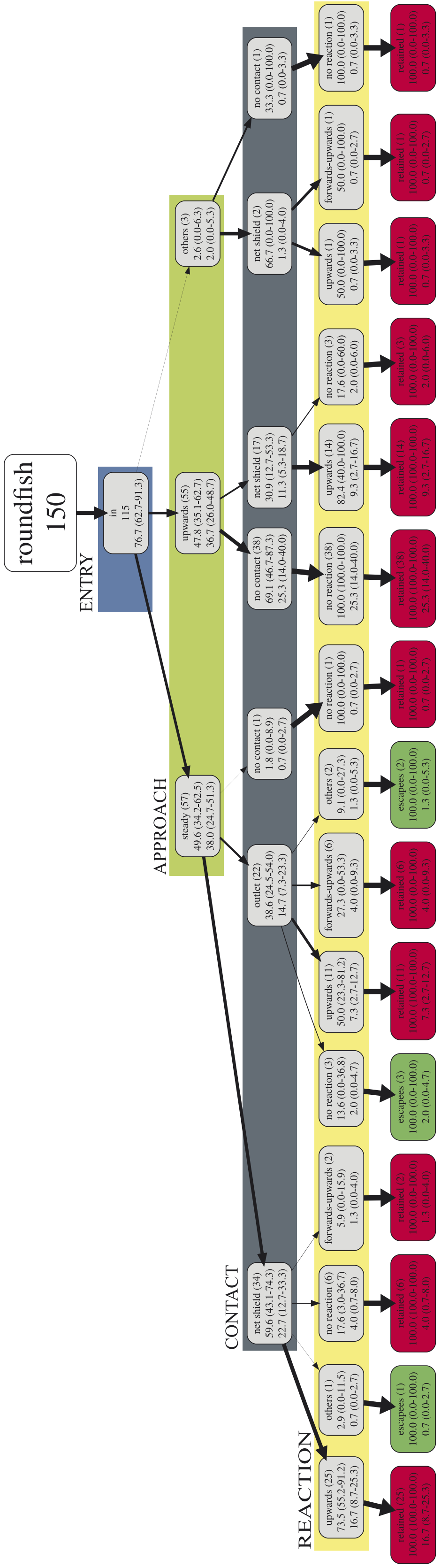

Figure 7. Behavioural trees resulting from the analysis of roundfish video observations. White box represents the root of the tree showing the total number of fish observed. Behavioural events are represented as grey nodes and organized in four different levels related to the behavioural stages. Red boxes represent leafs with counts of fish caught after following a specific sequence of behavioural events, while green boxes represent leafs with counts of fish that escaped through FLEX. The first text line within each node/leaf contains the label of the event plotted and the number of fish observed performing such event (in brackets). The second and third lines show the CP and MP with 95% confidence intervals (in brackets).

nE^* value obtained was very similar to the average nE value obtained for flounder (∼85 vs. ∼83%, respectively). Although the estimated percentile confidence intervals overlap each other, the average nE^* obtained for roundfish was considerably lower than the average nE values of cod and whiting (∼4% vs. ∼14% and ∼13%, respectively).

A selection of fish observations can be found in the Supplementary Material (Supplementary Footages S1–S3). In addition to the observations on fish behaviour in relation to FLEX, the videos also showed that the device consistently released benthic debris entering the trawl (Supplementary Video S4).

Discussion

This study demonstrates the applicability of a method for quantitative analysis of fish behaviour, which can be used to supplement catch-data analyses of performance of selection devices in trawl gears.

Results from this analysis are presented graphically by the so-called behavioural trees (Figures 5 and 6). Behavioural trees provide the researcher with several layers of information regarding fish behaviour in relation to the tested device; while an overview reveals general behavioural patterns and relationships between these patterns and the fate of the fish being selected, a detailed visualization provides information regarding the average probability of occurrence (marginal and conditional) of individual behavioural events. Furthermore, the method provides confidence intervals based on the same bootstrap resampling scheme applied in the catch comparison analysis, therefore properly accounting for different sources of variation potentially influencing fish behaviour in relation to the selection process. To the best of our knowledge, this is the first time the bootstrap scheme usually applied in selectivity analysis is adapted and incorporated into behavioural analysis based on video recordings.

The method has a broad scope of applicability to address questions regarding the functioning of selection devices currently in use. For example, the performance of square mesh panels or grids (Catchpole and Reville, 2008) is usually assessed using models able to quantify the probability that fish efficiently contact the device, and the size selection properties of the device (Zuur *et al.*, 2001; Alzorriz *et al.*, 2016; Santos *et al.*, 2016). However, these models do not provide further information regarding how fish contact the selection device, and which of the potential contact modes could be regarded as "efficient" in relation to the selection process. Our method could provide quantitative answers with uncertainties to such questions, providing guidance for further developing the intended selection.

In this study, we applied the proposed method to assess fish behaviour in relation to a flatfish excluder (FLEX), which was developed and tested in the cod-directed trawl fishery in the Baltic Sea. The potential of using fish behaviour to reduce bycatch remains largely unexploited in the Baltic Sea trawl fishery, and FLEX is probably one of the few selection devices developed in the region whose functioning fully relies upon species' behaviour. During the development phase, very limited quantitative behavioural information was available to guide the conceptual design of FLEX (Krag *et al.*, 2009a). The results from the behavioural analysis obtained in this study revealed that the assumptions regarding expected differences in the behaviour of flatfish and roundfish were valid. Moreover, the behavioural results obtained help to understand how fish interact with the device and provide quantitative information that can be used for future developments.

During the experimental sea trials, most flatfish catches occurred in hauls conducted on muddy or sandy fishing grounds. In these hauls, mud clouds entered the trawl reducing the visibility of the videos recorded, therefore limiting the possibilities to obtain sharp footage of fish behaviour. Attempting to maximize such possibilities, we adopted a systematic sampling scheme, whereby the behaviour of the first 30 flatfish and 30 roundfish observed per haul was evaluated. Due to the uneven presence of mud clouds, flatfish observations were drawn at different towing times. However, all roundfish observations were collected in the first 50 min of towing. Although the knowledge of the swimming capabilities of fatigued fish entering and escaping from a trawl is limited (Ingólfsson *et al.*, 2007), it could be argued that individuals approaching FLEX during the first half of the haul could be less fatigued than those observed during later stages, potentially influencing behavioural responses to the device and the final outcome of the selection process. We argue that such a potential effect would be of concern if observed fish tend to hold their position to avoid the device, maintaining a swimming speed equal to or greater than the towing speed (Krag *et al.*, 2009a). However, the short duration of the selection process observed for roundfish [$\Delta t = 1.97$ s (1.54–2.53)] indicates that the presence of FLEX induced, if any, low-demanding avoidance responses that might be affordable even for exhausted fish (Hannah and Jones, 2012). In any case, the presence of the device did not interrupt their travel towards the codend. An ad hoc inspection of roundfish behaviour during the later stages of towing showed no obvious difference between towing time and roundfish behaviour in relation to FLEX.

Based on catch comparison data from 33 experimental hauls, it was demonstrated that using FLEX greatly reduced the number of flatfish that otherwise would have entered the codend, providing a proof of efficiency required for the device before being considered for commercial adoption. The analysis of catch data from dab and flounder revealed an average escape efficiency of FLEX above 75%, independent of the fish size (Figure 4 and Table 3). Small catches of plaice were obtained during the experiment, resulting in an inaccurate estimate of escape efficiency for this species (Figure 4). However, having noted the low accuracy achieved, and considering the very similar results obtained for flounder and dab, there is no statistical evidence to reject the hypothesis that FLEX could perform for plaice as it did for the other two flatfish species.

Discrepancies between quantitative results from catch-data analysis and video observations can restrict the usability and interpretation of the latter source of information (Krag *et al.*, 2009a). In this study, the close average values and overlap of confidence intervals of the nE indicators estimated for dab and flounder based on the catch-data analysis ($nE = \sim$78 and $\sim$83%, respectively), and those from the estimated flatfish indicator based on video observations ($nE^* = \sim$85) demonstrate the validity of the behavioural analysis to assess escape efficiency of FLEX visually.

The behaviour of flatfish in trawl gears has been mostly studied during initial phases of the catch process in the fore part of the gear (Bublitz, 1996; Ryer, 2008; Underwood *et al.*, 2015); however, less effort has been invested in assessing flatfish behaviour in the trawl body. Krag *et al.* (2009a) quantified vertical preferences and behavioural responses of flatfish in the extension piece of a trawl, using a rigid separator grid that divided the codend into three vertically stacked compartments. Because the part of the trawl investigated, the catches and the behavioural events recorded were similar, the results reported in Krag *et al.* (2009a) are comparable to those presented in the current study. In Krag *et al.* (2009a), 83% of the observed flatfish were retained in the lower compartment of the separator grid, which is nearly the same value as the nE^* value obtained in this study. Our behavioural analysis shows that flatfish are inclined to escape through FLEX without performing avoidance reaction before or after contacting the device. This is also consistent with the findings from Krag *et al.* (2009a), which reported that most flatfish approached the separator grid calmly, without showing evident avoidance reactions before contacting the grid, or panic after passing through it. Moreover, most of the flatfish observed in this study (78%) entered the field of view heading aft towards the codend, a value which is consistent with the 70% reported in Krag *et al.* (2009a) or the 55% reported in He *et al.* (2008). The results obtained in Krag *et al.* (2009a), He *et al.* (2008), and the current study demonstrate that flatfish tend to travel across the aft of the trawl swimming near to the bottom panel of the trawl and oriented towards the codend, without significantly altering their swimming behaviour even when interacting with selection devices placed in their way, at least if such devices do not substantially impede the passing through them. These findings can be useful for future developments of flatfish selection devices located in the trawl body.

Previous studies demonstrated that cod can also be found swimming low at the trawl mouth (Main and Sangster, 1985; Beutel *et al.*, 2008), trawl body (Ferro *et al.*, 2007), and even in the aft end of the trawl (Krag *et al.*, 2009a,b; Melli *et al.*, 2019). Therefore, the potential for overlapping in the vertical distribution of cod and flatfish challenged the development of FLEX. The behavioural analysis demonstrated the need to take such concern seriously, since three quarters of the observed roundfish entered the extension piece through the lower layer of the water column, becoming available for FLEX. Our strategy to avoid losses of marketable cod was to connect a simple deterrent device consisting of a rectangular net shield with small fluttering floats to the outlet (Figure 1). This device was inspired by the findings in Herrmann *et al.* (2015), who demonstrated that the efficiency of escape windows can be improved by provoking upwards swimming reactions of Baltic cod with similar stimulation techniques. The behavioural analysis showed that nearly half of the observed roundfish swimming in the operative zone of FLEX detected the device in advance and displayed upwards-avoidance reactions. This result indicates that the use of stimulation devices in the design of FLEX successfully contributed to reduce potential roundfish escapes. Upwards-avoidance reactions were also the most observed roundfish reaction after contacting FLEX.

Although FLEX's escape efficiency for roundfish was estimated to be low and not significantly different from 0.0%, the comparison among catch-based indicators and the analogous indicators based on video recordings revealed a discrepancy between the nE value calculated for cod and whiting, and the lower nE^* value calculated for roundfish. One explanation for this discrepancy could be a potential effect of device's visibility on the roundfish escape efficiency. It was observed that muddy waters resulting from trawling on soft grounds significantly reduced visibility of FLEX. Under low visibility conditions, it is plausible that the stimulating effect of the net shield and fluttering floats of FLEX could be lower than when those device's elements are highly visible for the approaching fish. Following this argumentation, a reduced stimulation effect due to low visibility could increase the probability for roundfish to contact the device and escape. The inability of the camera system used in this study to collect fish observations under low visibility could therefore bias the estimation of nE^* to lower values. Another explanation is related with roundfish escapees observed during the haul-back, which were not accounted in the behavioural analysis. When bringing the trawl to the vessel, it was observed that some roundfish swam from the codend to the front of FLEX, contacted the outlet near the surface and escaped. These events could be related to the complex manoeuvres conducted by the vessel to retrieve the experimental DBT used in this study. In particular, the vessel had to stop towing before initiating the haul-back, and the process itself took double the time required for a standard trawl, since the crew only could handle the catches of each side one after the other. We speculate that the losses of roundfish observed during the haul-back could be largely avoided by using standard trawls in twin-trawl configuration, a common set-up in Baltic Sea trawl fisheries. Twin trawls are brought on board simultaneously and at towing speed, drastically reducing the duration and complexity of the haul-back process. However, this option was not available due to the lack of twin-trawl facilities on board the research vessel. In any case, since the selection of FLEX occurs in a very specific location at the aft part of the trawl, we argue that the escape efficiency of the device quantified in this study during towing should not be affected by the type of trawl used, at least under same fishing conditions and towing speeds.

Although the difference was not significant, the test codend caught on average fewer small-sized roundfish than the control codend. This was reflected in the average escape efficiency curve, which was >0.0% for smaller length classes. Previous studies quantitatively demonstrated that smaller gadoids tend to swim lower in the trawl body (Melli *et al.*, 2019). Therefore, it could be speculated that the probability of encountering FLEX is higher for small individuals of these species, consequently increasing their chances to escape relative to larger individuals. Since it was not possible to accurately determine the size of the fish observed in the video, this hypothesis could not be investigated in the current study. However, fish size could be obtained in future experiments by using other camera technologies, such as stereo cameras. The resulting size information could be added to the behavioural trees enabling investigations regarding length-dependent behavioural patterns influencing the performance of selection devices like FLEX.

FLEX was conceived as an alternative to the industry-driven FRESWIND device (Santos *et al.*, 2016). FRESWIND exploits differences in fish morphology to largely avoid flatfish catches without compromising the catchability of marketable sizes of cod. However, the device is relatively complex and includes rigid grids that fishermen might be reluctant to use, especially on vessels not equipped with stern ramps (Graham *et al.*, 2004). Furthermore, disabling FRESWIND requires changing the trawl's complete extension piece, limiting the fishermen's flexibility in adapting their fishing strategies on short notice. Therefore, despite the positive results obtained with FRESWIND (Santos *et al.*, 2016), we identified the need for a simpler and more adaptive device without rigid parts, able to reduce flatfish bycatch in the Baltic Sea trawl fishery. Our results demonstrate that it is possible to release a significantly large fraction of flatfish entering a trawl gear by applying a simple and adaptive technical modification in front of the codend. The possibility to easily activate or deactivate FLEX on board allows a dynamic control of trawl-species selectivity, even between hauls. This feature could help fishers adapt their exploitation patterns to changing scenarios in the fishery, which could be an advantage in fisheries regulated by limiting catch quotas or as adaptation to market requirements. Although the study was conducted in the Baltic Sea, the FLEX concept could also be of interest to fishers in other regions with a similar need for adaptive reduction in flatfish bycatch.

Other simple and adaptive devices have been recently proposed to address specific bycatch problems in trawl fisheries. For example, Kynoch *et al.* (2015) demonstrated that the bycatch of skate and sharks can be reduced significantly by removing the tickler chain usually connected to the mouth of demersal trawls. Another adaptive species-selection device proposed recently is FLEXSELECT (Melli *et al.*, 2018), a removable counter-herding device to reduce the bycatch of fish in crustacean trawl fisheries. The effectiveness of these two devices and FLEX mostly depends on species-specific behavioural patterns. It is known, however, that fish behaviour can be largely influenced by intrinsic or environmental factors (Claireaux *et al.*, 1995). Therefore, it should be expected that the efficiency of behavioural devices varies according to variations in fish and/or fishing conditions (Winger *et al.*, 2010). The method for behavioural analysis presented here could be also helpful to quantify and understand variations in the effectiveness of behavioural devices due to such variations in fish and fishing conditions.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Data availability

The datasets generated and analysed during the current study are available from the corresponding author on request.

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Paper III

"Broadening the horizon of size selectivity in trawl gears"

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Broadening the horizon of size selectivity in trawl gears

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ABSTRACT

The discussion of alternative harvest patterns in commercial fisheries has been raised by stock assessment and fishery modelers, especially in the wider context of balanced harvesting. But often, these theoretical approaches propose alternative exploitation patterns that are difficult to achieve within the current limitations in the selectivity characteristics of fishing gears, such as trawl gears. The aim of the present study is to broaden the horizon for size selectivity in trawl gears by demonstrating the feasibility of alternative selectivity patterns for trawls. As a case study, we combined two well-known selection devices to obtain a bell-shaped selectivity curve in trawls with low catch ability of both small and large individuals from the target species. We have successfully tested this gear in the Baltic Sea cod fishery. The results revealed that completely different exploitation patterns for trawl gears can be achieved by means of gear technology.

1. Introduction

Selectivity can be defined as the dependence of a fishing gear's capture efficiency on factors such as size, age, and species (MacLennan, 1992). Adapting the selectivity of fishing gears is the most important strategy used in many fisheries around the world to achieve the desired exploitation patterns. So far, a widely accepted paradigm is that "Improving selectivity leads to a more efficient exploitation of the stock's growth potential" (Macher et al., 2008), and that good fishery management requires fishing gears to catch large adult fish while allowing small juveniles to escape (Armstrong et al., 1990). According to classical theory, length at first catch is the key parameter to optimizing a stock's yield. (Armstrong et al., 1990; Beverton and Holt, 1957).

The size selection of fishing gears is described by selectivity curves, which quantify the probability that a given length class of a given fish species will be caught, assuming that it is available to the gear. Selectivity curves differ between gear types and configurations of gears (Dickson et al., 1995; Hovgård and Lassen, 2000; Wileman et al., 1996). Passive gears, such as gillnets, have size selection properties usually described as bell-shaped curves (Dickson et al., 1995; Hovgård and Lassen, 2000; Huse, 2000; Millar and Fryer, 1999; Millar and Holst, 1997). They are characterized by low retention probabilities at small length classes, as well as at large length classes, with the result that gillnets catch primarily medium-sized length classes.

Historically, the selective properties of trawls and other active gears were adapted by altering the size selection in the codend (Glass, 2000). This strategy assumes that most fish entering the gear drift toward the codend, where a simple size-selection process occurs: smaller fish with specific morphological characteristics have a greater probability of passing through the meshes and escaping, whereas larger fish have a greater probability of being retained in the codend. In contrast to passive gears, the selection curve in trawl gears is S-shaped. Thus, the retention probability increases with the size of fish (Dickson et al., 1995; Gulland, 1983; Huse, 2000; MacLennan, 1995; Millar and Fryer, 1999; Reeves et al., 1992; Wileman et al., 1996). To reduce unwanted bycatch, the classical codend selection is often supplemented with additional selectivity approaches, such as grids (He and Balzano, 2012; Sistiaga et al., 2010), escape windows (Armstrong et al., 1998; Bullough et al., 2007; Catchpole and Revill, 2008; Madsen, 2007), and other strategies (Herrmann et al., 2015). Currently, the selective properties of these types of devices are optimized by changing the S-shaped selectivity curve, resulting in a change in the position of the curve along the length range of the species (often described as the L50-value, length of 50% rejection/retention) and/or in the steepness of the curve often described as the SR-Value, L25–L75; (Dickson et al., 1995; Wileman et al., 1996). A good example of such a limited approach is the development of gear regulations for cod-

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directed fisheries in the Baltic Sea (Feekings et al., 2013; Madsen, 2007). Since 1999, fishery management and fishery science have tried repeatedly to adapt the size selectivity of legal codends to accomplish specific management goals. This effort, mostly limited to discard reduction, has been carried out without considering a broader set of fishery management objectives, such as optimal population dynamics and healthy population structure. Nevertheless, owing to a lack of alternative selectivity options, the standard S-shaped trawl selectivity curve was “only” moved left and right (Fig. 1).

The lack of possible alternatives to the S-shaped trawl selectivity curves also narrows the range of potential exploitation patterns to be investigated in fishery models, in the search for optimal harvest strategies. Typically, such studies only considered S-shaped selectivity scenarios (Kronbak et al., 2009; Macher et al., 2008). With the debate about balanced harvesting (Garcia et al., 2012; Jacobsen et al., 2013; Zhou et al., 2010), additional selectivity patterns are being discussed and used for modeling purposes (Jacobsen et al., 2013). However, it often remains unclear how the alternative harvest patterns could be implemented technically in the fisheries.

Apart from the fundamental concept of balanced harvesting and underlying aims, other rationales offer themselves as alternative harvest strategies for trawl fisheries: Although the importance of age structure for recruitment success is still under discussion (Brunel, 2010; Morgan et al., 2011), there are arguments for a healthy age structure, including large and old individuals (Berkeley et al., 2004; Hixon et al., 2014; Law et al., 2015). For several stocks, the positive influence on population dynamics caused by older individuals has been postulated, with varying driving factors, including parental effects (Cardinale and Arrhenius, 2000; Cerviño et al., 2013; Marteinsdottir and Begg, 2002; Trippel et al., 2005) and enhanced resilience against excessive fishing pressure and against climate variation (Ottersen et al., 2006). The extent of such effects is still being debated (Marshall et al., 2010; O’Farrell and Botsford, 2006). In addition, age-structure indices are also important to ecosystem-based fishery management.

In line with the above arguments, we aim in this study to reduce the catchability of trawl gears for both tails of the length distribution (juveniles and older fish) for a given target species. Achieving this through fishing technology would require finding ways to shift the traditional S-shaped trawl selection curves toward bell-shaped selection curves, commonly associated with passive gears such as gillnets (Dickson et al., 1995). The strategy adopted here emulates gillnet-like bell-shaped selectivity by adding the rejection of larger individuals during the selectivity process in a standard trawl gear. The technological approach is simple and is based on the combination of two well-known and widely used selection devices. The proof of concept was carried out in the Baltic Sea cod-directed fishery.

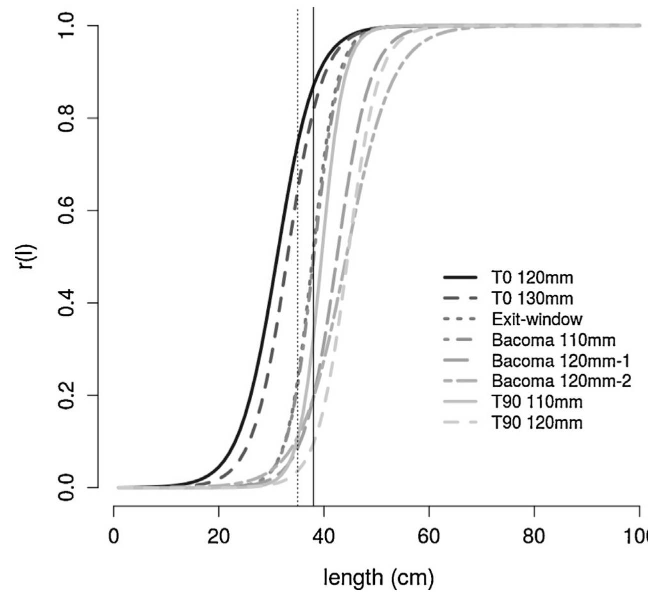

Fig. 1. Selection curves of legalized codends for the Baltic cod trawl fishery, 1999–2015. Vertical lines represent the corresponding minimum landing/reference sizes (MLS; 35 cm, 1999–2002 and 2015; 38 cm, 2003–2014). Codends are (a) T0 120 mm (1999–2001); (b) T0 130 mm (2002–2003); (c) Exit-window (1999–2001); (d) Bacoma 110 mm (2003–2009); Bacoma 120 mm (2001–2003 and 2010–2015); T90 110 mm (2006–2009); T90 120 mm (2010–2015). Selectivity curves were derived from personal, unpublished selectivity experiments conducted between 1999 and 2010. A description of the legislative development can be found in Feekings et al. (2013).

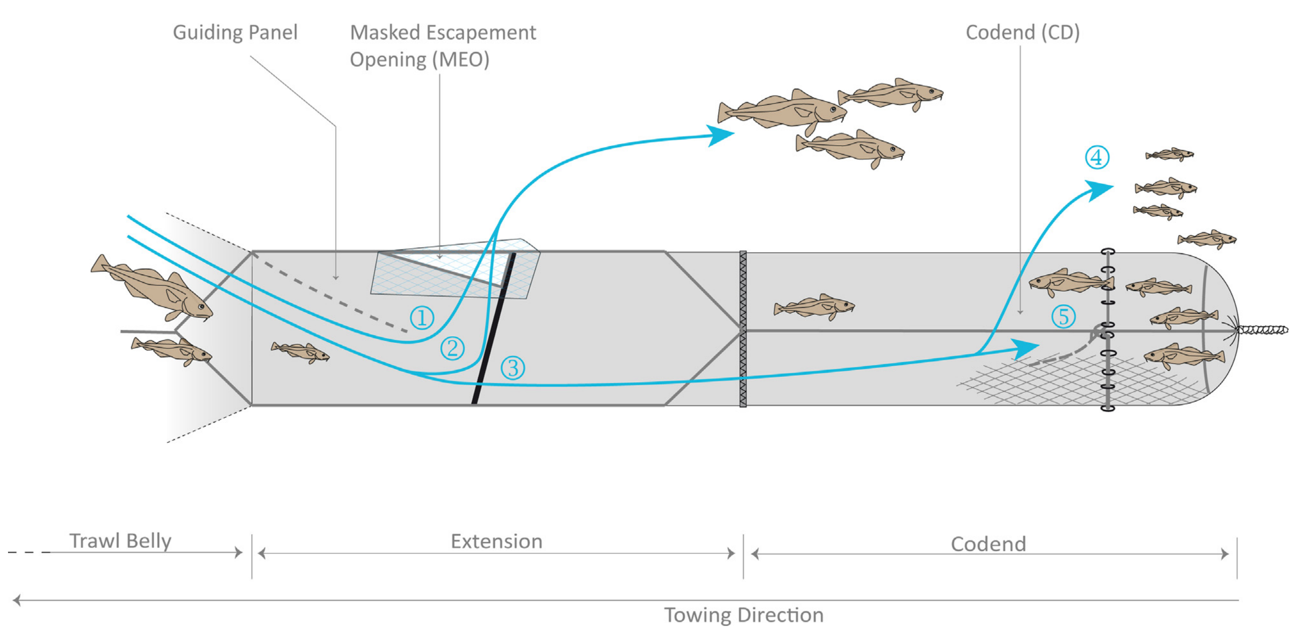

Fig. 2. Illustration of the grid and codend selection system used to obtain bell-shaped trawl selectivity. In addition to technical details, the different traits of fish entering the extension piece are illustrated: (a) fish not contacting the grid and escaping through the MEO; (b) fish contacting the grid, but not able to pass through; (c) fish contacting the grid, passing through, and entering the codend; (d) fish escaping through the codend meshes; (e) fish finally caught within the test codend.

The overall aim of the study is to demonstrate the feasibility of alternative selectivity patterns for trawls in general. Based on this demonstration, it is hoped that the study will stimulate further discussion and development that will broaden the scope of fishery management.

2. Material and methods

2.1. Selectivity concept

To achieve a bell-shaped size selectivity pattern for a target species in trawl fisheries, two selection devices —a grid system and a standard codend—were mounted sequentially (Fig. 2). The first selection device, a steel grid, was mounted in the extension piece between the belly section of the trawl and the codend. The purpose of the grid was to change the population structure entering the codend by rejecting large fish and allowing small and medium-sized fish to pass through it and continue the selection process. Large fish unable to pass through the grid would be excluded from the gear through the escape outlet placed in the upper panel in front of the grid. Ideally, all fish should contact the grid in their normal swimming orientation and be sorted according to size by the grid. However, not all fish entering the gear will necessarily contact the grid, and some may subsequently escape through the outlet, regardless of their size (Millar and Fryer, 1999; Sistiaga et al., 2010). Consequently, this study faced the challenge of ensuring that a large proportion of fish made proper contact with the grid to be sorted by size before encountering the escape outlet. To stimulate grid contact, we attached a rectangular piece of netting at the front of the escape outlet. The netting was mounted over the outlet to make the outlet less visible to fish (Fig. 2). The resulting masked escape outlet is denoted hereafter as MEO.

The small and medium-sized fish not rejected in the grid zone are sorted by the second size-selection process determined by the selectivity properties of the codend. At this stage, only small fish have any probability of escaping by passing through the codend meshes. The profile of the resulting catch is therefore determined by the combination of two size-selection processes, differing in purposes and acting sequentially along the gear. Because codend size selection acts only on fish that contact and pass through the grid in the first selection process, the second selection process is conditioned by the first.

2.2. Experimental setup

To estimate the individual and combined selectivity properties of both selection devices, it is helpful to use a three-compartment setup (Jørgensen et al., 2006; Kvamme and Isaksen, 2004; Sistiaga et al., 2010 (Fig. 3) to directly quantify fish escaping through the MEO (fish rejected by the grid or fish that did not contact the grid), fish retained in the codend, and fish that passed through the codend meshes. We used an experimental design based on the cover method (Wileman et al., 1996) to collect the experimental data. In addition to the common setup, based on covering the codend with a small mesh net cover, this experimental setup uses a top cover to collect the fish using the MEO to escape from the gear. Consequently, the experimental design includes three compartments:

(a) TC = top cover to collect all individuals escaping through the MEO ($n_{TC,l}$)
(b) CD = codend, containing the gear's final catch ($n_{CD,l}$)
(c) CC = cover codend to collect all individuals escaping through the codend meshes ($n_{CC,l}$)

2.3. Model for describing bell-shaped selection curves

The probability that a fish will be caught (*r(l), overall retention probability of the gear*) upon entering the experimental gear depends on the probability that it passes through the grid ($p_{grid}(l)$, *passage probability through the grid*) toward the codend, and that it is subsequently retained in the codend through size selection there ($r_{codend}(l)$, *retention probability in the codend conditioned entry*). The overall size selection of the gear can be described by the following model:

$$r(l) = p_{grid}(l, C_{grid}, L50_{grid}, SR_{grid}) \times r_{codend}(l, L50_{codend}, SR_{codend}) \tag{1}$$

Each of the partial selectivity functions on the right side of Eq. (1) has a specific structure and therefore must be described separately. The first is the probability that a fish will pass through the grid toward the codend ($p_{grid}(l)$). This is the combined probability that a fish efficiently contacts the grid (C_{grid}, *contact probability with grid*) and, once it contacts the grid, it is small enough not to be rejected by the selective properties of the grid ($1-r_{grid}(l)$); therefore:

$$p_{grid}(l, C_{grid}, L50_{grid}, SR_{grid}) = C_{grid} \times (1 - r_{grid}(l, L50_{grid}, SR_{grid})) \tag{2}$$

Second, $r_{codend}(l)$ in Eq. (1) refers to the probability that a fish will be retained in the codend, presupposing that it enters the codend.The probabilities $r_{grid}(l)$ and $r_{codend}(l)$ can be described by standard S-shaped size-selection models for trawl gears. We considered four different S-shaped models: *Logit*, *Probit*, *Gompertz*, and *Richard*. Details of these functions and the respective calculations of the selectivity parameters L50 (length of 50% rejection/retention) and SR (L75–L25) can be found in Wileman et al. (1996).

2.4. Model estimation and selection

The values for the parameters for the overall selection model (1) – C_{grid}, $L50_{grid}$, SR_{grid}, $L50_{codend}$, and SR_{codend} — were obtained using maximum likelihood estimation based on the experimental data, pooled over hauls *j* (1 to *m*) by minimizing:

$$-\sum_{l}\sum_{j=1}^{m}\left\{n_{TC,l,j} \times ln\left(1.0 - p_{grid}\left(l, C_{grid}, L50_{grid}, SR_{grid}\right)\right) + \left(n_{CC,l,j} + n_{CD,l,j}\right) \times ln\left(p_{grid}\left(l, C_{grid}, L50_{grid}, SR_{grid}\right)\right)\right.$$
$$\left. + n_{CC,l,j} \times ln(1.0 - r_{codend}\left(l, L50_{codend}, SR_{codend}\right)) + n_{CD,l,j} \times ln\left(r_{codend}(l, L50_{codend}, SR_{codend})\right)\right\} \tag{3}$$

In total, 16 models were considered to describe the overall size selectivity in the trawl, based on the number of combinations of the four different S-shaped functions considered for both $r_{grid}(l)$ and $r_{codend}(l)$ (Section 2.3). The 16 competing models were evaluated based on their AIC-values (Akaike, 1974); the model with the lowest value was selected. The diagnosis of goodness-of-fit of the selected model to describe the experimental data was based on the *p*-value, model deviance vs. degree of freedom, and finally the inspection of the model curve's ability to reflect the length-based trends in the data.

The maximum likelihood estimate using Eq. (3) with Eq. (1) and (2) and requires the aggregation of the experimental data over

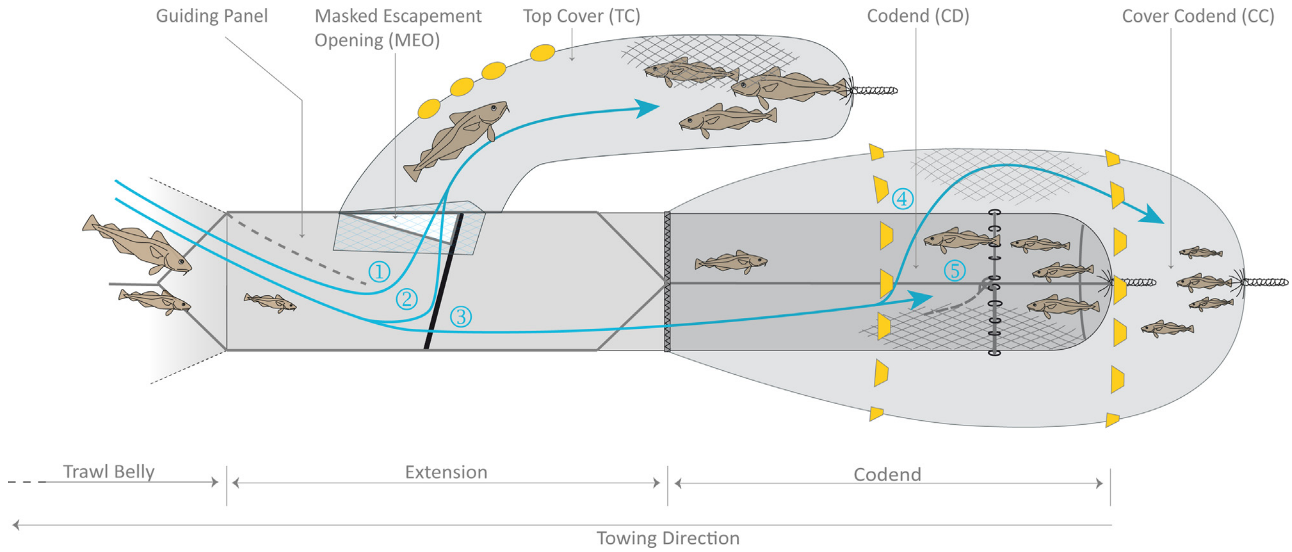

Fig. 3. Illustration of the experimental setup with three compartments. For a description of different numbers, see Fig. 2.

hauls. This results in stronger data to estimate the average size selectivity, at the expense of not considering explicit variation in selectivity between hauls (Fryer, 1991). To account correctly for the effect of between-haul variation in estimating uncertainty in size selection, we used a double bootstrap method to estimate the Efron percentile Confidence Intervals for both the estimated parameters in Equation (1) and the resulting curves for $p_{grid}(l)$, $r_{codend}(l)$, and $r(l)$. We used the software tool SELNET (Herrmann et al., 2012) for the analysis and applied 1000 bootstrap iterations to estimate the confidence intervals.

2.5. Specific setup of the trawl

The experimental trawl was a TV300/60 (300 meshes circumference behind the square with a 120 mm mesh opening in the belly and 60 mm in the extension piece), a standard trawl used in the Baltic cod-directed trawl fishery. The trawl and the codend were two-panel constructions, whereas the extension piece was a four-panel construction (Fig. 3). The extension piece included small transition sections that allowed the two-panel (belly and codend) and four-panel (extension piece) constructions to be joined.

To achieve the intended bell-shaped selection curve by using the proposed sequential selection system, it was necessary to define the grid's bar spacing and codend characteristics, considering the length structure of the population available at the moment of the experiment (obtained from Baltic International Trawl Survey, ICES SD24, first quarter 2014). The information about the population structure revealed very low abundance of large cod (above 50 cm, Fig. 4). We used SELNET's built-in parametric simulation facilities to predict the selection curves of a grid combined with a codend. This simulation (Fig. 4 left) indicated that it would probably not lead to sufficient coverage of the bell-shaped selection curve when combining a highly selective grid (for example with bar spacing of 70 mm) and a codend (for example the mandatory T90 120 mm codend). Therefore, it was proposed to combine a grid with reduced bar spacing (50 mm) and a less-selective codend (T90 105 mm). The grid was installed at an angle of 75° and a guiding panel was installed in front of the grid to further encourage fish contact with the grid, in addition to the use of MEO (Fig. 3). The codend was made of 4 mm PE double twine with an actual mesh size of 107 mm and 50 meshes along and 50 meshes around.

The top cover and cover codend were designed following recommendations of Wileman et al. (1996) (Fig. 3). The cover codend and the last part of the top cover were made of PE single twine 2.5 mm netting with a mesh size of 60 mm. The cover codend dimensions were 570 meshes in circumference and 275 meshes in length. The top cover construction followed the design guidelines from Wileman et al.(1996), therefore it comprises the assembly of net pieces with different dimensions and cutting edges. To avoid masking effects, 11 floats with a buoyancy of ~800 g each were attached to the top cover, while the combination of 5 kites with lead weights were used to separate the cover codend from the codend.

To understand the operation of the selectivity devices and the behavior of fish near such devices, we used GoPro cameras (GoPro Hero 3HD cameras without artificial light), installed at several positions on the trawl.

3. Results

The experimental fishing was conducted on board the German Fishery Research Vessel (FRV) "Solea" (total length = 42 m, 950 kW, stern trawler) over a period of 3 days (21–23 March 2014) in the Western Baltic Sea (Table 1). The water depth varied between 14 and 46 m. The average towing speed was 3 knots. The haul duration was either 90 or 120 min.

In all, eight valid hauls were achieved by the experimental fishing (Table 1). All cod observed in the different compartments were measured to the nearest half centimeter below their total length.

A total of 12 514 cod (5371.28 kg) were caught in experimental hauls used in the analysis (Table 1). All three compartments contained enough cod for proper analysis.

The 16 different models (Section 2.4) were successfully estimated, and the best model (considering the AIC-value) was determined to be the one that used the Gompertz function to describe both the grid and the codend selectivity (Table 2). The estimated curves for grid passage probability, conditioned codend retention, and overall selection together with their 95% confidence intervals are shown in Fig. 5 (left). Inspecting the p-values and deviance vs. DOF-from-the-fit statistics (Table 2) could have indicated lack of fit for the model. But inspecting the ability of the model curves to reproduce the trends in the experimental data revealed no systematic pattern of deviances for any of the curves (Fig. 5). Therefore, we consider the poor fit statistics a result of overdispersion in the data and, based on this, we are confident in applying the model to describe the trends in the data. The probability that a fish efficiently contacted the grid was estimated as $C_{grid} = 0.73$ (Table 2),

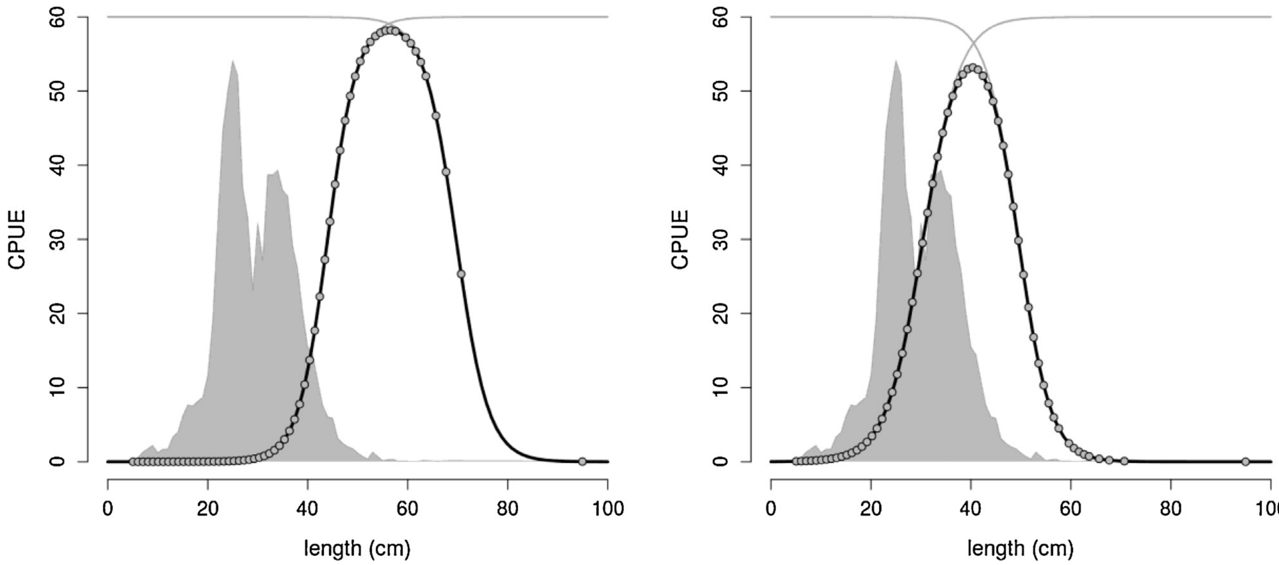

Fig. 4. A priori simulation of expected selectivity of the sequential selectivity system to be used during experimental fishing. Grey shaded area: expected length distribution for cod in the fishing area (derived from Baltic International Trawl Survey, ICES SD24, first quarter 2014). Grey lines: simulated selectivity curves for grid and codend (assuming 100% contact probability with the grid). Black line: resulting retention probability of the entire trawl. Dots indicate the distribution of length classes in population along the simulated retention curve. Left: combination of grid spacing 70 mm with T90 120 mm codend; right: combination of grid spacing 50 mm and T90 105 mm codend.

Table 1
Operational information of the experimental fishing hauls. TC = top cover, CC = cover codend, CD = codend.

Haul	Tow duration(min)	Latitude	Longitude	Depth (m)	Cod catch in different compartments Number (Catch weight in kg)		
					TC	CD	CC
1	120	54°12,227N	012°00,860E	14	321 (137.65)	835 (402.33)	657 (202.11)
2	120	54°12,568N	011°47,101E	23	375 (396.62)	1151 (433.63)	751 (246.03)
3	90	54°12,254N	012°00,422E	15	953 (176.15)	839 (526.22)	741 (238.89)
4	90	54°45,378N	013°29,785E	41	38 (16.40)	364 (148.26)	138 (32.09)
5	120	54°50,315N	013°27,635E	46	608 (239.47)	966 (418.59)	396 (115.05)
6	120	54°52,660N	013°15,529E	45	197 (80.44)	649 (254.39)	634 (147.39)
7	120	54°52,610N	013°15,166E	45	742 (331.47)	424 (167.88)	268 (63.46)
8	120	54°52,540N	013°30,885E	47	647 (225.76)	487 (266.01)	333 (104.99)
				Total	3881 (1608.44)	4715 (2617.31)	3918 (1150.01)

meaning that 73% of fish entering the trawl effectively contacted the grid and were sorted by it, based on size. Therefore, a number of individuals that could have passed through the grid escaped through the MEO and were released to the top cover (Fig. 5, top left). The underwater video recordings revealed that many fish hit the grid soon after entering the trawl, while others were actively swimming in front of the grid and not making immediately use of it. For those fish, the chances increased to find the way out through the escapement opening above the grid—even when covered by a net panel. This grid-avoidance response by cod could have contributed to the reduction in C_{grid}.

Owing to the value obtained for C_{grid}, which implies the loss of some fish belonging to the desired length classes, the bell-shaped selection curve did not reach the full catchability (retention probability) at the targeted mid-sized length classes. Nevertheless, the overall gear selectivity curve (Fig. 5, bottom left) clearly demonstrates the possibility of obtaining bell-shaped size selectivity in trawls.

Table 2
Selectivity parameters for the best models describing the size selections of the two selective devices in the test gear during the experimental sea trials; 95% confidence limits shown in parentheses; DOF: degree of freedom.

Selection device	Model	Parameter	Value
Grid	Gompertz	C_{grid}	0.73 (0.64–0.83)
		$L50_{grid}$	47.93 (46.45–49.46)
		SR_{grid}	8.40 (5.72–12.14)
Codend	Gompertz	$L50_{codend}$	29.70 (28.22–30.94)
		SR_{codend}	11.05 (10.17–11.82)
		p-Value	0.0093
		Deviance	217.57
		DOF	171
		Number of hauls	8
		AIC	27060.56

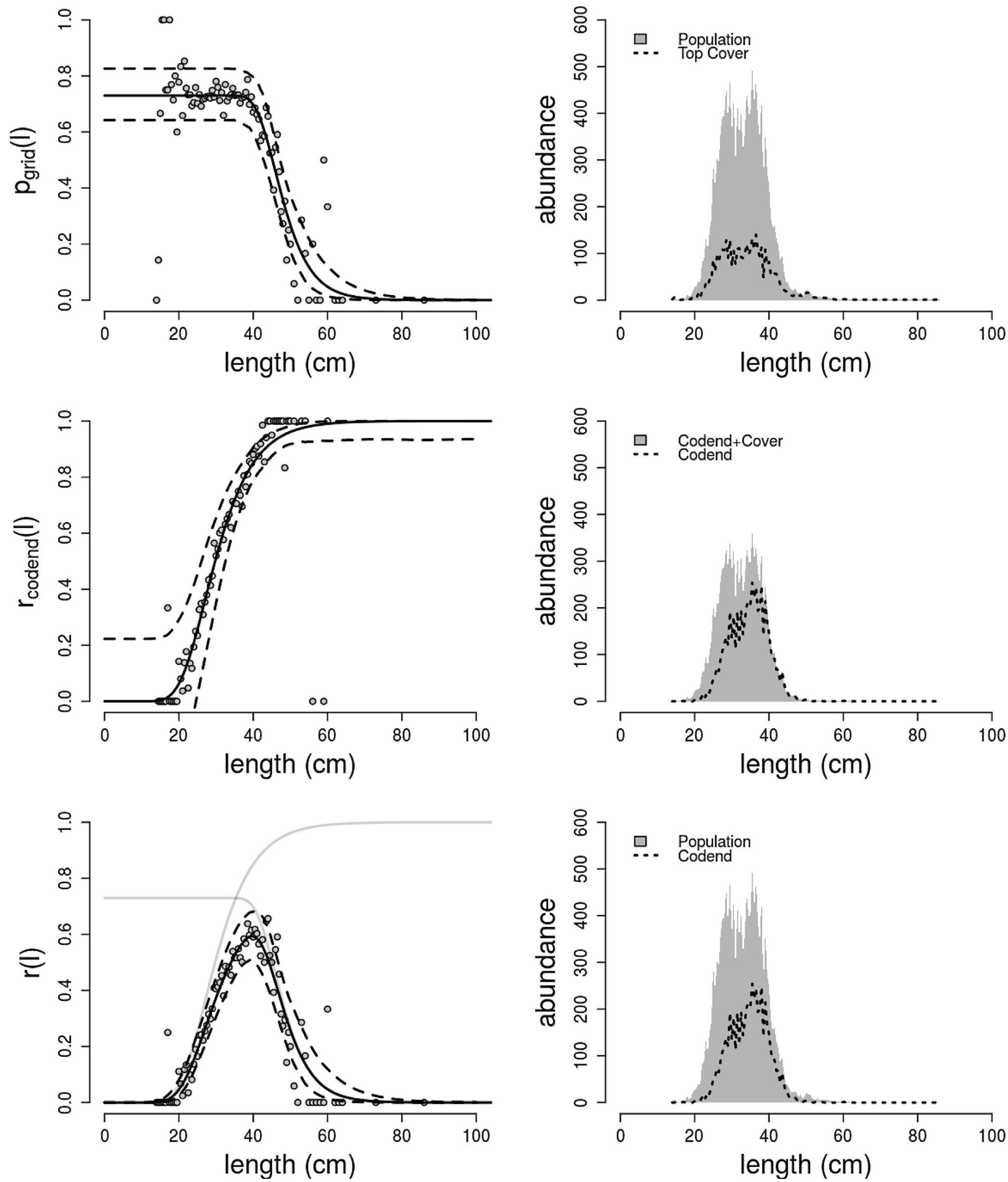

Fig. 5. Left: size selection curves of cod in different selectivity devices (including experimental data (points) and 95% confidence limits). Top: grid with vertical bars and 50 mm bar distance; Middle: T90 105 mm codend; Bottom: selectivity curves of grid and codend (grey lines) and resulting combined selectivity curve. Right: catch within a given compartment (stippled curve) in relation to the length distribution encountering the relevant selection device (grey shaded area).

Our results do not indicate any bias resulting from cover selection, because the model we applied was able to describe the full range of the data without any systematic pattern of deviation.

4. Discussion

The discussion of alternative harvest patterns in commercial fisheries has been raised by stock assessment scientists and fishery modellers, especially in the wider context of balanced harvesting

(Garcia et al., 2012; Jacobsen et al., 2013; Zhou et al., 2010). These theoretical approaches often propose alternative exploitation patterns, which cannot be achieved under the currently assumed paradigm for size-selection characteristics for target species with active fishing gears, such as trawl gears.

The aim of the present study was to broaden the horizon for size selectivity in trawl gears by demonstrating the feasibility of alternative size-selection patterns for trawls, in addition to the traditional S-shaped pattern.

Therefore, we have chosen one example to demonstrate that completely different exploitation patterns can be achieved in trawl fisheries to accomplish alternative fishery-management objectives. The practical exercise was to simultaneously obtain low catch probability of the smaller and larger individuals available in the targeted fish population. The underlying idea is based on the hypothesis that, in addition to short- and medium-term effects of the loss of reproductive potential of older and larger fish, size selectivity of trawls also has a long-term effect. It is known that the fishing pressure in combination with traditional S-shaped selectivity patterns of trawls can result in fishery-induced evolution (Andersen and Brander, 2009; Jørgensen et al., 2007; Kuparinen and Merilä, 2007; Law, 2000). Although the rate of evolution is assumed to be lower than previously published (Andersen and Brander, 2009), an alternative harvest pattern—targeting not only large individuals—may help to reduce the evolutionary effects of trawl selectivity.

The technological strategy adopted to achieve our goal was the combination of two well-known size-selection devices in fishing-gear technology, integrated sequentially in the trawl to establish a dual selection system. This has been tested for the cod-directed trawl fishery in the Baltic Sea. We used a grid to specifically sort out the large individuals of the target species, while allowing smaller fish to enter the codend. The use of a grid for this purpose is new for the target species. Until now, grids have been used to supplement codend size selectivity by allowing small individuals to escape (He and Balzano, 2012; Herrmann et al., 2013; Jørgensen et al., 2006; Kvamme and Isaksen, 2004; Sistiaga et al., 2010; Wileman et al., 1996) or to exclude the entire length range of specific bycatch species from the catch (He and Balzano, 2011; Isaksen et al., 1992; Sala et al., 2011). In some cases, both grid applications are combined in the same gear (He and Balzano, 2013).

In excluder-grid-based selectivity systems, it is also likely that selectivity patterns can be found that differ from the standard S-shape trawl selectivity curve. Possible examples are shrimp fisheries, where trawls are used to avoid catch of unwanted roundfish species (He and Balzano, 2011; Isaksen et al., 1992). If the grid-bar spacing allowed the passage of individuals of roundfish species within the length range, which is also relevant to codend selectivity, it may also be possible to find bell-shaped selectivity for these species. This bell-shaped selectivity curve releases the large individuals in front of the grid and the small individuals in the codend. In contrast to the design used in this study, this potential bell-shaped selectivity curve is derived by accident and is not obtained on purpose, and certainly not for the target species.

The experimental results presented here demonstrate that it is possible to obtain completely different exploitation patterns for trawl gears by means of gear technology.

Based on the length distribution of cod available during the experiments, the selective properties of the selection devices used did not necessarily result in an optimized harvest pattern for cod in the Baltic Sea, but were chosen based on experimental considerations (see Section 2.5) and, following the aim of this study, to act as a feasibility study. Optimal combinations of grid and codend selectivity for a variety of fisheries can be identified in future modelling studies. To improve the proposed selectivity pattern, attention has to be paid to increasing the probability of contact with the grid by specimens entering the trawl.

As mentioned above, the use of multiple selection devices gives more flexibility to obtain desired harvest patterns. On the other side, the complexity of the trawl has effects on costs and handling of the gear. Such aspects also have to be taken into account when identifying optimal harvest strategies to obtain a sustainable use of a population and a sustainable fishery.

It was shown that it is possible to achieve a bell-shaped selectivity in trawl fisheries, which is similar to the selectivity curve of gill-nets. Nevertheless, it is not clear whether the population effect of both fisheries is identical when using bell shaped curves. For instance, it could be influenced by potential differences in survival of escapees in both fisheries.

We hope this study will initiate further discussion and development that will broaden the scope and possibilities of fishery management. Modelers are encouraged to enlarge the scope of their models to include alternative selectivity patterns and to discuss with fishing gear technologists how to bring them into practice.

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Paper IV

"Reducing cod bycatch in flatfish fisheries"

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Reducing cod bycatch in flatfish fisheries

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Abstract:	Management measures to facilitate the recovery of fish stocks can lead to shifts in traditional fishing patterns and target species. In the Baltic Sea, drastic reductions in catch quota for cod (Gadus morhua) force mixed demersal trawl fisheries to avoid cod bycatch and focus on flatfish species. This study developed and tested a simple selection concept that aims to avoid cod bycatch in flatfish-directed trawl fisheries by removing a section of the top panel from the extension piece of the trawl (roofless concept). Sea trials testing the performance of a baseline roofless design, and two designs intended to enhance escape reactions of cod were conducted during two sea cruises. Analysis of the resulting catch data revealed that applying the baseline roofless design consistently reduced cod bycatch by ~75%. Catches of the target species plaice (Pleuronectes platessa) and flounder (Platichthys flesus) were reduced by less than 15%; however, we estimated that catch losses of the two flatfish species could be balanced by increasing fishing effort to ~8% and ~12%, respectively. Under the scenario of fishery choke caused by limited cod quotas, we estimate that the use of the roofless concept could increase fishing possibilities for flatfish by more than 300%.
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Reducing cod bycatch in flatfish fisheries

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Abstract

Management measures to facilitate the recovery of fish stocks can lead to shifts in traditional fishing patterns and target species. In the Baltic Sea, drastic reductions in catch quota for cod (*Gadus morhua*) force mixed demersal trawl fisheries to avoid cod bycatch and focus on flatfish species. This study developed and tested a simple selection concept that aims to avoid cod bycatch in flatfish-directed trawl fisheries by removing a section of the top panel from the extension piece of the trawl (roofless concept). Sea trials testing the performance of a baseline roofless design, and two designs intended to enhance escape reactions of cod were conducted during two sea cruises. Analysis of the resulting catch data revealed that applying the baseline roofless design consistently reduced cod bycatch by ~75%. Catches of the target species plaice (*Pleuronectes platessa)* and flounder (*Platichthys flesus*) were reduced by less than 15%; however, we estimated that catch losses of the two flatfish species could be balanced by increasing fishing effort to ~8% and ~12%, respectively. Under the scenario of fishery choke caused by limited cod quotas, we estimate that the use of the roofless concept could increase fishing possibilities for flatfish by more than 300%.

Keywords

Bycatch reduction device, roofless, landing obligation, catch comparison, fishing effort, dual-species indicators, fish behaviour

Introduction

The productivity of commercial fish stocks is affected by natural and anthropogenic pressure, caused most obviously by changes in marine ecosystems and fisheries (Eero et al., 2011; Cushing, 1995). The Baltic cod populations, especially the eastern stock, are examples of fish stocks affected by adverse fluctuations in environmental factors (e.g. increasing temperature, decreasing salinity, and lower levels of oxygen) and continued overfishing, which have driven the stocks to their current situation of distress (Köster et al., 2017; Eero et al., 2015). Current environmental conditions in the Baltic Sea and recent forecast stock scenarios (ICES, 2020a) render it unlikely that the Eastern Baltic cod stock will recover in the short term (ICES, 2019a). Based on the assessment of the International Council for the Exploration of the Sea (ICES), zero-catch quotas were advised for 2020 and 2021 for the management of the Eastern Baltic cod (ICES, 2020b, 2019b), also affecting the mixing zone of both stocks in the central Baltic Sea (ICES, 2019c). To allow the flatfish-directed fishery to continue, it was agreed to provide a small cod bycatch quota for the fishers. Traditionally, cod has been the most important target species in the demersal trawl fisheries in the Baltic Sea (Madsen, 2007). In these fisheries, cod is usually caught beside flatfish species (ICES, 2019c), such as plaice (*Pleuronectes plattessa*), flounder (*Platichthys flesus*), and dab (*Limanda limanda*). To maintain sustainable and economically viable demersal fishing activities in the current situation, the mixed fishery has to switch to a flatfish fishery, while avoiding cod bycatch as much as possible (ICES, 2019a). Avoiding cod bycatch is especially relevant considering the European landing obligation (European Union, 2013) implemented for the Baltic Sea in 2015. Under this regulation, using fishing gears optimised for catching cod can result in an early exhaustion of the limited bycatch quota, therefore choking fishing possibilities on the flatfish stocks, which are largely in a good state (ICES, 2020a).

Applying species-selection technologies to demersal trawl fisheries has been identified as a potentially efficient strategy to reduce the bycatch of Baltic cod (ICES, 2019a). Research into trawl selectivity in the Baltic Sea has traditionally focused on adjusting codend size selection (Madsen et al., 2021; Wienbeck et al., 2011, 2014; Madsen et al., 2007). In turn, few technologies developed specifically to avoid cod bycatch of any size are available to Baltic fishers. To the best of our knowledge, Madsen et al. (2006) is the only reference available that addresses the question of how to avoid cod bycatch in flatfish fisheries. Madsen et al. (2006) developed and tested a selective flatfish trawl to reduce the relative bycatch of cod, partly by increasing the fishing efficiency on flatfish. Such an increase in fishing efficiency on the flatfish species was achieved by mounting tickler chains in the groundgear, a controversial adaptation because it is associated with a greater impact on the seabed (Depestele et al., 2019). Additionally, following the approach of Madsen et al. (2006) would require the costly replacement of the entire trawl.

A simpler solution could be to add a specific selection device to the commercial trawls already in use. Selection devices designed to exploit differences in fish behaviour during the catch process can be efficient solutions to reduce the bycatch of unwanted species (Lomeli et al., 2018; Beutel et al., 2008; Bayse et al., 2016). Behavioural observations at the non-tapered rear section of trawls (i.e. the extension piece) have revealed the preference of flatfish to swim close to the bottom of the net towards the codend, without significantly altering their behaviour even when interacting with selection devices placed in their way (Santos et al., 2020; Krag et al., 2009; He et al., 2008). In contrast, cod exhibit no clear preferences for a vertical zone in the water column (Karlsen et al., 2019), but exhibit behaviour more active than flatfish in response to the presence of selection devices (Santos et al., 2020). Such differences in behaviour between cod and flatfish have been used recently to reduce flatfish catches by establishing a simple escape opening in the bottom panel of the extension piece (the non-tapered section of the trawl ahead of the codend) of a trawl (Santos et al., 2020). Following the same principle, it is relevant to investigate if establishing an escape opening in the upper panel of the extension piece can be an efficient strategy to reduce cod bycatch without affecting the catches of the targeted flatfish.

In practice, the use of selection devices often leads to catch losses of the target species, compromising the devices' adoption in commercial fisheries (Macher et al., 2008; Suuronen et al., 2007). In this scenario, and especially in fisheries subjected to landing obligations, it is of interest to quantify the trade-off between catch losses of targeted species per unit of effort and the additional fishing opportunities derived from a reduction in the bycatch of a potential choke species. However, such trade-offs cannot be quantified using traditional analytical methods that assess the selectivity of fishing trawls from a single-species perspective (Wileman, 1996). Key questions to be answered are: (i) How much must the fishing effort be increased to compensate for potential catch losses of targeted species owing to the use of a given selection device? (ii) To what extent would the reduction in the bycatch of the most limiting (potential) choke species improve the fishing opportunities for the target species? To answer such questions, this study introduces so-called fishing-effort and dual-species indicators. Combined with traditional selectivity analysis, these indicators should provide a wider picture of cost–benefit trade-offs related to the use of a given selection device, thus identifying the best technical solution for individual fishing and management scenarios.

This study will develop and test a selection device that provides an escape opening in the upper panel of the net, designed to reduce cod bycatch without affecting flatfish catch efficiency. The selection device can be applied directly to current commercial trawls without major gear modifications. We also investigate to what extent the escape rates of target and bycatch species could be affected by (i) the length of the escape opening, and (ii) active stimulation strategies to enhance the escape reaction in cod.

Material and methods

2.1. The roofless device

The species selection concept investigated here was established by removing a net section from the upper panel of the extension piece of the trawl. This simple modification is hereafter referred to as the roofless device. It is assumed that establishing the roofless device will create a zone of increased visual contrast and water flow disturbances that could trigger escape reactions in fish (Kim, 1997; Glass et al., 1995; Briggs, 1992). Following the different behavioural patterns observed for flatfish and cod at the non-tapered section of the trawl (Santos et al., 2020; Karlsen et al., 2019; Krag et al., 2009; He et al., 2008), the intended species selection was made on the assumption that the local visual stimuli and hydrodynamic disturbances created by the roofless device will attract cod towards the escape opening, whereas flatfish will not react to the presence of the device, continuing their path towards the codend.

The extension piece was made of four panels of diamond-mesh netting, 4 mm double PE twine, and a mesh size of ~114 mm (mesh measurements according to Fonteyne et al., 2007). The panels were 39.5 meshes long and 25 meshes wide. The extension piece was connected to the trawl body by a 2-to-4 panel adapter and to the codend by a 4-to-2 panel adapter, made of the same material as the extension and having a total length of 22.5 meshes each. The approximate length of the whole gear, combining the extension piece with the front and rear adapters, was ~10.1 m (estimated length of fully stretched netting). Connected to the gear was a mandatory T90 codend (European Union, 2019), made of 4 mm double PE twine, and measured mesh size of ~120 mm, 50 meshes in circumference and ~8 m long.

The roofless device was formed by removing a 14.5-meshes-long rectangular net section of the top panel (~175 cm long) and as wide as the panel, excluding the meshes in the selvedge. The longitudinal cut of the panel was straight (N-cut) and ran backwards from the first quarter of the total length of the extension. The transversal cut was also straight (T-cut). The section of the top panel directly in front of the escape opening was raised by two floats of 2.5 kg buoyancy mounted in line, one after another. To keep the escape opening stable, two plastic rods of 25 mm diameter and 90 cm long were attached crosswise to the extension, one to the bottom panel underneath the escape opening, and the other to the top panel at the rear end of the escape opening. Hereafter, this design is referred to as RL175 (derived from RoofLess 175 cm) or baseline design (Figure 1).

Further technical information on the test gear (extension piece, adapters, and RL175) can be found in the Supplemental Material (Figure S1).

In addition, two modifications of the baseline design thought to further stimulate cod escape behaviour were developed and tested. In the first modification, the length of the escape opening was increased to nearly double the length of the section removed from the top panel (27.5 meshes deep, ~330 cm long). In the second modification, float ropes were applied according to Herrmann et al. (2014). Each float rope consisted of six floats of 0.115 kg buoyancy attached to a PE rope. The lower tip of the rope was attached to the bottom net panel of the extension underneath the opening; the upper tip was attached to the rear edge of the escape opening. Four float ropes were mounted, one beside the other, across the tunnel, thus disturbing the free passage of fish swimming through the extension towards the codend. The ropes' upward inclination and their fluttering motion during towing were predicted to stimulate cod to swim upwards towards the escape opening. Hereafter, the stimulus-enhancing design with an elongated escape opening will be referred to as RL330 (derived from RoofLess 330 cm), and the design mounting float ropes will be referred to as RL175+ (Figure 1).

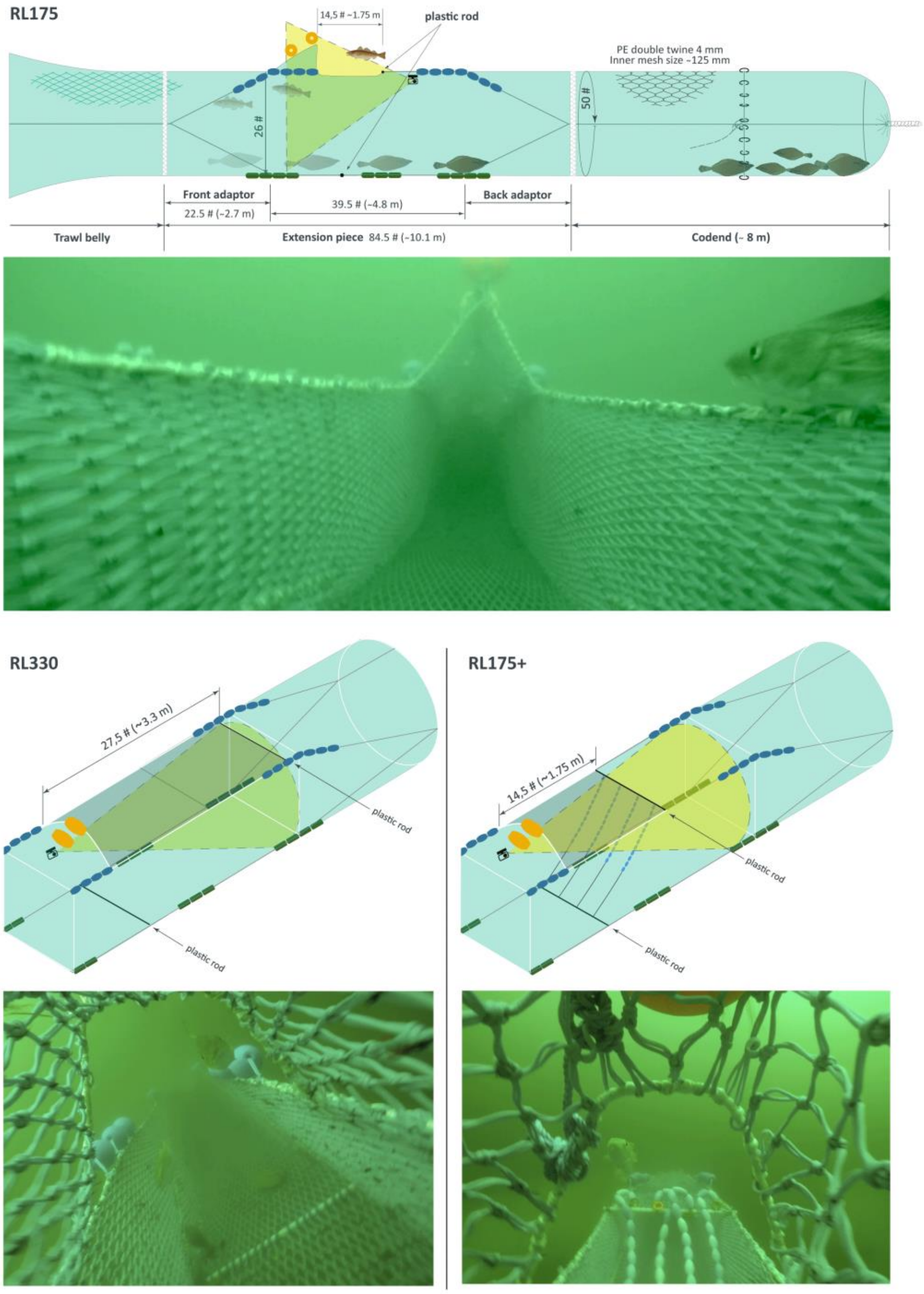

Figure 1. Design and underwater pictures of the baseline roofless device and its modifications. Top: technical characteristics and conceptual functioning of the baseline roofless device (RL175), mounted in the test gear together with the mandatory T90 codend. Bottom: technical characteristics of the two stimulus-enhancing designs RL330 (left) and RL175+ (right). The drawings also show the camera positioning and perspective from which the related underwater pictures were taken.

2.2. Experimental fishing and data collection

The performance of the three roofless designs was tested during two cruises. Fishing trials during Cruise 1 were conducted on board the German research vessel FRV Clupea (28.80 m LOA, 478 kW), and took place within the area of distribution of the western cod stock (Hemmer-Hansen et al., 2019; Weist et al., 2019), at the border zone between ICES Subdivisions 22 and 24. The roofless designs tested during Cruise 1 were the baseline (RL175) and the RL330 designs. The experimental design applied was a catch comparison (Herrmann et al., 2018; Krag et al., 2015) using twin-trawl type TV300/60 (Figure S2), similar in design to the commercial trawls used in demersal Baltic fisheries. One trawl mounted the extension piece with the roofless device (test gear); the other trawl mounted the same extension piece with the top panel unaltered (reference gear). The test trawl involved two selection processes, provided sequentially by the roofless device and the mandatory T90 codend. As selection device, the other trawl had only the same T90 codend as the test gear. Therefore, this trawl was considered the reference for the current selectivity in the commercial fishery.

Fishing trials during Cruise 2 were conducted on board the German FRV Solea (42.40 m LOA, 1780 kW), covering a wide spatial area, which included the same fishing grounds as Cruise 1, the overlapping zone between western and eastern cod stocks in ICES Subdivision 24 (Weist et al., 2019), and fishing grounds within the area of distribution of the eastern cod stock (ICES Subdivision 25). Tests on the performance of the baseline roofless design were replicated during Cruise 2, using the same extension pieces and codends as were used during Cruise 1, but under different experimental and fishing conditions. Furthermore, during Cruise 2, we assessed the effect of adding float ropes (RL175+) to the baseline escape efficiency. Owing to the lack of twin-trawl facilities on board FRV Solea, the catch comparison was performed using the same double belly trawl (DBT) as described in Santos et al. (2020; Figure S3).

The experimental design was applied consistently during both cruises. Each roofless design was tested one at a time for a given number of hauls. When possible, consecutive hauls were done in opposite towing directions in order to neutralise any potential influence of uncontrolled operational conditions (e.g. sea state) on the probability that a fish will enter either trawl. Previous trials with the same vessels and trawls have demonstrated equal fishing efficiency, independent of the side on which the trawls were mounted (see Figure S4 as proof of the lack of side effect for the DBT). Consequently, it was not considered necessary to switch the trawls between sides during the experiment. Catches from the test and reference gears were kept separate and sampled one after another. The catch from each codend was sorted by species, and all individuals from each of the analysed species were length-measured to the half centimetre below (total length), using Scantrol electronic measuring boards.

2.3. Data analysis

2.3.1. Catch comparison analysis

Based on a group of valid hauls *i = 1,..,h*, the expected average length-dependent catch efficiency of the test gear relative to the reference gear can be estimated as:

$$CC_l = \frac{\sum nt_{il}}{\sum (nr_{il} + nt_{il})} \qquad (1)$$

The experimental catch comparison data (CC_l) at fish length l expresses the effect of the roofless device on the catch efficiency of the test gear (Krag et al., 2014, 2015). A value of CC_l = 0.5 implies that the catches of a given species at length l would be shared equally among the test and the reference gears, which indicates no effect of the roofless device on the catch efficiency of the test trawl. Following the same interpretation, the lower the value below 0.5, the smaller the catch in the test gear compared with the reference gear, and so, the larger the catch reduction caused by the roofless device. The comparative assessment of the roofless effect across lengths is done by estimating the most likely catch comparison curve associated with the experimental CC_l data. In this study, the $CC(l)$ curve is defined as:

$$CC(l,v) = \frac{\exp(f(l,v))}{1.0 + \exp(f(l,v))} \qquad (2)$$

where $f(l,\mathbf{v})$ is a smooth function of fish length, with a functional form controlled by a 4-order polynomial basis with parameters $\mathbf{v} = (v_0, v_1, v_2, v_3, v_4)$. The length-dependent catch comparison analysis is therefore reduced to an optimisation problem, in which the values of the parameters $\mathbf{v}$ associated with the $CC(l)$ curve most likely related to the experimental data are estimated. Thus, the maximum likelihood function involving Equation (2) and the catch data is defined as:

$$logLik = -\sum_i \sum_l \left\{ nt_{il} \times \ln(CC(l,v)) + nr_{il} \times \ln(1.0 - CC(l,v)) \right\} \tag{3}$$

Equation (3) is minimised relative to $\mathbf{v}$, which is equivalent to maximising the probability for the observed data. Evaluation of a model's ability to describe the data sufficiently well using Equations (2 and 3) was based on the calculation of the corresponding *p*-value together with the visual inspection of residuals distribution. Wileman et al. (1996) provide details on how to apply and interpret these fit statistics.

Leaving out one or more of the parameters v_0–v_4 in Equation (2) led to 31 additional simpler models, which were also considered potential candidates for modelling the catch comparison data, therefore also estimated by Equation (3). The 32 competing models were ranked by decreasing AIC value (Akaike, 1974). The predicted catch comparison curve $CC(l,\mathbf{v})$ was obtained using a model averaging procedure involving all models considered, weighted by their relevance to decreasing values of AIC (Herrmann et al., 2017).

If the catch comparison curve $CC(l,\mathbf{v})$ has been estimated by Equations (2 and 3) at length *l*, the length-dependent curve describing the ratio of catches in the test trawl to the catches in the reference trawl can be derived as:

$$CR(l,v) = \frac{CC(l,v)}{1 - CC(l,v)} \tag{4}$$

The resulting $CR(l,\mathbf{v})$ curve directly relates the catch efficiency of the test trawl to the catch efficiency of the reference trawl, and so, it is better suited to quantitatively assess the escape efficiency of the roofless device than the *CC(l,**v**)* curve. For example, values of *CR(l,**v**)* close to 1.0 would imply similar catches in the test and reference gears. In the present study, such values would be desirable for marketable sizes of flatfish species, indicating low escape efficiency of the targeted flatfish. Conversely, low *CR(l,**v**)* values for cod would express high escape efficiency for the bycatch species. For example, a value of *CR(l,**v**)* = 0.2 would imply an escape efficiency of 80% at length *l* (20% catch efficiency).

Efron confidence intervals (95% CI) of the curves predicted by Equations (3 and 4) were obtained using the double bootstrap procedure (1000 iterations) traditionally applied in selectivity studies (Krag et al., 2014; Millar, 1993). This includes accounting for between-haul variation in the catch comparison curve and the uncertainty in individual hauls resulting from the capture of a finite number of fish. In addition, the bootstrap method accounts for the uncertainty related to the model-averaging procedure used to predict *CC(l,**v**)*. The catch comparison analysis described above was carried out using the software tool SELNET (Herrmann et al., 2018; Krag et al., 2014).

2.3.2 Quantifying the effect of stimulus-enhancing designs on the baseline escape efficiency

Similar to the method described in Melli et al. (2019), the effect of each of the two stimulus-enhancing modifications tested was assessed by quantifying the differences between the baseline catch ratio curve $CR_b(l,v)$ obtained with the RL175 design, and the catch ratio curves obtained from either the RL330 or the RL175+ designs ($CR^*(l,v)$):

$$\Delta CR(l,v) = CR_b(l,v) - CR^*(l,v) \qquad (5)$$

Confidence intervals associated with ΔCR(l,v) were obtained by synchronising the outer bootstrap resampling scheme from both the baseline and the stimulus-enhancing design being assessed.

2.3.3 Fishery usability indicators

Contrary to the curves estimated by Equations (3 and 4), the indicators defined in this section are point estimates that consider the size structure of the catches obtained during the experiments. The estimated indicators are used to answer relevant questions related to the usability of the roofless device in the fishery:

What is the relative performance of the test gear on catch fractions defined by management reference sizes?

The first three indicators are used to assess the catch efficiency of the test gear relative to the reference gear. Point estimates are obtained by grouping the catch data into fractions defined by a given reference size of the species being analysed:

$$
\begin{aligned}
nS &= \sum_{i=1}^{h} \sum_{l} \frac{nt_{il}}{nr_{il}} \\
nS- &= \sum_{i=1}^{h} \sum_{l<mrs} \frac{nt_{il}}{nr_{il}} \\
nS+ &= \sum_{i=1}^{h} \sum_{l \geq mrs} \frac{nt_{il}}{nr_{il}}
\end{aligned}
\qquad (6)
$$

Indicators in Equation (6) are calculated as the ratio of catches (in numbers) of species *S* in the test gear to catches in the reference gear. The catch ratios are estimated based on the total catch (nS), and catch fractions below ($nS-$) and equal to or greater ($nS+$) than a species-specific management reference size (mrs). The reference size used here for cod and plaice are the species minimum conservation reference sizes in the Baltic Sea (35 cm and 25 cm, respectively). The minimum conservation reference size used for flounder in the area where the sea trials were conducted is 23 cm. However, according to the current preferences in German markets, there is no commercial interest in flounder smaller than 25 cm. Therefore, we used the same reference size as for plaice.

How much should fishing effort be increased to compensate for potential catch losses of targeted flatfish?

Applying the roofless device to the test gear can lead to catch losses of targeted flatfish (*f*), expressed as $nS_f+ < 1.0$. In such a scenario, the indicator $\Delta Effort$ quantifies how much additional fishing effort would be required to balance the catch losses in the test gear relative to catches in the reference gear, after *h* hauls:

$$\Delta Effort = \times \left(\frac{h}{h \times nS_f +} - 1.0 \right) \quad (7)$$

What are the cost–benefit trade-offs related to potential reductions in cod bycatch and catch losses of target flatfish species?

In fisheries subjected to landing obligations, the costs associated with a loss in catchability of the target species derived from the use of the selection device need to be assessed considering the benefits associated with a potential reduction in bycatch from species with limited quota.

Considering cod (*c*) as the bycatch (choke) species and flatfish (*f*, either plaice or flounder) ≥ 25 cm as the target, the following dual-species indicators are calculated:

$$nR_t = \frac{\sum_{i=1}^{h} \sum_{l} ntc_{il}}{\sum_{i=1}^{h} \sum_{l \geq mrs} ntf_{il}}$$

$$nR_r = \frac{\sum_{i=1}^{h} \sum_{l} nrc_{il}}{\sum_{i=1}^{h} \sum_{l \geq mrs} nrf_{il}} \quad (8)$$

$$nRR_t = \frac{nR_t}{nR_r}$$

where nR_t and nR_r are bycatch ratios in test and reference gears, and nRR_t is the relative bycatch ratio of the test gear.

In a simulated scenario where the maximum allowable catches of the choke species would be achieved after conducting *h* hauls with the reference gear,

$$\sum_{i=1}^{h} \sum_{l} nrc_{il} = nc_{choke} \quad (9)$$

the indicator nRR_t can be used to project how many additional fishing possibilities for the targeted flatfish species could be expected by using the test trawl until the nc_{choke} *is* reached:

$$nf^*_t = \frac{\sum_{i=1}^{h} \sum_{l \geq mrs} nf_{r,i,l}}{nRR_t} \qquad (10)$$

$$nRf^*_t = \frac{nf^*_t}{\sum_{i=1}^{h} \sum_{mrs} nf_{r,i,l}}$$

where nf^*_t is the projected catches estimated for the test gear once nc_{choke} is reached; nRf^*_t is the ratio between the flatfish catches projected for the test gear to the empirical catches obtained in the reference trawl after *h* hauls. Values of $nRf_t^* > 1.0$ would indicate gains in fishing possibilities for the targeted species derived from the use of the roofless device.

Indicators described in Equations (6–10) were calculated for each roofless design by cruise and after combining the information from both cruises. The resulting values are presented in percentages. Efron confidence intervals (95%) associated with the fishery usability indicators were obtained using the same bootstrap scheme described in the previous section. The indicators analysis was conducted using R (R Core Team, 2020).

3. Results

3.1. Description of fishing operations and catches

Cruise 1 took place between 11 and 19 December 2019 (Table 1), yielding 16 valid hauls. The tows were conducted at fishing depths averaging 15.5 m (SD = 2.2), the towing speed was set at 3 knots, and the towing duration averaged 54 min (SD = 12). The first eight hauls (11–16 December) tested the escape efficiency of the RL330 design. Catches were made of cod (n = 1821), plaice (n = 1394), and flounder (n = 428). The remaining eight hauls were used to test the baseline roofless design RL175 (17–19 December). Although the catch profile was very similar to the previous experiments, catch volumes decreased to nearly half. Cod and plaice were again the most abundant species (n = 925 and n = 723, respectively), whereas catches of flounder were relatively small (n = 291).

Cruise 2 took place between 4 and 8 February, 2020 (Table 1). In all, 22 valid hauls were conducted, of which 15 hauls were located in ICES Subdivision 24 (average fishing depth = 22.9 m (SD = 15.5)), and the remaining seven in Subdivision 25 (average fishing depth = 65.2 m (SD = 5.4)). The towing speed was set to 3 knots, whereas the towing duration was, on average, shorter than the average haul duration from Cruise 1 (40.3 min, SD = 11.7). The baseline roofless (RL175) and RL175+ designs were alternated across hauls, totalling 12 and 10 hauls, respectively. The total cod catches obtained in each trial were comparable with those obtained in Cruise 1 (n = 1254 and n = 1098 for RL175 and RL175+ trials, respectively). Conversely, flounder was the most abundant flatfish species in Cruise 2 (n = 3267 and n = 2132 for RL175 and RL175+, respectively), whereas catches of plaice were small (n = 329 and n = 252 for RL175 and RL175+, respectively; Table 1).

3.2 Catch comparison analysis

Data from all experimental hauls were used to analyse the performance of the three roofless designs, except for the plaice data from Cruise 2, haul 14, owing to problems in the data collection. The models described in Equations (3–5) were successfully fitted to the data. Most of the fitted models present high goodness-of-fit to the experimental data (p-values > 0.05). However, four models present poor fit statistics (p-values < 0.05), likely caused by a combined effect of model overdispersion and weak length dependence of the observed catch comparison data (Table 2). The experimental catch comparison data reveal that cod was caught mostly in the reference codend, irrespective of the roofless design used. Consequently, the estimated catch comparison curves ($CC(l)$) are significantly lower than the value of CC = 0.5. This result is linked to significant escape efficiency for cod. Assessment of the resulting $CC(l)$ curves reveals no clear length dependence on cod escape efficiency; however three of the curves predict a slight negative trend throughout the most abundant lengths, which suggests a slight increase in escape efficiency for larger cod (Figure 2).

Table 1. Operational information of the hauls conducted during Cruise 1 and Cruise 2, and catches by species, haul, and gear (test and reference).

			Haul	Duration	Latitude	Longitude	Course	Depth	Cod (n fish)		Plaice (n fish)		Flounder (n fish)	
Cruise	Date	Tested design		(min)	(°)	(DD)	(°)	(m)	Test	Reference	Test	Reference	Test	Reference
1	2019/12/11	RL330	1	60	54°11.8	11°53.7	101	16	55	294	94	101	36	52
	2019/12/12	RL330	2	60	54°12.2	12°00.5	265	13	4	95	60	85	13	15
	2019/12/12	RL330	3	60	54°11.7	11°53.9	94	18	10	56	43	57	23	35
	2019/12/12	RL330	4	60	54°12.0	11°59.5	258	14	12	5	51	45	9	15
	2019/12/13	RL330	5	60	54°12.2	12°00.2	261	13	30	88	90	148	10	16
	2019/12/16	RL330	6	60	54°12.1	11°59.8	259	13	57	253	78	116	20	21
	2019/12/16	RL330	7	60	54°11.8	11°52.5	97	18	125	595	114	167	38	52
	2019/12/16	RL330	8	30	54°11.9	11°52.1	96	18	17	125	63	82	40	33
	2019/12/17	RL175	9	30	54°11.9	11°52.3	98	17	22	84	47	57	16	26
	2019/12/17	RL175	10	30	54°11.7	11°52.3	277	17	7	13	107	114	43	60
	2019/12/17	RL175	11	60	54°11.7	11°53.9	96	17	17	256	35	36	9	9
	2019/12/18	RL175	12	60	54°12.1	11°59.9	258	13	14	31	25	16	7	3
	2019/12/18	RL175	13	60	54°11.8	11°52.4	98	17	21	82	28	46	19	42
	2019/12/19	RL175	14	60	54°11.8	11°53.4	95	17	12	28	47	35	10	19
	2019/12/19	RL175	15	60	54°12.2	12°00.2	243	13	17	161	27	47	4	13
	2019/12/19	RL175	16	60	54°12.1	11°59.9	253	13	78	82	29	27	4	7
2	2020/02/04	RL175	1	15	54°12.2	12°00.2	270	12	9	27	12	21	2	0
	2020/02/04	RL175+	2	60	54°12.2	11°58.5	268	13	26	126	34	42	2	5
	2020/02/04	RL175+	3	60	54°11.8	11°52.4	286	17	33	88	16	21	2	0
	2020/02/04	RL175	4	60	54°12.0	11°49.1	115	19	47	319	20	38	0	1
	2020/02/05	RL175+	5	30	54°12.2	12°00.1	264	12	19	47	2	1	0	1
	2020/02/05	RL175	6	45	54°12.0	11°56.5	61	15	61	364	9	17	1	1

2020/02/05	RL175	7	45	54°11.5	11°55.1	237	16	96	167	32	22	4	3
2020/02/05	RL175+	8	45	54°11.6	11°50.9	114	17	45	397	0	12	0	0
2020/02/05	RL175	9	45	54°11.8	11°53.2	94	17	33	126	1	3	0	0
2020/02/06	RL175	10	45	54°32.3	13°47.9	22	21	0	0	1	1	0	3
2020/02/06	RL175	11	45	54°40.3	13°46.8	28	32	0	12	1	6	8	32
2020/02/06	RL175+	12	47	54°44.4	14°45.9	206	54	7	30	3	16	70	199
2020/02/06	RL175	13	45	54°42.5	14°44.0	32	53	5	30	6	6	92	103
2020/02/07	RL175	14	45	54°53.1	15°17.4	202	76	23	45	NA	NA	740	768
2020/02/07	RL175+	15	30	54°52.0	15°17.0	197	69	5	27	21	29	395	364
2020/02/07	RL175+	16	30	54°52.0	15°10.2	269	64	26	46	12	18	381	348
2020/02/07	RL175	17	30	54°51.9	15°09.0	271	63	6	12	15	24	279	314
2020/02/07	RL175	18	30	54°52.1	15°06.6	102	62	5	16	3	5	137	88
2020/02/08	RL175	19	30	54°53.1	15°10.8	272	62	0	8	0	0	168	222
2020/02/08	RL175+	20	30	54°53.0	15°10.3	275	61	1	11	6	12	88	131
2020/02/08	RL175+	21	30	54°47.8	14°42.9	211	45	0	5	1	2	71	75
2020/02/08	RL175	22	45	54°47.9	14°42.8	211	45	2	0	9	3	140	161

Table 2. Fit statistics obtained from the catch comparison models for Baltic cod, plaice, and flounder, based on the paired-catch data obtained during the trials with the three roofless designs tested.

Species	Test design	Cruise	Number of hauls	Deviance	*p*-value
Cod	RL175	1	8	37.0	**0.954**
		2	12	99.5	0.014
	RL330	1	12	56.1	**0.905**
	RL175+	2	9	82.3	**0.148**
Plaice	RL175	1	8	43.2	**0.162**

		2	11	35.8	0.007
	RL330	1	12	50.5	**0.386**
	RL175+	2	9	55.0	**0.104**
Flounder	RL175	1	8	52.5	0.047
		2	12	34.4	**0.875**
	RL330	1	12	36.9	**0.696**
	RL175+	2	8	73.5	0.001

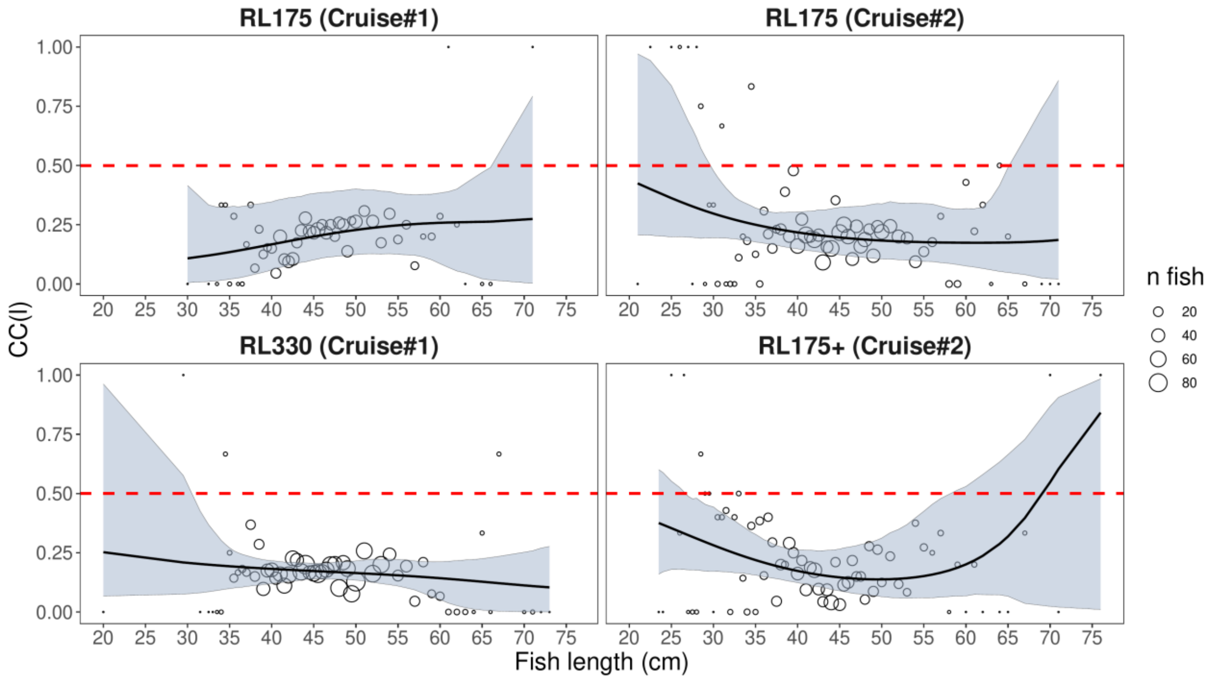

Figure 2. Catch comparison curves (solid line) estimated for cod by roofless design and trial. Grey shadowed areas: 95% confidence intervals of the estimation. Transparent circles: species catch comparison data. Red dashed line: value indicating equal catch share among test and reference gears (CC = 0.5).

The *CR(l)* curves estimated for cod reveal a decrease in cod catch efficiency to values clearly lower than 50% of the reference catch efficiency, at least within the range of most abundant lengths (Figure 3). Neither the increment in the length of the escape opening (RL330, Cruise 1) nor the addition of float ropes (RL175+, Cruise 2) significantly improved the escape efficiency obtained with the baseline RL75 design. It is worth noting, however, the negative trend of the average Δ*CR(l)* curve derived from the comparison RL330 vs. RL175, which indicates that the enlarged escape opening had a positive marginal effect on the escape efficiency of larger cod.

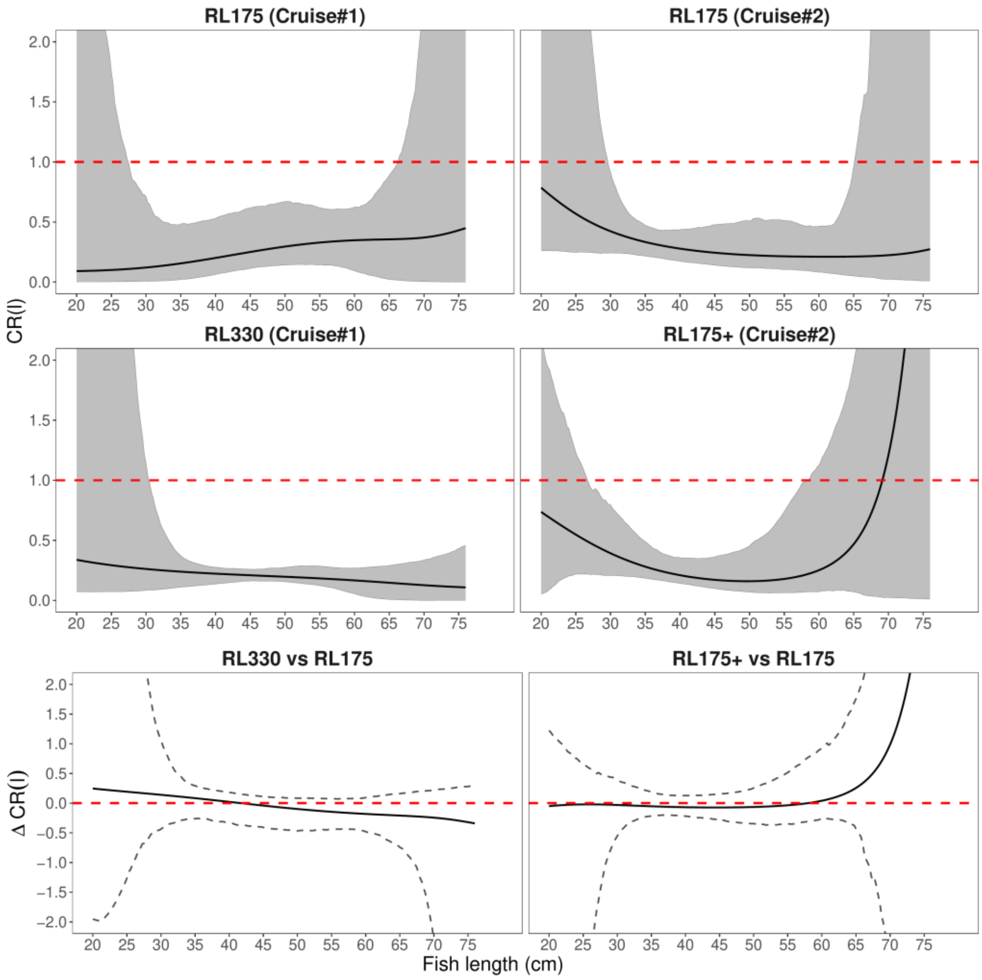

Figure 3. Left to right: Catch ratio curves for cod obtained in Cruise 1 and Cruise 2 by the baseline roofless design RL175 (first row), and the two other designs tested in each cruise, respectively (second row). Grey shadows: 95% confidence intervals of the estimation. Red dashed line: value indicating equal catch efficiency of test and reference gears (CR = 1.0). The third row shows the Δ*CR(l)* curves used to assess differences in performance of the baseline design vs. RL330 (Cruise 1) and RL175+ (Cruise 2). Red dashed line: value indicating no differences in performance between the baseline and the alternative designs (ΔCR = 0.0).

The *CC(l)* curves for plaice estimate a similar distribution of catches in the test and reference trawls and, as with cod, indicate no strong length dependence. The analysis related to the baseline roofless RL175 trial in Cruise 1, characterised by greater abundance of plaice catches, resulted in negligible deviation of the estimated *CC(l)* curve from the CC = 0.5 value. The replication of the baseline trial in Cruise 2, characterised by smaller catches of plaice, led to lower values of the *CC(l)* curve. However, there was no statistical evidence that the resulting curve differed from CC = 0.5 throughout the assessed lengths. Both increasing the length of the roofless section and applying float ropes significantly reduced the catches of larger plaice in the test gear relative to catches in the reference gear (Figure 4).

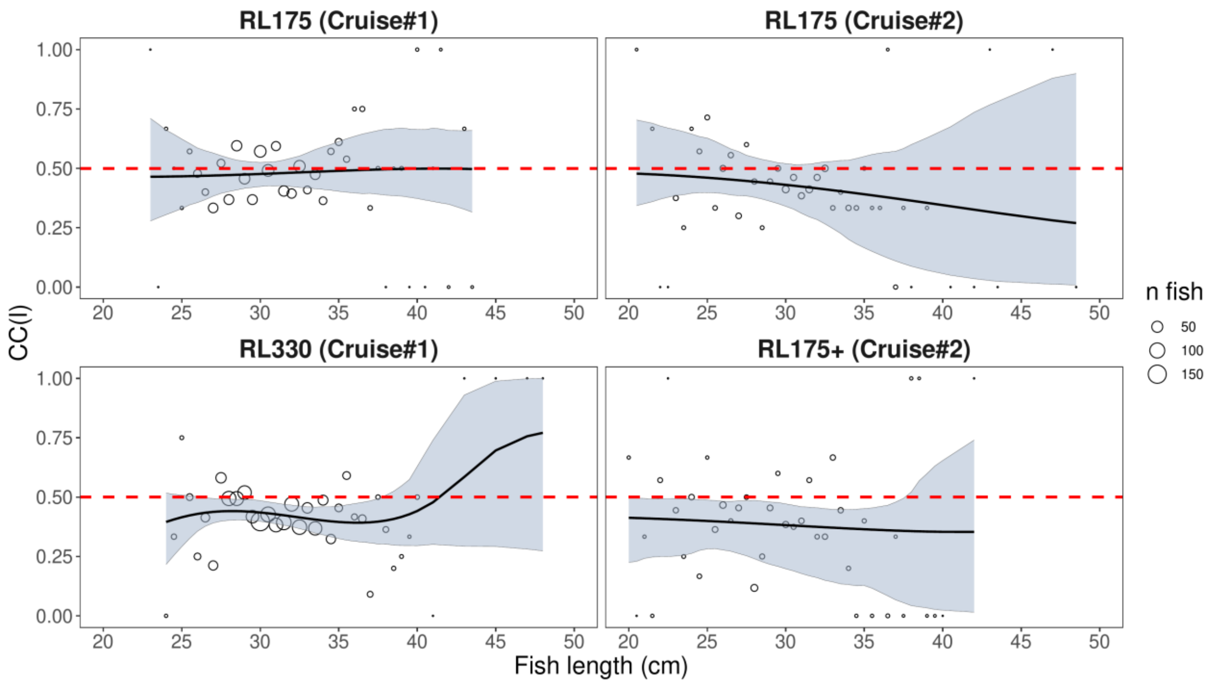

Figure 4. Catch comparison curves (solid line) estimated for plaice, by roofless design and trial. Grey shadowed areas: 95% confidence intervals of the estimation. Transparent circles: species catch comparison data. Red dashed line: value indicating equal catch share among test and reference gears (CC = 0.5).

The *CR(l)* curve estimated for the baseline RL175 design in Cruise 1 shows minimal reductions in catch efficiency lower than 10%. The *CR(l)* curves associated with the RL330 design reveal a larger and significant reduction in catch efficiency for plaice lengths between ~25 cm and ~37 cm. A similar decrease in catch efficiency was found for the RL175+, but extended to the whole range of lengths smaller than 37 cm (Figure 5). Although the significant losses in relative catch efficiency observed for the stimulus-enhancing designs, the respective Δ*CR(l)* curves detected no statistical differences compared with the relative catch efficiency of the baseline design. This was probably the result of the low inferential power resulting from the limited number of hauls, combined with a relative high between-haul variation in roofless performance.

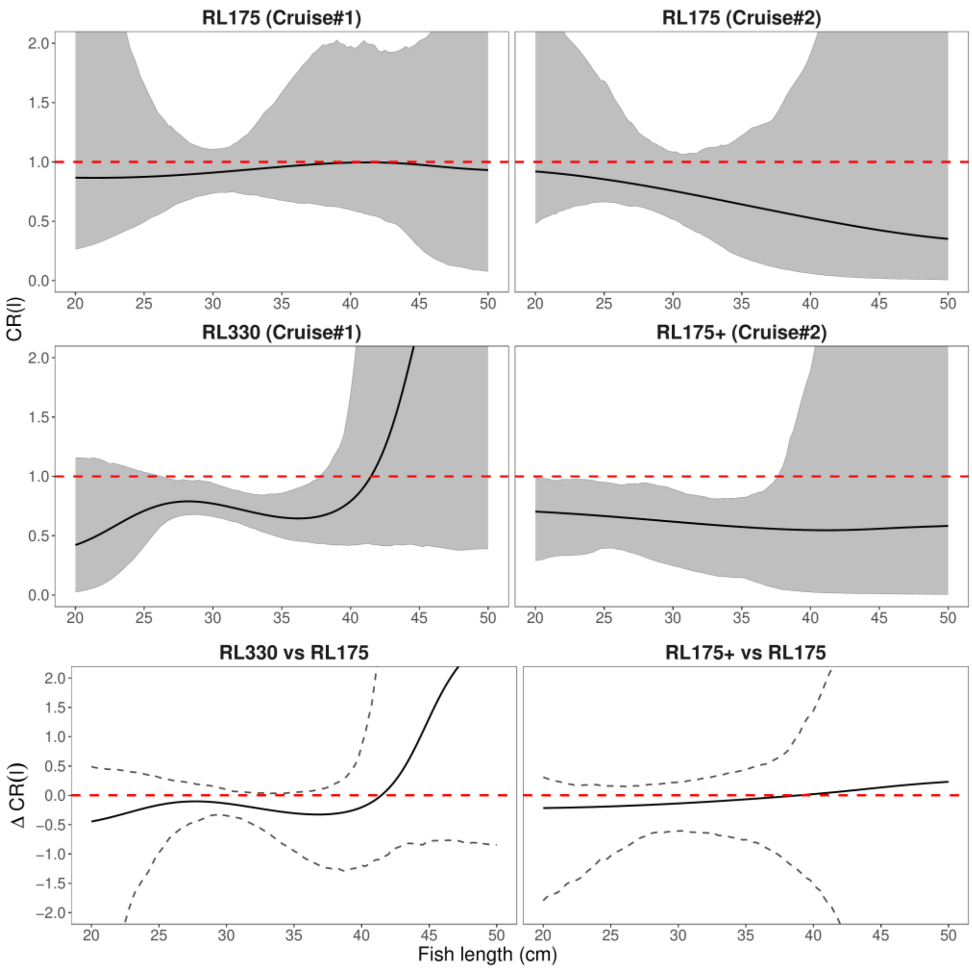

Figure 5. Left to right: catch ratio curves for plaice obtained in Cruise 1 and Cruise 2 by the baseline roofless design RL175 (first row), and the two other designs tested in each cruise, respectively (second row). Grey shadowed areas: 95% confidence intervals of the estimation. Red dashed line: value indicating equal catch efficiency of test and reference gears (CR = 1.0). The third row shows the Δ*CR(l)* curves used to assess differences in performance of the baseline design vs. RL330 (Cruise 1) and RL175+ (Cruise 2). Red dashed line: value indicating no differences in performance between the baseline and the alternative designs (ΔCR = 0.0).

The *CC(l)* curves for flounder were estimated close to CC = 0.5 in three out of the four experiments. As for plaice, a larger and significant deviation from CC = 0.5 occurred only when the species was caught in low abundance during Cruise 1 (Figure 6).

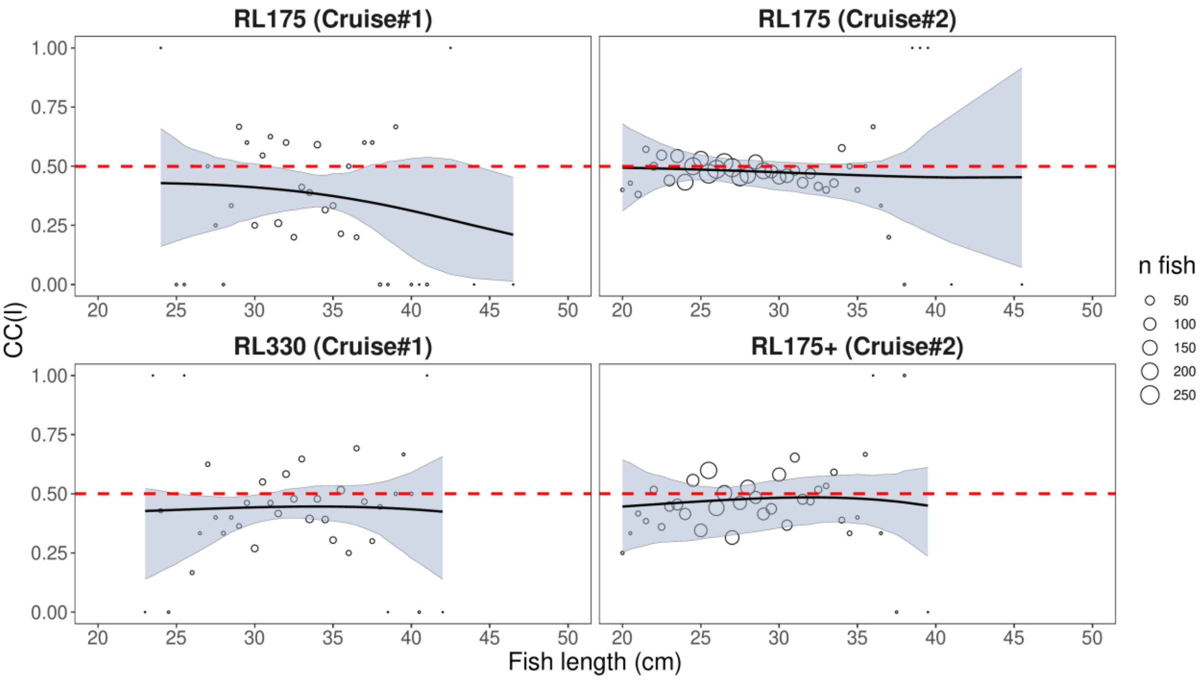

Figure 6. Catch comparison curves (solid line) estimated for flounder, by roofless design and trial. Grey shadowed areas: 95% confidence intervals of the estimation. Transparent circles: species catch comparison data. Red dashed line: value indicating equal catch share among test and reference gears (CC = 0.5).

The estimated *CR(l)* curves for the RL175 and RL175+ in Cruise 2 attained higher values than those obtained from Cruise 1, with decreases in catch efficiency lower than 10% (Figure 7). However, the Δ*CR(l)* curves detected no statistical catch efficiency differences between the baseline and the alternative roofless design.

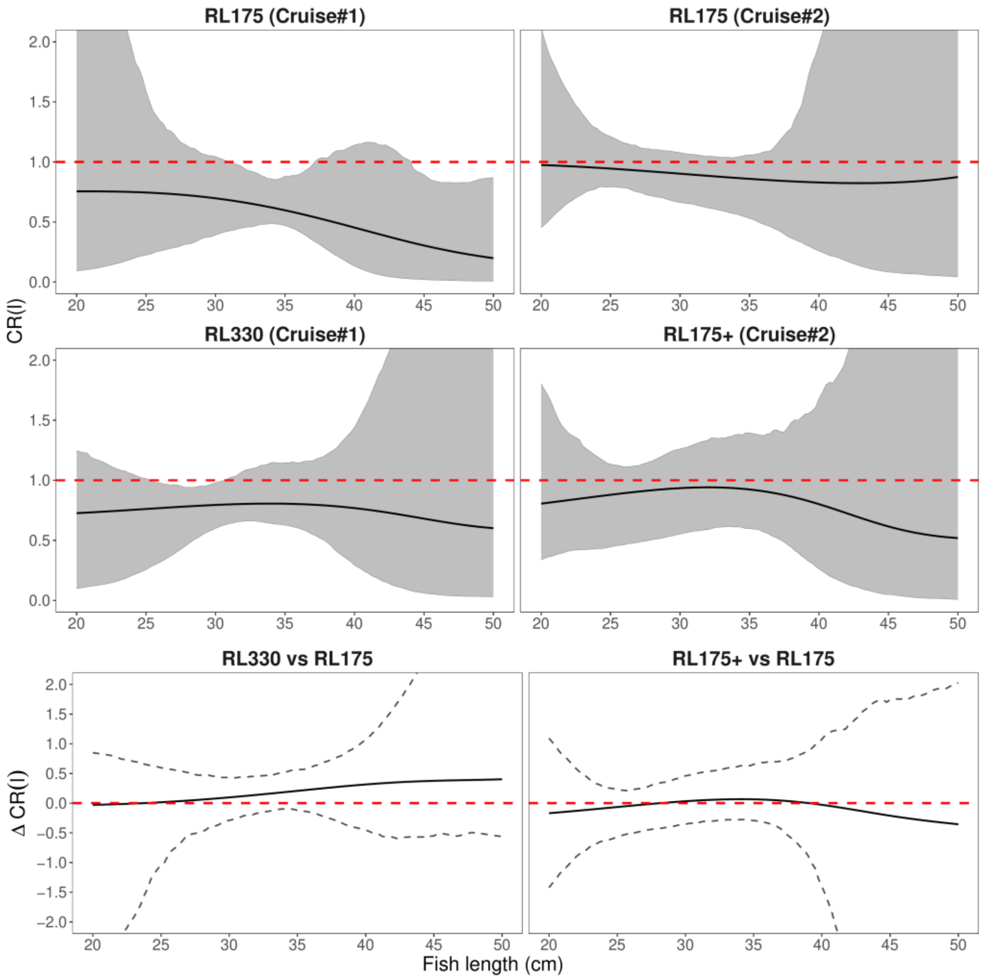

Figure 7. Left to right: catch ratio curves for flounder obtained in Cruise 1 and Cruise 2 by the baseline roofless design RL175 (first row), and the two other designs tested in each cruise, respectively (second row). Grey shadowed areas: 95% confidence intervals of the estimation. Red dashed line: value indicating equal catch efficiency of test and reference gears (CR = 1.0). The third row shows the Δ*CR(l)* curves used to assess differences in performance of the baseline design vs. RL330 (Cruise 1) and RL175+ (Cruise 2). Red dashed line: value indicating no differences in performance between the baseline and the alternative designs (ΔCR = 0.0).

3.3 Fishery usability indicators

In line with the results obtained in the modelling section, the catch ratio indicator for marketable cod (*nS+*; Equation (6)) yielded values ≤ 25%, irrespective of the roofless design used (Figure 8). Hence, a consistent reduction in catches ≥ 75% was achieved. Increasing the length of the escape opening (RL330), or adding float ropes (RL175+), reduced the relative catchability of cod further, by at least four percentage points. However, the overlap between confidence intervals around the mentioned *nS+* values for cod indicate no statistical differences across roofless designs (Figure 9). The small catches of cod less than the species mrs obtained during both cruises (< 5% of the total catches) probably explain the very strong uncertainty in the estimation of the species *nS−* (length classes < mrs), and also explains the minor differences between values from the species *nS* (accounting for all length classes) and *nS+* (accounting for length classes ≥ mrs).

The use of the baseline roofless design (RL175) yielded values of *nS+* > 90% for the most abundant flatfish species in catches (plaice in Cruise 1, flounder in Cruise 2). The upper confidence limits associated with these *nS+* > 90% values expanded beyond 100%, indicating no significant differences in the catch efficiency of sized flatfish between the test gear using the RL175 design and the reference gear. Unexpectedly, small flatfish catches (i.e. few flounder in Cruise 1 and few plaice in Cruise 2) resulted in lower values of *nS+*. Combining the catch data from Cruises 1 and 2 led to values of *nS+* > 85%, both for plaice and flounder. Increasing the length of the escape opening (RL330) reduced the *nS+* value for plaice with the baseline design RL175 (Cruise 1 trials) by ~15 percentage points. On the contrary, the *nS+* for flounder was higher for the RL330 design than for the baseline design. However, the later result needs to be treated with caution owing to the small catches of flounder during Cruise 1. The *nS+* values obtained for plaice and flounder with the RL175+ design (Cruise 2 trials) reveal no clear effect of the stimulus-enhancing designs on the catchability of flatfish. Similar to cod, catches of undersized flatfish were also small (~10% of total plaice catch, ~5% of total flounder catch; Figure 9).

Combining the catches from both cruises, the estimated *ΔEffort* indicator (Equation (7)) reveals that a trawl equipped with the baseline roofless design (RL175) would need an additional fishing effort of ~8% and ~12% to compensate for the catch losses of plaice and flounder, respectively (Figure 9). In return, the trawl equipped with the baseline roofless would have access to 373% and 347% more fishing opportunities for plaice and flounder (nRf^*_t; Equation (10)) than the reference trawl, respectively.

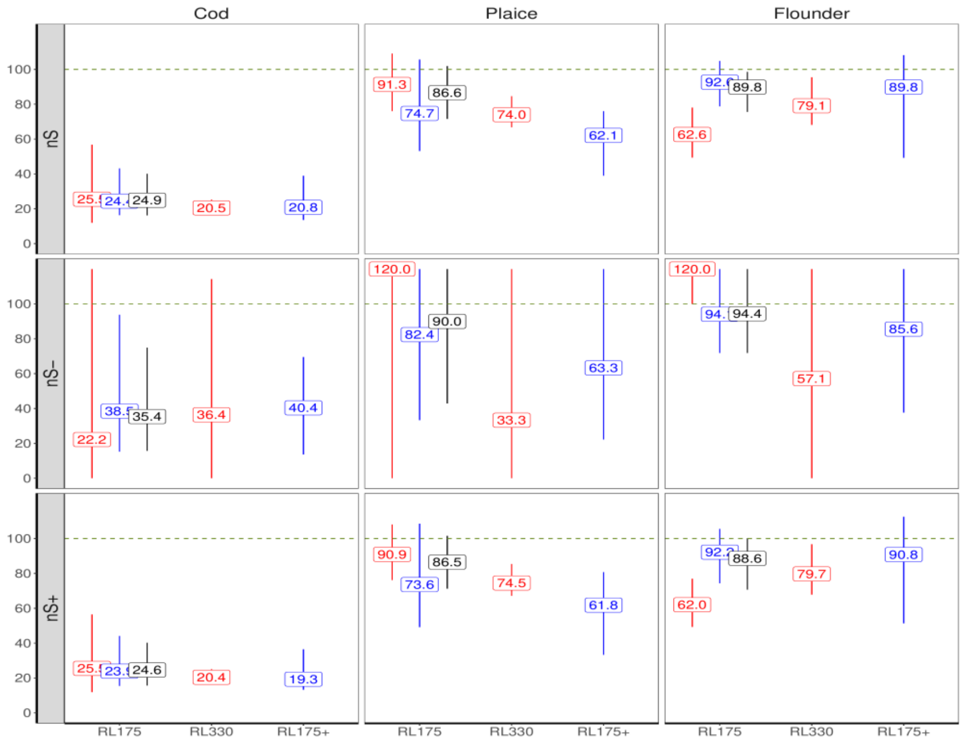

Figure 8. Catch ratio indicators (Equation (6)), by species, roofless design, and cruise (red = Cruise 1, blue = Cruise 2, black = combined). Rectangular labels indicate the average value of the estimated indicators. Vertical bars represent 95% confidence intervals.

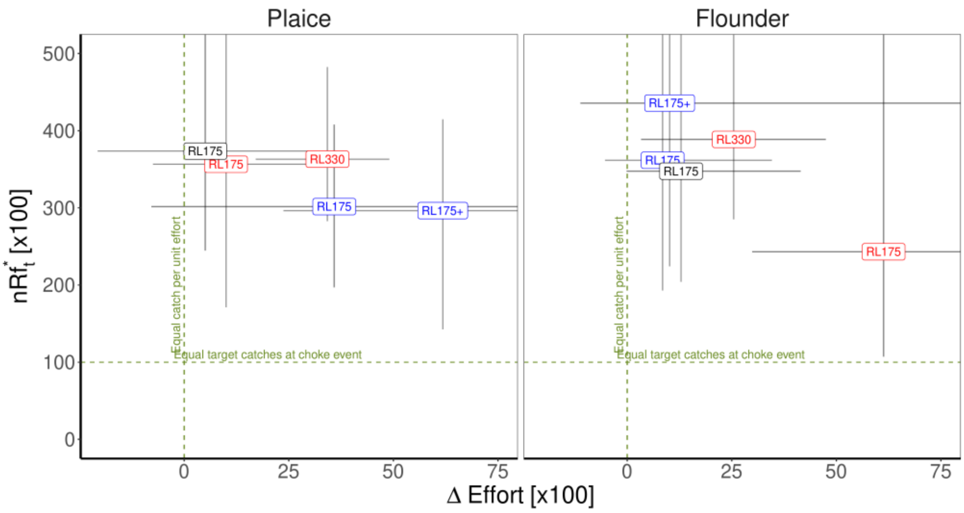

Figure 9. Relation of the increased effort needed to compensate for catch losses of targeted species derived from the use of the roofless device (indicator $\Delta Effort$, Equation (7)) and projection of

additional fishing possibilities caused by the reduced risk of a fishery choke event (indicator nRf^*_t; Equation (10)) by test gear and cruise (red = Cruise 1, blue = Cruise 2, black = combined). Rectangular labels indicate the relation between the average values from both indicators. Horizontal bars represent 95% confidence intervals associated with the average value of $\Delta Effort$; vertical bars represent 95% confidence intervals associated with the average value of nRf^*_t.

Discussion

This study demonstrates that the bycatch of Baltic cod can be reduced significantly by simply removing a section of the upper net panel in the extension piece of the trawl. Results with the baseline design of the roofless device with a 175-cm-long escape opening (RL175) showed an average reduction in cod catches by ~75% that otherwise would be retained in commercial fishing using the mandatory T90 codend. The consistency in performance achieved during the two cruises, conducted with different vessels, using different trawls, and operating in different fishing grounds, is solid proof of the devices' functional reliability.

The roofless concept represents the latest development in the search for simple technical solutions that release Baltic cod from the trawl before they enter the codend. Earlier attempts using square mesh panels (SMP) inserted in a position in the trawl similar to that of the roofless device (Herrmann et al., 2014) resulted in very low escape efficiency for cod. The poor performance observed in Herrmann et al. (2014) might be explained by the natural behaviour of many fish species to stay clear of the surrounding netting once it enters the trawl (Glass et al., 1993): Although the SMP could be perceived as a clear escape possibility, fish tend to be reluctant to approach and try to penetrate the open meshes (Glass et al., 1995; Briggs, 1992). A recent attempt to improve the attractiveness of SMP on Baltic cod used very large meshes (~400 mm square-mesh size) to mitigate the "wall effect" of the SMP netting (ICES, 2019d). The poor results related to escape efficiency obtained with the 400 mm SMP motivated the search for the more radical roofless concept introduced in this study, one whose purpose is to maximise the visual and mechanical stimuli for the activation of escape behaviour of Baltic cod.

The greatest concern associated with the roofless concept was the potential catch losses of targeted flatfish species. Our experimental results with the baseline roofless design (RL175) revealed a slight but not significant reduction in the catch efficiency of flatfish species. Pooling the catch data from both cruises resulted in average values of *nS+* close to 90% for both plaice and flounder. This result agrees with previous behavioural observations of flatfish species, often seen swimming close to the bottom net panel of the extension piece of the trawl (Santos et al., 2020; Krag et al., 2009; He et al., 2008), without altering their path, even in the presence of selection devices (Santos et al., 2020). When the catches of the analysed flatfish species were small (flounder in Cruise 1, plaice in Cruise 2), the *nS+* value unexpectedly dropped to values below 75%. We could find no plausible explanation for this pattern other than the large variation in the binomial process related to the share of low-abundance catches among the paired gears. The behaviour of fish in relation to fishing gears, and more specifically to selection devices, can be influenced by extrinsic factors such as light conditions, or intrinsic factors such as the physiological condition of the fish (Winger et al., 2010; Walsh and Hickey, 1993). Further investigations that combine experimental fishing using the roofless device with behavioural investigations based on underwater video recordings are planned to assess and understand the performance of roofless devices under fishing and fish conditions different from those associated with the current study.

Recent studies have demonstrated the potential of using codend selectivity to reduce the bycatch of Baltic cod beyond species minimum conservation reference size, without affecting the catchability of flatfish species (Madsen et al., 2021; Wienbeck et al., 2014). In particular, commercial sea trials using a square-mesh codend (so-called New Bacoma) of ~125 mm mesh size significantly reduced cod catches up to 50 cm (Madsen et al., 2021). Although the technological adaptations of the current mandatory codends proposed by Madsen et al. (2021) and Wienbeck et al. (2014) are simple, straightforward, and effective solutions to reducing cod bycatch, it is important to consider the risks associated with this strategy, given the current status of the Baltic cod stocks. Fishing with highly size-selective codends would increase the fishing pressure on larger cod, which are already rare, especially in the eastern stock (ICES, 2020a; Eero et al., 2015). The highly selective removal of older and larger spawners can accelerate the decline in size and age at maturity in the population (Garcia et al., 2012; Berkeley et al., 2004), thus reducing the quantity and the quality of total egg production (Cerviño et al., 2013; Berkeley et al., 2004), and therefore reducing even further the already low production in the population. It must also be noted that, according to the definition of size selection (Wileman et al., 1996), the degree of bycatch achieved using highly selective codends will depend strongly on the population structure encountered by the trawl. For example, considering the current population structure of Eastern Baltic cod, applying highly selective codends would be a fast and simple solution to reducing species bycatch. Nevertheless, as the length structure of the population changes, i.e. fish in the population grow, the efficiency of bycatch reduction provided by the codend will be reduced. Therefore, the bycatch reduction performance of codends must be evaluated regularly. Under the current technological development and state of the Baltic Sea cod stocks, we argue that combining the roofless device with a highly selective codend could lead to a large, balanced (across fish lengths), and stable reduction in cod bycatch without considerable catch losses of marketable flatfish. Future sea trials combining the roofless device with highly selective codends, such as those proposed by Madsen et al. (2021) and Wienbeck et al. (2014), should be conducted to assess the benefits and limitations of the proposed combined strategy.

The roofless device expands the available toolbox of technologies for reducing cod bycatch in demersal fisheries. The dual-species indicators estimated in this study reveal that, under a choking scenario, using the roofless device would help to increase the time during which other demersal resources may be fished, and it may provide individual fishers with flexibility to adapt the exploitation patterns and divide the annual quota use according to their own preferences. It should be noted that the roofless device could also be an effective solution for demersal fisheries in other regions, challenged by choking caused by limitations on cod bycatch or any other roundfish species.

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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Paper V

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ORIGINAL ARTICLE

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The efficiency of sieve-panels for bycatch separation in *Nephrops* trawls

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Abstract

This study investigated the efficiency of a sieve-panel concept, intended to separate bycatch species from *Nephrops* (Norway lobster) in a trawl gear via mechanical and behavioural means. Four different designs of varying panel mesh size or inclination were tested in experimental fishing. For each design, the length-dependent sieving efficiency, defined as the fraction of *Nephrops* or fish passing through the panel to the lower codend, was estimated. The sieving efficiency for *Nephrops* increased from ~17% to ~71% as mesh size increased, and decreased with increasing carapace length, but did so less as panel inclination and mesh size increased. The sieving efficiency for roundfish was low, as intended, while the efficiency for flatfish decreased with fish size. Although results are promising, the sieving efficiency for the largest, most valuable *Nephrops* remained too low. Therefore, further improvements are necessary before the concept is acceptable to the commercial fishing fleet.

KEYWORDS
bycatch, efficiency, landing obligation, *Nephrops*, sieve-panel, trawl

1 | INTRODUCTION

Nephrops norvegicus (L.)-directed fisheries are among the most economically important fisheries in European waters (Ungfors et al., 2013). Although some creel fisheries target *Nephrops* (Adey, 2007), 95% of total European landings are taken by demersal trawlers (Briggs, 2010; Ungfors et al., 2013). Catching *Nephrops* efficiently with trawls requires to use of relatively small mesh codends (Frandsen, Herrmann & Madsen, 2010; Krag, Frandsen & Madsen, 2008), which can lead to large bycatches of small fish co-habiting the fishing grounds (Alverson, Freeberg, Murawaski & Pope, 1994; Catchpole & Revill, 2008; Catchpole, Tidd, Kell, Revill & Dunlin, 2007; Kelleher, 2005; Krag et al., 2008).

The problem of unwanted bycatch in *Nephrops* fisheries has been addressed mainly by attempting to provide additional escapement possibilities for fish species before they enter the codend (Catchpole & Revill, 2008). Although different in concept and purpose, all current devices are designed to reduce bycatch by selecting fish out of the catch. Probably the most used bycatch reduction devices (BRDs) are the Swedish grid (Valentinsson & Ulmestrand, 2008) for monospecific *Nephrops* fisheries, and square mesh panels (SMPs) for mixed fisheries (Armstrong, Briggs & Rihan, 1998; Briggs, 1992). Although it has been demonstrated that using these BRDs can significantly reduce bycatch rates, to date none of them have delivered an efficient size selectivity for the target and bycatch species simultaneously. Depending on the population structure fished, this can lead to a considerable number of bycaught small fish (Frandsen, Holst & Madsen, 2009; Lövgren, Herrmann & Feekings, 2016; Nikolic et al., 2015; Valentinsson & Ulmestrand, 2008), or losses of marketable *Nephrops* (Catchpole, Revill & Dunlin, 2006; Frandsen et al., 2009).

Achieving an efficient size selection for both the target and bycatch species is an increasingly important requirement in the wake of the Common Fisheries Policy (CFP) reform (EU 2013), implemented in *Nephrops* fisheries since 2016. The reform adopted the landing

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obligation (LO) for listed species, which forces fishers to land all catches of those species and count them against their quota. Under such a scenario, a large bycatch of fish species with limited quota can alter the fishing strategy or even force fishers to stop fishing completely, without exhausting the quota of *Nephrops*. Improving species and size selectivity is required now more than ever to secure both the biological and economical sustainability of *Nephrops*-directed fisheries.

This study presents an alternative concept for reducing fish bycatch in these fisheries. The concept shares similarities with the sieve nets used in shrimp trawl fisheries, such as the brown shrimp fishery in the North Sea (Revill & Holst, 2004), and it is based on the assumptions that *Nephrops* has limited swimming activity and tends to roll over the floor of the trawl body (Briggs & Robertson, 1993; Main & Sangster, 1985), whereas fish tend to swim actively to stay clear of the surrounding net (Glass & Wardle, 1995). It consists of a 10-m-long square mesh sieve-panel, mounted in the extension piece of the trawl with a continuous upward inclination towards an upper and lower codend. The fore edge of the sieve-panel is attached to the floor of the gear, ensuring that all *Nephrops* and fish will enter on the upper side of the panel connected to the upper codend. Assuming that the behavioural differences between *Nephrops* and the fish species listed above can be used, the panel will sieve *Nephrops* towards the lower codend, and fish will be guided towards the upper codend. The mesh size used in the sieve-panel and its inclination should be sufficiently large to sieve all sizes of *Nephrops* towards the lower codend, without losing the ability to guide fish to the upper codend.

The aim of the study was to investigate and quantify the ability of different sieve-panel designs to separate *Nephrops* from different roundfish and flatfish species during the catching process.

2 | MATERIAL AND METHODS

2.1 | Sieve-panel designs and test gear

The 10-m-long sieve-panel was mounted in the four-panel extension piece of the trawl (Figure 1). The fore edge of the sieve-panel was attached at the front of the extension's lower panel, and the sides were connected to the lateral panels with a cutting rate of 6N2B. This construction provides a monotonous upward–backward inclination of ~2.5°, and splits the aft of the trawl into two horizontal compartments, ending in the lower and upper codend (Figure 1).

Four different panel designs were tested during experimental fishing. All designs used square mesh netting (Figure 1). Design 1 was made of knotless PA netting with 45.2 mm measured bar length and 2.5 mm nominal twine thickness. Design 2 used knotless PE netting with 60.9 mm bar length and 5 mm twine thickness. Design 4 was constructed similarly to Designs 1 and 2, but used PE standard netting, with 94.3 mm mesh bar length and 3 mm twine thickness. Design 3 used the same sieve-panel as Design 2, but the monotonous inclination was altered by inserting six floating lines, arranged in two groups of three and attached at two different positions on the panel's lower side. The configuration was intended to create a hilly surface to increase the inclination of the panel (Figure 1). For a sieve-panel to perform well, sieving efficiency should be high for all sizes of *Nephrops* and low for all sizes of the bycatch species.

During experimental fishing, the sieve-panels were mounted one at a time for a group of hauls in the same extension piece, which was 11. 5 m long, made of PE single netting with 1.8 mm twine thickness. The stretched mesh size obtained with the omega gauge (Fonteyne, Buglioni, Leonori & O'Neill, 2007) was 47.9 mm (Figure 1). The codends were 6 m long and made of PA netting with ~1.2 mm twine thickness. The stretched mesh sizes of the codends were 48.4 mm and 49.6 mm for the upper and lower codends, respectively. The codend mesh sizes applied were considered sufficiently small to retain all *Nephrops* available in the targeted population. The extension piece and the double codend system were connected to a demersal trawl model Spaeghugger, spread by two Thyborön doors Type 2 (1.78 m^2).

2.2 | Sea trials and data collection

The four sieve-panels were tested between 12 and 24 September 2015 on Danish *Nephrops* fishing grounds in the Skagerrak (ICES Division IIIa), using the German research vessel Solea (42 m, 1,780 kW). Catches obtained at haul level were sampled by species and for each codend separately. Catch weight was collected using electronic scales. The *Nephrops* carapace length (CL) was measured to the nearest 0.5 mm using digital callipers. Total length (TL) was measured to nearest 0.5 cm for the fish bycatch species using electronic measuring boards. Subsampling was avoided in most of the experimental hauls. When subsampling occurred, the subsampling factor was calculated by dividing the subsampling weight by the total catch weight.

Underwater video recordings were collected during the experimental hauls to assess qualitatively the shape of the sieve-panel and how different species interacted with it. The cameras used were GoPro model Hero 3+, mounted in deep-water housing, model GoBenthic2. The camera system was supplemented with flood-beam artificial light (1,400 lumens).

2.3 | Data analysis

The sieving efficiency was quantified separately for each of the sieve-panels and each species as described below.

$$S_{il} = \frac{nlc_{il}}{nlc_{il} + nuc_{il}}. \quad (1)$$

With nlc_{il} as the number of individuals of length l (CL or TL) caught in the lower codend during haul i, and nuc_{il} as the number of length l caught in the upper codend, the proportion of the total catch observed in the lower codend, can be interpreted as the experimental sieving efficiency of the sieve-panel for individuals with length l. S_{il} can only take values in the range 0.0–1.0. Values of S_{il} close to 1.0

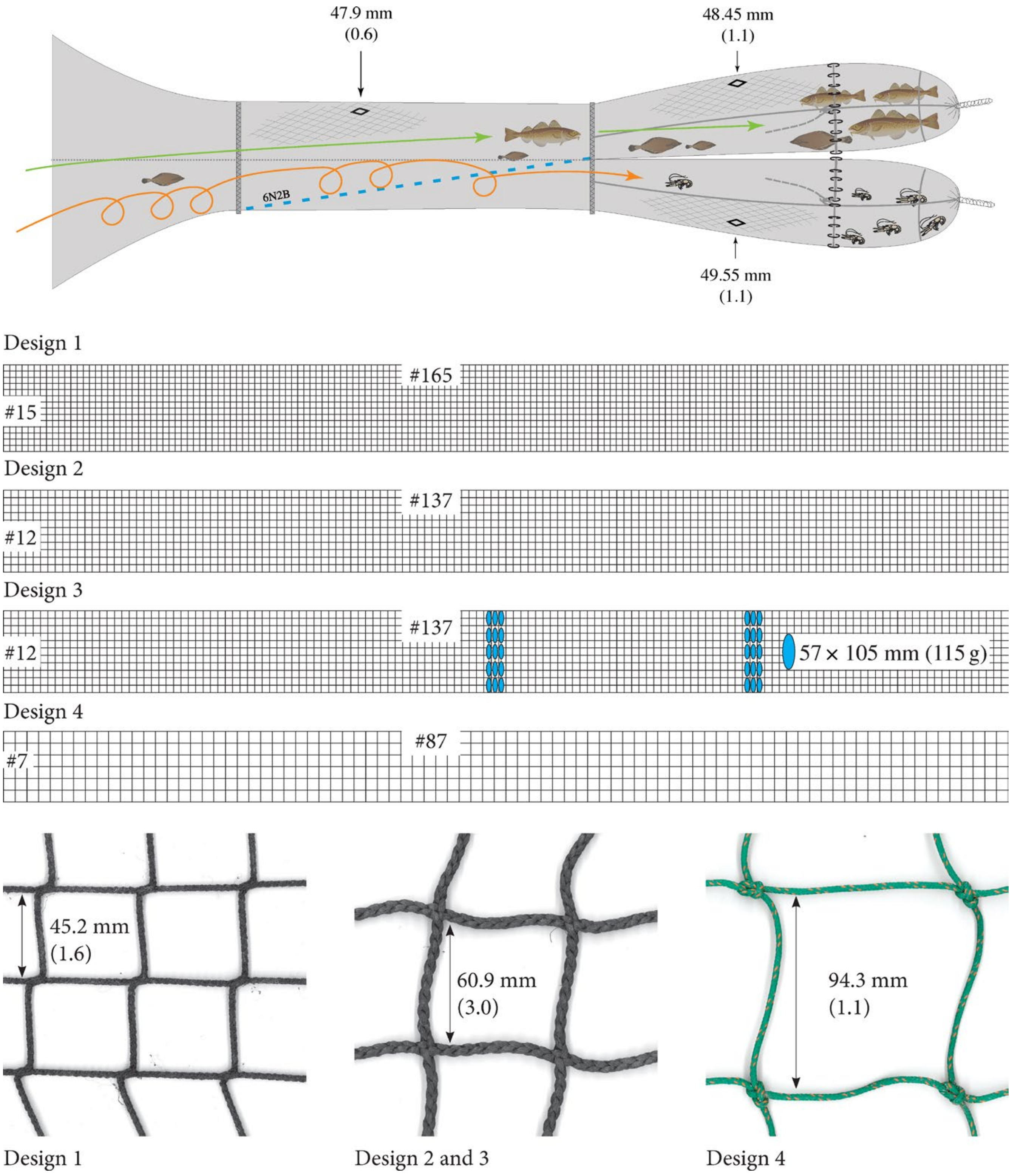

FIGURE 1 Top: Side view of the experimental gear with the general design of the sieve-panel (blue stippled line) mounted ahead of the double codend setup. For the sorting system to work efficiently, the following selection events have to take place consistently: (1) Assuming that *Nephrops* travels towards the codends by rolling and hitting the lower panel of the net, it is expected that they will be sorted by the sieve-panel to the lower codend (orange path); (2) the bottom–up inclination of the panel should guide fish upwards towards the upper codend (green path). Middle: Number of meshes of the different sieve-panel designs; additional floats (blue) were mounted in Design 3. Bottom: Netting used in the different designs and the measured mesh bar length of each (*SD* in parentheses). Nets were scanned using the same scale, allowing a direct comparison between meshes [Colour figure can be viewed at wileyonlinelibrary.com]

would mean that most individuals with length l were sieved and finally retained in the lower codend. On the other hand, S_{il} values close to 0.0 would mean low sieving efficiency, either because individuals of length class l were not physically able to pass through the meshes, or because the sieve-panel guided them towards the upper codend.

The sieving efficiency might be influenced by the size selection of the square meshes and by species behaviour when interacting with the sieve-panel, which at the same time might be length dependent. Therefore, length-dependent sieving efficiency is modelled by applying a highly flexible function $S(l,\boldsymbol{q})$:

$$S(l,\boldsymbol{q}) = \frac{\exp(f(l,q_0,\ldots,q_j))}{1+\exp(f(l,q_0,\ldots,q_j))}, \quad (2)$$

where f is a polynomial of order j, with coefficients q_0 to q_j, which provide great flexibility to the functional form of the resulting sieve efficiency curve. The estimation of the values of the parameters $\boldsymbol{q} = (q_0,\ldots,q_j)$, which make the observed experimental data averaged over hauls most likely, was carried out by minimising the negative log-likelihood function for the binomial data:

$$\log L_{\text{model}} = -\sum_{l}\sum_{i}\{nlc_{il}\times\ln(S(l,\boldsymbol{q})) + nuc_{il}\times\ln(1.0 - S(l,\boldsymbol{q}))\}, \quad (3)$$

where the summations are for group of hauls i with the specific sieve-panel design and length classes l. In Equation 2, f was considered as a polynomial up to the fourth order with parameters q_0, q_1, q_2, q_3 and q_4. Leaving out one or more of the parameters q_0–q_4 led to 31 additional simpler models that were also considered potential candidates for the sieve efficiency curves $S(l,\boldsymbol{q})$, and therefore, they were also estimated using Equation 3. Selection of the best model for $S(l,\boldsymbol{q})$ among the 32 competing models was based on a comparison of their respective Akaike information criterion (AIC) values (Akaike, 1974). The model with the lowest AIC value was selected to describe the experimental sieving efficiency.

The model's ability to describe the data was evaluated based on an inspection of the fit statistics, that is the p-value and the model deviance versus the degrees of freedom (df), following the procedures described by Wileman, Ferro, Fonteyne and Millar (1996). The p-value expresses the likelihood of obtaining a discrepancy at least as large as between the fitted model and the observed experimental data by coincidence. In case of poor fit statistics (p-value < 0.05; deviance $\gg df$), the poor result was examined to determine whether it was caused by structural problems when describing the experimental data using the model, or whether it was the result of overdispersion in the data (Wileman et al., 1996).

The 95% confidence intervals (CI) for the averaged sieve efficiency curve $S(l,\boldsymbol{q})$ were estimated using a double bootstrap method with 1,000 replications. This approach, which avoided underestimating confidence limits when averaging over hauls, is identical with the one described in Sistiaga, Herrmann, Grimaldo and Larsen (2010). Traditionally, the CIs are estimated without accounting for potentially increased uncertainty resulting from uncertainty in the selection of the model used to describe the curve (Katsanevakis, 2006). This additional uncertainty was accounted for by following

TABLE 1 Number of hauls conducted with the different *Nephrops* sieve-panel designs, including the average towing duration (standard deviation in round brackets), and the number of individual length-measurements obtained from each of the analysed species and sampling compartments

Design	Number hauls	Duration (min)	*Nephrops*		Cod		Blue whiting		American plaice		Witch flounder	
			Lower codend	Upper codend	Lower codend	Upper codend	Lower codend	Upper codend	Lower codend	Upper codend	Lower codend	Upper codend
1	13	54.5 (31.0)	19	89	18	2,082	33	2,530	1,609	6,246 [0.973]	0	1,085
2	10	100 (29.0)	1,349	806	76	1,693	24	3,863 [0.700]	2,561	6,799 [0.885]	12	1,034
3	7	100.9 (16.0)	2,537	1,132	31	563 [0.998]	376	3,606	2,570	7,110	14	898
4	11	96.4 (13.9)	1,156	471	106	1,135	18	664 [0.730]	5,393	5,220 [0.856]	134	1,209 [0.799]

Note. Subsampling rates are presented in square brackets for those cases where not all fish were measured.

the same method used by Krag, Herrmann, Karlsen and Mieske (2015), which incorporates an automatic model selection based on which of the 32 models produced the lowest AIC for each of the bootstrap iterations.

In addition to the assessment of the uncertainty of the individual averaged sieve curves, the bootstrap CIs were used to compare *Nephrops* sieving efficiencies obtained for the different sieve-panel designs. Such assessments were carried out as pairwise comparisons, and the differences within pairs were considered statistically significant only in the range of individual lengths, where the compared CIs did not overlap. The analysis of sieve-panel efficiency was carried out using the software tool SELNET (Herrmann, Sistiaga, Nielsen & Larsen, 2012).

3 | RESULTS

3.1 | Description of experimental hauls and catches

The experimental hauls were conducted in Danish fishing grounds within 57°–58°N and 009–010°E (Figure S1) at fishing depths between 54 and 136 m. Haul duration ranged from 28 to 118 min. In all, 13, 10, 7 and 11 valid hauls were conducted using Designs 1, 2, 3 and 4, respectively, a total of 41 experimental hauls. A total of 108 *Nephrops* were caught and measured with Design 1, a very small number compared with the 2,155, 3,669 and 1,627 individuals measured in Designs 2–4 (Table 1). Two roundfish and two flatfish species were caught in sufficient numbers to warrant investigating the sieving efficiencies on the fish species: American plaice (*Hippoglossoides platessoides* (Fabricius), 37,508 fish measured), blue whiting (*Micromesistius poutassou* (Risso), 11,114 fish measured), cod (*Gadus morhua* L., 5,704 fish measured) and witch flounder (*Glyptocephalus cynoglossus* (L.), 4,386 fish measured; Table 1).

Of the *Nephrops* caught in the hauls with Design 1, 17% were collected in the lower codend, increasing to 71% with Design 4 (Table 1). By contrast, <10% of the cod, blue whiting, and witch flounder caught were observed in the lower codend. Larger numbers of American plaice were observed in the lower codend than the other fish species, increasing from 12% with Design 1 to 50% with Design 4.

A short haul in shallow and clear waters was conducted to collect video recordings showing the shape and mechanical behaviour of the extension piece with the sieve-panel mounted. Video recordings were collected during seven of the experimental hauls (Table 1), for a total of 561 min. Exploratory analysis of catch data indicated no clear influence of the camera system on sieve-panel performance; therefore, these hauls were used in the quantitative analysis.

3.2 | Assessment of the length-dependent sieving efficiency

The sieving efficiency of each of the sieve-panel designs was successfully obtained using the model described in Equation 2. *p*-values > 0.05 were obtained in all cases, except for *Nephrops* in Design 4, confirming the model's ability to describe the length-dependent sieving efficiency in the experimental data (Table 2). The

TABLE 2 Sieving efficiency model statistics for the different species analysed (*df* = model degrees of freedom, *n* hauls = number of hauls included in the analysis)

Species	Parameter	Design 1	Design 2	Design 3	Design 4
Nephrops	*p*-value	0.90	0.86	0.15	0.04
	Deviance	36.79	72.07	98.68	101.29
	df	49	86	85	78
	n hauls	2	10	7	7
Cod	*p*-value	>0.99	>0.99	>0.99	0.99
	Deviance	56.90	50.54	34.57	64.78
	df	111	108	86	93
	n hauls	13	10	7	11
Blue whiting	*p*-value	0.87	0.99	0.98	0.98
	Deviance	41.62	30.8	29.96	23.35
	df	53	51	48	39
	n hauls	7	9	7	11
American plaice	*p*-value	0.13	>0.99	0.97	0.65
	Deviance	54.76	25.14	30.48	42.81
	df	44	50	47	47
	n hauls	7	10	7	11
Witch flounder	*p*-Value	>0.99	>0.99	0.95	0.64
	Deviance	0.00	23.52	35.41	46.89
	df	47	51	51	51
	n hauls	11	10	7	11

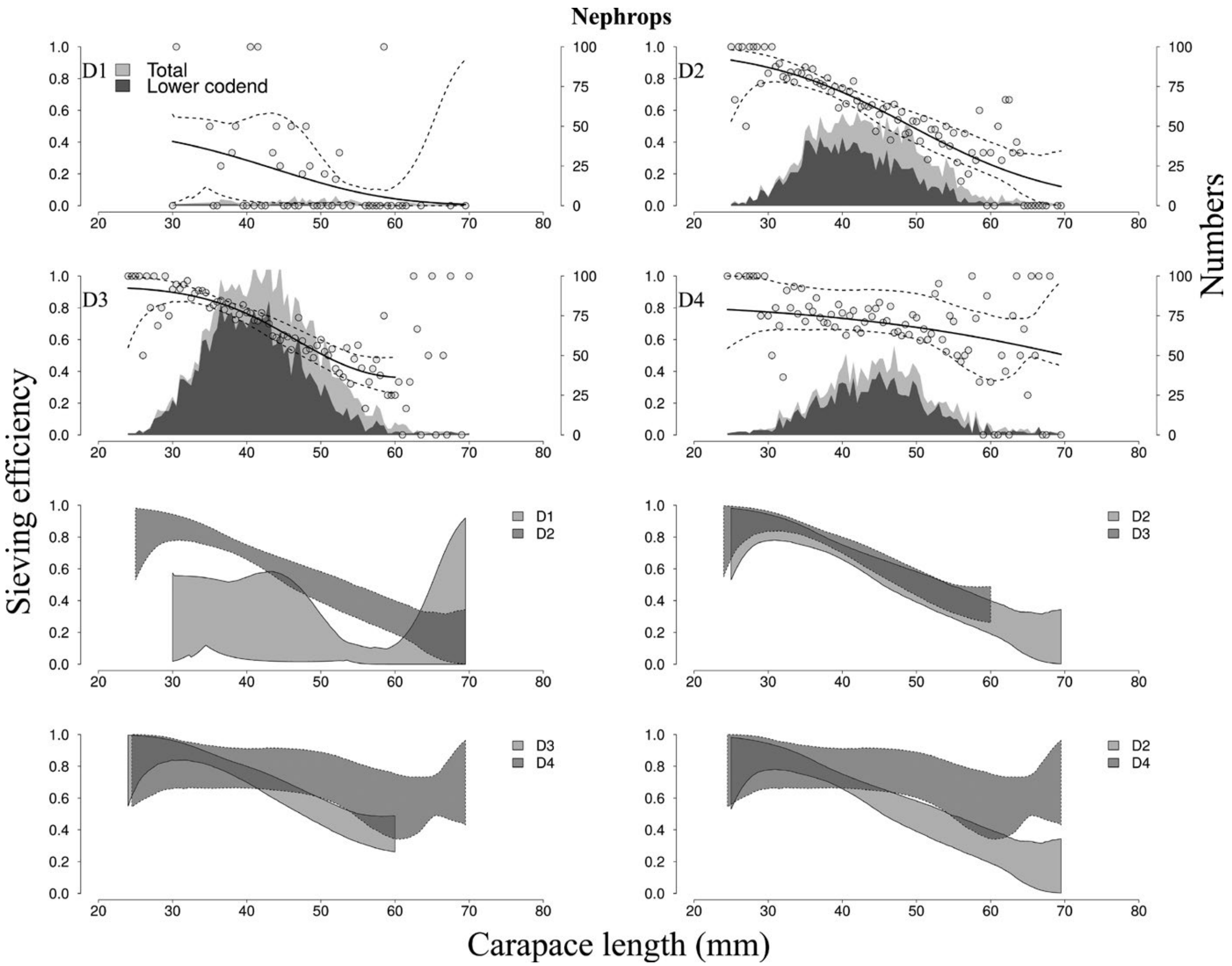

FIGURE 2 First and second rows show the sieving efficiency curves (solid lines), 95% bootstrap CIs (dashed lines), and experimental sieving data (points) obtained for *Nephrops* by each sieve-panel design (D1 = Design 1,..., D4 = Design 4). Total catches (light grey shading) and catches in lower codend (dark grey shading) are plotted in the background. Third and fourth rows show pairwise comparisons of the *Nephrops* sieving efficiency achieved by each of the designs. The grey bands represent the CI associated to each of the estimated sieving efficiency curves. The top-right to bottom-left diagonal can be used to assess the effect of increasing mesh size, and the opposite diagonal to compare the effect of uneven sieve-panel inclination

low p-value obtained for *Nephrops* Design 4 could indicate the model's inability to describe the experimental data. However, inspection of the deviations between the observed and modelled sieving efficiency did not reveal any clear pattern (Figure 2). Therefore, it was concluded that, in this case, the low p-value was caused by overdispersion in the experimental data, thus giving confidence in applying the model to describe the sieving efficiency curve for *Nephrops* in Design 4 as well.

The model for *Nephrops* predicted a sieving curve with values of <40% for Design 1, decreasing in efficiency as carapace length increased (Figure 2). Larger percentages of *Nephrops* catches were sieved using Designs 2–4, but many of the large individuals were still found in the upper codend. The larger mesh size applied in Design 2 improved the sieving efficiency of Design 1 significantly, estimated as being >86% for CL ≤ 30 mm, but decreasing drastically as CL increased. Increasing the inclination with the float lines applied in Design 3 reduced the monotonic decreasing trend in the sieving efficiency curve from Design 2, thereby reducing the loss in sieving efficiency for the largest sizes. Finally, Design 4 reduced the negative trend observed in the previous designs, and the average sieving efficiency was not lower than 45% throughout the experimental CL classes (Figure 2).

The increased mesh sizes from Design 1 to Design 2 resulted in an overall and significant improvement in sieving efficiency, except for CL, which was larger than ~60 mm. Design 3's sieving values were higher on average than Design 2's, but the improvement was not statistically significant over the available CL range. Design 4 improved the sieving efficiency of Designs 2 and 3 on CL ~50 mm significantly and the efficiency of Design 2 on CL >60 mm (Figure 2).

For the bycatch species, <1% of cod (18 fish) were caught in the lower codend using Design 1. A larger number of individuals

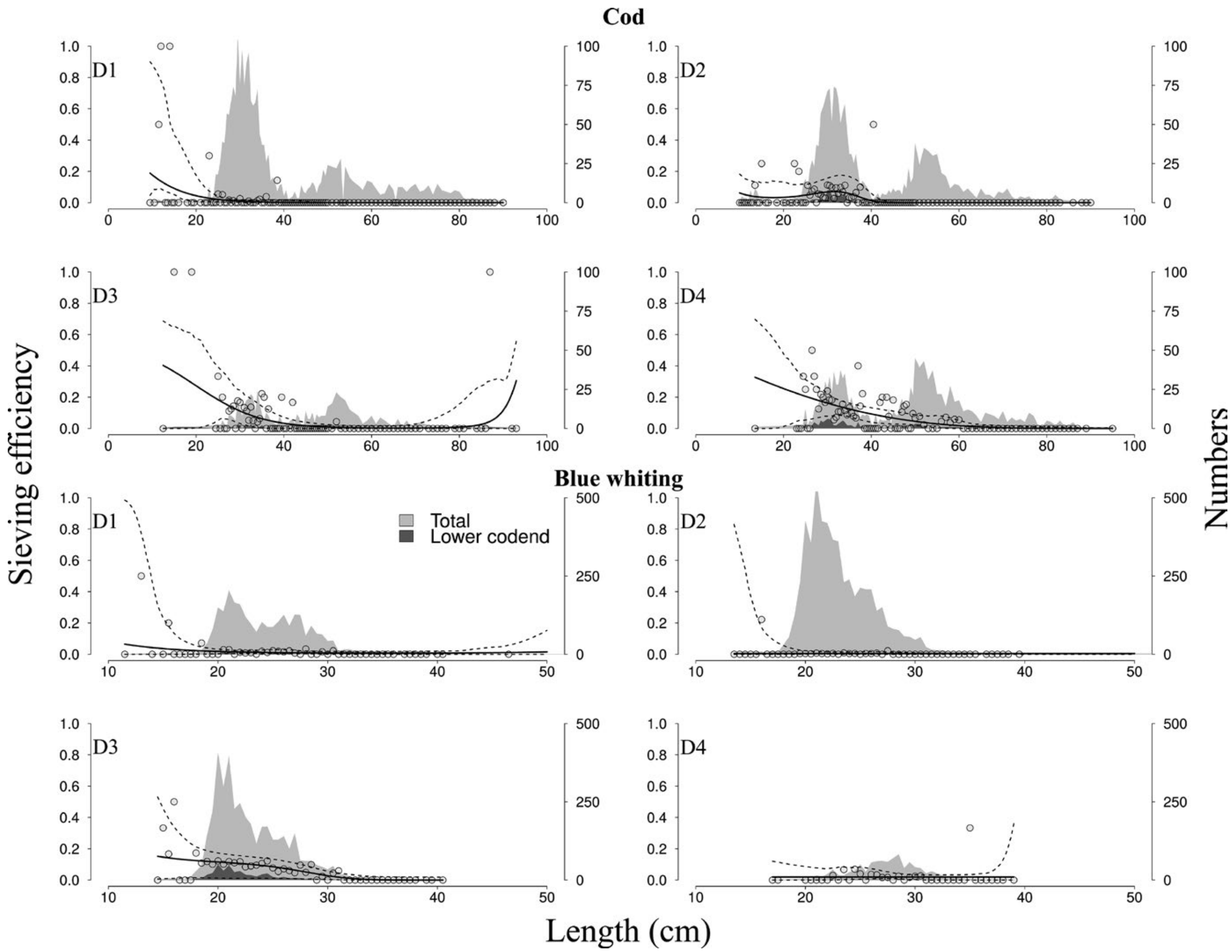

FIGURE 3 Sieving efficiency curves (solid lines), bootstrap CIs (dashed lines), and experimental sieving data (points) obtained by each design (D1 = Design 1,..., D4 = Design 4) on cod (top rows) and blue whiting (bottom rows). Total catches (light grey shading) and catches in the lower codend (dark grey shading) are plotted in the background

(4.3%) were sieved in Design 2, mostly in the range of 20–40 cm TL. Designs 3 and 4 increased the probability of small cod being sieved towards the lower codend. Nevertheless, the averaged sieve curve from Design 4 remains below 20% for most of the TL classes available (Figure 3).

Negligible catches (3%) of blue whiting were observed in the lower codend over the different designs. Only the steeper inclination of the panel in Design 3 resulted in an increased sieving efficiency for TL <30 cm; however, it was still <20% (Figure 3).

A considerable number of American plaice were observed in the lower codend and, as with *Nephrops*, the sieving efficiency was strongly and negatively related to fish length. Similar curves were obtained for Designs 1–3. Sieving efficiency was increased over the whole length range by Design 4 (Figure 4).

Sieve efficiency was lower and less dependent on fish length for witch flounder than for American plaice. Consistent with results from the previous flatfish species, Design 4 raised the sieving efficiency obtained by the other three designs considerably (Figure 4).

3.3 | Underwater video recordings

The images collected confirmed that the shape of the sieve-panels was as intended. The sieve-panel had a slight U-shape resulting from the drag of the water flow during towing (Figure S2).

The sediments suspended in the water column made it difficult to collect quality video sequences, and only a few of them revealed *Nephrops* interacting with the sieve-panels. Contrary to expectations, most observations of *Nephrops* passing through the sieve-panel meshes occurred through individuals' active behaviour. One observation involved a first swimming phase, where the individual contacted an open mesh tail-first (Figure S3: A.1). After penetrating the mesh tail-first, the individual pushed the body downwards attempting to burrow below the sieve-panel (Figure S3: A.2). At this stage, the individual stayed with the claws upwards above the panel surface, and most of the body below it (Figure S3: A.3), before pushing downwards again to pass the mesh completely and fall into the lower compartment (Figure S3: A.4). By contrast, other individuals

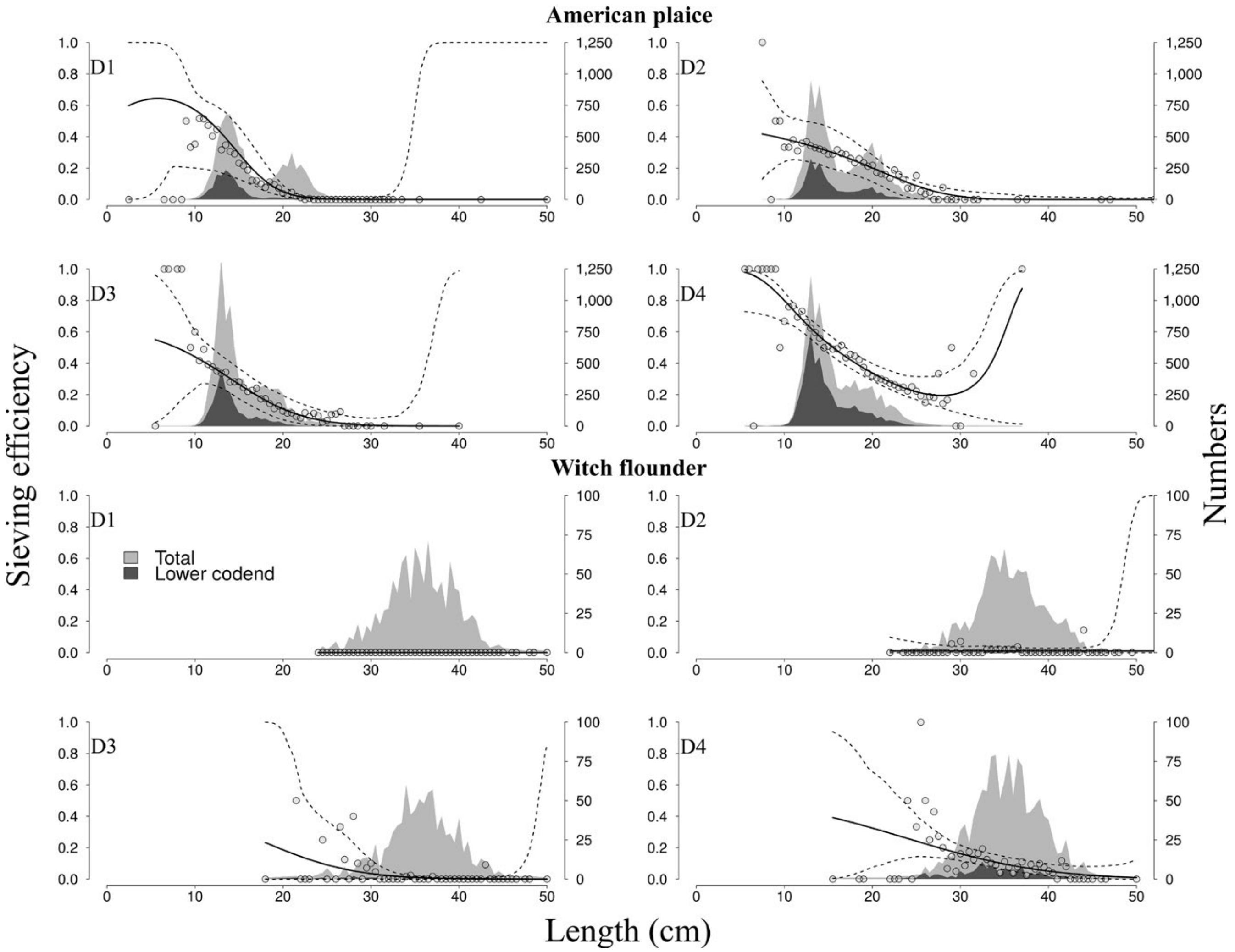

FIGURE 4 Sieving efficiency curves (solid lines), bootstrap CIs (dashed lines), and experimental sieving data (points) obtained by each design (D1 = Design 1,..., D4 = Design 4) on American plaice (top rows) and witch flounder (bottom rows). Total catches (light grey shading) and catches in the lower codend (dark grey shading) are plotted in the background

actively avoided being sieved by lying on the bar meshes (Figure S3: B), holding the mesh twines with the chelipeds, both in the natural or reverse body orientation (Figure S3: C–E), or simply by walking over the panel. In the last case, some specimens were observed walking over the panel until they lost their balance and finally drifted with the water flow towards the upper codend.

Most fish observed in the recordings followed the bottom–up inclination of the sieve-panel without attempting to pass through the meshes. Few active passages of cod were observed during the haul-back process, when cod attempted to swim downwards to balance the decrease in hydrostatic pressure caused by the loss of depth.

4 | DISCUSSION

The progressive improvement in *Nephrops* sieving efficiency from Design 1 to Design 4 was related to increments in the mesh size applied to the different panels. Although Design 2 improved on the performance of Design 1, the strong and negative length dependence in the efficiency of this design makes it unfeasible for commercial adoption. Further increasing the mesh size in Design 4 reduced the length dependence of the average sieve curve, but even with such improvement, only 45% of the *Nephrops* larger than 55 mm CL were found in the lower codend. Although Design 3 did not improve significantly on the efficiency of Design 2, the form of the predicted curve indicates that increasing the inclination of the panel might benefit the sieving efficiency.

Contrary to the original design assumptions, many sieving events observed in the underwater video recordings occurred when individuals actively positioned the body in an optimal orientation towards the open meshes (Figure S3: A1–A4), whereas other active interactions counteracted the sieving process (Figure S3: B–E). Based on the quantitative results and observation of the video recordings, it is speculated that, in addition to the passive process assumed in the design of the device, the sieving of *Nephrops* might also be influenced by avoidance behaviour, which could be stronger in large individuals.

Investigations conducted in tank aquariums demonstrated length-dependent avoidance behaviour only for male *Nephrops* (Newland, Chapman & Neil, 1998). In particular, it was observed that larger males reacted to tactile stimulus by producing fewer swimming bouts with more tail-flips per bout than smaller individuals. Assuming that these findings can be extrapolated to the fishing grounds, it is speculated that avoidance behaviour expected for large individuals could reduce the number of times they contact the surface of the sieve-panel compared with smaller individuals, reducing therefore the sieving occurrences. Since the relationship between swimming performance and individual length was found to be sex-dependent, *Nephrops* sex ratios in both the lower and upper codend could be used as indicators to clarify whether the behavioural observations in Newland et al. (1988) could explain the length-dependent efficiency of the gear.

The sieving efficiency of cod was estimated at <20% for all reference lengths considered (Figure 3). In particular, the efficiency of TL = 34 cm was 13%, meaning that 87% were directed towards the upper codend. It was assumed that using *Nephrops*-selective netting in the lower codend would provide some escapement possibilities for small fish, thus lowering even further the catch probability of undersized cod. The combination of a sieve-panel and selective codends would therefore significantly improve the cod bycatch rates in trawls mounting the Swedish grid, estimated at ~30% for lengths ~34 cm (Lövgren et al., 2016).

The sieve-panel performed differently on roundfish and flatfish. The greater and strongly length-dependent sieving efficiency observed for flatfish species is a consequence of their natural behaviour, tending to swim in close contact with the floor of the net (Ryer, 2008), and therefore increasing the probability of being mechanically sieved to the lower codend.

Although the sieve-panel concept tested here is a promising tool for improving the exploitation patterns in *Nephrops* fisheries, further improvements are necessary before the concept will be acceptable to commercial fishing fleets. The results of the present study provide further development opportunities of the concept in three different dimensions. First, a steeper inclination of the sieve-panel could improve the sieving efficiency for *Nephrops*. This alteration in the original design might reduce the longitudinal transportation of Nephrops over the panel, enhancing the possibility of being sieved through the meshes. On the downside, a steeper angle might reduce the guiding effect, leading to larger fractions of fish passing through the panel into the lower codend. Alternative mounting angles to be considered for future designs should be between 30° and 45°, a range used for other devices applied in *Nephrops* fisheries such as the Swedish grid (Valentinsson & Ulmestrand, 2008), or separator panels (Rihan & McDonnell, 2003). Increasing the mesh size used in Design 4 could facilitate the sieving efficiency for *Nephrops*, whereas changing the mesh geometry to a rectangular shape with the longitudinal opening oriented in the towing direction might reduce the sieving efficiency for flatfish, because of the species' flat body shape. Finally, using thicker twine in the panel construction might limit the *Nephrops'* ability to hold the twines and avoid being sieved.

Efficient separation of *Nephrops* and fish species might substantially reduce the unwanted bycatch in European *Nephrops*-directed fisheries. By securing the *Nephrops* catch in a lower codend, fishers could mount an upper codend with a larger mesh size to catch larger fish. Under fish quota exhaustion, catches of fish might be avoided by opening the upper codend during towing. In addition to a better utilisation of available quotas, other benefits can be expected by dividing the species efficiently into separate codends. A proper separation would improve the quality of marketable fish catches, as they are not subjected to damages in the skin and internal tissues caused by the contact with the spiny appendixes of *Nephrops* (Galbraith & Main, 1989; Karlsen, Krag, Albertsen & Frandsen, 2015). Exemptions to the landing obligation are contemplated in the European legislation for species with scientific evidences of high survival rates after catch and release. Most recent studies on *Nephrops* reported survival rates in the range of ~20%–60% (Castro, Araújo, Monteiro, Madeira & Silvert, 2003; Méhault, Morandeau & Kopp, 2016); therefore, *Nephrops* could be one of these exemptions under evidence of improved survival rates. Achieving "clean" *Nephrops* catches would drastically reduce the overall catch volume in the lower codend, sorting time on deck and air exposure, improving survival probability (Castro et al., 2003; Harris & Andrews, 2005; Méhault et al., 2016).

Further investigations combining quantitative analysis of *Nephrops* behavioural patterns with sieve-panels having different inclinations, mesh geometries and twine thickness would be of benefit for a better understanding on how mechanical and behavioural size selection contributes to the observed sieving efficiency for *Nephrops*. This information is required to create design guides for more efficient *Nephrops* sieve-panels, able to achieve clean *Nephrops* catches in the lower codend, while ensuring minimal or no losses of marketable individuals, so providing the industry with new technological alternatives to dealing with the landing obligation enforced by the new European Fishing Policy.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Paper VI

“Predictive framework for codend size selection of brown shrimp (*Crangon crangon*) in the North Sea beam-trawl fishery”

RESEARCH ARTICLE

Predictive framework for codend size selection of brown shrimp (*Crangon crangon*) in the North Sea beam-trawl fishery

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Abstract

The brown shrimp (*Crangon crangon*) fishery is of great socio-economic importance to coastal communities on the North Sea. The fishery is exploited by beam trawlers often using codends with very small mesh sizes, leading to concerns about catch rates of undersized shrimp. However, little information is available on codend size selection, making it difficult to provide scientifically based advice on alternative codend designs. Therefore, this study establishes a predictive framework for codend size selection of brown shrimp, based on a large selectivity dataset from 33 different codend designs tested during four experimental fishing cruises, during which more than 350,000 brown shrimp were length measured. Predictions by the framework confirm concerns about the exploitation pattern in the fishery, because the retention probability of undersized shrimp reaches 95% with the currently applied designs. The framework predictions allow the exploration of obtainable exploitation patterns depending on codend design. For example, increasing codend mesh size to 25–29 mm would reduce the retention rate of undersized shrimp to a maximum of 50%, depending on codend mesh type.

Introduction

The brown shrimp (*Crangon crangon*) fishery is socio-economically one of the most important fisheries in the North Sea [1,2]. It supports an international fleet of approximately 560 vessels [3], employing more than 1,000 fishermen, and producing yearly revenues of up to ~€100 million [4]. Landings have been consistently larger than 30,000 tonnes since 2003, with Dutch and German beam-trawl fleets in the length category 10–30 m making up approximately 90% of the total landings [5].

Despite its relevance, the brown shrimp fishery is one of the least regulated fisheries in European waters [6]. The European fishery management applied to this fishery does not include quotas or fishing-effort restrictions, while the minimum landing size is based on

and Niedersachsen (http://www.niedersachsen.de/startseite/). Additionally, SINTEFF Fisheries and Aquaculture provided support in the form of salary to BH but did not have any additional role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript. The specific roles of this author are articulated in the 'author contributions' section.

Competing interests: SINTEFF Fisheries and Aquaculture provided support in the form of salary to BH but did not have any additional role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript. This does not alter the authors' adherence to PLOS ONE policies on sharing data and materials.

market preferences, since only shrimps with total lengths >50 mm are commercially exploited [7]. However, in recent years, brown shrimp producer organisations have initiated a certification process of the fishery by the Marine Stewardship Council. A key finding for successful certification was the need to investigate gear technology on codend selectivity, which should improve the exploitation patterns of brown shrimp [1,4].

Codends made of diamond mesh (mesh in standard net orientation, T0) with small mesh sizes of ca. 20–22 mm are currently used to avoid the loss of commercial sizes of brown shrimp, at the expense of a large bycatch of small individuals [2,8,9,10]. One obvious strategy for reducing unwanted catches of small shrimp would be to increase the mesh size, but it has not been determined what that mesh size should be. Revill and Holst [9] studied the selectivity of diamond-mesh codends with mesh sizes of 16, 22, 24, and 26 mm, but only relative changes in selectivity were estimated. Therefore, the effect of mesh size on codend selectivity of brown shrimp is largely unknown and prevents the identification of optimal codend mesh size. In addition to mesh size, it has been demonstrated that altering codend mesh geometry using square mesh or T90 mesh (mesh orientation turned by 90˚) can provide better selectivity for crustaceans than standard diamond-mesh codends [11–14]. Therefore, square-mesh codends or T90 codends may be alternative codend designs for the brown shrimp fishery. However, this leads again to the question: What mesh size should be used for such codends?

It is the objective of this study to fill the knowledge gap about codend selectivity in the brown shrimp fishery, by developing a framework for predicting codend size selectivity for different mesh sizes and mesh types. This framework will allow the prediction of size-selective retention probabilities for brown shrimp in codends varying in mesh size and mesh type, including diamond-mesh, square-mesh, and T90 codends. The predictive framework is intended to improve decision-making about fishery exploitation patterns.

Material and methods

Ethic statement

Experimental fishing was conducted on board a German Fishing Research Vessel owned and operated by the Federal Office for Agriculture and Food (BLE), the legal entity which regulates and controls the fishing activity in German waters. The use of the Research Vessel for conducting the fishing trials implicitly granted the authors with the fishing permission from the German authorities. No other authorization or ethics board approval was required to conduct the study. Information on animal welfare and steps to ameliorate suffering and methods of sacrifice is not applicable, since the animals were not exposed to any additional stress other than that involved in commercial fishing practices. This study did not involve endangered or protected species.

Experimental codends

A total of 33 different codends were used for experimental fishing. Among them, 13 were made of standard diamond mesh, with mesh sizes ranging from ~19 mm to ~36 mm; 8 square-mesh codends, with mesh sizes ranging from ~17 mm to ~29 mm; and 12 T90 codends, with mesh sizes ranging from ~19 mm to ~36 mm. The square-mesh codends were constructed using standard diamond netting turned 45˚ (T45), and the netting used for T90 codends was turned 90˚ (Fig 1). Codend mesh sizes were measured using OMEGA gauge according to Fonteyne *et al.* [15].

The number of meshes in circumference applied in the codends decreased with mesh size to attempt neutralising the potential effect of the number of meshes on codend size selectivity [16]. All codends were made of 210 Deniers–mass in grams per 9,000 m of the fibre–PA twine netting.

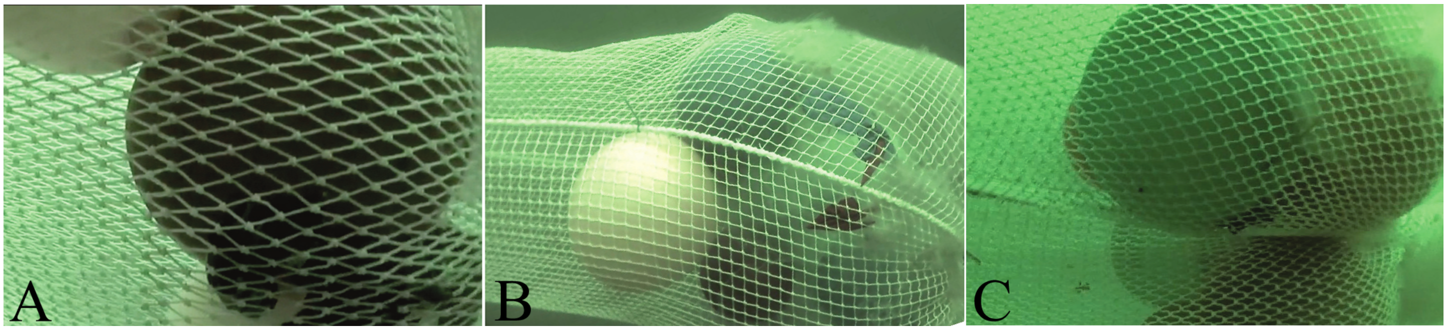

Fig 1. Netting configurations applied in the experimental codends. (A) traditional diamond mesh (T0), (B) square mesh (T45), (C) T90 mesh. A, B, and C Pictures were taken underwater using plastic balls to simulate catch volume.

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Sea trials and experimental design

Experimental fishing was conducted during four cruises on board the German research vessel *RV/Solea* (42 m, 950 kW) in commercial fishing grounds off the Wadden Sea coast, in the south-eastern part of the North Sea. Three of the cruises were conducted during the main fishing season (April, September, and November 2013), and one was conducted during low season in January 2013. The collection of size-selection data was based on the paired gear method [17]. Two identical beam trawls, similar to those used in the commercial fishery were mounted on each side of the vessel. The beam width was 7 m with a U-shaped groundrope of 9.2 m. The vertical opening of the net was 0.5 m. The trawl bodies were made of standard diamond netting with 30 mm mesh size in the front, decreasing to 20 mm in the rear. A sieve net of 60 mm mesh size [18] was mounted in both trawls, as it is mandatory in the commercial fishery to reduce fish bycatch. During each of the experimental hauls, one of the two nets mounted a control codend of 11 mm nominal mesh size, and the other mounted one of the 33 test codends. The mesh size of the control codend was not measured, since its nominal value met the lower limit of measurable sizes by the Omega gauge (10 mm ± 1 mm precision). Control and test codends were exchanged between trawls after several hauls to level out potential differences in catch efficiency between the two trawls. It was assumed that the control codend was not selective for the relevant sizes of brown shrimp; therefore, catches from this codend were considered representative of the population available for the experimental test codends. The differences in catches observed in the control and test codend were used to estimate the size-selection properties of the test codends at haul level.

Catch sampling was carried out for each codend separately. Brown shrimp catches were sorted from the bulk of the catch and weighted. A random subsample of brown shrimp was collected from the total catch and frozen for later length measurement in the laboratory. Once in the laboratory, the subsamples were thawed and placed on a plate to be photographed. The total length of each individual was obtained by digital image analysis. Total lengths where rounded to the half millimetre below, to provide count data of the number of shrimp in each half millimetre-width length groups for the subsequent size selectivity analysis.

Assessing the selectivity of individual hauls

The logistic function [17] was used to describe the size selection of each experimental haul:

$$r(\mathrm{l}, \mathrm{L50}, \mathrm{SR}) = \frac{\exp\left(\frac{\ln(9)\times(l-L50)}{\mathrm{SR}}\right)}{1+\exp\left(\frac{\ln(9)\times(l-L50)}{\mathrm{SR}}\right)} \tag{1}$$

Eq (1) quantifies the probability that a brown shrimp with length *l* will be retained in the test codend. It is defined by two selectivity parameters: *L50* represents the shrimp length with 50% retention probability, and *SR* (selection range) represents the range of lengths between 75% and 25% retention probabilities. The two selectivity parameters were obtained at haul level by modelling the length-dependent catch share of brown shrimp between the test and control codends. Assuming that the selectivity of the test codend can be described by the logistic function (Eq (1)), the proportion of a given length class *l* in the test codend to the total catch can be modelled by:

$$\varphi(l, L50, SR, SP) = \frac{SPxr(l, L50, SR)}{(1 - SP) + SPxr(l, L50, SR)} \tag{2}$$

where the split parameter (*SP*) is the length-independent probability for brown shrimp to enter the test codend. A value of *SP* ~0.5 indicates an equal probability of entering the control or the test codend; $SP > 0.5$ indicates a greater probability of entering the test codend. Although the *SP* parameter is not of primary interest in this study, its estimation is required to estimate the selection parameters of the test codend correctly [19]. The value for parameters *L50*, *SR*, and *SP* were obtained by minimising the following likelihood function:

$$\sum_l \left\{ nt_l \times ln\left(\frac{qt \times \varphi(l, L50, SR, SP)}{qt \times \varphi(l, L50, SR, SP) + qc \times (1 - \varphi(l, L50, SR, SP))}\right) + nc_l \times ln\left(\frac{qc \times (1 - \varphi(l, L50, SR, SP))}{qt \times \varphi(l, L50, SR, SP) + qc \times (1 - \varphi(l, L50, SR, SP))}\right)\right\} \tag{3}$$

In Eq (3), nt_l is the number of shrimps with length *l* measured in the test codend; nc_l is the number of shrimps with length *l* measured in control codend. Values qt and qc are the length-independent subsampling factors, calculated as the ratios of shrimp length measured to the total catch of shrimps for the test and control codends, respectively.

The ability of Eq (2) to describe the experimental data sufficiently well was evaluated based on the model *p*-value, model deviance vs. degrees of freedom (DOF), and inspection of how the model curve reflects the length-based trend in the data [17]. In case of a poor fit statistics (p-value being <0.05; deviance being $>>$DOF), the predicted curve from the analysed haul was inspected to determine whether the poor result was caused by structural problems when describing the experimental data, or by overdispersion in the data [17]. In case of no clear pattern in deviation, it was assumed that poor fit statistics would be the result of overdispersion in data, and the specific haul would be kept for further analysis.

Meta-analysis of codend selectivity

The values of *L50*, *SR*, and *SP*, estimated for each experimental haul (Eqs (1–3)), were used to model the variation of brown shrimp codend selectivity over the range of experimental codend designs tested during the four research cruises. The meta-analysis was conducted using the Fryer method [20], which quantifies the influence of a set of fixed factors on the experimental codend selectivity, including codend mesh size and other factors measured at haul level. Further, the Fryer method accounts for uncertainty in the estimation of selectivity for individual hauls owing to finite sample sizes, known as within-haul variation, and between-haul variation caused by variations in the fishing process due to uncontrolled changes in fishing conditions. We therefore applied the Fryer method to the experimental selectivity parameters, including information on their covariance (within-haul variation) and a set of fixed factors, as follows:

$$L50_{mean} = \alpha_0 + \alpha_1 \times m + \alpha_2 \times m^2 + \alpha_3 \times w + \alpha_4 \times m \times w + \alpha_5 \times s + \alpha_6 \times p$$

$$SR_{mean} = \beta_0 + \beta_1 \times m + \beta_2 \times m^2 + \beta_3 \times w + \beta_4 \times m \times w + \beta_5 \times s + \beta_6 \times p$$

$$SP_{mean} = \gamma_0 + \gamma_1 \times m + \gamma_2 \times m^2 + \gamma_3 \times w + \gamma_4 \times m \times w + \gamma_5 \times s + \gamma_6 \times p \quad (4)$$

In Eq (4), the coefficients α_j, β_j, and γ_j (j = 0,. . .,6) quantify the effect of each of the fixed factors on $L50_{mean}$, SR_{mean}, and SP_{mean}, respectively. The first terms considered are the intercept terms α_0, β_0, and γ_0. The effect of mesh size (m) is accounted for by the terms $\alpha_1 \times m$, $\beta_1 \times m$, $\gamma_1 \times m$. The second-order terms $\alpha_2 \times m^2$, $\beta_2 \times m^2$, and $\gamma_2 \times m^2$ were considered because exploratory scatterplots indicated a potential non-linear relationship between the values of the experimental size selectivity parameters and mesh size. Some studies have demonstrated that codend catch weight in some cases can affect codend size selection [10,21]. Consequently, the potential effect of catch weight (w) in the test codend is accounted for by the terms $\alpha_3 \times w$, $\beta_3 \times w$, and $\gamma_3 \times w$, while $\alpha_4 \times m \times w$, $\beta_4 \times m \times w$, and $\gamma_4 \times m \times w$ quantify the potential interaction effect between catch weight and codend mesh size. Additionally, the sea state can potentially influence codend selectivity [22]. Therefore, sea state (s) was measured using the vessel's bridge facilities (scale range 0–9). An average value of s was calculated for every experimental haul and accounted for by the terms $\alpha_5 \times s$, $\beta_5 \times s$, and $\gamma_5 \times s$. Beam trawls can have different fishing power, even in the twin configuration used in this study. Therefore, the mounting position p of the test codend was recorded for each haul (port = 0 or starboard = 1), and included in Eq (4) as $\alpha_5 \times p$, $\beta_5 \times p$, and $\gamma_5 \times p$.

For the analysis based on Eq (4), it is required that the size selection of the experimental codends included in the model have comparable between-haul variability. However, this assumption might not be fulfilled for codends with different mesh orientation [16]. For this reason, Eq (4) was applied separately for the three different mesh configurations considered in the study (diamond-mesh, square-mesh, and T90 codends).

Based on the full model (Eq (4)) with 21 fixed factors, many submodels can be formulated leaving out one or more terms at a time for $L50_{mean}$ and/or SR_{mean} and/or SP_{mean}. Considering all combinations, this led to 2,097,152 different competing models that were all candidates to model the size selection in diamond-mesh, square-mesh, and T90 codends separately. Analogue to the procedure in Wienbeck et al. [16], the candidate models were automatically ranked by decreasing value of AICc [23], and the model with the lowest AICc was selected to predict the size selection for diamond-mesh, square-mesh, and T90 codends, respectively.

Before the selected models could be used, it was necessary to validate their predictive capabilities, by inspecting their ability to describe the main trends in codend selectivity observed experimentally. This was done by plotting the $L50$ and SR values obtained from the experimental hauls against the predicted values, which involve considering the mean predictions ($L50_{mean}$, SR_{mean}), the uncertainty in mean parameters ($varL50_{mean}$, $varSR_{mean}$), and the estimated between-haul variation (D_{L50}, D_{SR}). Therefore, the following lower and upper 95% limits of the CI for $L50_{mean}$ and SR_{mean} were used in the comparisons:

$$limL50_{mean} = l50_{mean} \pm 1.96 \times \sqrt{varL50 + D_{L50}}$$

$$limSR_{mean} = SR_{mean} \pm 1.96 \times \sqrt{varSR + D_{SR}} \quad (5)$$

Predictive framework

Once the predictive capabilities of the selected models for diamond-mesh, square-mesh, and T90 codends were validated, they were applied to calculate the size of brown shrimp L_r associated to given retention probabilities r from a wide range of codend designs, differing in mesh size separately for the three types of codends investigated:

$$L_r = L50_{mean} + \frac{SR_{mean}}{ln(9)} \times ln\left(\frac{0.01 \times r}{1.0 - 0.01 \times r}\right) \quad (6)$$

The retention probabilities assessed in Eq (6) ranged from $r = 0.05$ to $r = 0.95$, with intermediate probabilities in steps of 0.05. Retention probabilities were plotted in percentage terms (for ease of reading) against codend mesh size and their associated L_r, providing isolines of codend retention probability. Sizes of shrimp with less than 5% retention probability ($r < 0.05$) and sizes of shrimp with more than 95% retention probability ($r > 0.95$) were considered to be fully released or fully retained by the codend, respectively.

Although the predictive framework of retention probability provides information independent of the size structure of the available brown shrimp population, it is of interest to give an example of codend performance for a given population structure. This assessment was conducted by applying the predictive capabilities of the selected models on the size structure of brown shrimp population ($nPop_l$) used during the sea trials. The structure of $nPop_l$ was therefore obtained by pooling the brown shrimp catches from the control codend over the experimental hauls (Fig 2). The predicted size-selection curve for a given codend design was applied to $nPop_l$, to produce simulated catches ($nCatch_l$) of brown shrimp. Based on $nPop_l$ and $nCatch_l$, the following codend usability indicators were calculated for diamond-mesh, square-mesh, and T90 codends with 21 mm (midpoint mesh size considering the commercial range), 23 mm, 25 mm, 27 mm, and 29 mm mesh sizes:

$$nR = \frac{100 \times \sum_{l<mls} nCatch_l}{\sum_{l} nCatch_l}$$

$$nP = \frac{100 \times \sum_{l} nCatch_l}{\sum_{l} nPop_l}$$

$$nPa = \frac{100 \times \sum_{l \geq mls} nCatch_l}{\sum_{l \geq mls} nPop_l}$$

$$nPb = \frac{100 \times \sum_{l<mls} nCatch_l}{\sum_{l<mls} nPop_l} \quad (7)$$

where $mls = 50$ mm is the minimum landing size established by the fleet for market reasons [7]; nR is the percentage of catches of undersized shrimp relative to the total catch, therefore, quantifying the expected proportion of brown shrimp bycatch associated with a given codend. The indicator nP represents the percentage of brown shrimp entering the codend, which is

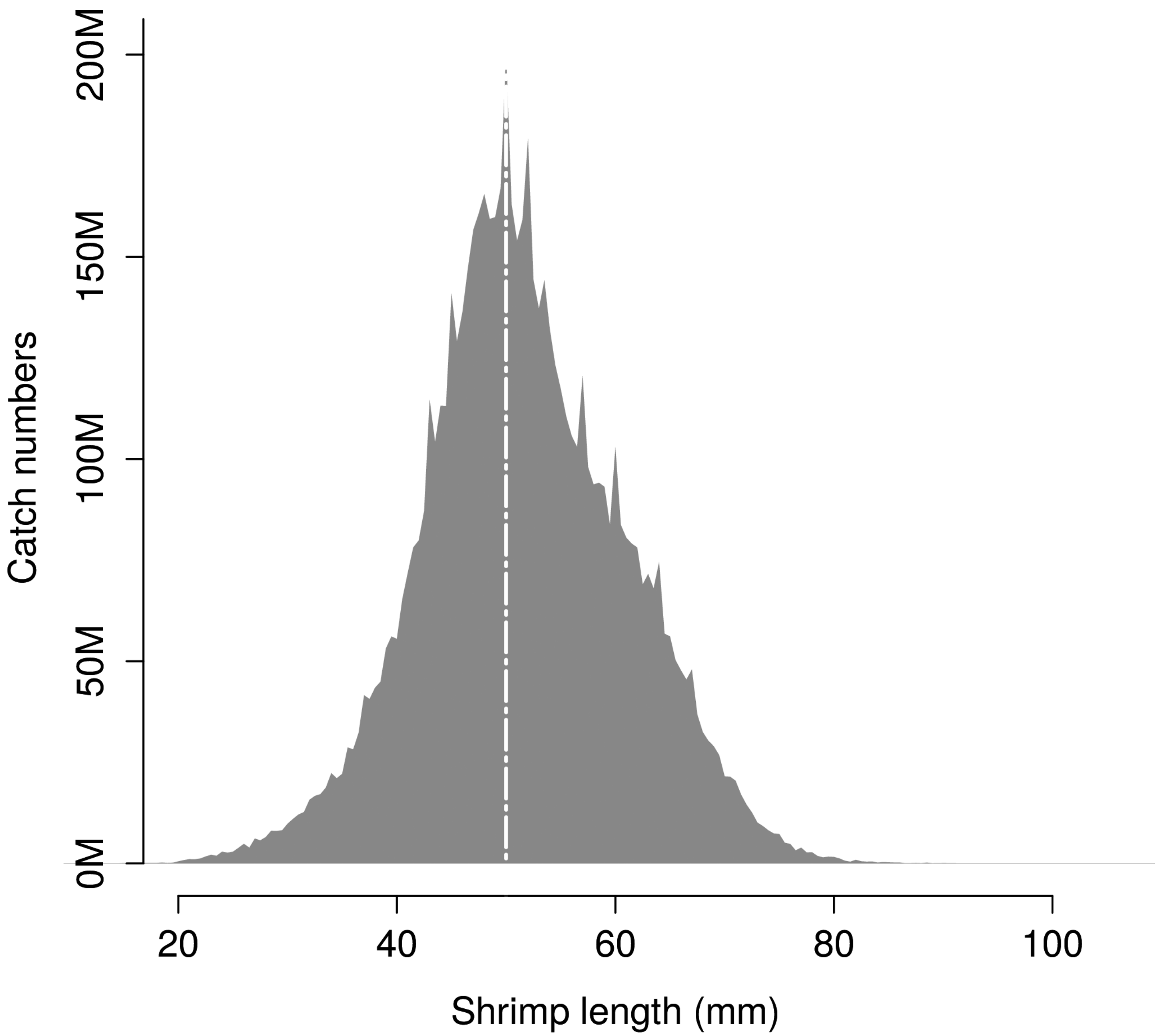

Fig 2. Size structure of the brown shrimp population fished during the sea trials. Numbers (in thousands, M) obtained after pooling the catches from the control codend over the experimental hauls.

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finally caught, providing information on the length-independent retention efficiency of the codend. Finally, *nPa* and *nPb* indicate codend retention efficiencies for length ranges of brown shrimp greater than and less than *mls*, respectively. Therefore, a codend with a good compromise between retention of commercial shrimp and release of undersized shrimp would have *nR* and *nPb* values close to 0%, and an *nPa* value close to 100%. All analysis described above were conducted with the software SELNET [24].

Results

A total of 208 hauls were conducted during the four research cruises carried out in January (27 hauls), April (85 hauls), September (63 hauls), and November (33 hauls) 2013. Most of the hauls were conducted in a rectangle defined between 54.25N-55.00N and 008.00E-008.40E, in the German waters of the Wadden Sea (Fig 3 and S1 Table). In all, 89 hauls were conducted using diamond-mesh codends, 51 using square-mesh codends, and 68 using T90 codends (Table 1). Beam trawls were towed at a speed of ~3 knots with a towing duration of 60 min, on fishing grounds between 11 and 24 m deep, confirming that fishing conditions were similar among hauls, codends and cruises (S1 Table). In 75% of the experimental hauls, the catch weight in the test codend did not exceed 40 kg. On average, smaller catches in the test codends were observed during the first two cruises (14.98 kg, (standard deviation, s.d. = 5.24) and 8.80 kg (s.d. = 4.73)) compared with the catches in September and November (50.43 kg (s.d. = 46.50) and 82.41 kg (s.d. = 39.53)). Shrimp catches were systematically subsampled, and approximately 1 kg of shrimp was used for length measurement per codend. In total, 160,612 brown shrimp were measured from hauls using diamond-mesh test codends, 85,304 individual measurements were obtained from hauls using square-mesh codends, and 109,451 individual measurements from hauls using T90 codends. The subsampled factors ranged between 0.03 and 0.47 in test codends and between 0.02 and 0.26 in the control codend (Table 1).

Size selectivity of individual hauls

A visual inspection of the experimental data demonstrated clear size-selection trends (S1 Fig), except in three hauls (two hauls using diamond-mesh codends and one haul using a T90 codend). For these three hauls, it was not possible to estimate the covariance matrix of the selectivity parameters. Therefore, these hauls were excluded from further analysis. The selectivity parameters (*L50* and *SR*), the split parameter (*SP*), and the covariance of the remaining 205 hauls were successfully estimated using Eqs (1–3). For all 205 valid hauls, the selectivity parameters, fit statistics, the characteristics of the codends used (codend type and mesh size), and the additional fixed factors considered for the subsequent meta-analysis (Eq (4)) are summarised in S2 Table. The inspection of the fit statistics for each estimation on haul level resulted in 39 fits (~19% of the total estimated models) with p-values <0.05. However, inspection of the residuals associated with these hauls did not show any systematic trend. Therefore, it was decided to use the selectivity data from all 205 hauls for subsequent analysis.

Meta-analysis of codend selectivity

The Fryer method was successfully applied in the selectivity meta-analysis for diamond-mesh, square-mesh, and T90 codends. The results from the full model (Eq (4)) and the associated 2,097,151 reduced models for each codend type were ranked by increasing the AICc value. The models with lowest AICc values for each codend type were selected. The three resulting models allowed predictions of the mean size selectivity for each of the codends used in experimental fishing (Fig 4). In general, the position of the predicted size-selection curves in relation to the distribution of experimental curves indicates good predictive capabilities of the selected models. Further details from each of the selected models are described in the subsections below.

Model for diamond-mesh codends. The selected model for predicting diamond-mesh codend selectivity has the following fixed factor structure:

$$L50_{mean} = \alpha_1 \times m + \alpha_2 \times m^2$$

$$SR_{mean} = \beta_1 \times m$$

$$SP_{mean} = \gamma_0 \quad (8)$$

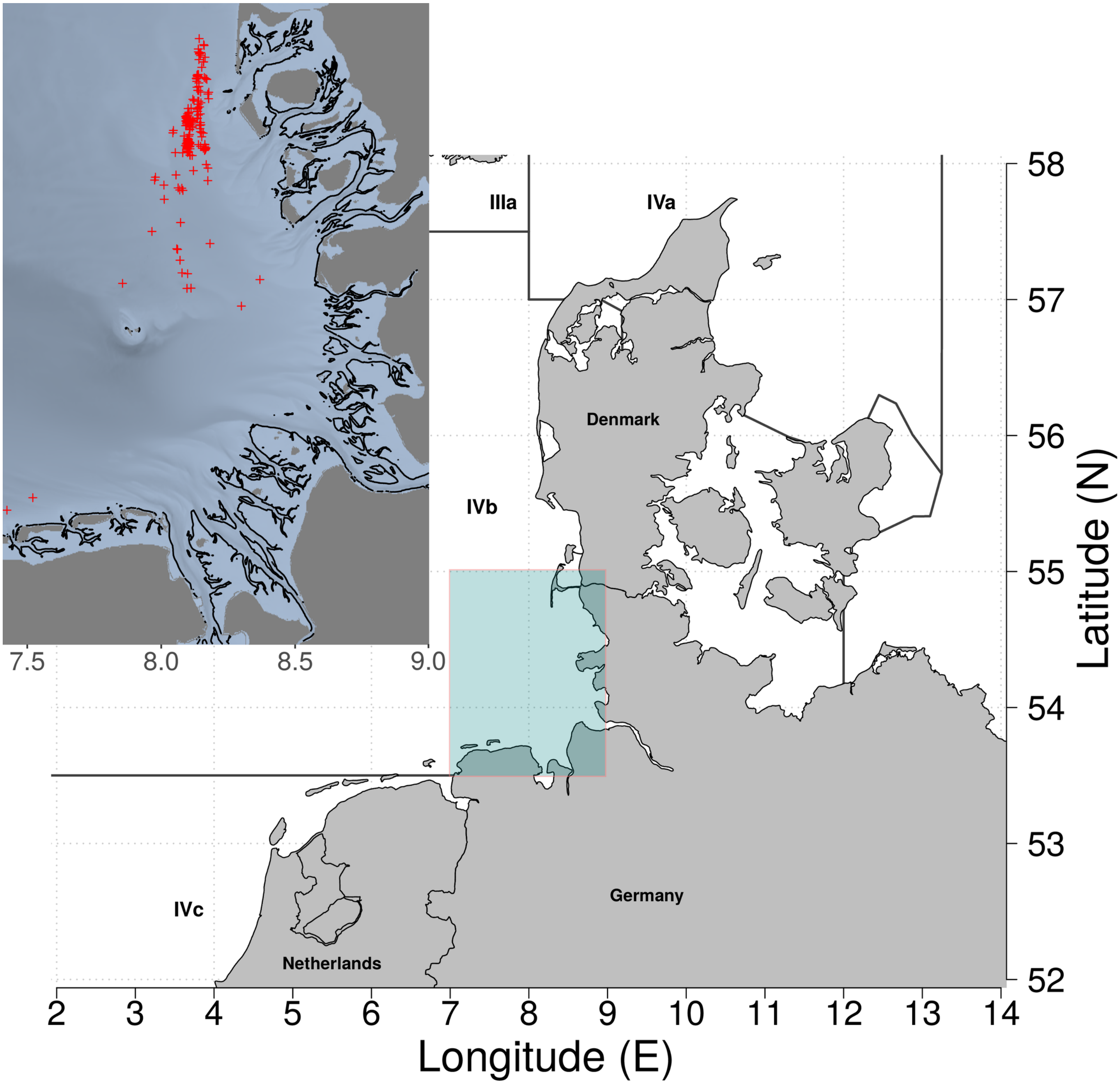

Fig 3. Location of the experimental hauls conducted during the four different cruises.

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Only four of the terms used in the full model structure (Eq (4)) were kept in the selected model. The linear (m) and quadratic mesh size (m^2) were the two factors used to describe the experimental *L50* values. The effect of the linear term is positive and stronger than the negative value of the quadratic term (Table 2), resulting in a nearly linear trend with a positive slope over the range of experimental mesh sizes (Fig 5). SR_{mean} increases linearly with mesh size, and

Table 1. List of codends tested in experimental trials, and brown shrimp catch information related to each codend.

	Test codend					Control codend		
Codend type	Codend mesh size (mm)	Number of hauls	Number measured	sub-sample factor (qt)	Lengths (mm)	Number measured	sub-sample factor (qc)	Lengths (mm)
Diamond mesh	19.05 (0.07)	6	6857	0.06	50.6 (21.0–81.0)	7414	0.06	49.1 (12.5–83.0)
(T0)	20.19 (0.34)	9	8780	0.18	50.0 (10.5–86.5)	10037	0.13	47.9 (13.5–93.0)
	21.45 (0.07)	9	7158	0.26	51.1 (24.5–90.0)	8498	0.21	49.0 (19.5–81.5)
	22.95 (0.19)	6	5376	0.09	53.2 (24.5–84.0)	5765	0.07	50.3 (15.0–84.0)
	24.65 (0.07)	6	4441	0.28	53.7 (25.5–82.5)	5054	0.20	50.1 (20.5–85.0)
	25.10 (0.29)	5	4482	0.20	51.9 (18.0–82.0)	4707	0.15	49.8 (19.0–83.5)
	27.15 (0.60)	6	5665	0.07	55.2 (25.5–89.5)	8692	0.03	48.0 (20.0–88.5)
	27.83 (0.24)	8	5537	0.16	54.9 (17.5–81.0)	7453	0.09	49.2 (19.5–81.0)
	29.35 (0.26)	5	3351	0.12	54.3 (18.0–86.5)	4331	0.05	50.5 (15.0–80.5)
	31.58 (0.28)	6	4643	0.23	54.7 (24.0–88.0)	6549	0.05	48.0 (20.0–82.0)
	32.25 (0.13)	6	3602	0.23	58.2 (25.0–81.0)	4816	0.19	51.3 (22.5–85.5)
	32.28 (0.13)	12	7899	0.34	56.5 (23.0–87.0)	10828	0.18	50.4 (15.0–87.5)
	36.38 (0.45)	5	3639	0.41	57.4 (33.5–95.5)	5038	0.13	51.2 (20.0–87.5)
Square mesh	17.25 (0.07)	2	1900	0.47	48.7 (18.5–75.5)	2312	0.26	47.3 (21.5–83.0)
(T45)	18.75 (0.21)	5	4483	0.09	52.4 (24.5–81.0)	4545	0.08	51.6 (11.0–80.5)
	20.98 (0.88)	12	8577	0.06	55.2 (23.0–84.5)	9161	0.06	52.5 (18.5–89.5)
	23.40 (0.12)	6	4943	0.07	54.6 (26.0–85.0)	6704	0.04	49.1 (19.5–87.5)
	24.95 (0.21)	8	6387	0.08	54.6 (20.5–87.5)	8172	0.04	49.7 (17.5–85.5)
	25.20 (0.18)	6	3232	0.11	57.0 (35.0–81.5)	3615	0.07	53 (20.5–80.0)
	27.78 (0.15)	6	4040	0.12	56.8 (27.5–86.0)	6546	0.05	49.1 (15.0–99.5)
	29.28 (0.21)	6	4392	0.29	55.9 (24.5–87.0)	6295	0.13	49.4 (17.5–85.0)
T90	18.88 (0.33)	6	5133	0.10	52.3 (20.5–84.5)	6729	0.06	49.1 (16.5–89.0)
	20.18 (0.56)	3	3581	0.11	49.0 (25.5–82.0)	3568	0.09	47.4 (14.5–76.5)
	21.15 (0.49)	6	3678	0.15	55.6 (27.5–82.0)	4248	0.14	52.6 (20.5–77.5)
	22.50 (0.48)	6	5690	0.18	51.4 (9.5–79.0)	6670	0.13	48.3 (10.0–80.5)
	24.35 (0.66)	7	4221	0.27	57.2 (33.5–81.5)	4672	0.22	53.9 (21.5–83.0)
	24.63 (0.59)	5	3800	0.09	57.8 (24.5–86.0)	4308	0.03	52 (20.0–92.5)
	27.55 (0.13)	6	3923	0.06	56.5 (26.0–88.5)	5793	0.02	51.5 (20.0–90.0)
	27.83 (0.29)	6	3363	0.36	59.0 (28.5–79.5)	3766	0.19	53.8 (26.0–84.0)
	29.03 (0.63)	6	4174	0.04	55.8 (25.0–85.5)	5741	0.03	50.6 (21–87.5)
	31.28 (0.55)	6	3254	0.29	59.0 (30.5–85.0)	3984	0.18	51.7 (14.5–80.5)
	31.40 (0.34)	5	3686	0.05	55.5 (21.0–88.0)	5102	0.03	50.4 (17.0–88.5)
	36.50 (0.20)	6	4498	0.03	56.1 (24.5–88.5)	5869	0.02	51.0 (20.5–84.0)

Average mesh size of the test codends with standard deviation (sd, in brackets) was taken as the inner distance from knot to knot in stretched meshes (sd in brackets), obtained using OMEGA gauge. Number of brown shrimps measured in test and control codend obtained after pooling catches from all hauls conducted with a given codend. Description of length structure of brown shrimp caught in the test and control codends includes the mean length and the length range (in brackets) found in the measured sub-samples. Sub-sampled factors presented are averaged over hauls conducted with each of the tested codends.

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no other term was found influential (Table 2 and Fig 5). The structure of the *SP* equation only included the intercept term, which was found to be not significantly different from 0.5 (γ_0 = 0.49 (0.48–0.52)), indicating equal probability that brown shrimp entered either the control or the test codend.

The $L50_{mean}$ and SR_{mean} predictions from Eq (8) describe well the experimental data (Fig 5), because most of the experimental values fall within the CI of $L50_{mean}$ and SR_{mean}, whereas the outer points overlap their own CIs with the CI from the predictions.

Model for square-mesh codends. The selected model for square-mesh codends has the following structure:

$$L50_{mean} = \alpha_1 \times m$$

$$SR_{mean} = \beta_2 \times m^2 + \beta_3 \times w$$

$$SP_{mean} = \gamma_0 \qquad (9)$$

Mesh size (m) was the only fixed factor included in Eq (9) to describe the distribution of the experimental $L50$ values. The estimated linear coefficient was similar to the one estimated for diamond-mesh codends (Table 2); however, the lack of a quadratic term results in a linear trend of $L50_{mean}$ over the range of mesh sizes (Fig 5). The fixed-factors structure related to SR is more complex, combining the effect of the second-order polynomial mesh size (m^2) and catch weight (w). The value of both terms is positive (Table 2). Therefore, SR_{mean} also increases with increasing catch weight. As for diamond-mesh codends, the predicted SP_{mean} was not significantly different from 0.5 (Table 2).

Predictions from Eq (9) using a fixed catch weight of 35 kg (a value near the average catch weight obtained during the sea trials in the test codend) describe well the distribution of the experimental $L50$ and SR obtained by square-mesh codends (Fig 5), with all experimental values or their respective CIs falling within the CI of the predictions.

Model for T90 codends

The selected model for T90 codends has the following structure:

$$L50_{mean} = \alpha_1 \times m + \alpha_3 \times w + \alpha_4 \times m \times w$$

$$SR_{mean} = \beta_1 \times m$$

$$SP_{mean} = \gamma_0 \qquad (10)$$

Eq (10) includes the fixed-factors mesh size (m), catch weight (w), and the interaction term ($m \times w$) to describe the variation of experimental $L50$ values obtained with T90 codends. The main-factors mesh size and catch weight affect the $L50_{mean}$ positively, whereas the negative value of the interaction term (Table 2) lead to an opposite effect of catch weight depending on mesh size. In particular, increasing catch weight increases $L50_{mean}$ for mesh sizes less than 25 mm, whereas the opposite effect is predicted for mesh sizes greater than 25 mm. As with the diamond-mesh model (Eq (8)), the T90 model incorporated only the linear mesh size term (m) for SR, and the associated coefficients are very similar (Table 2). As in Eqs (8) and (9), only the intercept was used to describe the experimental SP values, and the predicted SP_{mean} was not significantly different from 0.5 (Table 2).

Predictions from Eq (10) using 35 kg as fixed catch weight describes well the distribution of the experimental $L50$ and SR obtained by T90 codends (Fig 5), with most experimental values or their respective CIs falling within the CI of the predictions.

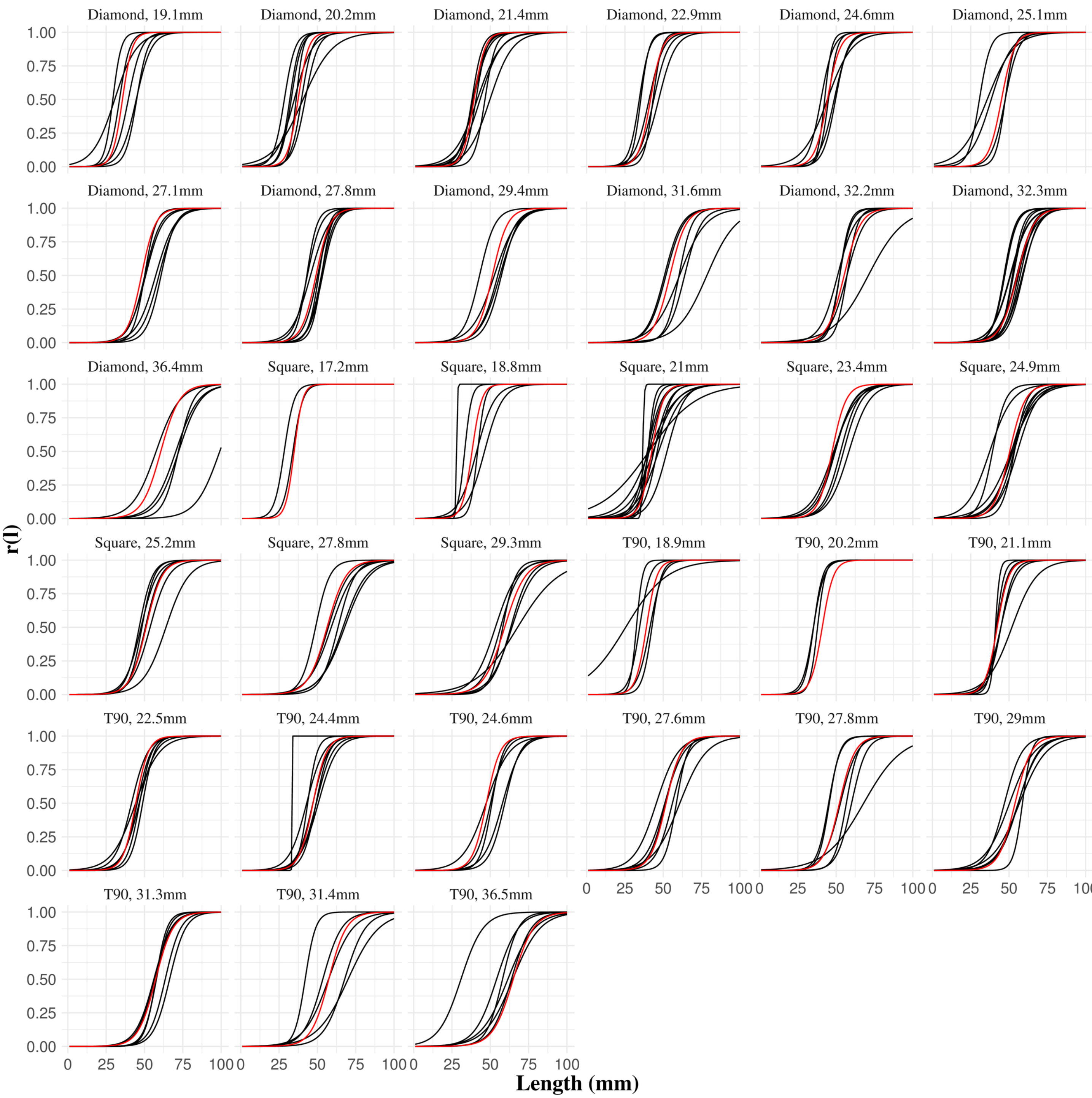

Fig 4. Predicted size selection curves for each of the experimental codends. For visual comparison, the mean curves predicted by the selected models (red lines) for each codend are plotted together with the size selection curves obtained experimentally (black lines).

https://doi.org/10.1371/journal.pone.0200464.g004

Predictive framework

The good predictive capabilities of the three models shown in Figs 4 and 5 allowed the establishment of the predictive framework. Isolines in Fig 6 describing codend retention

Table 2. Estimated parameters of the selected predictive models for different mesh types (diamond, square and T90).

Mesh configuration	Parameter	Fixed factor	Coefficient	Value	SE	95% CI	p-value
Diamond-mesh	*L50 (mm)*	*m*	α_1	2.05	0.12	1.821 to 2.287	<0.001
		m^2	α_2	-0.01	>0.01	-0.018 to -0.002	0.011
	SR (mm)	*m*	β_1	0.37	0.01	0.350 to 0.396	<0.001
	SP	*intercept*	γ_0	0.49	0.01	0.476 to 0.518	<0.001
Square-mesh	*L50 (mm)*	*m*	α_1	2.02	0.03	1.960 to 2.082	<0.001
	SR (mm)	m^2	β_2	0.02	>0.01	0.014 to 0.017	<0.001
		w	β_3	0.04	>0.01	0.023 to 0.053	<0.001
	SP	*intercept*	γ_0	0.51	0.01	0.484 to 0.540	<0.001
T90	*L50 (mm)*	*m*	α_1	1.93	0.03	1.866 to 1.988	<0.001
		w	α_2	0.31	0.06	0.193 to 0.438	<0.001
		mxw	α_3	-0.01	>0.01	-0.017 to -0.009	<0.001
	SR (mm)	*m*	β_1	0.40	0.02	0.366 to 0.427	<0.001
	SP	*intercept*	γ_0	0.51	0.01	0.483 to 0.530	<0.001
Between haul variation		*Diamond-mesh*	*Square-mesh*	T90			
	D_{11}	26.14	22.11	26.44			
	D_{22}	6.38	7.93	7.43			
	D_{33}	0.01	0.01	0.01			

Top: fixed factors included in the model matrix (see also Eqs (8–10)). Bottom: Diagonal of the D-Matrix presenting the estimated between-haul variation of the selective parameters. SE = standard errors, CI = confidence interval.

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probabilities for the three different mesh types, covering the range of mesh sizes applied experimentally, were estimated using the established framework (see S3 Table to assess the numerical values used in Fig 6). Predictions for square-mesh and T90 codend were obtained assuming a fixed catch weight of 35 kg. Isolines of retention probability show that lengths equal to or greater than *mls* = 50 mm are fully retained (greater than 95% retention probability) by diamond-mesh codends between 20 and 21 mm. The retention probability in this range of mesh size remains great for smaller lengths. For example, the retention probability for 45 mm brown shrimp is still greater than 80%. The framework reveals that it would require codends with diamond-mesh size of 29 mm to reduce the retention probability for the species *mls* to ca. 50%, whereas the probability of retaining 45 mm brown shrimp individuals would drop to 25%. On the other hand, the framework predicts retention probabilities between 80% and 95% for square-mesh and T90 codends using commercial mesh sizes between 20 and 22 mm. Applying a square-mesh codend with a mesh size of ~25 mm, or a T90 mesh size of ~27 mm, would result in a retention efficiency similar to diamond-mesh codends with 29 mm mesh size.

The percentage of undersized shrimp relative to the total catch (*nR* indicator in Eq (7)) for the diamond-mesh codend with commercial mesh size of 21 mm is ~42% (Table 3). For the same codend, it is expected to catch 85 of every 100 shrimps entering the codend (*nP* ~85%). As reflected by the isolines for this codend design, the indicator *nPa* shows nearly full retention efficiency for individuals equal to or greater than species *mls* (*nPa* ~99%), at the expense of retaining a large number of undersized shrimp (*nPb* ~72%). By changing the mesh type to square mesh or T90, a considerable reduction in the retention efficiency of the undersized shrimp (*nPb* ~55% and *nPb* ~57% for square-mesh and T90 codends, respectively) is expected, without considerable effects on the retention efficiency for marketable sizes (*nPa* ~96%). Using a T90 codend with 23 mm mesh size, or increasing the diamond-mesh size to 25 mm, would reduce the retention efficiency for undersized shrimps to less than 50% (*nPb* ~43%),

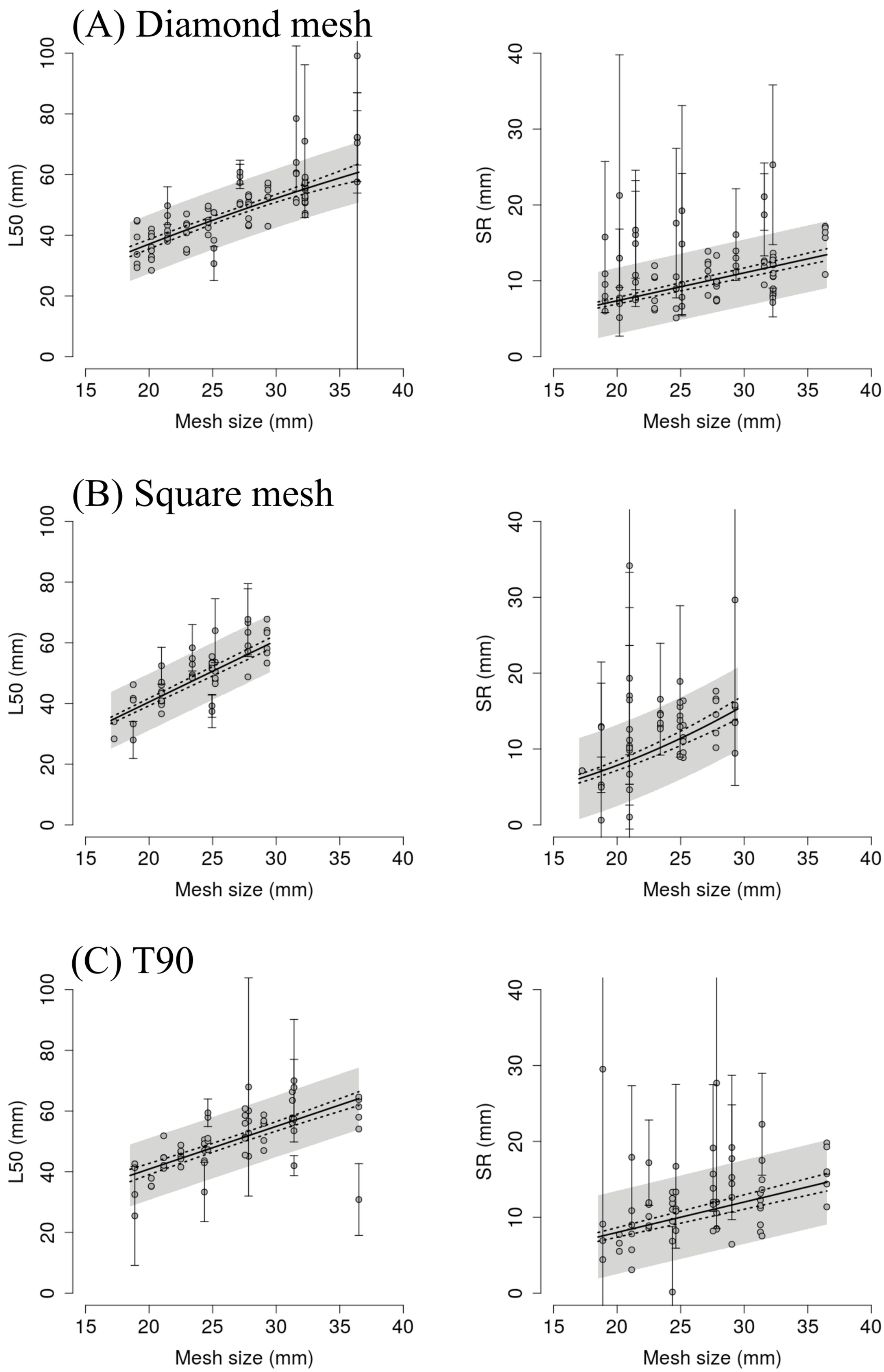
(A) Diamond mesh
(B) Square mesh
(C) T90
L50 (mm)
SR (mm)
Mesh size (mm)

Fig 5. *L50* and *SR* mean values (solid line) estimated by the predictive models for the three different codend mesh types ((A) Diamond mesh, (B) Square mesh, and (C) T90). Predictions are plotted against the L50 and SR values obtained from individual hauls (circle marks). Dotted lines represent the CIs accounting for the uncertainty of the estimation, while the grey band represents the CIs accounting for the total variation in the data, including the between-haul variation. CIs associated to experimental values (vertical lines) only plotted for the experimental points falling outside the grey band. *SR* predictions for the square-mesh codends and *L50* predictions for T90 codends were estimated using a fixed total catch weight of 35 kg, a value near the mean total catches observed in the test codends.

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while maintaining the retention efficiency for marketable shrimps at greater than 90% (*nPa* ~91%). Implementing any of these codend designs would reduce bycatch to *nR* = ~32%. Likewise, applying either a square-mesh codend with 25 mm mesh size, a T90 codend with 27 mm mesh size, or increasing the diamond-mesh size to 29 mm would reduce the retention efficiency for undersized shrimps to values smaller than 25% (nPb ~23 and *nPb* = 21.5, respectively), while the retention efficiency for the commercial shrimp would be reduced to nearly 75% (nPa ~74%).

Discussion

This study attempts to fill gaps in knowledge of codend size selection in the brown shrimp beam-trawl fishery in the North Sea. Based on a comprehensive dataset derived from experimental fishing, we deliver a framework to predict the codend size selectivity for a wide range of codend designs. These predictions can be used to identify suitable codend specifications under a given harvesting strategy.

Polet [10] studied the selectivity of a standard codend with commercial mesh size of 21.7 mm, estimating *L50* = 39.4 mm (37.0–41.4 mm) and *SR* = 11.6 mm (10.2–13.0). As a benchmarking exercise, we used our tool to predict the selectivity parameters for a codend with the same mesh size and mesh configuration, giving an $L50_{mean}$ = 39.8 mm (38.2–41.3 mm), nearly the same *L50* as Polet [10], and a slightly lower SR_{mean} = 8.0 mm (7.5–8.5). These similar results, obtained from the different studies–and different experimental designs–support the usability of our predictive framework.

In addition to the ability to predict the size-selection parameters for a wide set of codend designs, the predictive framework is further applied to estimate codend usability indicators. It is important to mention here that the given codend usability indicators depend on the actual population structure and so need to be recalculated if they are applied to other brown shrimp populations.

The predictions highlight the very poor selectivity delivered by the codends currently used in the commercial fishery. For a 21 mm diamond-mesh size, the framework predicts almost full retention for the *mls* of brown shrimp (Fig 6 and Table 3). Accordingly, the *nPa* value (retention of marketable sizes) for this codend was estimated to be ~99%. Simultaneously, the *nR* (rate of bycatch of undersized shrimp) indicator was ~40%, which indicates an average bycatch rate of ca. 40% in the fishery for this codend and population structure. Using the predictive capabilities of the framework provide different alternatives to mitigate the bycatch problem. For example, it would be possible to reduce the bycatch rate by half (*nR* ~20%), while maintaining the catchability of commercial sizes greater than 70%, by implementing either codends with ~29 mm diamond-mesh size, square-mesh codends with ~25 mm mesh size, or T90 codends with ~27 mm mesh size. This example illustrates how the framework can provide predictions and thereby recommendations on codend design, suitable for specific management strategies.

This study quantifies for the first time the selectivity properties of square-mesh and T90 codends in the North Sea brown shrimp fishery. As with diamond-mesh codends, the present analysis shows $L50_{mean}$ and SR_{mean} values from square-mesh and T90 codends increasing with increasing mesh sizes. The predictions using a fixed catch weight of 35 kg show $L50_{mean}$ values

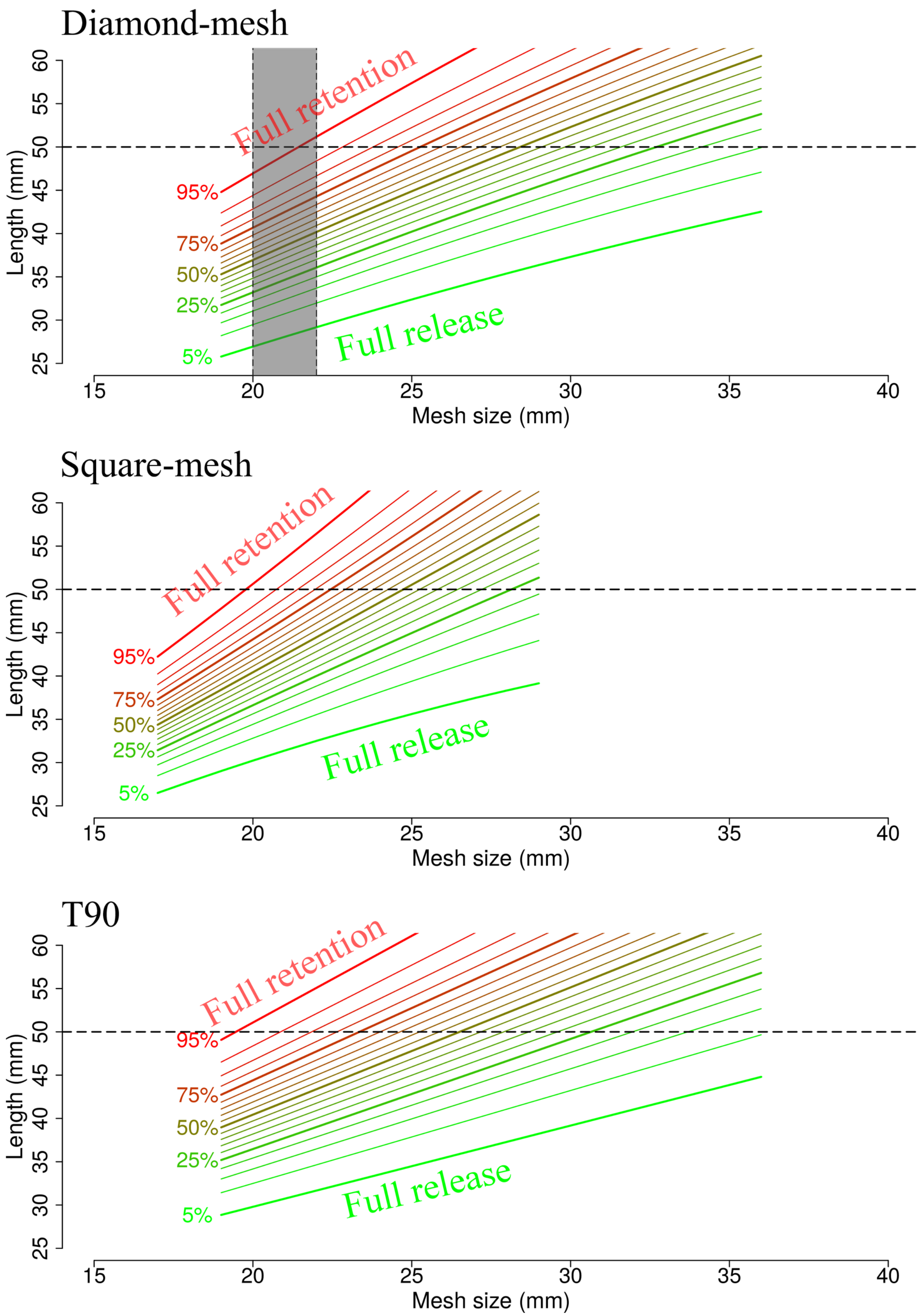
Diamond-mesh
Full retention
Full release
95%
75%
50%
25%
5%
Length (mm)
Mesh size (mm)
Square-mesh
Full retention
Full release
95%
75%
50%
25%
5%
Length (mm)
Mesh size (mm)
T90
Full retention
Full release
95%
75%
50%
25%
5%
Length (mm)
Mesh size (mm)

Fig 6. Isolines of predicted retention probabilities (5%–95% in steps of 5%). Grey bars represent the range of codend mesh sizes currently used in the fishery. Horizontal dashed lines represent minimum commercial size at 50 mm shrimp length (See S3 Table).

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of T90 codends to be greater than those of diamond-mesh codends of the same mesh size. For example, the $L50_{mean}$ expected for the mesh size of 21.7 mm used by Polet [10] is $L50$ = 43.3 mm (41.6–44.9 mm) for T90 mesh configuration, a value significantly greater than the $L50_{mean}$ value expected from the diamond-mesh codend. Square-mesh codends with small mesh sizes provide $L50_{mean}$ values similar to T90 codends; however, differences arise for mesh sizes greater than 25 mm. For example, the expected $L50_{mean}$ for square-mesh codends at 26 mm mesh size is estimated to be 52.7 mm (51.0–54.2 mm), whereas for T90 it is estimated to be $L50_{mean}$ = 49.3 mm (47.9–50.8 mm). The SR_{mean} for diamond-mesh and T90 codends is similar, presenting a linear trend over mesh size, while the SR_{mean} for square-mesh codends present a quadratic functional form, making the estimated values significantly greater than the diamond-mesh and T90 estimations for mesh sizes larger than 25 mm. Based on these results, it is demonstrated that mesh type influences significantly the size selectivity of brown shrimp. Therefore, mesh type should be considered together with mesh size in the search for specific harvesting strategies.

In addition to mesh size, catch weight (w), sea state (s), and the side on which the test codend was mounted (p) were considered to be fixed factors in the development of the predictive framework. The selected model for diamond-mesh codends only incorporated mesh size (m) and the square of mesh size (m^2) as influential terms; therefore, the effect of the remaining factors was not sufficiently strong to be selected by AICc. This result contrasts with the results obtained by Polet [10], who estimated negative and positive effects of catch weight and sea state on $L50$ values, respectively. Contrary to the method applied in this study, Polet [10] did not account for the between-haul variation in the analysis. Because the methodology applied in this study meets the standard approach to multivariate regression modelling in size-selection studies, we consider the results of our approach to be reliable.

Only mesh size was necessary to explain the $L50$ variation from square-mesh codends, whereas the structure for SR_{mean} includes mesh size and catch weight as influential effects. We

Table 3. Values for the codend usability indicators nR, nP, nPa nPb.

Mesh size (mm)	Mesh configuration	nR (%)	nP (%)	nPa (%)	nPb (%)
21	Diamond	42.31	85.48	98.79	72.21
	Square	36.47	75.48	96.07	54.96
	T90	37.41	76.93	96.47	57.46
23	Diamond	37.62	77.08	96.32	57.9
	Square	29.28	61.8	87.55	36.13
	T90	32.18	67.45	91.64	43.34
25	Diamond	32.21	67.21	91.28	43.22
	Square	23.57	48.28	73.92	22.72
	T90	27.03	57.38	83.89	30.97
27	Diamond	26.95	56.93	83.32	30.63
	Square	20.18	36.76	58.77	14.81
	T90	22.63	47.60	73.78	21.50
29	Diamond	22.55	47.19	73.22	21.25
	Square	18.74	27.79	45.25	10.40
	T90	19.26	38.71	62.61	14.88

Predictions for the square-mesh codends and T90 codends considering a fixed catch weight of 35 kg.

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speculate that the positive effect of catch weight on SR_{mean} might be related to decreasing possibilities for brown shrimp to contact the codend meshes, or an increasing longitudinal deformation of the meshes with increasing catch weight, providing different escapement opportunities for a given length of shrimp. The positive effect of catch weight on $L50_{mean}$ for T90 codends with meshes smaller than 25 mm agrees with the effect found for roundfish species in diamond-mesh codends [25]; however, the presence of the negative interaction term in Eq (10) leads to an opposite effect of catch weigh for T90 codends with mesh sizes larger than 25 mm, in accordance with results previously obtained for T90 codends and very large catches [26]. The ambivalent effect of catch weight on $L50_{mean}$ for T90 codends should be interpreted with caution owing to the low catch weights obtained in this study, less than catch weights usually found in the commercial fishery. To what extent this could influence the applicability of our results is unknown. Further investigations aiming to obtain larger catches, and involving theoretical studies of brown shrimp selectivity, would be required to better understand the effect of catch size on the selectivity of square-mesh and T90 codends.

In addition to *L50* and *SR* (Eq (4)), the parameter *SP* was modelled to detect any factor compromising the entrance of brown shrimp in the test codends. The three selected models (Eqs 7–9) only accounted for the intercept term to describe experimental *SP* values. Therefore, there is no indication that any of the fixed factors (included mesh size) affect the probability that brown shrimp will enter the test codend.

The analysis applied in this study allows the quantification of non-controlled variation between the experimental hauls [20]. Because the modelling was conducted separately for diamond-mesh, square-mesh, and T90 codends, their between-haul variation can be compared. Although the between-haul variation associated with *L50* and *SR* was great, no remarkable differences were found between the three different mesh orientations (Table 2). This result indicates that applying either square-mesh or T90 codends in the commercial fishery would not result in a greater variation in the size-selection patterns of the fleet, compared with the currently applied diamond-mesh codends.

Often, size-selection studies focus on investigating individual codend designs to meet specific needs in a given fishery. As the needs change with time, similar studies are repeated over decades without a clear and unified strategy [27]. Our approach goes beyond the standard strategy. Based on a comprehensive dataset, collected during a single year, the predictive framework presented in this study can provide advice regarding the expected selectivity of a wide span of codend designs. This is the basis to support current and future scientifically based management decisions to be applied in the North Sea brown shrimp fishery.

Supporting information

S1 Table. Operational information of the test hauls. Geographical coordinates (decimal degrees) refer to the start and end of each haul. Operational information is completed with towing direction (°), distance towed (in nautical miles, nm), and the average fishing depth in meters (m) (n.a. = not available). Hauls ordered by codend type, mesh size, and cruise.
(DOCX)

S2 Table. Results from the selectivity analysis for individual hauls. Catch weight, sea state and trawl side are the fixed factors measured at haul level, and included together with mesh size in the meta-analysis. Standard deviation of the estimated *L50*, *SR*, and *SP* are shown in brackets. CO11 to CO33 are the vectorised form of the covariance matrix from the estimated *L50*, *SR*, and *SP*. Hauls ordered by codend type, mesh size, and cruise.
(DOCX)

S3 Table. Predicted lengths of brown shrimps associated to given retention probabilities (from *r* = 5% to *r* = 95%) for different codend types and mesh sizes. Values $L50_{mean}$ and SR_{mean} estimated by the predictive framework. The numerical information presented here was used to plot the isolines for codend retention in Fig 5.
(DOCX)

S1 Fig. By-haul catch sharing between control and test codends. Grey polygon and black line represent the length distributions of brown shrimp in control and test codends, respectively. Mark circles represent the experimental catch proportion in the test codend relative to the total catch, obtained upon raised data. Blue line is the φ(l) curve estimated according to Eqs 2 and 3. Dotted red line represents species minimum landing size at 50 mm length. Hauls ordered by codend type, mesh size, and cruise.
(PDF)

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