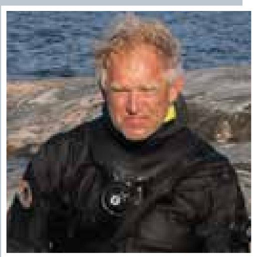
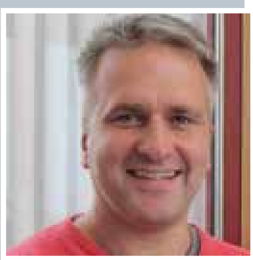
Underwater observations of cod

Peter Ljungberg



Sven-Gunnar Lunneryd



Johan Lövgren

Sara Königson

Ljungberg, Lunneryd, Lövgren, and Königson study the importance of using funnels in pot entrances.

Who should read this paper?

Gear technologists interested in the development of passive fishing gear, along with fish ecologists focusing on knowledge about differences in target species behaviour.

Why is it important?

A number of applied research programs around the rim of the North Atlantic Ocean have been focusing on improving the performance of baited pots for Atlantic cod. Evidence has shown that the main challenge is not attracting cod to pots, but rather encouraging cod to enter pots. Doing so requires individual fish to overcome the risk and inhibition to enter a restricted space.

Underwater cameras provide a unique opportunity to study the behaviour of individual cod as they approach and interact with the entrances to baited pots. Without this knowledge, researchers are forced to infer animal behaviour simply by observing the catch rates as the pots come aboard the vessel.

In this paper, the authors respond to the need for seal-safe fishing technologies for the Baltic Sea. Cod pots are of interest because, unlike gillnets, they suffer less seal-inflicted damage. This provides a powerful opportunity to maintain the social and economic viability of small scale coastal fisheries. One of the challenges to widespread uptake, however, is the need for commercially viable catch rates. In this paper, the team of Swedish scientists uses underwater cameras to study the importance of pot entrance on subsequent entry and escape of cod. With over 190 hours of video to analyze, the authors have learned much about the behaviour of this species. They introduce a novel statistical technique called a *conditional inference tree*, which helps in the interpretation of behaviour patterns and the identification of potential bottlenecks in the capture process.

About the authors

The four authors are affiliated with the Swedish University of Agricultural Sciences, located in Lysekil, Sweden. Peter Ljungberg has a PhD in limnology and marine ecology from Lund University. Since 2013, he has worked in the field of fishing gear development in small-scale, coastal fisheries as a response to changing environments. Sven-Gunnar Lunneryd is the project leader/senior scientist at the Institute of Coastal Research, working with different aspects of the conflict between man and marine mammals and birds. Johan Lövgren has PhD in freshwater fish interactions from the University of Umeå. He joined the Institute of Marine Research in 2005 and has specialized in statistical analyses of selective fishing gear trials. Sara Königson studies marine mammal and fisheries interactions. She works with fishing gear development for small-scale fisheries with a focus on sustainable and seal-safe fishing gear.

INCLUDING COD (*GADUS MORHUA*) BEHAVIOURAL ANALYSIS TO EVALUATE ENTRANCE TYPE DEPENDENT POT CATCH IN THE BALTIC SEA

Peter Ljungberg[1], Sven-Gunnar Lunneryd[1], Johan Lövgren[2], and Sara Königson[1]

[1]*Institute of Coastal Research, Department of Aquatic Resources, Swedish University of Agricultural Sciences, Lysekil, Sweden*

[2]*Institute of Marine Research, Department of Aquatic Resources, Swedish University of Agricultural Sciences, Lysekil, Sweden*

ABSTRACT

In order to allow cod pots to be an alternative to gillnet fisheries, catch has to be increased. In this study we evaluate pot entrance modifications as a means to increase pot catch efficiency. We connect entrance modifications to in-situ cod behavioural events in relation to pot entrances. Pots with entrances lacking funnels allow for a higher proportion of entering cod but also to a larger extent allow cod to exit pots. We show how pots equipped with funnel entrances generate increased catch by preventing escape and, through that, serve as an important factor in regulating cod pot catches. Importantly, we show how entrances equipped with funnels, although inducing a higher proportion of turn behaviour along with increased time in entering, result in a higher net effect in catch than the positive effect in entry if not using funnels. With target species behaviour being a strong regulator of gear catch efficiency, we stress the importance of in-situ observations of specific behavioural components in the fishing gear development process.

KEYWORDS

Cod; Pot; Entrance; Entry; Exit; Video; Behavioural traits

INTRODUCTION

The grey seal (*Halichoerus grypus*) population in the Baltic Sea has increased rapidly since 1990 with the number of counted seals in 2014 exceeding 32,000 individuals [Kauhala et al., 2015]. Along with an increasing seal population, there is an increase in seal-inflicted damage on fishing gear and catch, causing a conflict with coastal fisheries [Lunneryd et al., 2005; Hemmingson and Lunneryd, 2007; Königson et al., 2009; Varjopuro 2011]. With small-scale coastal fisheries being both economically and socially important for Swedish coastal communities [Neurnan and Piriz, 2000; Bruckmeier and Larsen, 2008; Waldo et al., 2010], it is essential to find solutions that reduce conflicts between seal and fisheries. The most sustainable solution is seal-safe fishing gear as an alternative in fisheries subjected to seal damage [Königson et al., 2015A].

Cod (*Gadus morhua*) gillnet fisheries in Sweden are mainly carried out in the southern Baltic Sea, where the increasing seal population causes a dramatic increase in seal-induced damages to the fisheries [Königson et al., 2009]. An alternative to gillnets which can easily be made seal-safe is baited cod pots. Cod pots consist of an enclosed compartment equipped with a conical entrance ending with a metal frame which, in contrast to traditional gillnets, hinder seals from reaching the fish [Königson et al., 2015B]. Pots offer advantages in relation to several other gear types as they are selective towards target species [Ovegård et al., 2011], yield high quality (undamaged) and fresh fish [Safer, 2010], have generally low by-catch mortality [Thomsen et al., 2010], ensure a high survival rate of releases of unmarketable or undersized fish, and tend to have minimal habitat impact [Kaiser et al., 2000]. Moreover, low energy use, effective species selectivity and low gear construction costs classify pots as low impact and fuel efficient fishing gear [Suuronen et al., 2012]. However, to allow for implementation of cod pots as an alternative in coastal fisheries, cod pots have to be commercialized and daily catches must remain in the same range as catches from traditional fishing gear as gillnets. Königson et al. [2015A] showed that daily catches from cod pots are comparable to gillnet catches during certain fishing seasons and areas; however, there is a need to increase the pots' overall capture efficiency, i.e., the proportion of available fish in the population retained in the catch [MacLennan, 1992].

Differences in catch among pot types have been frequently studied with variability in multiple factors such as pot shape, size and entrance type [Collins, 1990; Whitelaw et al., 1991; Furevik and Lokkeborg, 1994; Archdale and Kuwahara, 2005; Cekic et al., 2005; Bagdonas et al., 2012; Jørgensen et al., in press]. However, in studying multiple factors comes the difficulty in excluding individual components, e.g., entrance modifications only, which is why these kinds of studies are not suitable for isolating factors determining catch efficiency [Archdale and Kuwahara, 2005; Li et al., 2006]. Entrance design is crucial for pot efficiency [Furevik, 1994], regulating both target species and size, and has been the subject of several studies aiming for increased ingress rate [Furevik and Lokkeborg, 1994] and pot catch efficiency [Thomsen et al., 2010 and references therein]. However, with entrance design comes not only the ability to enter, but also hindrance of escape. Within the catch process, high escape rate is assumed to be a limiting factor for catch and has been detected for blue cod (*Parapercis colias*) by Cole et al. [2003] and Atlantic cod (*Gadus morhua*) by Anders et al. [in press], along with non-fish species such as lobster (*Homarus americanus*) by Jury et al. [2001]. In the Baltic Sea pot catch per unit effort did not start to decrease until soak time reached six to seven days, after which catch per unit effort decreased most likely due to fish escaping from the pot [Königson et al., 2015A]. To progress and increase catch efficiency, focus has to be placed upon the developments in entrance design as a single component of studies, allowing for pair-wise comparisons. Moreover, the effectiveness of baited gear is highly influenced by the behaviour of the target species [Stoner et al., 2006], with general findings showing high interspecific and intraspecific variability in fish behaviour [Magnhagen and Borcherding, 2008]. Up to recent years, in-situ studies of fish behaviour have been both expensive and hard to control; however, recent advancements in video technology including extensions through both low cost and increased recording time allow for progress in fish behavioural studies in relation to gear used in natural habitats.

The capture process of pots may be separated into several behavioural phases such as near-field behaviour, entry/exit behaviour and within-pot behaviour. By comparing the ratios among behavioural phases as numbers of entries in relation to numbers of exits, bottlenecks in the capture process may be identified [Bravener and McLaughlin, 2013]. In order to successfully maintain fishing gear development, there is a need for in-situ studies connecting target species' behaviours with entrance design, not only to increase gear efficiency but also to reduce by-catch of non-target species [Thomsen et al., 2010].

Aim

Recent advances in underwater video technology allow for extended behavioural observation along with repeatable analysis, as demonstrated by e.g., Jury et al. [2001], Favaro et al. [2012], Favaro and Duff [2015] and Anders [in press]. By using in-situ video recordings, we quantified aspects of fish behaviour in relation to pot entry and exit and analyzed catching performance with three main goals:

- Test for potential differences in catch efficiency based on entrance type.
- Analyze how differences in entrance type affect fish behaviour when approaching baited pots, with focus on exploration, rejection, entry and exit.
- Evaluate behavioural studies as a tool in fishing gear development.

MATERIAL AND METHODS

Experimental Setup and Catch

The study was carried out in Hanö Bay near Simrishamn, in the southwestern Baltic Sea (Figure 1) in collaboration with commercial cod fishermen. The floating pots used were of a D-shaped construction (110 x 70 cm, height 70 cm with a volume of 0.7 m^3), made positively buoyant using seven oval shaped floats, each with an uplifting power of 700 g

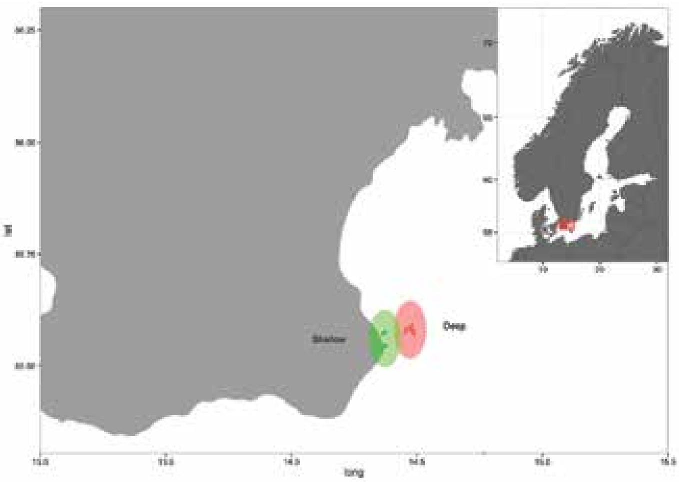


Figure 1: Map of the experimental area located in the southwestern Baltic Sea. Points indicate fishing locations, with green points showing shallow-set strings and red deep-set strings.

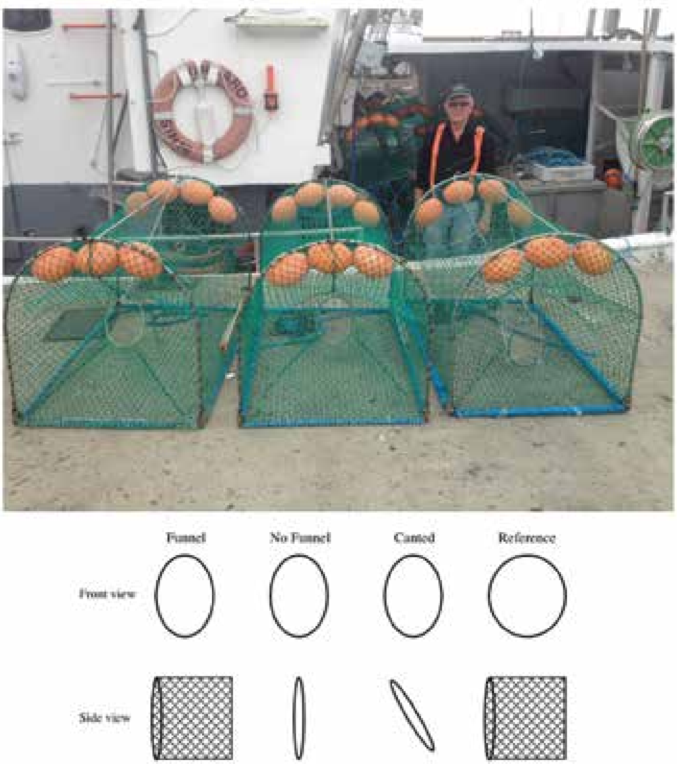


Figure 2: Upper photo: Cod pots used within the trials with the three different evaluation entrance types, from left: canted, no funnel, and funnel. Lower schematic: Entrances from both a frontal and side view. Evaluation entrances are oval-shaped while the reference is circular. Funnel and reference entrances were equipped with mesh, hindering cod from exiting through the entrance.

(Figure 2). The mesh material was green nylon with 25 mm between knots' bar length except for the back, which was constructed as a selection panel using a green nylon mesh with 45 mm between knots' bar length, releasing cod below 38 cm in length [Ovegård et al., 2011]. The entrance side was made from 25 mm green nylon and was slightly funnel shaped, 30 cm total, prior to the entrance ring. Pots were also equipped with a holding chamber with the potential to retain the catch. Pots were tethered to a string orienting them with entrances in a down-current direction.

In total, four different entrance types were used in the experiment, one with the original entrance type termed "reference" along with three newer types termed "evaluation." The entrance ring in the reference pot was circular and constructed of metal with a diameter of 22 cm, equipped with a 33 cm-long fine meshed, transparent, monofilament funnel. The entrance ring used in the evaluation pots was oval-shaped with a width of 15 cm and circumference of 56 cm. A prior study has shown that the reference entrance ring displayed both lower seal exclusion potential (although seal presence and seal-induced damage is low in the experimental area) and lower cod catch rate in relation to the oval evaluation entrance [Königson et al., 2015B]. However, because the reference entrance ring has been used in several experimental setups and in a larger array of areas prior to this study, we opted to use that pot type as a reference to allow for cod catch comparisons in relation to previous trials. The ring in the evaluation pots was modified with three different entrances: a funnel entrance equipped with a fine-meshed, transparent, monofilament funnel; no funnel entrance equipped with just the metal ring; or a canted entrance where the oval metal ring was set at a 45° angle horizontally, following Bacheler et al. [2013].

Experimental fishing was conducted between October 9 and November 7, 2013, at fishing depths ranging from 20 to 60 m. Two strings were used, each containing two reference pots and three evaluation pots equipped with each of the three evaluation entrances, at 11 pots per string in total. Chopped frozen herring (250 g) was used as bait and placed in the side adjacent to the entrance. Pot order was randomized within a string prior to every re-set to exclude potential within-string effects. As this was part of a large scale pot study by commercial fishermen, string collection was regulated by weather conditions, with soak time ranging from one to six days. Still, soak time was the same for the two different strings during each set. Strings were spatially separated, with one string deployed at a larger depth in an area allowing for the highest potential catch. Data from the experimental fisheries was taken by an onboard observer. Each pot string was deployed and collected on 22 occasions giving a total of 126 individual pot catch collections for each of the evaluation entrance pot types (funnel, no funnel, canted) and 84 for the reference pot. Number of fish and total weight in every emptied pot along with date, time and depth of deployment was noted. Only cod above 38 cm in length were kept, being the minimum landing size at the time, while cod less than 38 cm were registered and immediately released. Catch per unit effort (CPUE) was thereafter calculated as the number of cod per emptied pot and the weight per unit effort (WPUE) as the weight of cod per emptied pot of only those fish above 38 cm.

Video Setup and Recording

The second string was deployed at a shallow depth, with natural light being sufficient enough to allow for video recording. For analysis of in-situ cod entry behaviour, three pots in the shallow set string (one pot of each of the evaluation entrances) were equipped with a camera for recording. We excluded the reference pot due to a shortage of camera gear and to allow for continuous recording of all three evaluation entrance types. As pot setup was kept identical for the two strings used, video analyses are made with the assumption that a difference in light was not affecting entry behaviour. The cameras used were GoPro Hero 3+ equipped with GoPro BacPac add-on batteries and placed in GoPro underwater housings. The camera can record in high definition colour at up to 1080 p, saving recordings onto a MicroSD card, in our case 64 GB, with a maximum record time of approximately seven hours, making it suitable for detailed behaviour studies. However, it was required that video recordings were started prior to pot string deployment. Cameras were attached inside the pot on the lower portion of the back end, facing the entrance. The distance from the camera to pot entrance was about 0.7 m, allowing a horizontal field of view of approximately 2 m at the pot entrance level. Horizontal visual length varied between two and approximately 10 m depending on water clarity. Recorded video was collected and batteries and memory cards replaced each time pots were emptied and rebaited. Video recordings were transferred from memory cards to a hard drive for storage until further analysis. For analyses, we excluded pots which for various reasons did not stand correctly in the current's direction, which resulted in cod not being able find the entrance. Moreover, we were interested in video data due to the potential to reveal non-functional or damaged entrances, affecting pot entry. Both of these aspects stress the importance of pot deployment and construction as regulators of catch efficiency.

Behavioural Data and Activity

Underwater videos were manually analyzed and characterized into the following behavioural events: approach, inspection, turn, enter and exit through entrance. Behavioural events are presented in Figure 3. Approach was defined as a cod coming into the camera's visual field until it either would turn, stop for an inspection of the pot entrance or swim directly into the pot. Inspection was defined as a cod halting its approach to investigate the pot entrance, until it would either turn away or enter. Turn was defined as a cod actively moving away from the entrance without any further inspection. Entry was defined as when the cod started to swim into the pot with its snout at entrance ring level, until two-thirds of the body had passed the inner part of the funnel/ring with no possibility of backing out. Exit was defined as the opposite to entry, i.e., when the snout was at the level of the ring, until two-thirds of the body was out of the pot. Furthermore, the time taken for each event was recorded. We were unable to determine if the same cod returned after being out of the visual field of the camera, so there may be a slight bias for one fish performing repeated inspections of the pot entrance.

To analyze how a certain behavioural event affected the subsequent behaviour and how entrance type affected the results, we used a conditional inference tree. A conditional inference tree creates a binary split tree with the advantage of ordering input variables hierarchically, starting with the variable showing the strongest association (lowest p-value) of the response variable, i.e., being the most important for the outcome. This association is measured by a p-value corresponding to a test for the partial null hypothesis of a single input variable of the response. Advantages in using the method include allowing for null hypothesis testing for each of the input variables independently against the response variable, which stops if this hypothesis cannot be rejected, along with prohibiting overfitting of data. Moreover, this statistical approach ensures that the correctly-sized tree is built without any pruning or cross-validation needed. The method was developed by Strasser and Weber [1999] and implemented by Hothorn et al. [2006]. For our study, a conditional inference tree was hierarchally constructed for each of the

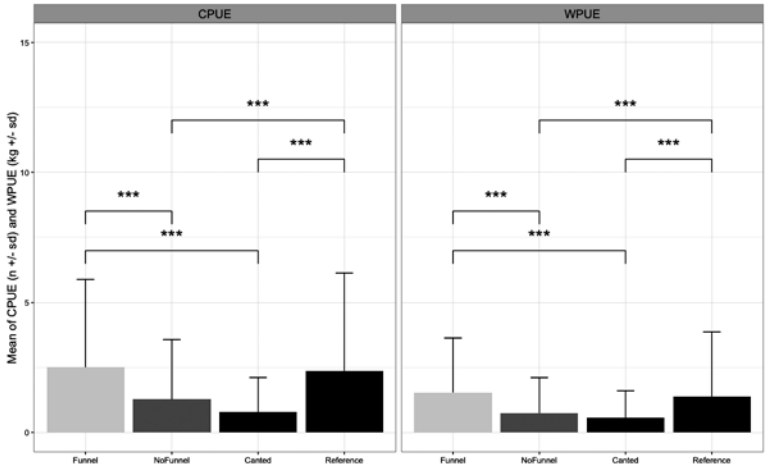


Figure 3: Mean catch in number per pot, CPUE (n +/- 1 sd), and weight, WPUE (kg +/- 1 sd) of cod, depending on entrance type: funnel (light grey), no funnel (grey), canted (dark grey) and reference (black). Stars show significance level, where *** indicates p<0.001 according to Dunn's test.

behavioural events: turn, inspect, entry and exit. Data was organized so that each cod was one replicate. Entrance type was set as a three-level categorical factor (funnel, no funnel and canted) and behavioural events (approach, inspect, turn, enter and exit) as binary factors.

Statistics were performed using *R* [R Development Core Team, 2010] for Macintosh. Conditional inference tree analysis was tested using the function ctree in the R package "party."

RESULTS

Catch

There was no difference in mean cod weight influenced by differences in entrance design ($\chi2 = 5.11$, df=3, p=0.16). Catch data was pooled independently of soak time. Catch data, both CPUE (number of cod per pot and collection) and WPUE (weight of cod per pot and collection), are presented in Table 1 and Figure 3. CPUE differed between fishing areas, with the deep-set string showing significantly higher catch (Kruskal-Wallis $\chi2 = 31.90$, df=1, $p<0.001$). When comparing entrance types in relation to CPUE and WPUE there was a difference in both CPUE (Kruskal-Wallis $\chi2 = 33.29$, df=3, $p<0.001$) and WPUE (Kruskal-Wallis $\chi2 = 25.91$, df=3, $p<0.001$). With both CPUE and WPUE being dependent on entrance type, post-hoc analyses were conducted to reveal between-level differences within each of the factors. With pot entrance types being unequal in their number of observations and with either two or three pots of each type used in each string, Dunn's z test is preferred for post-hoc analysis, according to Zar [2004]. Post-hoc comparisons revealed significant differences primarily between pots with mesh and non-meshed entrances, for both CPUE and WPUE (Table 2).

Behavioural Comparisons

A total of 190 hours and ten minutes of useable underwater video was analyzed, generating in total six hours and 30 minutes of behavioural data for analysis. Entrance type specific numbers of behavioural events are presented in Figure 4. Conditional inference trees are presented in Figure 5. Generally, turning behaviour is critical for all other events tested (investigate, entry and exit), which was

	Funnel	No funnel	Canted	Reference
Total catch (n)	317	161	99	200
Emptied pots (n)	126	126	126	84
CPUE	2.52±3.37	1.28±2.30	0.79±1.33	2.38±3.76
Total catch (kg)	185.36	90.2	68.77	111.32
WPUE	1.54±2.10	0.75±1.36	0.57±1.03	1.39±2.48
Mean weight/cod (kg)	0.68±0.22	0.72±0.44	0.72±0.29	0.61±0.19
Catch prop. relative to Reference pot	1.05	0.54	0.33	1

Table 1: Total catch in the different pot types along with CPUE, mean number of cod per pot (n ± 1 sd), and WPUE, mean total weight of cod per pot (kg ± 1 sd).

	CPUE				**WPUE**			
	Funnel	No Funnel	Canted	Reference	Funnel	No Funnel	Canted	Reference
Funnel	-				-			
No Funnel	**3.44 p<0.001**	-			**3.31 p<0.001**	-		
Canted	**4.51 p<0.001**	-1.06 p=0.14	-		**4.05 p<0.001**	-0.75 p=0.23	-	
Reference	0.48 p=0.31	**3.56 p<0.001**	**4.51 p<0.001**	-	0.12 p=0.45	**3.08 p<0.01**	**3.75 p<0.001**	-

Table 2: Dunn's pairwise z test statistics (upper) and p-value (lower) for each combination of CPUE and WPUE, respectively.

expected as it creates a permanent end point to cod ingress behaviour. Notably, entrance type mattered only for turning and exiting behaviour, while inspection behaviour impacted turning and entering behaviour. Finally, in Figure 6, net catch rate are presented for the three different entrance types.

Activity

The timing of each behavioural event was analyzed for potential differences between entrance types. We analyzed timing for the events inspect, enter and exit, but excluded turn (being a binary choice) along with approach (as we were not able to correct for differences in visibility among different sampling occasions, making it difficult to determine at which point an approach started), with data presented in Figure 7. There were no differences in timing among entrance types for neither inspect behaviour (Kruskal-Wallis $\chi2$ = 5.21, df = 2, p-value = 0.073) nor exit behaviour (Kruskal-Wallis $\chi2$ = 2.71, df=1, p=0.1). However, there was a difference in the timing of the entry (Kruskal-Wallis $\chi2$ = 7.44, df=2, p<0.05), where cod showed shorter entry time in canted entrances in relation to both funnel-equipped (1.77, p<0.05) and no funnel-equipped entrances (-2.49, p<0.01), while there were no differences between funnel- and no funnel-equipped entrances (-0.48, p=0.32), according to a following up Dunn's z test.

DISCUSSION

With catch of cod being regulated by soak time [Königson et al., 2015A], factors affecting pot catch efficiency are related to both entry as well as exit behaviour. We demonstrate how catch efficiency is tightly connected to gear modifications and, further, how differences in behavioural traits are connected to gear type. We show that when equipped with funnel entrances, cod catch in

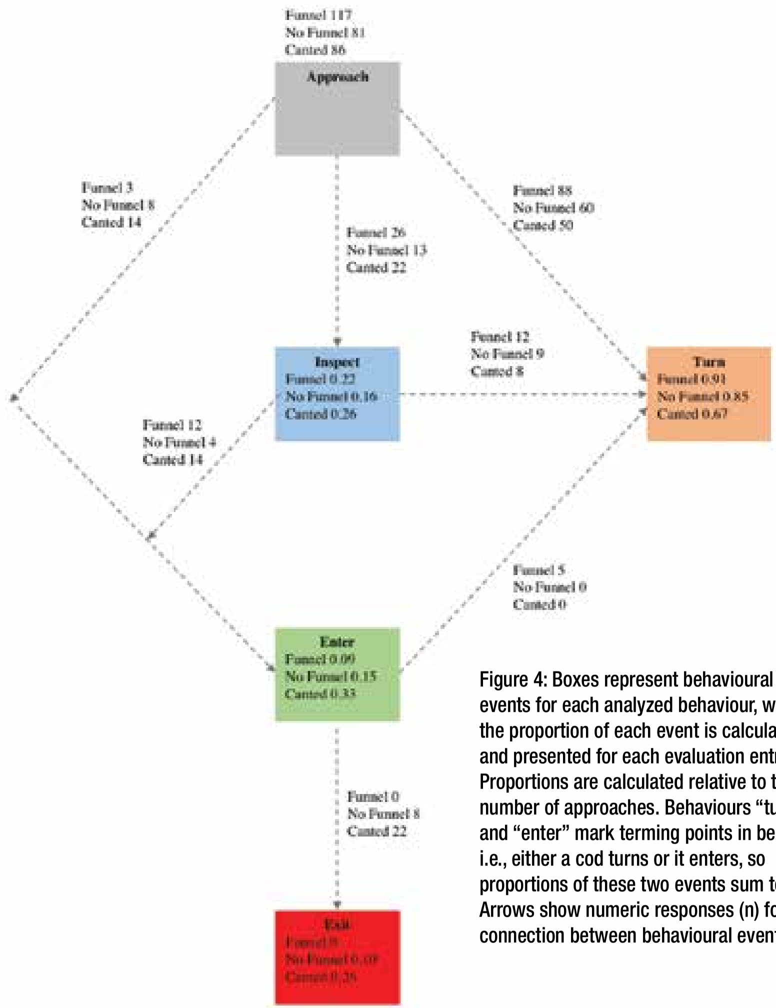


Figure 4: Boxes represent behavioural events for each analyzed behaviour, where the proportion of each event is calculated and presented for each evaluation entrance. Proportions are calculated relative to total number of approaches. Behaviours "turn" and "enter" mark terming points in behaviour, i.e., either a cod turns or it enters, so proportions of these two events sum to 1. Arrows show numeric responses (n) for each connection between behavioural events.

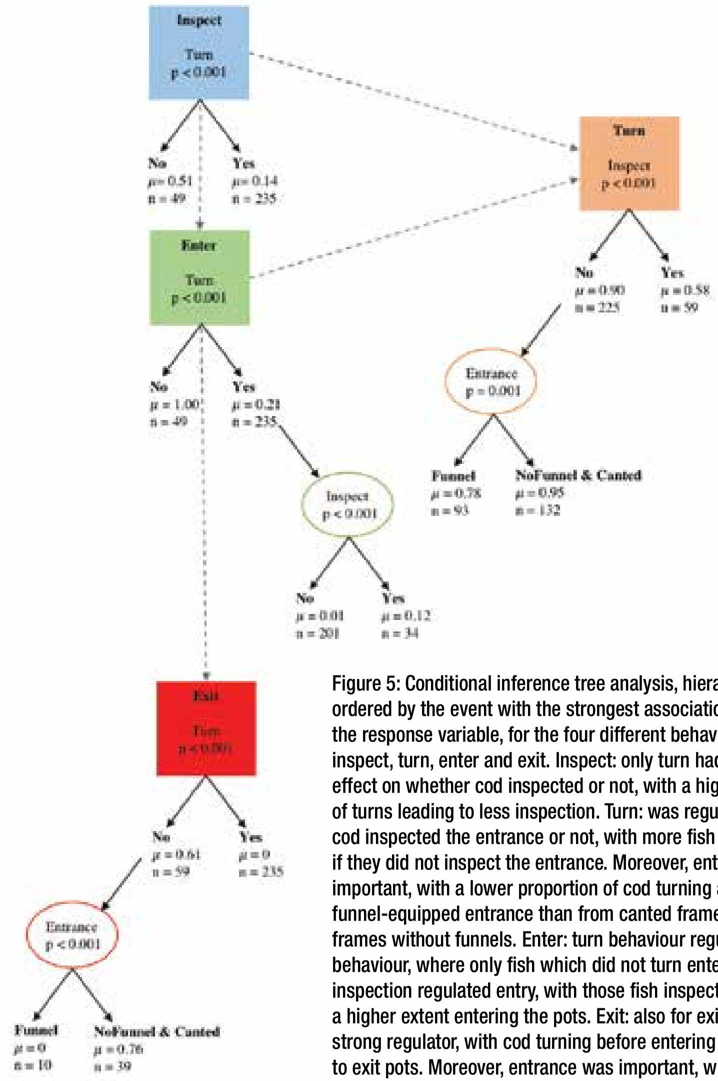


Figure 5: Conditional inference tree analysis, hierarchically ordered by the event with the strongest association (p-value) to the response variable, for the four different behaviour events: inspect, turn, enter and exit. Inspect: only turn had a significant effect on whether cod inspected or not, with a higher proportion of turns leading to less inspection. Turn: was regulated by whether cod inspected the entrance or not, with more fish turning away if they did not inspect the entrance. Moreover, entrance type was important, with a lower proportion of cod turning away from the funnel-equipped entrance than from canted frames and entrance frames without funnels. Enter: turn behaviour regulated entry behaviour, where only fish which did not turn entered pots. Also, inspection regulated entry, with those fish inspecting entrances to a higher extent entering the pots. Exit: also for exiting, turn was a strong regulator, with cod turning before entering not being able to exit pots. Moreover, entrance was important, with a significant difference in the amount of exiting cod between funnel-equipped entrances in relation to canted and no funnel-equipped entrances.

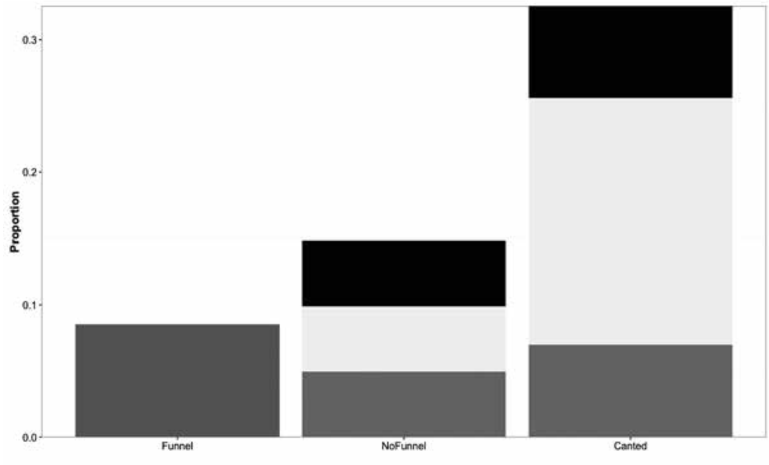


Figure 6: Net catch (grey) based on differences between entries (black) and exits (white), i.e., mean proportion of cod still present in the pots at the end of recording. Catch rates were funnel: 8.6%, no funnel: 4.9%, and canted: 7.0%.

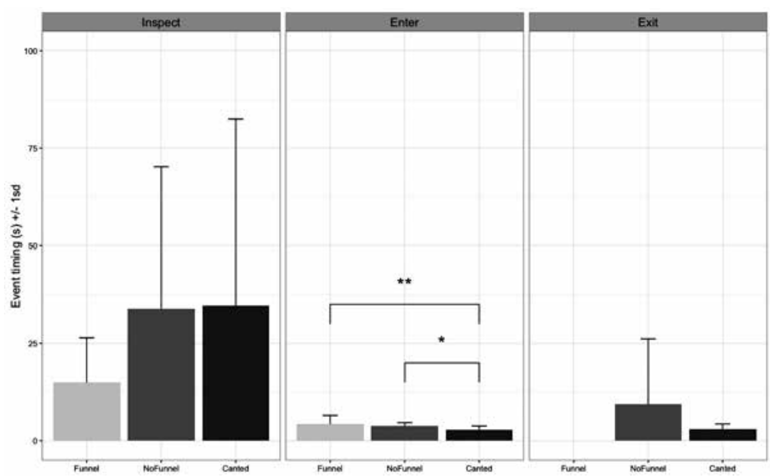


Figure 7: Timing (s ± 1 sd) of the behavioural events inspect, enter and exit for three entrance types: funnel (light grey), no funnel (grey) and canted (dark grey). Stars show significance level, where * indicates p<0.05 and ** indicates p<0.01.

pots increases in relation to pots lacking funnels (Figure 3). We also show how catch is regulated by funnels hindering cod from escaping the pots through the entrance (Figure 4). However, more fish turned away from the pots when entrances were equipped with funnels. Still, funnels did not affect the entry behaviour itself as this was merely driven by whether cod inspected the entrance, where more fish entered without inspection when no funnel was used. Moreover, entrance type affected the amount of time taken to enter the pot, with cod entering canted entrances faster than both funnel- and no funnel-equipped entrances. For all behavioural events connected to entrances, we conclude that turning behaviour (Figure 4) functions as an endpoint. This demonstrated significance in all behavioural analyses (Figure 5), which is connected to the fact that cod were rejecting entry; though, for the behavioural event of turn, there was an effect of whether cod inspected entrances and thereafter, turn behaviour was regulated by entrance type, with funnel-equipped entrances inducing a higher rate of turning behaviour.

Earlier studies have stressed the importance of examining factors which may explain variability in pot entry rates along with how the outcome of certain behaviours may regulate gear catch efficiency [He, 2010 and references therein; Jørgensen et al., in press; Anders et al., in press]. Here we explore behavioural events associated to near-field, entry/exit and inside-pot behaviour and how they vary depending on entrance type. We show how entry was affected by entrance type, where funnel-equipped entrances induced cod turning behaviour to a higher extent. The decrease in catch, along with a direct relationship between individual behaviour and gear design, indicate that funnels seem to deter cod. For both funnel- and no funnel-equipped entrances, cod took a longer time to enter (Figure 7). The significant role of funnels tends to be highest in the early phase between approach and entry, where fewer individuals choose to enter without inspecting when funnels are present, yet while inspecting, the role of funnels seems to be of less importance (Figure 4). The differences in approach induced by differences in entrance type are connected to the near-field behaviour of entering pots. Motivation for cod to enter a pot can be assumed to be higher for cod entering funnels as funnels likely represent a novel object, reflected by prolonged entry time and which likely requires higher individual motivation. Inside-pot behaviour is dominated by cod escaping the pot through the entrance. We could conclude that canted entrances not only allowed for the easiest entry but also facilitated a simple escape, making canted entrances unsuitable in cod fisheries.

With high variability in entry rate, our study generally supports earlier studies [Valdemarsen, 1977; Thomsen et al., 2010]. Entry rate differed largely among entrance types (Figure 4), ranging from 8.5 to 33% of approaching individuals, which is considered a high proportion of entries in relation to earlier studies [Thomsen et al., 2010]. Generally, motivation to enter is regulated by several factors such as hunger, light level, temperature and time of day [High and Beardsle, 1970; High and Ellis, 1973; Stoner, 2004; Stoner et al., 2006], which are difficult to control and evaluate in natural environments. However, there may also be intraspecific differences driven by a combination of environmental factors and individual behaviour. Literature shows how both gear selectivity [Huse et al., 2000; Ovegård et al., 2012] and condition [Damsgard and Dill, 1998; Chapman et al., 2010] may alter behavioural responses both on a population and individual level. With fish entering pots having to display higher motivation or be bolder, ingress behaviour may also be ruled by a variation in behavioural traits. The Baltic Sea cod population in the area where this experiment was conducted are under high nutritional stress, with cod displaying low condition due to prey limitations [Eero et al., 2012], especially in pots [Ovegård et al., 2012]. This has the potential to increase boldness [Damsgard and Dill, 1998; Chapman et al., 2010] and, through that, induce elevated entry numbers. Variation in prey resources may therefore affect behavioural traits, potentially affecting the ingress-related behaviours (turn and funnel entry), ultimately altering catch efficiency. Importantly, with a lack in knowledge in the combined effects of prey abundance, individual condition and behavioural consistency regarding fishing gear, there is a need for an increased understanding of their combined effects on gear catch efficiency.

CONCLUSION

In this study we relate gear modifications to isolated behavioural events in a setup allowing for pairwise comparisons in pot catch efficiency. Pots with funnel-equipped entrances generated increased catch efficiency by preventing escape and through that, serve as an important factor in regulating cod pot catches. Importantly, we show how entrances equipped with funnels, even though inducing a higher proportion of turn behaviour along with increased time in entering, result in a higher catch than the positive effect of increased entry if not using funnels (Figure 6). Being the first trials to evaluate the effect of funnels, there is still room for improvement – we suggest that further development should focus on modifications which decrease the negative effect of funnel entrance to allow for increased catch, i.e., modifications in length, shape, mesh size and colour, for example. A natural next step would be to evaluate optimal funnel length. In this experiment funnels led to an elevated amount of turn behaviour at all stages (Figures 4 and 5). In a controlled experimental setup, funnel length may be varied so that turn behaviour may be reduced to a minimum, determining an optimal funnel length for Baltic cod pot fisheries. Also, with funnels effectively preventing escape, the use of holding chambers may be re-evaluated. With the removal of holding chambers, and given that pot saturation is not affected, pot size may potentially be decreased allowing for decreased handling time per individual pot and through that, increased net catch. This study also supports the video analysis of behavioural traits as a valuable tool when evaluating catch efficiency, allowing for analysis of specific behavioural components, which allows for rapid gear development. Our results also stress the importance of behaviour as a strong regulator of gear catch efficiency. However, incorporating behaviour into gear development is a delicate matter as responses of fish may show both strong interspecific and intraspecific variability, warranting the consideration of the importance of multi-temporal and spatial examination of gear modifications.

ACKNOWLEDGMENTS

We thank the participating fisherman Olle Viberg, SIN 18 Vingarö (Figure 2), for his efforts in making this study possible, along with Patrik Jonsson for helpful discussions and comments on early versions of the manuscript. Furthermore, the comments of three anonymous reviewers improved this manuscript. This study was funded by the European Structural Fund for Fisheries, South Baltic Flag and the Program Seal and Fishery with financial support from the Swedish Agency for Marine and Water Management.

REFERENCES

Anders, N.; Fernö, A.; Humborstad, O.-B.; Løkkeborg, S.; and Utne-Palm, A.-C. [in press]. *Species specific behaviour and catchability of gadoid fish to floated and bottom set pots*. ICES Journal of Marine Science.

Archdale, M.V. and Kuwahara, O. [2005]. *Comparative fishing trials for Charybdis japonica using collapsible box-shaped and dome-shaped pots*. Fisheries Science, Vol. 71, pp. 1229-1235.

Bacheler, N.M.; Schobernd, Z.H.; Berrane, D.J.; Schobernd, C.M.; Mitchell, W.A.; and

Geraldi, N.R. [2013]. *When a trap is not a trap: converging entry and exit rates and their effect on trap saturation of black sea bass* (*Centropristis striata*). ICES Journal of Marine Science: Journal du Conseil, Vol. 70, pp. 873-882.

Bagdonas, K.; Humborstad, O.-B.; and Lokkeborg, S. [2012]. *Capture of wild saithe* (*Pollachius virens*) *and cod* (*Gadus morhua*) *in the vicinity of salmon farms: three pot types compared*. Fisheries Research, Vol. 134, pp. 1-5.

Bravener, G.A. and McLaughlin, R.L. [2013]. *A behavioural framework for trapping success and its application to invasive sea lamprey*. Canadian Journal of Fisheries and Aquatic Sciences, Vol. 70, pp. 1438-1446.

Bruckmeier, K. and Larsen, C.H. [2008]. *Swedish coastal fisheries - from conflict mitigation to participatory management*. Marine Policy, Vol. 32, pp. 201-211.

Cekic, M.; Dal, T.; Basusta, N.; and Gokce, M.A. [2005]. *Comparison of two different types of basket trap on fish catches in Iskenderun Bay*. Turkish Journal of Veterinary and Animal Sciences, Vol. 29, pp. 743-749.

Chapman, B.B.; Morrell, L.J.; and Krause, J. [2010]. *Unpredictability in food supply during early life influences boldness in fish*. Behavioral Ecology, Vol. 21, pp. 501-506.

Cole, R.G.; Alcock, N.K.; Handley, S.J.; Grange, K.R.; Black, S.; Cairney, D.; Day, J.; Ford, S.; and Jerrett, A.R. [2003]. *Selective capture of blue cod Parapercis colias by potting: behavioural observations and effects of capture method on peri-mortem fatigue*. Fisheries Research (Amsterdam), Vol. 60, pp. 381-392.

Collins, M.R. [1990]. *A comparison of 3 fish trap designs*. Fisheries Research, Vol. 9, pp. 325-332.

Damsgard, B. and Dill, L.M. [1998]. *Risk-taking behavior in weight-compensating coho salmon*, *Oncorhynchus kisutch*. Behavioral Ecology, Vol. 9, pp. 26-32.

Eero, M.; Vinther, M.; Haslob, H.; Huwer, B.; Casini, M.; Storr-Paulsen, M.; and Koster, F.W. [2012]. *Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish*. Conservation Letters, Vol. 5, pp. 486-492.

Favaro, B.; Lichota, C.; Côté, I.M.; and Duff, S.D. [2012]. *TrapCam: an inexpensive camera system for studying deep-water animals*. Methods in Ecology and Evolution, Vol. 3, pp. 39-46.

Favaro, B. and Duff, S.D. [2015]. *Observations of feeding behaviour of quillback rockfish* (*Sebastes maliger*) *around spot prawn* (*Pandalus platyceros*) *traps using an underwater camera*. Journal of Ocean Technology, Vol. 10, No. 4, pp. 56-64.

Furevik, D.M. [1994]. *Behaviour of fish in relation to pots*. In Marine Fish Behaviour in Capture and Abundance Estimation.

Furevik, D.M. and Lokkeborg, S. [1994]. *Fishing trials in Norway for torsk* (*Brosme brosme) and cod (Gadus morhua) using baited commercial pots.* Fisheries Research (Amsterdam), Vol. 19, pp. 219-229.

He, P. [2010]. *Behavior of marine fishes: capture processes and conservation challenges*. Blackwell Publishing Ltd.

Hemmingson, M. and Lunneryd, S.G. [2007]. *Pushup-fällor i Sverige, Introduktionen av ett nytt sälsäkert fiskeredskap*. (*Push-up traps in Sweden, the introduction of a new seal-safe fishing gear*). Finfo Fiskeriveket informerar 8 (in Swedish, with English summary).

High, W.L. and Beardsle, A. [1970]. *Fish behavior studies from an undersea habitat*. Commercial Fisheries Review, Vol. 32, pp. 31-37.

High, W.L. and Ellis, I.E. [1973]. *Underwater observations of fish behavior in traps*. Helgolander Wissenschaftliche Meeresuntersuchungen, Vol. 24, pp. 341-347.

Hothorn, T.; Hornik, K.; and Zeileis, A. [2006]. *Unbiased recursive partitioning: a conditional inference framework*. Journal of Computational and Graphical Statistics, Vol. 15, pp. 651-674.

Huse, I.; Lokkeborg, S.; and Soldal, A.V. [2000]. *Relative selectivity in trawl, longline and gillnet fisheries for cod and haddock*. ICES Journal of Marine Science, Vol. 57, pp. 1271-1282.

Jury, S.H.; Howell, H.; O'Grady, D.F.; and Watson, W.H. [2001]. *Lobster trap video: in situ video surveillance of the behaviour of Homarus americanus in and around traps*. Marine and Freshwater Research, Vol. 52, pp. 1125-1132.

Jørgensen, T.; Løkkeborg, S.; Furevik, D.; Humborstad, O.-B.;and De Carlo, F. [in press]. *Floated cod pots with one entrance reduce probability of escape and increase catch rates compared with pots with two entrances*. Fisheries Research.

Kaiser, M.J.; Spence, F.E.; and Hart, P.J.B. [2000]. *Fishing-gear restrictions and conservation of benthic habitat complexity*. Conservation Biology, Vol. 14, pp. 1512-1525.

Kauhala, K.; Kurkilahti, M.; Ahola, M.P.; Herrero, A.; Karlsson, O.; Kunnasranta, M.; Tiilikainen, R.; and Vetemaa, M. [2015]. *Age, sex and body dondition of Baltic grey seals: are problem seals a random sample of the population?* Annales Zoologici Fennici, Vol. 52, pp. 103-114.

Königson, S.; Lunneryd, S.G.; Stridh, H.; and Sundqvist, F. [2009]. *Grey seal predation in cod gillnet fisheries in the central Baltic Sea*. Journal of Northwest Atlantic Fishery Science, Vol. 42, pp. 41-47.

Königson, S.; Fredriksson, R.E.; Lunneryd, S.G.; Strömberg, P.; and Bergström, U.M. [2015A]. *Cod pots in a Baltic fishery: are they efficient and what affects their efficiency?* ICES Journal of Marine Science, Vol. 72, pp. 1545-1554.

Königson, S.; Lövgren, J.; Hjelm, J.; Ovegård, M.; Ljunghager, F.; and Lunneryd, S.G. [2015B]. *Seal exclusion devices in cod pots prevent seal bycatch and affect their catchability of cod*. Fisheries Research, Vol. 167, pp. 114-122.

Li, Y.; Yamamoto, K.; Hairaishi, T.; Nashimoto, K.; and Yoshino, H. [2006]. *Behavioral responses of arabesque greenling to trap entrance design*. Fisheries Science, Vol. 72, pp. 821-828.

Lunneryd, S.G.; Hemingsson, M.; Tarnlund, S.; and Fjalling, A. [2005]. *A voluntary logbook scheme as a method of monitoring the by-catch of seals in Swedish coastal fisheries*. ICES Annual Science Conference Location, Aberdeen; UK.

MacLennan, D.N. [1992]. *Fishing gear selectivity: an overview*. Fisheries Research, Vol. 13, pp. 201-204.

Magnhagen, C. and Borcherding, J. [2008]. *Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness?* Animal Behaviour, Vol. 75, pp. 509-517.

Neurnan, E. and Piriz, L. [2000]. *Svenskt smaskaligt kustfiske-problem och mejligheter. The Swedish small-scale coastal fisheries-problems and prospects*.

Fiskeriverket rapport 2000:2 (in Swedish, with English summary).

Ovegård, M.; Könıgson, S.; Persson, A.; and Lunneryd, S.G. [2011]. *Size selective capture of Atlantic cod* (*Gadus morhua*) *in floating pots*. Fisheries Research, Vol. 107, pp. 239-244.

Ovegård, M.; Berndt, K.; and Lunneryd, S.G. [2012]. *Condition indices of Atlantic cod* (*Gadus morhua*) *biased by capturing method*. ICES Journal of Marine Science, Vol. 69, pp. 1781-1788.

R Development Core Team [2010]. *R: a language and environment for statistical computing*. Version 2.12.0 ed. R Foundation for Statistical Computing, Vienna, Austria.

Safer, A. [2010]. *Newfoundland cod pot fishery looks promising*. Commercial Fishery News, Vol. 38, pp. 1-3.

Stoner, A.W. [2004]. *Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment*. Journal of Fish Biology, Vol. 65, pp. 1445-1471.

Stoner, A.W.; Ottmar, M.L.; and Hurst, T.P. [2006]. *Temperature affects activity and feeding motivation in Pacific halibut: Implications for bait-dependent fishing*. Fisheries Research, Vol. 81, pp. 202-209.

Strasser, H. and Weber, C. [1999]. *On the asymptotic theory of permutation statistics*. Mathematical Methods of Statistics, Vol. 8, pp. 220-250.

Suuronen, P.; Chopin, F.; Glass, C.; Lokkeborg, S.; Matsushita, Y.; Queirolo, D.; and Rihan, D. [2012]. *Low impact and fuel efficient fishing - looking beyond the horizon*. Fisheries Research, Vol. 119, pp. 135-146.

Thomsen, B.; Humborstad, O.-B.; and Furevik, D.M. [2010]. *Fish pots: fish behavior, capture processes, and conservation issues*. Wiley-Blackwell.

Valdemarsen, J.W. [1977]. *Analysis of pot as a bottom gear and studies of some factors influencing the catch efficiency*. Department of Fishery Biology, University of Bergen, Bergen, Norway.

Varjopuro, R. [2011]. *Co-existence of seals and fisheries? Adaptation of a coastal fishery for recovery of the Baltic grey seal*. Marine Policy, Vol. 35, pp. 450-456.

Waldo, S.; Paulrud, A.; and Jonsson, A. [2010]. *A note on the economics of Swedish Baltic Sea fisheries*. Marine Policy, Vol. 34, pp. 716-719.

Whitelaw, A.W.; Sainsbury, K.J.; Dews, G.J.; and Campbell, R.A. [1991]. *Catching characteristiscs of 4 fish-trap types on the north-west shelf of Australia*. Australian Journal of Marine and Freshwater Research, Vol. 42, pp. 369-382.

Zar, J.H. [2004]. *Biostatistical analysis*. Upper Saddle River, NJ, Prentice Hall.