Fishing gear technology to mitigate harbour porpoise and seabird bycatch in the Baltic Sea: Gillnet modifications and alternative fishing gear fish pot

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Contents

Figures

Table

Abbreviations

ALDFG	Abandoned, lost or otherwise discarded fishing gear
AF	Acrylic fingers
ASCOBANS	Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas
BACI	Before-After-Control-Impact
CEC	Council of the European Community
CPUE	Catch-per-unit-effort
EC	European Commission
EU	European Union
FAD	Fish-aggregating device
GLMM	Generalised linear mixed model
GPS	Global positioning system
HELCOM	Baltic Marine Environment Protection Commission (Helsinki Commission)
ICES	International Council for the Exploration of the Sea
IR	Infrared
IUCN	International Union for Conservation of Nature
LED	Light-emitting diode
MCRS	Minimum conservation reference size
MSD	Minimum surfacing distance
PAM	Passive acoustic monitoring
PAL	Porpoise ALarm, now marketed as “Porpoise-PAL” by manufacturer F3 Maritime Technology
REM	Remote electronic monitoring
RFID	Radio-Frequency Identification
SED	Seal exclusion device
SSF	Small-scale fisheries

Summary

Gillnets are the main fishing gear for small scale fisheries (SSF) globally. They are affordable, easy to use, have a well-adjustable size selectivity and most importantly a high catch efficiency for target species. In recent times, they are increasingly criticized for resulting in a significant amount of bycaught marine mammals, diving seabirds, and turtles, threatening many of those megafauna species. Gillnets have the highest bycatch intensity of all fishing gears for these taxa. In the Baltic Sea, gillnet fishing is used to fish i.a. cod (*Gadus morhua*), herring (*Clupea harengus*), turbot (*Scophthalmus maximus*), and plaice (*Pleuronecta platessa*). It causes considerable bycatch of harbour porpoises (*Phocoena phocoena*) and one the highest gillnet bycatch rates worldwide for diving seabirds in that sea basin. Several of these bird species and one of the two harbour porpoise sub-populations are classed as endangered and considered particularly threatened by gillnet bycatch. Baltic European Union Member States have legal obligations to mitigate the bycatch of these species.

This thesis focusses on bycatch mitigation approaches for the Baltic Sea. It starts from the assumption that gillnet bycatch is not solvable by one single technical solution. Rather, a “toolbox" of different measures is required.

In line with the toolbox thinking, the thesis took a two-pronged approach: In Part A, an acoustic device for mitigating western Baltic harbour porpoise bycatch in gillnet fishing was tested. In Part B, several alternative gears to gillnets were assessed through a literature review and discussions with gear technologists and fishers. Fish pots were identified as the most suited alternative for Baltic SSF. Cod pots (fish pots for targeting cod) were then developed further to increase their catch efficiency.

In **Part A** (Paper I), an improvement of the cetacean bycatch reduction technology pinger (acoustic deterrent devices attached to gillnets), the “Porpoise ALert” (now marketed as “porpoise-PAL” by manufacturer F3 Maritime Technology, “PAL” hereafter), was tested. Previous pingers emit *artificial sounds* with no biological significance for cetaceans. Concerns with view to their effectivity and other non-intended effects detrimental to cetaceans, such as habitat exclusion, have been raised. The PAL has been developed to avoid the pingers’ adverse effects. It is an acoustic device which emits a *natural aversive communication signal* of western Baltic harbour porpoises.

Central question in Part A was, if the PAL effectively reduces western Baltic harbour porpoises’ bycatch in commercial gillnet fisheries. A fisheries trial was undertaken with three commercial gillnet vessels conducting 778 trips during their standard gillnet fishing operations from 2014 to 2016. The bycatch probabilities of 1120 PAL-equipped gillnet strings and of 1529 simultaneously set control strings with no PAL-devices were compared.

In total, 18 harbour porpoises were bycaught in control strings, and five harbour porpoises were taken as bycatch in strings equipped with PALs. Using a generalised linear mixed model (GLMM), it is shown that PAL usage significantly reduces western Baltic harbour porpoise bycatch by 79.7% when spaced with maximum distance of 200 m in between PAL.

The results of Part A further revealed that increasing the distance between PAL-devices to 210 m reduces their bycatch reduction effect to 64.9 %. This adds to findings of studies investigating pingers that distance between acoustic devices is an important factor influencing their bycatch mitigation effect.

No indications were found that the PAL reduces target species catch – an important factor for the uptake of the PAL by gillnet fisheries. The fact that the PAL is currently used by over 100 German SSF vessels underlines the validity of this finding. In conclusion, the PAL significantly reduces harbour

porpoise bycatch in gillnets deployed in the western Baltic Sea. It can be used for effective bycatch mitigation in that Sea region, with a comparable efficiency as conventional pingers.

The PAL is the first acoustic device which mitigates bycatch of a cetacean species using the species' own communication signals. It is an important proof-of-concept opening a distinct new cetacean gillnet bycatch mitigation pathway to be explored in further studies.

While PAL and conventional pingers were not directly compared in this study, it is discussed if the PAL could have comparable or similar detrimental effects. This includes a discussion of a Before-After-Control-Impact (BACI) study of harbour porpoise distribution in the area where PAL are now being used by fishers. Results indicate that habitat displacement does not occur. Evidence is limited though and the BACI study also does not assess possible detrimental habituation to the PAL signal. Habitat displacement and habituation in relation to the PAL require further investigation.

Part B focussed on gear alternatives with lower bycatch risk compared to gillnets. Most gear alternatives are not widely used by SSF in the Baltic Sea because they are not as suitable for small vessels, and they often have low catch efficiency and thus lower economic revenue. They have furthermore lower versatility compared to gillnets. Some can only be deployed in certain areas, for instance only from the coast.

In a first step to find the most suitable alternative, gear alternatives to gillnets were systematically assessed against operational, economic, as well as environmental criteria. Information was collated through a literature review and discussions with gear technologists and professional fishers. The following gears were assessed: pneumatically liftable large scale traps, so-called "pontoon traps"; hook-based gears such as longlines and jigging machines; the active gear Danish seine; and fish pots. Fish pots were identified as the most appropriate alternative gear for Baltic SSF. They offer high versatility, delivery of high-quality catch, and can be used from the smallest fishing vessels. And most importantly in this context they have a low risk of seabird and harbour porpoise bycatch.

The key aim of the studies undertaken in Part B was to improve the catch efficiency of fish pots for cod fishing. This would increase their economic viability and thus their uptake by commercial fisheries. In a literature review of cod pot-catch efficiency studies, influencing factors of pot catch efficiency were identified. This review revealed that fish pot entrances are a key influencing factor. They should ideally lead to easy entry of fish approaching a pot and prohibit their subsequent escape. However, this is rarely attained.

The review further showed that most pot-catch efficiency studies are field trials comparing catches. During these trials, different fish pot types are used under the same conditions in one fishery. Their catch-per-unit-effort (CPUE), i.e., the fish caught per number of pots fished, is the main metric by which their catch efficiency is compared. They do not provide any information about how the target species interact with the fish pots. This information is essential for efficient gear development, including the increase of pot catch efficiency. Catch-comparisons have several other drawbacks, for instance varying fish densities around pots over time, or unknown size and condition of approaching fish.

To avoid these limitations of catch comparison studies, a new and more effective study method was developed: the net pen-based observation method. It allows direct comparison of the behaviour of fish in relation to pot characteristics and consists of physical and statistical elements. The physical setup consists of a custom-made fish pot with two easily exchangeable entrances and an underwater video system with long term recording capabilities. The video system has infrared light (IR) capabilities which allows for unobtrusive day- and night-time observation (Paper II). It allows recording *all* interactions of fish with the pot entrances, including successful as well as unsuccessful fish entry- and exit attempts. Pot and video system are placed in a net pen, in which fish can be set and their interactions with the pot observed. The statistical components of the method include an ethogram for fish-pot entrance interactions for describing and assessing observed fish interaction with the entrances. Observed entrance catch efficiency – a function of entry- as well as of exit probability through an entrance – is quantified and compared using a bundle of two further analysis methods. The statistical methods permit to "dissect" the event chains of fish interactions with the entrance. The reasons for the observed differences between the entrances can thus be pinpointed. For each experimental trial, the same number of fish are set into the net pen, assuring a constant fish presence at the pot for each trial.

The target species for pot catch efficiency improvements was cod, one of the main target species of Baltic Sea SSF at that time. Two studies were undertaken using this method to improve understanding of cod–pot entrance interaction and to then capitalize on that knowledge to improve cod pots. In the first study (Paper III), the influence of basic parameters of cod pot entrances on catch efficiency was assessed. Parameters analyses comprised funnel presence, funnel length and funnel colour, and funnel type. Fundamental findings were made which enhance the understanding of cod-pot entrance interactions: Foremost, a pronounced diurnal pattern of entrance interactions with few nocturnal entrance passages could be revealed. Also, an unobstructed view of the pot inside or pot outside when cod try to enter or exit the pot, was identified as key factor for entrance passage. Regarding the parameters analysed, it was shown that funnel presence increases cod entrance encounter rate by enlarging the outer opening of the entrance and channelling approaching cod towards the entrance opening. At the same time funnels decrease exit rates, assumedly by deflecting cod away from the inner entrance opening and by reducing the area in which the exit is perceptible to cod inside the pot. Funnels are thus crucial for maximising cod pot catch efficiency. Increasing funnel length further reduces the area inside the pot from which cod can see the exit unobstructed and may further deter cod from exiting by the longer passage length. Funnel netting colour (colours tested: white, green, and transparent netting material) influences entrance passage rates, with significantly higher entrance passage rates for a transparent funnel.

Overall, the study results indicate that cod–pot interactions are primarily guided by vision. This improved understanding can directly be used to enhance cod pot fishing strategies. For example, traditional olfactory bait such as cut herring has been shown to lose most of its attracting effect in less than two hours. Cod pots baited with such bait thus should assumedly perform better when set during day and at latest two hours before sunset.

The aim of the second study (Paper IV) was to increase pot catch efficiency by reducing cod pot exit rate without also reducing cod entry rate. Based on the finding of the first study that cod primarily use vision to navigate cod pot entrances, the "Acrylic fingers" (AF) were developed. AF are a novel kind of "fish-retention devices" (FRDs) of a finger like type, so-called "triggers". In contrast to precursor triggers, AF are made of transparent acrylic glass and are hence almost invisible under water. The AF were compared to a conventional, commercially available trigger, named "Neptune fingers" (NF) that is clearly visible under water. Both trigger types significantly reduced exit rates compared with an entrance without triggers. However, the rigid NFs also reduced entry rates by visually deterring cod. In contrast, AF did not result in changes of entry rates compared to an entrance without triggers. AFs have higher entry-to-exit ratios than entrances without AF and therefore improve catch efficiency. They almost double it compared to entrances without AF. Moreover, combining AFs with funnels further increased catch efficiency. Therefore, transparent acrylic triggers present a promising innovative approach to increase catch efficiency of cod pots, as well as allowing alternative entrance designs to e.g. support multispecies pot designs. They could increase the uptake of pots in commercial fisheries as environmentally low-impact gear.

Concluding Part B, the findings made in the two studies show the net pen-based observation method's advantages compared to prior catch comparison studies. With the method, an in-depth understanding of how different entrance parameters affect cod–pot entrance interactions is obtained. It can be used to develop and evaluate improved entrances. It was used to deliver important insights into cod–pot entrance interactions, laying the groundwork for further structural entrance improvements. It also led to the development of a new trigger type which increased the retention efficiency without reducing entry rates. Thus, further pot gear development studies will benefit from using this method.

The findings of Part B also have direct management relevance. Due to the critical conservation status of the Baltic proper harbour porpoise sub-population, gillnets will be prohibited in the future in certain protected areas of the Baltic Sea. These prohibitions will be a strong restriction for Baltic SSF. Fishers will have to switch to alternative passive gear (such as fish pots), if they want to continue fishing in the protected areas. The findings on diurnal entrance passage differences and the improved understanding of entrance interactions can already facilitate fishers' gear switch to fish pots.

This thesis contributes to the bycatch mitigation "toolbox" and thus addresses the divide between fisheries and nature conservation objectives in the Baltic Sea. The PAL concept as well as the developed pot study method and its findings can furthermore be directly or perspectively transferred to the bycatch mitigation "toolboxes" of other sea regions.

Zusammenfassung

Stellnetze sind das weltweit wichtigste Fanggerät der kleinen Küstenfischerei („small scale fisheries" (SSF)). Sie sind kostengünstig und einfach einzusetzen, ihre hohe Größenselektivität ist gut einstellbar und vor allem weisen sie eine hohe Fangeffizienz für ihre Zielarten auf. In jüngster Zeit wird ihre Verwendung zunehmend kritisiert, denn sie führen zu einem erheblichen Beifang von Meeressäugern, tauchenden Seevögeln sowie marinen Schildkröten, den Fortbestand vieler dieser Megafaunaarten bedrohend. Stellnetze haben die höchste Beifangintensität aller fischereilichen Fanggeräte für diese Taxa. In der Ostsee werden Stellnetze u. a. zum Fang von Dorsch (Gadus morhua), Hering (Clupea harengus), Steinbutt (Scophthalmus maximus) und Scholle (Pleuronecta platessa) verwendet. Die Stellnetzfischerei führt dort zu einem erheblichen Beifang von Schweinswalen (Phocoena phocoena) sowie zu einer der höchsten Stellnetzbeifangraten für tauchende Seevögel weltweit. Mehrere dieser Seevogelarten sowie eine der beiden dortigen Schweinswalunterpopulationen gelten als gefährdet und werden als besonders durch Stellnetzbeifang bedroht angesehen. Die baltischen EU-Mitgliedsstaaten sind rechtlich dazu verpflichtet, die Beifänge dieser Arten zu begrenzen.

Ziel dieser Dissertation ist die Entwicklung neuer Ansätze zur Beifangverringerung. Ausgangspunkt ist die Annahme, dass Stellnetzbeifang nicht durch einen einzelnen technischen Lösungsansatz ausreichend vermindert werden kann. Zielführend ist vielmehr die Entwicklung eines Werkzeugkastens unterschiedlicher Maßnahmen.

In Teil A dieser Dissertation (Paper I) wurde der "Porpoise ALert" (jetzt vom Hersteller F3 Maritime Technology unter dem Namen "porpoise-PAL" vertrieben; "PAL" hiernach) als eine Weiterentwicklung der sog. „Pinger"-Technologie getestet. Pinger sind an Stellnetze zu befestigende Geräte zur akustischen Vergrämung von Walen, Delfinen und Schweinswalen. Dazu senden herkömmliche Pinger künstliche Geräusche ohne biologische Bedeutung aus. Es bestehen wissenschaftliche Bedenken im Hinblick auf ihre Wirksamkeit und andere unbeabsichtigte Auswirkungen auf die damit zu schützenden Meeressäuger, wie zum Beispiel weiträumige Habitatvertreibung. Ziel der Pinger-Weiterentwicklung PAL war die Vermeidung dieser negativen Pingereffekte. Dazu sendet der PAL natürliche, aversive Kommunikationssignale von Schweinswalen der westlichen Ostsee aus.

Leitfrage von Teil A war, ob der PAL den Beifang von Schweinswalen der westlichen Ostsee in der kommerziellen Stellnetzfischerei wirksam reduziert. Dazu wurde ein Fischereiversuch mit drei Fahrzeugen der kommerziellen Stellnetzfangflotte durchgeführt, die von 2014 bis 2016 insgesamt 778 Tages-Fangreisen im Rahmen ihrer üblichen Fischereiaktivität durchführten. Die Beifangwahrscheinlichkeit von insgesamt 1.120 PAL-ausgestatteten Stellnetzfleeten sowie 1.529 Kontrollfleeten ohne PAL wurde verglichen.

Über die gesamte Versuchsdauer wurden insgesamt 18 Schweinswale in Kontrollfleeten sowie fünf Schweinswale in PAL-Fleeten beigefangen. Mittels eines „generalised linear mixed model" (GLMM) wurde nachgewiesen, dass PAL den Beifang von Schweinswalen der westlichen Ostsee um 79,7% signifikant verringern, wenn der Abstand zwischen an den Fleeten aufeinanderfolgenden PAL nicht mehr als 200 m beträgt.

Die Studie von Teil A zeigt des Weiteren, dass eine Erhöhung der Distanz zwischen aufeinanderfolgenden PAL auf 210 m den Beifang-verringernden Effekt auf 64.9% verringert. Diese Erkenntnis unterstützt die Ergebnisse früherer Pingerstudien, die zeigten, dass die Distanz zwischen aufeinanderfolgenden Pingern ein wichtiger Einflussfaktor auf deren Beifang-verringernden Effekt ist.

In der Teil-A Studie wurden keine Hinweise darauf gefunden, dass PAL die Stellnetzfängigkeit auf die Zielarten verringert – ein wichtiges Ergebnis für den Einsatz von PAL in der Stellnetzfischerei. Die

Tatsache, dass über 100 deutsche Stellnetzfahrzeuge in der westlichen Ostsee die PAL mittlerweile schon seit mehreren Jahren einsetzen, belegt dies. Somit kann geschlussfolgert werden, dass der PAL Stellnetz-Schweinswalbeifang in der westlichen Ostsee signifikant verringert. Der PAL kann für effektive Schweinswalbeifangvermeidung in dieser Region genutzt werden, mit vergleichbarer Effektivität zu konventionellen Pingern.

Der PAL ist das erste akustische Gerät, dass den Beifang von Schweinswalen mittels ihrer eigenen kommunikativen Lautäußerungen verringert. Er stellt somit ein wichtiges „proof-of-concept" dar und eröffnet damit einen neuen Ansatz zur Beifangvermeidung von Walen, Delfinen und Schweinswalen.

Obwohl PAL und konventionelle Pinger in der Studie von Teil A nicht direkt verglichen wurde, wird argumentativ erörtert, ob der PAL vergleichbare oder sogar gleichartige schädliche Effekte bewirken könnte. Bei einer Before-After-Control-Impact (BACI) Studie von Schweinswalverbreitung in dem Gebiet, in dem der PAL seit mehreren Jahren eingesetzt wird, wurden keine Belege für Habitatsvertreibung gefunden. Die Belege der BACI-Studie sind jedoch nicht stark aussagekräftig und eine potentiell schädliche Habituation der Schweinswale an das PAL-Signal konnte nicht untersucht werden. Somit bedürfen mögliche Habitatsvertreibung und Habituation weiterer Untersuchungen, um ausgeschlossen werden zu können.

In Teil B der Dissertation lag der Fokus auf möglichen Fanggerätealternativen mit geringerem Beifangpotential im Vergleich zu Stellnetzen. Die meisten bekannten Fanggerätealternativen werden von der kleinen Küstenfischerei der Ostsee nicht genutzt, da sie für den Einsatz von kleinen Fischereifahrzeugen weniger geeignet sind. Auch haben sie meistens eine geringere Fangeffizienz und ihr Einsatz ist somit ökonomisch weniger rentabel. Des Weiteren weisen sie oft eine geringere Einsatzvielseitigkeit auf: Manche Fanggerätealternativen können nur in bestimmten Gebieten eingesetzt werden, zum Beispiel nur in flachen Küstengewässern.

Im ersten Schritt wurde zur Identifikation des als Stellnetzalternative am besten geeigneten Fanggeräts, Fanggerätealternativen systematisch nach operativen, wirtschaftlichen und ökologischen Kriterien bewertet. Grundlage für die Bewertung war eine Literaturrecherche sowie Diskussionen mit Fischereifangtechnikern und professionellen Fischern. Die folgenden Fanggeräte wurden analysiert: pneumatisch-hebbare Großreusen, sog. „Ponton-Fallen", Fanggeräte mit Haken wie Langleinen und sog. „Jigging-Maschinen", das aktive Fanggerät Snurrewade oder „Danish seine" sowie Fischfallen. Letztere wurden als beste Stellnetzalternative für die kleine Küstenfischerei der Ostsee identifiziert. Sie sind ebenso vielseitig einsetzbar, liefern den hochwertigsten Fang und können selbst von kleinsten Fischereifahrzeugen eingesetzt werden. Und im Kontext dieser Dissertation entscheidend: Fischfallen haben ein geringes Risiko für Beifang von Schweinswalen sowie tauchender Seevögel.

Wichtigstes Ziel der im zweiten Schritt in Teil B unternommenen Studien war, die Fangeffizienz von Fischfallen bei der Dorschfischerei zu erhöhen. Denn damit würde ihre Wirtschaftlichkeit verbessert werden und somit auch ihre Aufnahmewahrscheinlichkeit durch die Stellnetzfischerei. Mittels einer Literaturstudie von Fischfallen-Fangeffizienzstudien wurden Einflussfaktoren identifiziert und bewertet. Fischfalleneingänge wurden dabei als zentraler Einflussfaktor herausgearbeitet. Fischfalleneingänge sollen idealerweise den Eintritt von sich der Fischfalle nähernden Fischen in die Fischfalle möglichst erleichtern und einen darauffolgenden Austritt verhindern. Diese zentrale Eigenschaft wird bei der Fischfallenfischerei jedoch meist nicht erreicht.

Weiterhin zeigte die Literaturstudie, dass die meisten Fischfallen-Fangeffizienzstudien Fischereifangvergleiche im Feld sind. Bei solchen Studien werden unterschiedliche Fischfallentypen unter gleichen Bedingungen in einer Fischerei parallel gefischt. Ihr Fangertrag (catch-per-unit-effort

(CPUE)), also die Anzahl gefangener Fische pro eingesetzter Fischfalle eines bestimmten Fischfallentyps, ist dabei der Hauptmesswert, mit dem die Fangeffizienz der Fischfallen verglichen wird. Dieser Messwert erlaubt jedoch keine Rückschlüsse darauf, wie die Zielart mit den Fischfallen interagiert. Dabei ist diese Information essenziell für effiziente Fanggeräteentwicklung, einschließlich Studien zur Steigerung der Fangeffizienz. Fischereifangvergleiche im Feld haben mehrere weitere Nachteile, zum Beispiel die so nicht zu erfassende, variierenden Zielartabundanzen um die getesteten Fischfallen, oder die nicht zu erfassende Größe und Kondition sich den Fallen nähernder Fische.

Zur Vermeidung dieser Nachteile von Fischereifangvergleichen, wurde in Teil B eine neue, effektivere Methode entwickelt: Die netzkäfigbasierte Beobachtungsmethode („net pen-based observation method“). Sie erlaubt den direkten Vergleich des Verhaltens von Fischen in Relation zu Fischfallencharakteristika. Die Methode umfasst physische und statistische Elemente. Der physische Aufbau umfasst eine speziell für den Versuchsaufbau angefertigte Fischfalle, derer zwei Eingänge leicht austauschbar sind und an der ein Unterwasser-Videosystem mit Langzeitaufnahmekapazitäten angebracht ist. Das Videosystem hat Infrarotlicht (IR)-Aufnahmefähigkeiten und erlaubt so eine Fische nicht beeinflussende Tag- und Nachtbeobachtung (Paper II). Damit können alle Interaktionen von Fischen mit den Eingängen während der Versuche aufgezeichnet werden, also erfolgreiche wie nicht-erfolgreiche Durchtrittsversuche. Fischfalle samt Videosystem werden in einen Netzkäfig platziert, in denen ausgesuchte Fische eingesetzt werden können.

Das erste statistische Element der Methode ist ein Ethogramm für die Interaktion von Fischen mit Fischfalleneingängen, mit dem diese beschrieben und bewertet werden können. Die beobachtete Fischfalleneingangseffizienz – eine Funktion aus Eintritts- und Austrittswahrscheinlichkeit durch einen Eingang – wird mit einem Bündel aus zwei statistischen Methoden quantifiziert und verglichen. Diese statistischen Elemente erlauben die Ereignisketten von Fisch-Eingangsinteraktionen zu „sezieren“. Die Ursachen für die zwischen den getesteten Eingängen beobachteten Unterschiede können so präzise bestimmt werden. Bei jedem Versuchsdurchgang wird die gleiche Anzahl an Fischen in den Netzkäfig gesetzt, und so eine gleichbleibende Fischabundanz um die Fischfalle gewährleistet.

Die Zielart für die Effizienzsteigerung der Fischfallen war Dorsch, derzeit eine der Haupt-Zielarten für die kleine Küstenfischerei der Ostsee zu dieser Zeit. Um das Verständnis der Interaktion von Dorschen mit Fischfalleneingängen zu erhöhen, wurden mittels der entwickelten Methode zweier Fischfallenstudien durchgeführt. In der ersten Studie (Paper III) wurde der Einfluss von grundlegenden Parametern von Fischfalleneingängen untersucht. Analysierte Parameter waren Präsenz von angebrachten Netz-Kehlen, Kehlenlänge, Kehlenfarbe sowie Kehlentyp. Wichtige, grundlegende Erkenntnisse für das Verständnis der Interaktion von Dorschen mit Fischfalleneingängen wurden erzielt: Zum einen wurden ausgeprägte Tag/Nacht Unterschiede aufgezeigt, mit sehr wenigen nächtlichen Eingangsdurchtritten. Zum anderen wurde eine unbehinderte Durchsicht durch die Eingänge des Falleninneren oder -äußeren für von außen oder innen mit den Eingängen interagierenden Dorschen als Schlüsselfaktor für eine erfolgreiche Eingangspassage identifiziert. Bezüglich Einfluss der Eingangsparameter wurde gezeigt, dass eine angebrachte Kehle die Wahrscheinlichkeit erhöht, dass sich nährende Dorsche den Eingang finden, weil sie die äußere Eingangsöffnung vergrößert und so Dorsche auf den Eingang hinleiten. Des Weiteren verringern Kehlen die Austrittsrate, mutmaßlich indem Dorsche von der inneren Eingangsöffnung abgelenkt werden und indem sie den Bereich in der Falle verringern, von dem die Ausgangsöffnung unversperrt sichtbar ist. Kehlen sind somit entscheidend, um die Fischfallenfängigkeit zu maximieren. Durch Verlängerung der Kehlenlänge wird der Bereich in der Falle, von der die Ausgangsöffnung unversperrt sichtbar ist, weiter verringert. Auch wird mutmaßlich die Austrittswahrscheinlichkeit durch die längere

Distanz, die Dorsche beim Austritt wieder zurückschwimmen müssen, reduziert. Kehlenfarbe (getestete Netzfarben: weiß, grün sowie transparentes Netzmaterial) beeinflusst Kehlendurchtrittsraten, mit signifikant höherer Durchtrittsrate bei transparenten Kehlen.

Ziel der zweiten Fischfallenstudie (Paper IV) war, Fischfallenfängigkeit durch Reduktion der Austrittswahrscheinlichkeit, bei gleichzeitiger Vermeidung einer Reduzierung der Eintrittswahrscheinlichkeit, zu erhöhen. Aufbauend auf der Erkenntnis der ersten Studie, dass Dorsche vor allem ihr Sehvermögen zum Durchtritt von Fischfalleneingängen nutzen, wurden die sog. „Acrylic fingers“ (AF) entwickelt. AF sind ein neuartiger Typ von fingerförmigen Fischrückhaltevorrichtungen, sog. „Trigger“. Im Gegensatz zu Vorgänger-Trigger, bestehen AF aus transparentem Acrylglas und sind unter Wasser daher fast durchsichtig.

AF wurden mittels der netzkäfigbasierten Beobachtungsmethode mit einem konventionellen, kommerziell erhältlichen und unter Wasser deutlich sichtbaren Triggertyp, den „Neptune fingers“ (NF), verglichen. Beide Typen verringerten signifikant die Austrittsrate aus der Fischfalle im Vergleich zu Eingängen ohne Trigger. Die rigiden NF reduzierten jedoch auch die Eintrittsrate, indem sie Dorsche visuell abschreckten. Die AF hingegen bewirkten keine Änderung der Eintrittsrate im Vergleich zu Eingängen ohne Trigger. AF haben somit ein höheres Eintritt-zu-Austrittverhältnis als Eingänge ohne AF und verdoppeln somit fast die Fangeffizienz.

Diese transparenten Acrylglastrigger stellen insgesamt einen vielversprechenden Ansatz zur Erhöhung der Fischfallen-Fangeffizienz und erlauben die Entwicklung neuer, innovativer Eingänge für Fischfallen zur gleichzeitigen Befischung mehrerer Zielarten (Mehrartenfischfalle). Damit könnte die Aufnahme von Fischfallen als alternatives Fanggerät mit geringen Umweltauswirkungen für die kleine Küstenfischerei der Ostsee vorangebracht werden.

Die in Teil B der Dissertation gewonnenen Erkenntnisse zeigen die Vorteile der netzkäfigbasierten Beobachtungsmethode im Vergleich zu den üblichen Fischerei-Fangvergleichen auf. Die Methode erlaubt ein tiefgehendes Verständnis für den Einfluss verschiedener Eingangsparameter auf die Interaktion von Dorschen mit Fischfalleneingängen zu gewinnen. Sie ermöglicht somit eine zielgerichtete Entwicklung und Evaluation verbesserter Eingänge. In dieser Dissertation wurde sie genutzt, um entscheidende Erkenntnisse zur Interaktion von Dorschen mit Fischfallen zu gewinnen und so eine Grundlage für weitere Eingangsverbesserungen zu legen. Darüber hinaus wurde mit ihr ein verbesserter Trigger-Typ entwickelt, der die Rückhaltekapazität von Eingängen erhöht, ohne die Eintrittswahrscheinlichkeit zu verringern. Weitere Fischfallenstudien werden von dieser Methode und den so gewonnenen Erkenntnissen profitieren können.

Die Erkenntnisse von Teil B haben darüber hinaus auch direkt Fischerei-Managementrelevanz. Denn aufgrund des kritischen Erhaltungszustands der Schweinswal-Population der zentralen Ostsee werden in Zukunft Stellnetze in bestimmten Schutzgebieten der zentralen Ostsee verboten sein. Diese Verbote stellen eine erhebliche Einschränkung für die kleine Küstenfischerei dar. Fischer werden auf alternative Fanggeräte (wie zum Beispiel Fischfallen) umstellen müssen, wenn sie in den Schutzgebieten weiter fischen wollen. Die Erkenntnisse bezüglich Tag/Nacht-Unterschieden bei Eingangspassagen sowie das verbesserte Verständnis der Interaktion von Dorschen mit Fischfalleneingängen können den Fischern beim erfolgreichen Umstieg auf Fischfallen nützlich sein.

Die vorliegende Dissertation bestückt den Beifangverringerungs-Werkzeugkasten für die Ostsee mit neuen, innovativen und effizienten Werkzeugen. Sie kann so dazu beitragen, den Dissens zwischen Fischerei- und Arterhaltungsinteressen zu verringern. Das PAL-Konzept sowie die netzkäfigbasierte

Beobachtungsmethode und die damit gewonnenen Erkenntnisse können zudem teils direkt, teils perspektivisch auf andere marine Regionen übertragen werden.

List of Papers and contribution of authors

Paper I: Synthetic harbour porpoise (*Phocoena phocoena*) communication signals emitted by acoustic alerting device (Porpoise ALert, PAL) significantly reduce their bycatch in western Baltic gillnet fisheries

Jérôme Chladek, Boris Culik, Lotte Kind-Larsen, Christoffer Moesgaard Albertsen, Christian von Dorrien

This paper has been published in the journal Fisheries Research:

Chladek, J., Culik, B., Kindt-Larsen, L., Albertsen, C. M., and von Dorrien, C. (2020). Synthetic harbour porpoise (*Phocoena phocoena*) communication signals emitted by acoustic alerting device (Porpoise ALert, PAL) significantly reduce their bycatch in western Baltic gillnet fisheries. *Fish. Res.* 232, 105732. doi:10.1016/j.fishres.2020.105732.

JC led the data collection, including liaising with the participating fishers and undertaking observer trips on their vessels. He supervised other observers. The REM analysis was also supervised by JC. Data curation and validation was performed by JC, assisted by CvD. JC analysed the data, assisted by LKL, CMM and CvD. JC was the principal author of the manuscript, from the first draft to the final accepted version. All co-authors provided feedback to the manuscript.

BC and CvD conceptualized the study and acquired the funds. CvD further developed the initial study methodology and carried out project supervision and administration.

LKL helped acquiring Danish fishers willing to participate in the study and led the REM analysis of the Danish vessel data.

CMA participated in the statistical analysis of data, both by advising on methodology and undertaking of data analysis.

Paper II: An open source low-cost infrared underwater video system

Andreas Hermann, Jérôme Chladek, Daniel Stepputtis

This paper has been published in the journal Hardware X:

Hermann, A., Chladek, J., and Stepputtis, D. (2020). iFO (infrared Fish Observation) – An open source low-cost infrared underwater video system. *HardwareX* 8, e00149. doi:10.1016/j.ohx.2020.e00149.

JC and AH conceptualized the IR camera. AH designed and built the camera and was the principal author of the manuscript, from the first draft to the final accepted version. JC and DS provided feedback to the manuscript.

Paper III: Using an innovative net-pen-based observation method to assess and compare fish pot-entrance catch efficiency for Atlantic cod (*Gadus morhua*)

Jérôme Chladek, Daniel Stepputtis, Andreas Hermann, Isabella M. F. Kratzer, Peter Ljungberg, Paco Rodriguez-Tress, Juan Santos, Jon C. Svendsen

This paper has been published in the journal Fisheries Research:

Chladek, J., Stepputtis, D., Hermann, A., Kratzer, I. M. F., Ljungberg, P., Rodriguez-Tress, P., Santos, J., Svendsen, Jon C. (2021). Using an innovative net-pen-based observation method to assess and compare fish pot-entrance catch efficiency for Atlantic cod (*Gadus morhua*). *Fish. Res.* 236, 27. doi:https://doi.org/10.1016/j.fishres.2020.105851.

JC conceptualized the study, designed the study setup and supervised its assembly. He led the data collection, performed data curation and validation and performed the data analysis, assisted by JS, PRT and DS. JC was the principal author of the manuscript, from the first draft to the final accepted version. All co-authors provided feedback to the manuscript.

DS and PL assisted study conceptualization.

DS supervised the project in which this study was performed and assisted in study design, setup and implementation.

AH took care of setting up and maintaining the electronic equipment of the study setup.

JCS advised on RFID-technology.

Paper IV: Development and testing of fish-retention devices for pots: transparent triggers significantly increase catch efficiency for Atlantic cod (*Gadus morhua*)

Jérôme Chladek, Daniel Stepputtis, Andreas Hermann, Peter Ljungberg, Paco Rodriguez-Tress, Juan Santos, Jon C. Svendsen

This paper has been published in the journal ICES Journal of Marine Research:

Chladek, J., Stepputtis, D., Hermann, A., Ljungberg, P., Rodriguez-Tress, P., Santos, J., Svendsen, Jon C. (2020). Development and testing of fish-retention devices for pots: transparent triggers significantly increase catch efficiency for Atlantic cod (*Gadus morhua*). *ICES J. Mar. Sci.* doi:10.1093/icesjms/fsaa214.

JC conceptualized the study, designed the study setup and supervised its assembly. The Acrylic fingers were conceptualized and designed jointly by JC and DS. JC led the data collection, performed data curation and validation and performed the data analysis, assisted by JS, PRT and DS. JC was the principal author of the manuscript, from the first draft to the final accepted version. All co-authors provided feedback to the manuscript.

DS assisted in study conceptualization, supervised the project in which this study was performed and assisted in study design, setup and implementation.

AH took care of setting up and maintaining the electronic equipment of the study setup.

JCS advised on RFID-technology.

Overview of thesis chapters

The thesis is structured in five chapters as follows:

Chapter 1 introduces the gillnet fishing technology and lays out its ecological impacts, including the issue of marine mammal, turtle and bird bycatch. Current, insufficient approaches to reduce that bycatch of air-breathing megafauna are summarised and discussed. This is followed by a rendering of the particular megafauna bycatch situation in the Baltic Sea. In the final sub-chapter, the thesis concept to further mitigate that bycatch in the Baltic Sea is deduced.

Chapter 2 presents the PAL ("Porpoise ALert") bycatch mitigation device and the need for a fisheries test of the device. Paper I, the PAL fisheries test follows that chapter.

Chapter 3 presents the bycatch mitigation approach "gillnet alternative gear" and an assessment of several alternative gear candidates. This is followed by the result of this assessment, which identifies fish pots as the most suited alternative gear for German Baltic SSF. The chapter finishes by an elaboration of the research questions developed to increase fish pot catch efficiency. Fish pot study Papers II, III and IV follow this chapter.

Chapter 4 sets the studies performed in this thesis into context and discusses their relevance, including identifying further research questions resulting from these studies. It finishes with a conclusion and outlook how the study already now and perspectively in the future will be taken up in further studies and by Baltic Sea Fisheries managers.

1. Introduction

1.1 Relevance and history of gillnet fishing

Gillnet fishing is one of the most widespread used fishing gear (Sahrhage and Lundbeck, 1992). And it is one of the earliest fishing technologies developed, dating back to at least 6000 B.C. when gillnets were used on the Peruvian coast (Sahrhage and Lundbeck, 1992). Until the industrialization of fisheries in the 1950s and 1960s, gillnets were made from strings of natural fibres like cotton or hemp, which limited their durability. The introduction of synthetic netting (mainly nylon) and rope materials led to greatly improved durability and versatility, also because synthetic gillnets do not require periodic drying to increase their durability (Pycha, 1962; Kristjonsson, 1971; He, 2006; Bekker-Nielsen and Casasola, 2010). Synthetic gillnets additionally had a higher catch efficiency due to the higher tensile strength, allowing a lower twine thickness and higher flexibility of the netting (Pycha, 1962; Kristjonsson, 1971; Potter and Pawson, 1991). Introduction of mechanized net haulers further improved efficiency of gillnet fisheries (Pycha, 1962; Potter and Pawson, 1991).

These advantages led to a rapid global uptake of synthetic fibre gillnets that nowadays are considered easily accessible, cheap, versatile, easy to use from small vessels, and catch as well fuel efficient with high size selectivity (Suuronen *et al.*, 2012). They can be used to catch a wide variety of pelagic, demersal and even benthic species. Notwithstanding their adverse ecological consequences such as ghost fishing (see sub-chapter 1.3), gillnets are thus currently one of the main gears of coastal small scale fisheries (SSF), fishing mainly in freshwater and coastal areas (Chuenpagdee *et al.*, 2006; He, 2006; Waugh *et al.*, 2011; Suuronen *et al.*, 2012; Cashion *et al.*, 2018; Lucchetti *et al.*, 2020a; Thomas *et al.*, 2020).

52.3% of all fishing vessels registered in the European Union (EU) have gillnets as registered primary gear. In Germany, 981 of 1307 vessels have gillnets as primary gear of which 98.7% are small scale fisheries (SFF)[1] vessels (EC, 2020). Globally, gillnets are used to catch approximately 20% of all marine small scale catches, with strong differences between countries (Waugh *et al.*, 2011).

1.2 Description of gillnet gear and catch process

A gillnet is a curtain of webbing hanging in the water column suspended from a buoyant ‘float line’ (also ‘head rope’) and stretched downward with a weighted ‘lead line’ (also ‘foot rope’). Several gillnet units are often bound together to form a whole gillnet ‘string’ or ‘fleet’ (also ‘gillnet gang’ (Pycha, 1962)), reaching from a few hundred meters to several kilometres.

Gillnets are marked with a buoy attached to each of the two ends with a buoy line connecting the buoys at the surface with the net in the water (Figure 1). The buoys serve as location marker for the gillnets and are used to retrieve the gillnet through the connecting line. Usually, the buoys are complemented with a highflyer flag to alert other maritime users of the area of their presence. This is especially important in case of surface reaching gillnets such as herring gillnets in the Baltic Sea or when the encountering vessel deploys ground contacting devices such as trawls, sediment samplers or other gillnets. There are four different gillnet sub-categories:

I. **set gillnets**: stationary gillnets fixed to the ground with anchors at both ends;

[1] Defined as all vessels <12 m length in the EU (EU, 2014).

II. **drift gillnets**: not anchored and drift with the current, sometimes also connected to the fishing vessel. Since their usage is banned in the EU (Caddell, 2010), they are not addressed further in this manuscript;

III. **trammel nets**: a compound gillnet consisting of three webs, with the middle web possessing smaller mesh size than the two outer webs;

IV. **fixed gillnets**: gillnets set into tidal currents with strong stakes firmly planted in the ground.

For reading ease, unless otherwise stated, the term 'gillnet' is used here to both depict gillnets and trammel nets as those are the main categories used in the Baltic Sea.

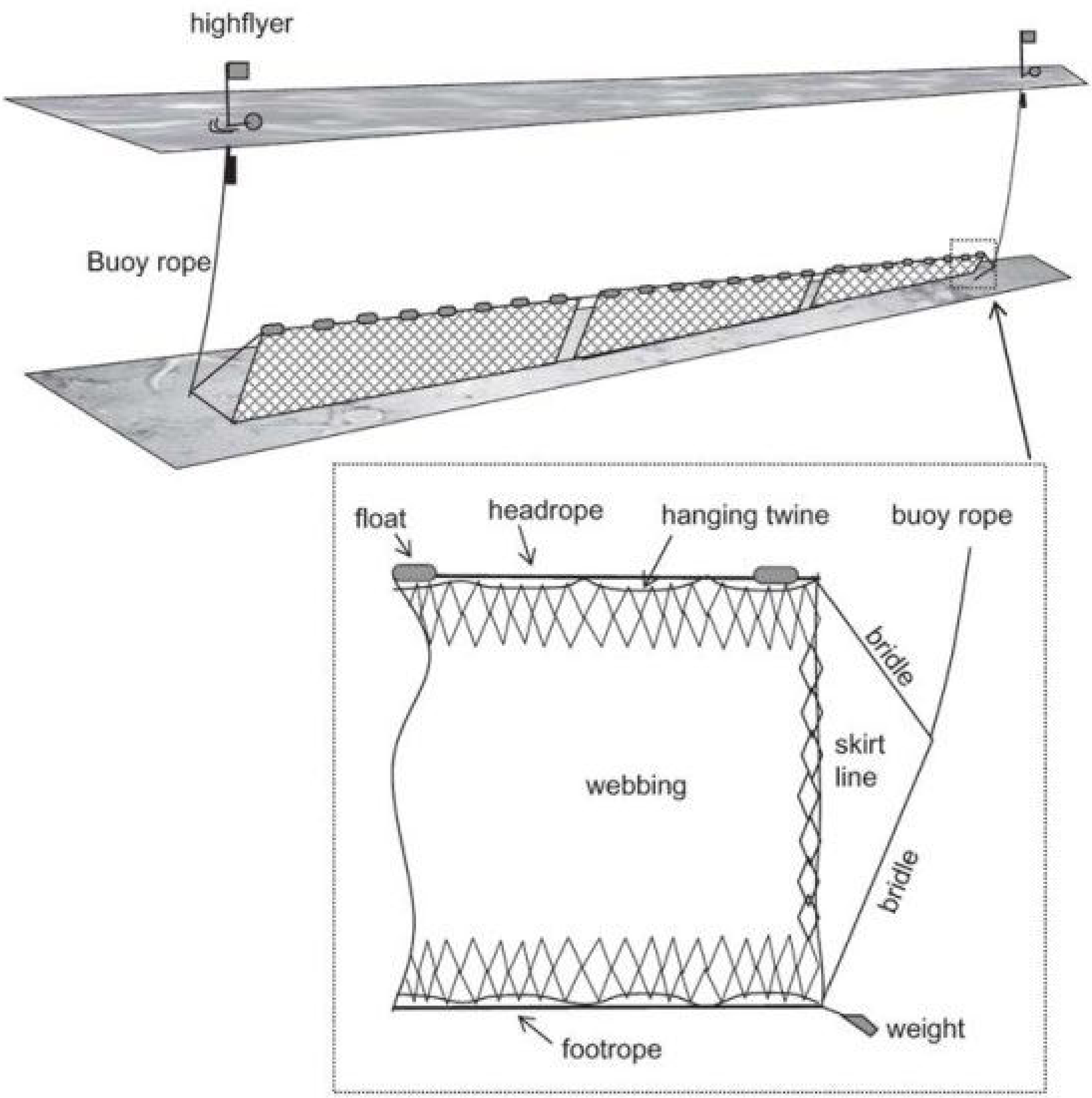

Figure 1: Schematic illustration of a bottom set gillnet (from He, 2006).

The gillnet basic catch principle is that fish do not perceive the thin netting and swim into it and then are retained. They can then either become stuck in a mesh, often behind their gills (termed 'gilling', hence the term 'gillnet') but also at the largest body diameter ('wedging'). Fish can also become entangled in the net, as well as 'snagged', meaning catching fish by rigid body protrusions such as teeth or spines (He, 2006). Since fish essentially entrap themselves, gillnet is classified as passive fishing gear. The principal metric determining catch efficiency of a gear is selectivity, which is the "*process which causes the catch of the gear to have a different composition to that of the [fished] population*" (Wileman *et al.*, 1996a). Gillnet size selectivity is the proportion of fish of a given size being retained after encountering a gillnet. It is typically bell-shaped: gillnets catch fish in a narrow size range 'window' (Figure 2, He, 2006). These bell-shaped selection curves may have more than one peak when more than one principal catch mechanism affects the fished species (Hovgård and Lassen, 2000; He, 2006).

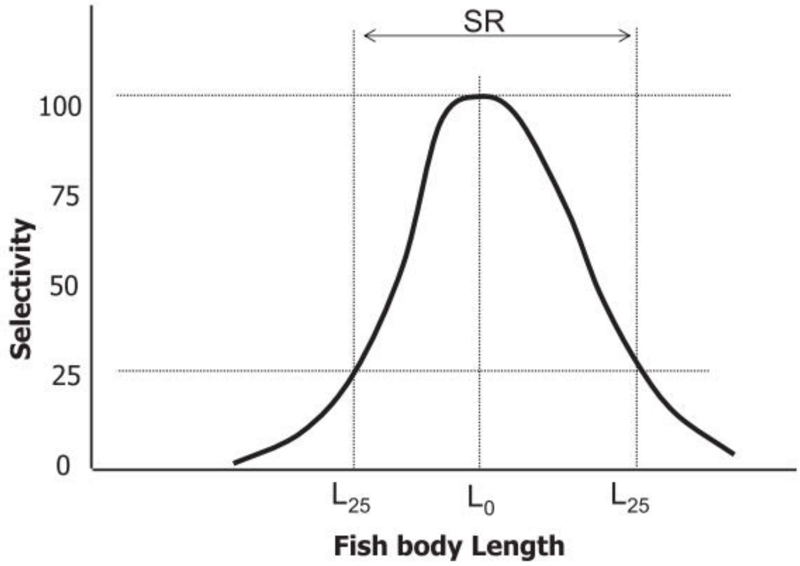

Figure 2: Typical bell-shaped gillnet size selection curve (from He, 2006).

The principal net parameters determining gillnet selectivity are net height, mesh size, hanging ratio (the ratio between the length of the rigged gillnet and the length of its stretched webbing, determining the mesh stretch and thus shape) and webbing material (He, 2006; He and Pol, 2010). Net height determines the gillnet area size per length unit fishing the water column, and in which part of the water column it catches (He, 2006; Sala *et al.*, 2018). Net height should be chosen in relation to the expected migration depth of target species as well of the bycatch species one possibly wants to avoid (He, 2006; Sala *et al.*, 2018).

<u>Mesh size</u> is the main net characteristic determining selectivity, as gillnet selectivity is to a large part determined by Baranov's principle of geometric similarity (Baranov, 1948), describing the catchability dependence of fish body circumference and mesh size (Hamley, 1975; Holst *et al.*, 1998; He, 2006). Mesh size is usually reported as the distance between the two opposite knots of a mesh stretched with a mesh wedge gauge ('stretched mesh size'; e.g. Wileman *et al.*, 1996b; ICES, 2005; Petetta *et al.*, 2020). This definition is used hereafter in the manuscript. Depending on target species, mesh size ranges from just over 20 mm for small fish such as the Big-scale sand smelt (*Atherina boyeri*; Rodríguez-Climent *et al.*, 2012a) to over 200 mm for large bodied fish such as sharks and rays (Lucchetti *et al.*, 2020b). In trammel nets, the mesh size of the two exterior nets is larger than of the inner net and can range to over 600 mm, e.g. to target turbots (Scophtalmidae) in the Mediterranean (Lucchetti *et al.*, 2020b). Mesh size is central in determining not only which species, but also which size of fish is caught (He, 2006).

By determining the shape of the meshes, <u>hanging ratio</u> influences how fish entangle in the net as well as the water flow through the net and thus how the net hangs in the water. The latter is also connected to the uplift and the downward force of the head-, respectively footrope, which also influences catch properties (Angelsen *et al.*, 1979; Machiels *et al.*, 1994; Sala *et al.*, 2018).

The synthetic gillnet twine can be mono- or multifilament or a strand of several parallel, untwisted monofilament threads called multimono-filament (Hovgård and Lassen, 2000). Monofilament twine is considered more efficient because of its reduced visibility and higher rigidity compared to multifilament and multimono-filament twine (He, 2006).

Twine thickness is target species dependent and usually ranges between 0.2 and 0.6 mm in diameter (Sala *et al.*, 2018). But in some fisheries can be >1.0 mm and as wide as 4.0 mm for larger bodied fishes such as sandbar sharks (*Carcharhinus plumbeus*, Lucchetti *et al.*, 2020). Decreasing twine thickness usually increases catch efficiency (e.g. Ayaz *et al.*, 2011; Grati *et al.*, 2015). For some species a negative relation between catch efficiency and the ratio between twine thickness and mesh size has been proposed (Hovgård, 1996). Thinner twines are however less tear resistant (Hovgård and Lassen, 2000; He, 2006; He and Pol, 2010) and can also increase unwanted bycatch (Sala *et al.*, 2018). Additionally, thinner twines may have a larger selection range due to increased elongation when fish push into the webbing (He and Pol, 2010). Thus, twine thickness choice is a compromise between catch efficiency, handling time and durability. Even though twine/netting colour in any particular gillnet fleet varies considerably, there is evidence that it can influence catch success for some species (Hamley, 1975; Hovgård and Lassen, 2000; Balık and Çubuk, 2001; He and Pol, 2010; Orsay and Dartay, 2011).

Soak time is the time between setting and retrieving of passive gears. For gillnets, it can range from several hours (e.g. Larsen *et al.*, 2007) to several days (e.g. Kennedy *et al.*, 2019; Paper I). Soak time length depends principally on water temperature because the latter influences the potential swimming speed of target species and thus the probability of encountering the gillnet (He, 2003; He and Pol, 2010). Soak time is furthermore dependent on the time caught target species can survive in the gillnet (Kennedy *et al.*, 2019). This is influenced by water temperature and thus season (Veneranta *et al.*, 2018). Additionally, soak time can be reduced in times of high algal growth rapidly clogging gillnets, e.g., in late summer off the German Baltic coast.

The parameters outline above all influence catch efficiency and selectivity of gillnets, which explains the high variability in possible fishing outcomes for this gear of a merely at first glance simple design and catch process (He and Pol, 2010).

1.3 Ecological impacts of gillnetting

From an environmental sustainability perspective, gillnets have several advantages: a high target species size selectivity (e.g., He, 2006), low greenhouse gas emissions per catch unit rate (Suuronen *et al.*, 2012) as well as little bottom impact compared to active gears (Macdonald *et al.*, 1996; Grabowski *et al.*, 2014; Savina *et al.*, 2018). At the same time, gillnet fishing has several ecological disadvantages.

Gillnet fishing has a high susceptibility to catch depredation by marine mammals, reducing or even eliminating the economic viability of gillnet fishing in some areas (Buscaino *et al.*, 2009a; Cosgrove *et al.*, 2013; Königson *et al.*, 2015a; Geraci *et al.*, 2019; Waldo *et al.*, 2020).

Gillnet fishing can cause ghost fishing, which occurs through abandoned, lost, or discarded fishing gear (ALDFG) at sea that continues to catch and kill marine organisms without providing economic fishing revenue or marine protein for human consumption (Gilman, 2015; Suuronen *et al.*, 2017). It is predominantly problematic with passive gear such as gillnets and fish pots (Gilman, 2015). ALDFG can continue fishing for months to years and is reinforced by 'automated re-baiting' by caught organisms dying and then in turn attracting further scavenging organisms. Furthermore, still living caught organisms can attract conspecifics. This process is called 'cyclic fishing' (Gilman, 2015; Link *et al.*, 2019). For experimentally 'lost' gillnets, ghost fishing has been found to decrease in the first three months by around 80% and then stabilizing at 5-6% catch efficiency for up to 27 months and possibly beyond (Tschernij and Larsson, 2003). Ghost gillnet catches are not sold and not used for human consumption and possibly contributes from 0.5 % to 30% of the landed catch for some European and North American fisheries (Suuronen *et al.*, 2017).

The most controversially discussed drawback is the poor species selectivity of gillnets (He, 2006; He and Pol, 2010) leading to <u>substantial bycatches of marine mammals, turtles and diving seabirds</u> (e.g. D'agrosa *et al.*, 2000; Gilman *et al.*, 2010; Žydelis *et al.*, 2013; Northridge *et al.*, 2016; Christensen-Dalsgaard *et al.*, 2019). Many of these gillnet-bycaught air-breathing species are endangered or threatened (e.g. Gilman *et al.*, 2010; Croxall *et al.*, 2012) and protected under diverse national and international laws and regulations, such as the EU Habitats and Species Directive (CEC 1992). In some cases, gillnet bycatch directly threatens the survival of populations (e.g. Žydelis *et al.*, 2009; Croxall *et al.*, 2012; Dias *et al.*, 2019) or species (e.g. Brownell Jr *et al.*, 2019; D'agrosa *et al.*, 2000; Jaramillo-Legorreta *et al.*, 2019). Gillnets have the highest bycatch of air-breathing megafauna intensity of all fishing gears (Lewison *et al.*, 2014). Therefore, gillnet bycatch of air-breathing megafauna is an increasingly contentious issue between the fisheries sector and wider society raising concerns over sustainability of fisheries (Christensen-Dalsgaard *et al.*, 2019).

Figure 3: Gillnet bycaught harbour porpoise (*Phocoena phocoena*).

Air-breathing species bycaught in gillnet fisheries of the Baltic Sea are: its only cetacean species, the small odontocete harbour porpoise (*Phocoena phocoena*; Benke *et al.*, 2014), the three Baltic seal species, harbour-, ringed-, and grey seal (*Phoca vitulina, Phoca hispida, Halichoerus grypus;* Lunneryd *et al.*, 2005; Bäcklin *et al.*, 2011; Reeves *et al.*, 2013; Vanhatalo *et al.*, 2014; Königson *et al.*, 2015b) as well as several diving seabirds species (Table 1; Bellebaum *et al.*, 2013; Sonntag *et al.*, 2012; Žydelis *et al.*, 2013, 2009; Figure 4).

Figure 4: Gillnet bycaught common guillemot (*Uria aalge*).

The IUCN red list assesses the global threat status of harbour porpoise as "Least concern", including the sub-population in the western Baltic Sea. The Baltic proper sub-population however is assessed as "Critically endangered". It was estimated to have a population size of around only 497 individuals (SAMBAH, 2016). For diving seabirds, the Baltic Sea is one of the regions with the highest gillnet bycatch rate worldwide (Žydelis *et al.*, 2013). There, the bycatch species composition generally reflects species distribution (Žydelis *et al.*, 2009). Bycatch is considerably higher for pursuit-foraging diving birds such as loons or cormorants than benthivorous ducks (Dagys and Žydelis, 2002; Žydelis *et al.*, 2013).

Table 1: Diving seabird species bycaught in gillnets in the Baltic Sea (summarized from Žydelis *et al.*, 2009, 2013; Sonntag *et al.*, 2012; Bellebaum *et al.*, 2013) with IUCN redlist Europe conservation status (IUCN, 2020) and HELCOM Baltic Sea conservation status (HELCOM, 2021).
Conservation status abbreviations: LC – Least concern; VU – Vulnerable; NT – Near threatened; EN – Endangered; CR – Critically endangered; *NA* – not available.

Group	Common name	Latin name	IUCN redlist Europe status	HELCOM Baltic Sea status
Diving ducks	Pochard	*Aythya ferina*	VU	*NA*
	Tufted duck	*Aythya fuligula*	LC	NT
	Greater scaup	*Aythya marila*	VU	VU
	Goldeneye	*Bucephala clangula*	LC	*NA*
Sea ducks	Long-tailed duck	*Clangula hyemalis*	VU	EN (winter population)
	Velvet scooter	*Melanitta fusca*	VU	VU (breeding population) EN (wintering population)
	Common scooter	*Melanitta nigra*	LC	EN (winter population)
	Steller's eider	*Polysticta stelleri*	LC	EN
	Common eider	*Somateria mollissima*	VU	VU (breeding population) EN (wintering population)
Mergansers	Goosander	*Mergus merganser*	LC	*NA*
	Red-breasted merganser	*Mergus serrator*	NT	VU (wintering population)
Grebes	Great crested grebes	*Podiceps cristatus*	LC	*NA*
	Red-necked grebe	*Podiceps grisegena*	LC	EN (wintering population)
	Slavonian grebe	*Podiceps auritus*	NT	VU (breeding population) NT (wintering population)
Divers	Black-throated divers	*Gavia arctica*	LC	CR (wintering population)
	Red-throated diver	*Gavia stellata*	LC	CR (wintering population)
Cormorants	Great cormorant	*Phalacrocorax carbo*	LC	*NA*
Rails	Coot	*Fulica atra*	NT	*NA*
Auks	Razorbill	*Alca torda*	NT	*NA*
	Common guillemot	*Uria aalge*	NT	*NA*
Gulls	-	*Laridae spp.*	-	-

Contrary to harbour porpoise and diving seabird bycatch, gillnet bycatch of pinniped species is currently not discussed as major concern for the Baltic. In the first half of last century, seals had been hunted to almost extinction in the Baltic Sea. Then, numerous Baltic states had set bounties on seals. The usual goal of the bounty schemes was to limit fishing gear damage and catch depredation (Olsen *et al.*, 2018) and competition with fishers for fish (Harding and Härkönen, 1999; Bowen and Lidgard, 2013; Calamnius, 2017). After the Second World War, pollution through organochloride became the main reason for further Baltic seal population declines (Bergman *et al.*, 2003). All three species showed strong population increases in the last decades and are currently listed as "Least concern" on the IUCN red list (European Mammal Assessment team, 2007a, 2007b; Harding *et al.*, 2007; Bowen, 2016). This is probably the main reason why gillnet bycatch is currently not discussed as major concern for these species.

The current main concern of fisheries–seal interactions are about catch depredation of passive gear by the grey seal. This creates conflict between seals and fishers (Hemmingsson *et al.*, 2008; Königson *et al.*, 2010, 2015a; Varjopuro, 2011) or, more accurately, between fisheries and conservation interests (Ferretti, 2020). The gillnet depredation rates by the growing Baltic grey seal population are rapidly increasing. This makes economically viable gillnet and traditional trap fisheries difficult or even impossible in an increasing number of Baltic localities (Hemmingsson *et al.*, 2008; Westerberg *et al.*, 2008; Varjopuro, 2011; Königson *et al.*, 2015a; Plikshs and Pilāts, 2017), including along the German coast (Barz *et al.*, 2020; Ferretti, 2020).

1.4 Approaches to reduce bycatch of air-breathing megafauna in gillnet fishing

Air-breathing diving megafauna species are particularly threatened by gillnets because their entanglement usually leads to drowning in a short time. Therefore, bycatch of its different taxonomic groups (mammals, birds, and sea turtles) is often treated jointly (e.g. Northridge *et al.*, 2016) and several approaches to mitigate their bycatch have been proposed which will be discussed in the following.

Fisheries closures in areas or periods of high bycatch probabilities and/or high population vulnerability (e.g., breeding season) are a generally appropriate management approach for all bycaught taxa (Murray *et al.*, 2000; Gilman *et al.*, 2010; Gormley *et al.*, 2012; Regular *et al.*, 2013; van Beest *et al.*, 2017). Adjusting structural gillnet properties is also often explored (see Dawson, 1991; Gilman *et al.*, 2010; Northridge *et al.*, 2016 and references therein). Mesh size and net height were found to influence bycatch of the three taxa in a review of multiple bycatch studies (Northridge *et al.*, 2016), and mesh size in particular also for harbour porpoise (Moan *et al.*, 2020).

Several technical gillnet modifications specifically for sea turtles are reviewed in Gilman *et al.* (2010): Net illumination using submersible light-emitting diodes are a promising recently developed modification ("LED"; Wang *et al.*, 2010; Virgili *et al.*, 2018; Bielli *et al.*, 2020; Senko *et al.*, 2022).

Visual approaches were also investigated to mitigate seabird bycatch. This includes adding high-contrast panels or sections (Melvin *et al.*, 1999; Martin and Crawford, 2015; Field *et al.*, 2019) in the net or illuminating the net using the same approach as for sea turtles, by attaching LEDs (Mangel *et al.*, 2018a; Field *et al.*, 2019; Bielli *et al.*, 2020).

Net illumination has recently been used for successful small odontocete bycatch reduction (Bielli *et al.*, 2020). Most cetacean bycatch reduction studies however aim at exploiting the importance of the acute acoustic sensibilities of cetaceans. Another approach for odontocete-specific bycatch reduction approaches builds on their echolocation capabilities and consists of structural modifications of the gillnet netting to increase acoustic reflectivity (Koschinski *et al.*, 2006; Larsen *et al.*, 2007; Trippel *et al.*, 2009; Kratzer *et al.*, 2020, 2021, 2022).

Another approach investigated to mitigate bycatch of air-breathing megafauna is to acoustically alert or deter them with so-called "pingers" (Kraus *et al.*, 1997a; Melvin *et al.*, 1999). For sea turtles, this option has so far not been explored (Gilman *et al.*, 2010). Reasons are possibly the increasing success of LEDs for turtle deterrence (e.g. Wang *et al.*, 2010; Mangel *et al.*, 2018b; Bielli *et al.*, 2020) as well as concerns that pinger further increase detrimental anthropogenic noise in the oceans (Southwood *et al.*, 2008). For seabird bycatch mitigation, pingers have been tested by Melvin *et al.* (1999), with limited success but possibly still promising regarding recent findings of auditory orientation capabilities in diving seabirds (Hansen *et al.*, 2017; Sørensen *et al.*, 2020).

For marine mammals, pinger research has been ongoing since over 30 years and a large part of this research assesses the development and usage of pingers for their bycatch (e.g. Dawson, 1991; Kraus *et al.*, 1997; Larsen, 1999; Buscaino *et al.*, 2009; Carretta and Barlow, 2011; Larsen *et al.*, 2013; Mangel *et al.*, 2013). A review by Dawson *et al.* (2013) concluded that pingers are effective with view to small cetaceans. However, several possible concerns have been raised, including:

I. Potential **habituation to the pinger sound signal**, leading to reduction of the aversive effect and thus reduction of the acoustic signal efficiency over time (Gearin *et al.*, 2000; Cox *et al.*, 2001; Carlström *et al.*, 2009; Kyhn *et al.*, 2015). This was however either not confirmed in most more recent studies (Carretta and Barlow, 2011b; Dawson *et al.*, 2013; Omeyer *et al.*, 2020) or appears to be preventable by using alternating acoustic signals (Kindt-Larsen *et al.*, 2019), with the possible exception of inshore resident populations with small home ranges (Amano *et al.*, 2017).

II. **Echolocation rate reduction** of porpoises as a reaction to pinger signals (as to other loud noises (Wisniewska *et al.*, 2018a; Teilmann and Sveegaard, 2019)), possibly leading to reduced gillnet-detection capability (Cox *et al.*, 2001; Culik *et al.*, 2001; Teilmann *et al.*, 2006; Carlström *et al.*, 2009; Hardy *et al.*, 2012).

III. Potential **habitat exclusion** of porpoises by large-scale pinger deployment. Porpoises were shown to distance themselves from active pingers for several hundred meters (Culik *et al.*, 2001; Carlström *et al.*, 2009; Kyhn *et al.*, 2015; van Beest *et al.*, 2017; Kindt-Larsen *et al.*, 2019) possibly decreasing survival rate and thus population size via indirect effects such as reduced forage efficiency (van Beest *et al.*, 2017).

IV. **Target catch depredation** by marine mammals, especially seals, attracted by the pinger sound and depredating fish caught in the net, decreasing target catch of pinger-equipped gillnets (Melvin *et al.*, 1999; Bordino *et al.*, 2002; Carretta and Barlow, 2011b; Götz and Janik, 2013). Evidence suggests that this so called "dinner bell effect" could also occur with odontocetes (Cox *et al.*, 2004).

The above list is central for the first part of this thesis, as those concerns were the starting point forthe development of the acoustic bycatch reduction device assessed in Part A.

1.5 Thesis concept

1.5.1 Problem description and aims of the thesis

The preceding chapter illustrated that more options are called for to mitigate harbour porpoise and diving seabird bycatch in the Baltic Sea. Essentially, an "bycatch of air-breathing megafauna reduction toolbox" with a diverse tool-collection, encompassing management as well gear technology options, to be used individually as well as in combination, is needed. The overall goal of this thesis was to contribute to this with a two-pronged approach, centred on the study area western Baltic Sea.

The aim of Part A of the thesis was to evaluate the bycatch reduction efficiency of a new kind of acoustic porpoise bycatch mitigation device, the Porpoise ALert (PAL; Culik *et al.*, 2015). This device is similar to conventional pingers but emits a *synthetic* harbour porpoise communication signal instead of an *artificial* signal with no biological relevance to harbour porpoises. Compared to conventional pingers, its signal could potentially avoid the pinger concerns I (habituation), II (echolocation rate reduction) and IV (target catch depredation) for porpoise bycatch mitigation. In Part A, a PAL effectivity test was conducted with three commercial gillnet fishing vessels in the western Baltic Sea.

Nevertheless, since porpoise also increase their distance from an active compared to an inactive PAL (Culik *et al.*, 2015), large-scale PAL deployment could still lead to some habitat exclusion (pinger concern III). Furthermore, the PAL is aimed exclusively at harbour porpoises. Its lower spectral bandwidth of 60 kHz (Culik *et al.*, 2015; Paper I) is well above the auditory range of diving birds (Crowell *et al.*, 2015; Maxwell *et al.*, 2016; Hansen *et al.*, 2017; Maxwell *et al.*, 2017; Mooney *et al.*, 2019; Larsen *et al.*, 2020b; Mooney *et al.*, 2020), thus cannot mitigate their bycatch. Additionally, with only one short study investigating distancing behaviour of porpoise vis-à-vis an active PAL in the comparatively narrow Little Belt at Frederica (Denmark) (Culik *et al.*, 2015), its conclusions are uncertain. Therefore, pinger concern III (habitat exclusion) for the PAL cannot be ruled out with certainty and a possible detrimental large-scale displacement effect hypothesized by van Beest (2017) not be excluded.

The aim of thesis Part B was to explore alternative gears to gillnets as a complementary mitigation approach. An alternative gear with lower or best no bycatch potential for harbour porpoises and diving seabirds was identified and further developed. Ideally, it should be similarly usable by the German Baltic gillnet vessels largely consisting of small-scale fishing vessels (Meyer and Krumme, 2021). And it should provide a comparable catch-per-unit-effort (CPUE) to gillnets to assure the economic sustainability of a gear switch towards it. For instance, a recent study demonstrated that longlines can economically sustainably replace gillnets in south-western Atlantic SSF and almost eliminate Franciscana dolphin (*Pontoporia blainvillei*) and sea turtle bycatch (Berninsone *et al.*, 2020).

As a further important benefit to Baltic SSF and conservation interests, this second approach to gillnet bycatch mitigation is to develop SSF gear that protects the catch from depredating seals ('seal-safe fishing gear') while permitting economically sustainable fisheries and thus reducing seal-fisheries conflicts (Königson, 2011; Varjopuro, 2011; Königson *et al.*, 2015b, 2015a; Brownell Jr *et al.*, 2019). In these analyses, fish pots were identified as most appropriate alternative gear for cod fishing if not for their low-catch efficiency. Subsequently, an analysis for possible ways to increase fish pot CPUE to a comparable level to gillnets was conducted and two studies for fish pot entrance modification conducted to further this goal.

1.5.2 Structure of the thesis

This thesis consists of two main parts. Part A (chapter 2) is centred around the PAL. First, the conception and development of the PAL are laid out in (sub-chapters 2.1 and 2.2). Then follows a summary of the results of Paper I of this thesis, the PAL test in commercial western Baltic gillnet fisheries (sub-chapter 2.3).

In Part B of the thesis (chapter 3), the gillnet bycatch mitigation approach “alternative gear” is set out and its importance for an effective SSF bycatch mitigation toolbox explained. Different alternative gears for Baltic Sea SSF are presented and evaluated in sub-chapter 3.1, leading to fish pots being identified as the most promising one. Their low catch efficiency compared to gillnets is identified as the main obstacle for uptake by Baltic Sea SSF in sub-chapter 3.2. This leads to Papers II, III and IV of this thesis, undertaken with the main goal to increase pot-catch efficiency.

In the final chapter ‘General discussion’ (chapter 4), the key contributions to gear development research and the bycatch mitigation toolbox are first summarized and discussed (sub-chapter 4.1). Further considerations expanding the discussions of Papers I-IV are then made (sub-chapters 4.2 and 4.3). Both sub-chapters include a discussion on how the developed methods and the findings of the PAL test and the fish pot studies can feed into further research.

The chapter closes with an outlook reflecting developments around recently started and planned bycatch mitigation efforts in the Baltic Sea and how the results of this thesis will inform these efforts (sub-chapter 4.4).

Part A - PAL

2. Gillnet modification to reduce harbour porpoise bycatch

The study presented in **Paper I** is the first of a device developed to acoustically alert harbour porpoises of gillnet presence. The PAL is a novel acoustic device, building on the pinger concept. In contrast to pingers, which use synthetic sounds unknown to harbour porpoises, the PAL emits synthetically reproduced porpoise-proper aversive communication signals.

In the following two sub-chapters the PAL concept, its development and the need for an in-depth investigation of its effectiveness for harbour porpoise bycatch mitigation are explained.

2.1 Porpoise ALert (PAL) concept

The development rationale of the PAL followed an early recommendation regarding the effect mechanism of pingers. Pingers would effectively mitigate cetacean bycatch if they fulfilled the following conditions: "*(a) the sounds are intrinsically aversive, (b) they encourage echolocation, and therefore make detection of the net more likely, and/or (c) the porpoises learn to associate the sound with the danger of the net, and hence perceive it as indicating danger*" (Dawson *et al.*, 1998; see also Dawson, 1994).

Since unknown sounds can be expected to be intrinsically aversive to harbour porpoises, described as shy and neophobic (e.g. Dawson *et al.*, 2013; Teilmann and Sveegaard, 2019), it seems doubtful that porpoises would investigate an unknown sound acoustically. That porpoises are known to reduce or even cease echolocating when confronted with anthropogenic sound such as ship noise (Wisniewska *et al.*, 2018b), and specifically also when confronted with pinger sounds (Cox *et al.*, 2001; Culik *et al.*, 2001; Teilmann *et al.*, 2006; Carlström *et al.*, 2009; Hardy *et al.*, 2012; pinger concern II), substantiates this assumption. Furthermore, to learn to associate pinger sound with gillnet presence, porpoises would need to closely approach the pinger to detect the gillnet net and permit establishing the connection between its presence and the pingers' acoustic stimuli.

However, maximum distance at which harbour porpoises can acoustically detect gillnets has been estimated 4-25 m to the net (Kastelein *et al.*, 2000; Mooney *et al.*, 2004; Koschinski *et al.*, 2006). In a field study, free swimming harbour porpoises were shown to change their swimming paths to avoid a set gillnet in distances of >80 m (Nielsen *et al.*, 2012). This is still considerably shorter than the considerably larger reported maximum distancing reactions to pingers (Culik *et al.*, 2001; Carlström *et al.*, 2009; van Beest *et al.*, 2017; Kindt-Larsen *et al.*, 2019). A review of pinger effects on harbour porpoises therefore concluded that deterrence is the most likely effect mechanism of pingers (Dawson *et al.*, 2013). Hence, harbour porpoises learning to associate an aversive pinger sound with net presence appears unlikely. Finally, even if they could learn this association, it is unclear if this would lead to bycatch reduction, because it is not sure if harbour porpoise perceive a detected gillnet as obstacle (Goodson, 1997; Kratzer *et al.*, 2020, 2022).

Consequently, the development rationale for the PAL was to address the pinger concerns and to create an acoustic device that would lead to harbour porpoises to learn to associate the devices' signal with gillnet presence. When perceived by a harbour porpoise, this signal should a) elicit acoustic investigation of the sound source and thus of the gillnet the PAL is attached to (addressing pinger concern II) and b) alert it instead of deterring it, thus not displace it (addressing pinger concern III).

This assumption stemmed from a study demonstrating that some sounds also increase rather than decrease echolocation rates of harbour porpoises, such as a 2.5 kHz sound tested on free-ranging harbour porpoises by Koschinski *et al.* (2006, see also Koschinski *et al.* 2003). Such a sound-elicited acoustic investigation of the sound emitter could potentially lead to learning of a PAL signal–net presence association by harbour porpoises as well as avoiding habitat exclusion (addressing pinger concern III). Lastly, the developers assumed that the biological significance of a harbour porpoise acoustic signal used as PAL signal would be constantly reinforced because of its continuous usage in harbour porpoise interspecific communication. This would counter possible habituation (pinger concern I) (Culik and Conrad, 2013; Culik *et al.*, 2015).

2.2 PAL development

The PAL development consisted of several steps. In a behavioural study with captive harbour porpoises, aggressive signals were first described (Clausen *et al.*, 2011). These signals were then used to develop three synthetic harbour porpoise signals to be employed as alerting signal for the PAL.

The three signals were tested on naïve western Baltic harbour porpoises by Culik *et al.* (2015). The study area was in the Danish Baltic Sea strait "Little Belt". Study time were several weeks in the summers 2012 and 2013. During times of reduced sea state (<2), surface positions of porpoise groups observed were recorded via theodolite and surfacing distance to the study buoys each carrying an experimental acoustic emitter and a CPOD, an echolocation signal recorder. Minimum surfacing distance (MSD) to the signal emitter and recorded acoustic activity of the observed porpoise groups were compared between periods when the acoustic emitters were active to periods when they were inactive.

Of the three signal tested, the one named "F3" was found to slightly increase MSD by 32 m while simultaneously slightly increasing echolocation rate towards the acoustic emitters by 10% (Culik *et al.*, 2015). Hence, its effect on harbour porpoises is likely to differ from conventional pinger signals: it potentially does not decrease echolocation rate or largely deter harbour porpoises. And it could still have the potential for reducing bycatches in gillnets. For these reasons, it was chosen as the signal to be tested in a bycatch study in commercial gillnet fisheries in the western Baltic Sea (**Paper I**), the first study of this thesis.

2.3 PAL bycatch reduction test

Following the identification of a harbour porpoise-proper acoustic communication signal with bycatch reduction potential by Culik *et al.* (2015), this signal had to be tested under realistic fishing conditions. It had to be tested in the fisheries in which bycatch rates were to be mitigated. A PAL casing was developed, small and robust enough to be attachable to gillnets and to endure the straining conditions of regular gillnet setting and hauling.

Figure 5: PAL attached to head line of a gillnet during the PAL test of thesis Part A.

Paper I is the result of this PAL test in the gillnet fisheries in the distribution area of the western Baltic harbour porpoise. It shows that the PAL significantly reduces bycatch rates, with indications that distances <200 m between subsequent PAL increase their efficiency. Based on Kindt-Larsen *et al.* (2019), habituation (pinger concern I) might not occur with PALv.2 (used in the last year of the PAL test) because of its variable signal repetition rate and pause duration.

Paper I does nonetheless not provide conclusive proof against habituation of harbour porpoise to PAL (but see also chapter 0 below). And like conventional pingers, PAL does not permit ruling out habitat exclusion, with potentially more detrimental population level effects than the bycatch itself (van Beest *et al.*, 2017). Moreover, the study only confirms the bycatch mitigation effect for western Baltic Sea harbour porpoises from which the PAL F3 signal was derived. The results of Paper I are not transposable to other harbour porpoise (sub-)populations.

Therefore, PAL usage by itself does not permit attaining the overarching political goal to reduce Baltic Sea harbour porpoise anthropogenic mortality to a maximum 1% of the population per year ('Bergen Declaration', ASCOBANS, 2002). The PAL should thus not be viewed as the "silver bullet" for mitigating harbour porpoise bycatch. And equally important, it does not mitigate Baltic Sea diving seabird bycatch. Therefore, the PAL should be considered as just one of several tools needed for the gillnet harbour porpoise and seabird bycatch mitigation toolbox for the Baltic Sea.

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Synthetic harbour porpoise (*Phocoena phocoena*) communication signals emitted by acoustic alerting device (Porpoise ALert, PAL) significantly reduce their bycatch in western Baltic gillnet fisheries

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ABSTRACT

Gillnet fisheries are one of the main anthropogenic causes of harbour porpoise (*Phocoena phocoena* L., 1758) mortality in the Baltic Sea. A new kind of acoustic alerting device (Porpoise ALert, PAL) was tested in commercial gillnet fisheries in the western Baltic. PAL emits 133 kHz synthetic harbour porpoise communication signals, unlike conventional acoustic deterrent devices (pingers), which emit artificial noise. Trials were undertaken by three commercial gillnet vessels conducting 778 trips during standard fishing operations from 2014 to 2016. In all, 1120 PAL-equipped net strings were tested against 1529 simultaneously set control strings with no devices. We tested two versions of the PAL (v1 and v2) consecutively. These were spaced $<=210$ m apart on the gillnet floatlines, with all devices pointing in the same direction to ensure complete acoustic coverage of the strings. Two vessels fished in Kiel Bight and around Fehmarn Island in German waters, and the third vessel fished in the Øresund, in inner Danish waters. Overall, 18 harbour porpoises were bycaught in control strings (mean 0.01 ± 0.1/haul), and five harbour porpoises were taken as bycatch in strings equipped with PALs (0.004 ± 0.07/haul). The number of net string bycatches was analysed using a generalised linear mixed model (GLMM). The model applied to all observations revealed that the expected bycatch was significantly influenced by PAL deployment ($p < 0.05$), decreasing the expected bycatch by 64.9 % (95 % confidence interval (CI): 8.7–88.7 %). PAL effectiveness was also increased by reducing device spacing to $<=200$ m (16 bycatches in control, three in PAL strings; mean bycatch reduction 79.7 %). Additional model cases were applied to the data and are discussed. We conclude that, with this specific communication signal, PAL can significantly reduce harbour porpoise bycatch in gillnets deployed in the western Baltic Sea, thus reconciling anthropogenic activities with protection of the marine environment.

1. Introduction

Gillnets are a fuel-efficient fishing gear with high target species size selectivity, low greenhouse gas emissions (Suuronen et al., 2012), and little bottom impact compared with active gear (Grabowski et al., 2014). They are widely employed in small-scale Baltic fisheries. Gillnet fisheries, however, present a pressing conservation threat to air-breathing species taken as bycatch, such as marine mammals or diving birds (e.g. Brownell et al., 2019; Gilman, 2015; Northridge et al., 2016; Reeves et al., 2013; Žydelis et al., 2013). Many of these species are endangered and protected under diverse national and international laws and regulations, e.g. the European Union (EU) Habitats and Species Directive (CEC, 1992).

For more than 30 years, scientists have addressed marine mammal bycatch and its mitigation (see e.g. Dawson, 1991 and references therein; Kraus et al., 1997). Proposed mitigation measures include placing acoustic deterrent devices (ADD), so-called pingers, on the strings (e.g. Gearin et al., 2000; Gönener and Bilgin, 2009; Larsen and Eigaard, 2014), structurally modifying the gillnet twine to increase acoustic reflectivity (e.g. Koschinski et al., 2006; Kratzer et al., 2020;

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Larsen et al., 2007; Trippel et al., 2003), adjusting fishery operational factors such as net height or twine diameter (see Northridge et al., 2016 and references therein), and enacting spatial and/or temporal fisheries closures (e.g. Gormley et al., 2012; Murray et al., 2000).

Pingers can reduce the bycatch of many small cetacean species (see Dawson et al., 2013, for a review). Concerns have been raised that pingers might initially deter cetaceans from the gillnet, but then lose their effectivity through habituation to the deterring sound, at least in harbour porpoises (Carlström et al., 2009; Dawson et al., 2013; Gearin et al., 2000; Kyhn et al., 2015). Another concern is that the deterring pinger effect might exclude marine mammals from a potentially large and important ensonified habitat (Carlström, 2002; Culik et al., 2001; van Beest et al., 2017; Kyhn et al., 2015). It is also possible that pingers reduce harbour porpoise echolocation rate (Carlström et al., 2009; Cox et al., 2001; Hardy et al., 2012; Teilmann et al., 2006), thus reducing their ability to detect acoustically unmarked gillnets nearby.

To address these concerns, Culik and Winkler (2011) propose equipping gillnets with a device that synthetically reproduces natural aversive communication signals of harbour porpoises. In a field test in the Little Belt in Danish waters, Culik et al. (2015) demonstrated that harbour porpoises there reacted to one of three tested signals (F3) described for Belt Sea animals by Clausen et al. (2011), by increasing their distance to the signal source by 32 m, while increasing their echolocation rate by 10 %. Based on these results, Culik and Conrad (2013; Culik and Conrad (2013; DPMA Patent No. 10 2011 109 955) developed a rugged, individually programmable sound emitting device for deployment in fisheries, the Porpoise ALert (PAL).

To determine if the chosen PAL signal "F3" effectively reduces harbour porpoise bycatch, we tested the device with commercial gillnet vessels during their standard operations in the western Baltic. Thus, fishers did not invest additional fishing effort in these trials, which might have increased bycatch, so avoiding ethical conflicts.

We compared simultaneously deployed net strings equipped with the mitigation devices (PAL strings) and strings without them (control strings) with the expectation that PALs would lower bycatch rates (*null hypothesis:* no difference in bycatch rates between PAL and control strings).

2. Materials and methods

2.1. Criteria to select fisheries for the tests

Fisheries to conduct the tests were chosen based on these criteria:

a) Tests should be conducted in the area occupied by the Belt Sea porpoise population (cf. Culik et al., 2015).
b) In the test area, harbour porpoise densities should be sufficiently high to expect statistically sound results (i.e. sufficiently high bycatch numbers) with a reasonable experimental effort.
c) Only fishing vessels that ensured a sufficiently intensive fishing effort, based on string lengths set per trip and number of trips conducted per month, were selected for the project.

2.2. Study area, fishing vessels, and weather

From 2014 to 2016, three gillnet vessels, under the condition of anonymity, participated in this study in the western Baltic gillnet fishery. One Danish commercial gillnet vessel (Vessel A, approximately 11 m long) fished in the Øresund (International Council for the Exploration of the Sea (ICES) Area 3.b.23; Fig. 1). Two German commercial gillnet vessels fished in ICES Area 3.c.22 (Vessel B, approximately 8 m long, around Fehmarn Island, and Vessel C, approximately 11 m long, in the western part of Kiel Bight). The main target species was cod (*Gadus morhua* L., 1758), targeted with gillnets and trammelnets with 110–160 mm stretched mesh sizes (hereafter mesh size). Secondary target species were flatfish: mainly flounder (*Platichthys flesus* L., 1758), plaice (*Pleuronectes platessa* L., 1758), and turbot (*Scophthalmus maximus* L., 1758). In addition, Vessel A fished in spring with 240 mm mesh size for lumpfish (*Cyclopterus lumpus* L., 1758).

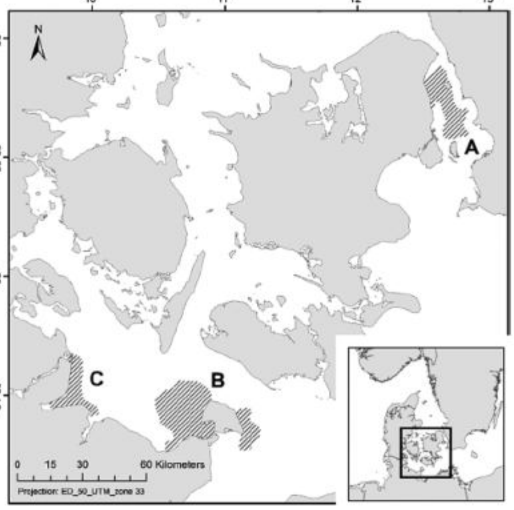

Fig. 1. Map of study area where three commercial gillnet vessels fished during this study (hatched areas). Letters indicate vessels operating in the Øresund (A), around Fehmarn Island (B) and western part of Kiel Bight (C). Note that the fishing areas shown are approximate, because a buffer was added to the setting positions to ensure confidentiality.

Vessels participating in this project were to pursue their usual fishing activities and operating conditions using their own nets. When setting and recording the deployment of both PAL and control strings, they were paid a small compensation. The catch-optimised fishery continued to be their main source of income and thus, PAL trials followed realistic operational conditions.

A research design coupling control and PAL strings was followed: Fishers were instructed to set half of their strings with PALs (PAL strings) and the other half without PALs (control strings) on the same trip. A trip was defined as the period from a vessel's departure from port to conduct fishing until its return to port. Both strings had to have identical net characteristics (mesh size, net panel length, and panel height) and string lengths. Fishers, however, had a limited number of PALs at their disposal. Sometimes there were not enough PAL to equip 50 % of the strings they chose to set for commercial purposes. As a result, fishers often set more control than PAL strings. Therefore, we decided later to include these additional control strings as well, to expand the number of observations available for analysis (see the Results section). PAL and control strings set by the same fisher during the same period were considered as "coupled." Fishers were instructed to space PAL and control strings at least 500 m apart, to ensure that porpoises would not detect the PAL signal near the control strings. Maximum porpoise detection range was conservatively estimated at 460 m by Culik et al. (2015) for a source level of 158 dB peak–peak re 1 μPa, 1 m, which is 6 dB higher than the PALs used here. Using the method of Culik et al. (2015), PAL received levels were simulated, demonstrating that harbour porpoises should detect the signal at wind conditions 0 Beaufort wind force scale (Bft) within a range of approximately 230–320 m, depending on porpoise orientation and position with respect to the PAL. This is reduced to 90–150 m at 7 Bft.

To determine if PAL efficacy is diminished by bad weather conditions through increased environmental noise (Urick, 1983), we acquired windspeed (m/s) and swell height (m) from the sea state model of the

German Meteorological Office (Deutscher Wetterdienst, Marine Meteorological Service) for the three fishing areas during the project time frames. This model contains archived 12 h-forecasts based on recorded meteorological data in a 0.05° grid over Baltic Sea areas with greater than 10 m average water depth. Forecast values are modelled for every 3 h. The forecast datapoints are non-homogenised forecast values and most accurate in areas of average depths greater than 15–20 m. The German Meteorological Office informed us that they assume an error of 0.1 % for the data (M. Gerber, German Meteorological Office, pers. Comm.). In a GIS software (ArcGIS version10.3.1; ESRI, 2014), each recorded gillnet string was assigned to the forecast grid point nearest to its setting point. Using the statistical software R (version r74432; R Core Team, 2018), each string was subsequently assigned the maximum windspeed and swell height during its setting period (distances between starting position of net setting and nearest forecast grid point: mean 2497 m, min. 1 m, max. 7428 m).

2.3. PAL hardware and attachment

PAL is a spindle-shaped acoustic transducer optimised for use in fisheries. In water, the device has a positive buoyancy of approximately 80 g. Two PAL versions were used in the experiment: PALv.1 was equipped with a 1.5 V carbon-zinc battery and a saltwater switch allowing for approximately six weeks or 35 days of operation. PALv.2 is equipped with a 3.6 V lithium-ion battery and a saltwater switch delivering autonomy for approximately two years under standard operating conditions, where the nets are in the water and the PAL is active for approximately 50 % of the time. PALs were acoustically checked on board after each haul by crew and observers, and defective devices were replaced immediately. Because device failures could occur under any normal fishing operations, strings with defective devices were included in the analysis.

The first PAL version (PALv.1) was programmed to emit acoustic signals while in water and continue to emit for approximately 20 min after being hauled on board. It emits a single synthetic signal termed "F3" consisting of two upsweep chirps beginning with a click rate of 173 clicks/s and ending with 959 clicks/s. PAL characteristics were measured by M. Conrad (pers. comm.) in the calibration tank at L3-Elac Nautic, Kiel, using the calibrated reference hydrophone Brüel & Kjær Type 8104, No. 2 393 700, and digital oscilloscope OWON SDS 7102 V. PAL has a centroid frequency of 133 ± 8.5 kHz; mean source level 147 dB peak–peak re 1 µPa@1 m (± 5 dB Standard Deviation; $n = 36$ measurements in 10° around the longitudinal axis (Fig. 2), and a close range audible signal envelope 8 kHz). Signal duration is 1.22 s followed by a pause lasting 20 s (approximately 3 signals/minute). The new PAL version (PALv.2) became available in April 2016 and replaced PALv.1 on all three vessels. PALv2 has a slightly different signal repetition pattern in order to fulfil the requirements for ADDs set in EU Regulation 812/2004 (CEC, 2004), and it emits a series of one to three signals at random followed by a randomised pause of 4–30 s (on average 5.5 signals/minute).

To ensure that the PAL signal acoustically covered the whole of the net string, fishers were instructed to attach the device horizontally to the floatline, spacing each a maximum of 200 m from the next. This is in accordance with EU Regulation 812/2004 (CEC, 2004) concerning the use of ADD. Maintaining this spacing limit is crucial because other studies have found that pinger effectiveness may decrease with increased spacing distance (Kindt-Larsen et al., 2019; Larsen et al., 2013). As in all acoustic devices, the battery compartment causes an acoustic "silent zone." Signal emission is thus slightly directional towards the end where the transducer is located, opposite the battery compartment (Fig. 2). Fishers were instructed to take care to attach all PALs pointing in the same direction of the net string to ensure complete acoustic coverage. The PALs were attached to the connecting bridle between the floatlines of two net panels (distance between subsequent net panels ranged approximately from 0 to 1.0 m, Fig. 3) This ensured optimal acoustic coverage, avoided net tangling, and allowed us to gauge the spacing between two subsequent PALs. PAL spacing ranged from a minimum of 120 to 210 m during the trials (cf. Results section, Table 3).

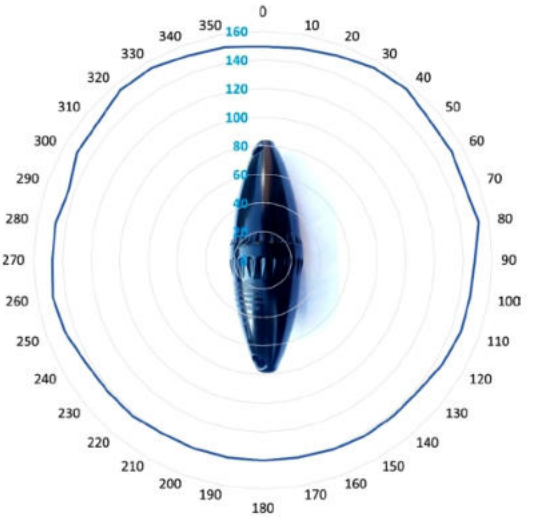

Fig. 2. PAL seen from above as attached to the net floatline. Source Level (peak–peak, in dB re. 1µPa 1 m) is not totally omnidirectional around the PAL along the long axis (in degrees). Source level towards the transducer side (top) is approximately 7 % higher than towards the battery compartment (bottom).

2.4. Trial monitoring

Participating fishers were instructed to self-report the following data about their fishing operations during PAL trials: date and start time of setting and hauling process (yielding soak time), type of gillnet (single or trammelnet), stretched mesh size, panel height and length, total number of panels per string set, geographical (GPS) position of string start and string end, and whether PALs in the string were identified as working or defective after hauling. Each harbour porpoise bycatch observed in a string was to be recorded, including relative position in the string and net type (PAL or control).

Observers regularly accompanied the vessels during operations to inspect PAL attachment, functioning, orientation, and spacing, and to replace depleted PAL batteries, confirm a correct experimental setup,

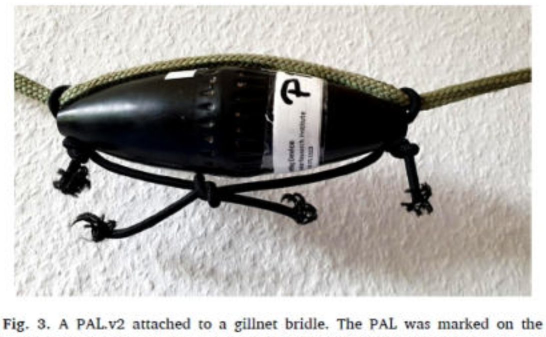

Fig. 3. A PAL.v2 attached to a gillnet bridle. The PAL was marked on the battery compartment (right) to ensure fishers positioned them all pointing in the same direction.

obtain feedback on possible problems concerning PAL usage (e.g. entanglement in nets), maintain a good understanding of the fishery tactics pursued by the fishers, and observe possible bycatches.

The Danish gillnet vessel (Vessel A) was equipped with a remote electronic monitoring (REM) system during the study. The REM system (Anchorlab, Denmark) records time, position, and video footage of all trips (port to port), and allows the recording of setting and hauling positions. By linking both positions, it is possible to deduce string soak time. Fishers, however, were tasked to record the same information in paper logs, as well as net characteristics because these are not recognisable from REM records. Two cameras film the net coming out of the water from different points of view, allowing detection of the entire catch breaking the surface (Kindt-Larsen et al., 2012). In addition, the fishers kept a paper log of their sets and harbour porpoise bycatch. One hundred per cent of all trips fulfilling the experimental conditions and used in the analysis (hereafter valid trips) of Vessel A were observed with REM. The fisher on German gillnet Vessel B only agreed to the installation of a REM system (Archipelago Marine Research, Canada) several months after the trials began (start of project participation 8 May 2015; REM system coverage beginning 9 January 2016). Two cameras filmed the point when the net exited the water. Vessel B is <8 m long, with only an open cab and very restricted berthing space. The single fisher, therefore, was reluctant to admit an observer on board owing to safety concerns. Therefore, only 18.3 % of Vessel B's trips were covered by REM or an observer. The crew of German gillnet Vessel C did not agree to have a REM system installed for the PAL project. Therefore, observation was only achieved with observers, and 28.5 % of all valid trips had observer coverage. Of the total 778 fishing trips with PAL trials in all three vessels, 49.2 % were observed by REM and/or on-board observers. All REM data were analysed by trained staff who recorded all harbour porpoise bycatch events (Vessel A data with Anchorlab software BlackBox Analyser, v. 2.0 and 3.0; Vessel B data with Archipelago Marine Research REM Interpret Pro, v. 2.1.5). Thus, the data collected is a mixture of monitoring data (REM/observer) and self-sampling data (fishers' logs).

2.5. Statistical analysis

All recorded data were checked for plausibility; data were excluded from analysis (classified as invalid) if implausible, according to the following criteria.

a) Harbour porpoise density is highly variable over time and space; therefore, control strings set without coupled PAL strings of the same net characteristics were not included in the analysis.
b) Spacing, coverage: Control strings set closer than 500 m from PAL strings. In these cases, an effect of the nearby PAL strings could not be ruled out, and those control strings were also classified as invalid. This could result in PAL strings being coupled only with distance-invalidated control strings. These PAL strings were also classified as invalid. Strings with only partial PAL coverage, or trips with missing data in the records, were not included (cf. the Results section for details).
c) An invalid trip is a trip on which all strings were classified as invalid, e.g. resulting from poor REM image quality.

Strings, where PALs were found to be defective after hauling, were included in the analysis, because device failure cannot be entirely ruled out in commercial fishing operations as well.

Because fishers on Vessel A often did not note the correct string length, distances between GPS points at fleet start and end were entered as a proxy for string length. For all three vessels, the PAL and control strings had the same length; mean lengths of PAL and control string were 1.79 ($\pm$ 0.92) km and 1.64 ($\pm$ 0.84) km, respectively. However, the total number and total length of control strings exceeded that of PAL strings (in total, 1529 valid control strings 2506.3 km long vs. 1120 PAL strings 2003.8 km long). Therefore, the length of each string was incorporated into the statistical model.

Between 17 February 2016 and 11 April 2016, spacing of the PALs on the strings set by Vessel A was at least 210 m (plus a short bridle length of approximately 0.3–3.0 m). This violated the experimental design by overstepping the PAL spacing limit by at least 10 m. Two PAL bycatches and two control bycatches occurred in this period. Although it seems unlikely that this short extra spacing would have a profound effect on the PAL bycatch effect, we decided to analyse the PAL effect in two separate models, one *including* the PAL strings with 210 m spacing, and another *excluding* these PAL strings (as well as *including/excluding* the corresponding control strings set on the same days, respectively).

Trials with the slightly modified version PALv.2 were begun eight months before the end of the trials. The few resulting data fulfilling all trial conditions (two bycatches occurred in control strings classified as valid, one bycatch in a control string classified as not valid according to the criteria given above) did not allow for statistical analysis of separate effects of version PALv.2 on expected bycatch. Therefore, we chose to analyse the complete PAL-trial dataset in two models, one *including* and one *excluding* the PALv.2 trial data.

Therefore, each of four datasets (hereafter named cases) was analysed with a generalised linear mixed model (GLMM). Case 1 served as the base dataset and included all 2649 observations with strings classified as valid (Table 1). To avoid overfitting caused by the limited number of bycatches, only a limited set of predictors could be included in the model.

The number of harbour porpoise bycatch per string ($N_i \in \{0, 1, 2, 3, \ldots\}$) was modelled for each of the four cases using a GLMM with Poisson distributed observations and a log link function with the glmmTMB (version 0.2.2.0; Brooks et al., 2017) package of the statistical software R (R Core Team, 2018). In addition to the Poisson distribution, negative-binomial and zero-inflated models were investigated. However, no indication of over-dispersion or zero-inflation was found. In the full model, "Fishing vessel" was included to account for different fishing strategies pursued by different vessels, while the "Trip" random effect was included to account for spatial and temporal porpoise density variability, which is expected to vary by year, month (Hammond et al., 2013), and even day.

The model had "Number of porpoise bycatches" as the response variable. As fixed effects, the model included an intercept (the parameter β_0), along with effects of "PAL presence" (β_1), "Log-string length" (β_2), and "Fishing vessel" (β_3 for Vessel B and β_4 for Vessel C). Further, the "Trip" (combination of fishing vessel and day) was included as a random effect ($\tau_{t(i)}$). To correct for different exposures to risk, "Log-soak time" was included as an offset ($\log(s_i)$). No interactions were included to prevent overfitting the data. In the full model, therefore, the logarithm of the expected bycatch for the i th haul was[1]

$$\log E(N_i) = \log(s_i) + \beta_0 + \beta_1 P_i + \beta_2 \log(L_i) + \beta_3 V_i^B + \beta_4 V_i^C + \tau_{t(i)},$$

where $s_i > 0$ is soak time, $P_i \in \{0, 1\}$ is a dummy variable reflecting presence (P = 1) or absence (P = 0) of PALs on the string, $L_i > 0$ is string length, $V_i^B \in \{0, 1\}$ is one if the haul is from Vessel B, $V_i^C \in \{0, 1\}$ is one if the haul is from Vessel C, $\tau_{t(i)} \sim N(0, \sigma_\tau^2)$ is a random effect on trips, and $\beta_0, \ldots, \beta_4 \in \mathbb{R}$, $\sigma_\tau > 0$ are the parameters described above. In this model, the intercept corresponds to a one kilometer control string from Vessel A with one hour soak time on an average trip.

Covariates with missing data were assumed to be missing completely at random, and entire observations were excluded if a covariate was missing. All model parameters were estimated using maximum likelihood. Before testing the hypothesis of no effect of PAL presence, the model was reduced as much as possible by likelihood ratio tests (LRT).

[1] In the notation of the programming language R and the glmmTMB package, this corresponds to the model: Bycatch ~ 1 + offset(log(SoakTime)) + PAL + I (log(StringLength)) + Vessel + (1|Trip).

Table 1
Results of valid PAL trials with model Cases 1-4 and vessels A, B, and C. Strings are split into control and PAL strings. Means are given with standard deviation. Cases 1 to 4 represent inclusion/exclusion of trials with 210 m PAL distance and PALv.2, respectively.

Case	PAL spacing 210 m included	PALv.2 included	Vessel	Trips			No. bycatch events		No. string		String length [km]			
				No.	No. observed	% observed	Control	PAL	Control	PAL	Total control	Mean control	Total PAL	Mean PAL
1	yes	yes	A	242	242	100 %	9	3	732	432	830.0	1.13 ± 0.3	481.7	1.12 ± 0.29
1	yes	yes	B	115	21	18.3 %	4	1	130	127	361.2	2.78 ± 1.2	358.8	2.83 ± 1.16
1	yes	yes	C	421	120	28.5 %	5	1	667	561	1315.2	1.97 ± 0.78	1163.3	2.07 ± 0.8
1	yes	yes	All	778	383	49.2 %	18	5	1529	1120	2506.3	–	2003.8	–
2	yes	no	A	194	194	100 %	9	3	608	349	683.0	1.12 ± 0.32	387.5	1.11 ± 0.31
2	yes	no	B	100	6	6 %	4	1	106	105	328.7	3.1 ± 1.02	324.4	3.09 ± 1.07
2	yes	no	C	309	88	28.5 %	3	1	525	444	1086.9	2.07 ± 0.74	965.3	2.17 ± 0.74
2	yes	no	All	603	288	47.8 %	16	5	1239	898	2098.7	–	1677.2	–
3	no	yes	A	216	216	100 %	7	1	630	392	715.2	1.14 ± 0.31	435.0	1.11 ± 0.29
3	no	yes	B	115	21	18.3 %	4	1	130	127	361.2	2.78 ± 1.2	358.8	2.83 ± 1.16
3	no	yes	C	421	120	28.5 %	5	1	667	561	1315.2	1.97 ± 0.78	1163.3	2.07 ± 0.8
3	no	yes	All	752	357	47.5 %	16	3	1427	1080	2391.6	–	1957.1	–
4	no	no	A	168	168	100 %	7	1	506	309	568.3	1.12 ± 0.33	340.7	1.1 ± 0.31
4	no	no	B	100	6	6 %	4	1	106	105	328.7	3.1 ± 1.02	324.4	3.09 ± 1.07
4	no	no	C	309	88	28.5 %	3	1	525	444	1086.9	2.07 ± 0.74	965.3	2.17 ± 0.74
4	no	no	All	577	262	45.4 %	14	3	1137	858	1984.0	–	1630.4	–

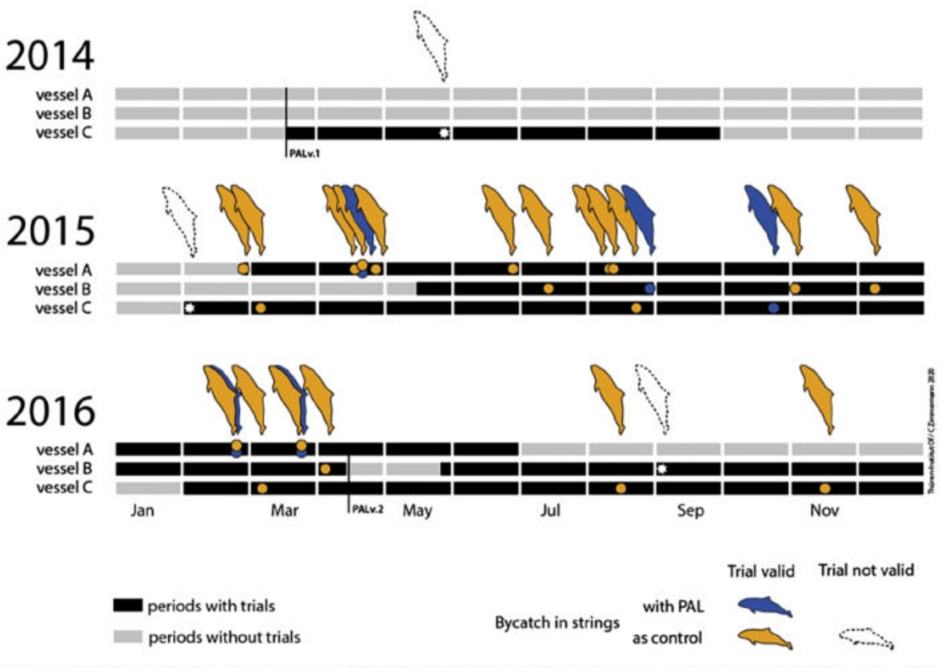

Fig. 4. Occurrence of harbour porpoise bycatches over time in PAL and control strings in trials conducted by three vessels (A, B, C) 2014–2016. Different colours of porpoise silhouettes indicate occurrence in PAL and control strings, as well as whether or not the bycatch events were valid for inclusion in the statistical analysis. Invalid bycatch are those where the experimental design was violated. Start of trials with different PAL versions (PALv.1, PALv.2) is indicated by vertical lines.

3. Results

3.1. Fishing effort and bycatch numbers

Trials with PALv.1 were carried out from 19 March 2014 to April/May 2016 (13 April 2016 for Vessel A, 8 May 2016 for Vessel B, and 15 April 2016 for Vessel C; Fig. 4), followed by trials with PALv.2, which ran until December 2016 (Fig. 4). Vessel A ended gillnet fishing and thus trial participation first, in June 2016. A total of 3357 strings were set during these trials.

The following data were not included in the analysis. (a) Vessel A hauled 119 strings where REM image quality was too low to discern whether or not these were equipped with PALs. The quality, however, was always sufficient to detect a porpoise, and none of these strings had any porpoise bycatch. (b) For 13 strings from all three vessels, the length is unknown because the fishers did not note plausible GPS coordinates of either a start- or endpoint, and (c) exact soak time is missing for 129 sets from all three vessels. None of these had porpoise bycatch. (d) In 2014, one control bycatch on Vessel C was observed by an on-board observer, but occurred in a control string tied directly to a string with PALs, thus violating the experimental design. (e) In addition, 446 strings were either control strings set closer than 500 m to the next PAL string or PAL strings coupled only with control strings that were closer than 500 m to their next PAL string. Two of those distance-invalidated control strings, in 2015 and 2016, each had one bycatch. Therefore, 708 strings with three control bycatches were excluded from the data set.

In all, 2649 string observations from 778 trips were included in the statistical analysis (Table 1). Eighteen porpoise bycatch events in the control strings and five bycatch events in the PAL strings classified as valid were included in the analysis (Fig. 4). They occurred over the whole range of mesh sizes used (110–240 mm; Table 3), during all weather conditions, and throughout the year. Each event was a bycatch of a single individual in one string. For the statistical analysis, the number of bycatch events were aggregated per string, and an observation was defined as the number of bycatch (and corresponding covariates) per net string. Thirteen (56.5 %) of all bycatches were observed either by REM or an on-board observer. Two of the 18 control bycatches occurred during PALv.2 trials (with no PAL bycatch).

Fishing strategies were unique to each vessel and mostly changed over the year, illustrated by individual variation in gillnet characteristics (Table 2). Usually, soak time lasted approximately 24 h, except for the lumpfish fishery of Vessel A with large-mesh size (240 mm), where soak time could extend up to several days. Catch data were not part of the data collected in this study, but all fishers stated during the study, until the study's end, that they did not perceive any PAL-related effect on their catches.

3.2. Modelling of PAL effect on bycatch rate

The four cases were analysed using a GLMM with string length, fishing vessel (Vessel), and PAL deployment as fixed effects. In a first step, the model was reduced by testing for no effect of string length on the response (null hypothesis: $\beta_2 = 0$), which could not be rejected at the 5 % significance level for any of the cases (Case 1 test size: 0.0160, p-value: 0.8994; Case 2 test size: 0.0050, p-value: 0.9437; Case 3 test size: 0.0113, p-value: 0.9155; Case 4 test size: 0.0288, p-value: 0.8653). Likewise, in the subsequently reduced model, the hypothesis of no fishing vessel effect (null hypothesis: $\beta_3 = \beta_4 = 0$) could not be rejected at the 5 % significance level (Case 1 test size: 1.5817, p-value: 0.4535; Case 2 test size: 2.0011, p-value: 0.3677; Case 3 test size: 1.3903, p-value: 0.4990; Case 4 test size: 1.6460, p-value: 0.4391).

Therefore, the model was reduced for all four cases to[2]:

$$\log E(N_i) = \log(s_i) + \beta_0 + \beta_1 P_i + \tau_{t(i)}.$$

Finally, in the reduced model, the hypothesis of no PAL effect was tested (null hypothesis: $\boldsymbol{\beta}_1 = 0$) using LRT and was rejected at the 5 % level for cases 1 (all trials), 3 (excluding trials with 210 m PAL spacing), and 4 (excluding trials with 210 m PAL spacing and PALv.2; Table 4). For Case 2 (excluding trials with PALv.2), the PAL effect was not significant (p-value: 0.0741). The estimated mean reduction rates in numbers of bycatch in strings where PALs were deployed varied between 59 % and 80 % (Table 4).

The estimates and Hessian-based standard errors for the intercept $\boldsymbol{\beta}_0$, the effect of PAL presence $\boldsymbol{\beta}_1$, and the logarithm of the standard deviation of the random effect on trips $\mathbf{log}(\boldsymbol{\sigma}_\tau)$ of the final reduced model in all four cases are reported in Table 5.

4. Discussion

4.1. PAL mitigates bycatch

This is the first scientific test of the PAL devices in an operational gillnet fishery and the first scientific test of a technical harbour porpoise bycatch reduction measure in the western Baltic Sea, involving two German and one Danish vessel, each operating in different fishing areas. During the trials, 18 harbour porpoises were taken as bycatch in control strings, i.e. nets without PALs, whereas five were taken as bycatch in strings equipped with PALs in a total of 778 trips. These 23 bycatch observations occurred in a total of 2649 hauled gillnet strings. The GLMM including all observations classified as valid (Case 1) and, with soak time as offset and fishing trips as a random effect, revealed that the deployment of PALs in strings significantly reduces harbour porpoise bycatches by 64.9 %.

During some of the trials carried out during a limited period of this study, the pre-set limit of PAL spacing of 200 m was exceeded by 10–13 m, depending on the length of the bridle connecting adjacent net panels. Two bycatch events occurred in PAL strings during these trials. Therefore, we included these results in the models as a separate case to test for any effects. Although some pinger types have been found to work with intervals of more than 400 m between individual pingers (Larsen et al., 2013), a long-term bycatch monitoring study in an operational fishery has found that too few functioning pingers in a string increases bycatch probability compared with a string where all pingers are functional (Palka et al., 2008). A more recent study demonstrated that pinger effect decreases as distance from the pinger increases (Kindt-Larsen et al., 2019). As demonstrated by Culik et al. (2015), received levels of the PAL signal decrease with distance as well as with sea state. Here we estimated PAL range at 5 Bft. as 150–200 m. This compares well with the fishery results: Omitting trips with PAL spacings 210 m (cases 3 and 4) from the model increases estimated PAL effectiveness values. In this study, four of the total of five recorded PAL bycatches occurred in strings with PAL spacing $\geq$195 m and windspeeds of 4–5 Bft. (Table 3). The effect of windspeed and sea state on ambient noise is well known (Richardson et al., 1995). How these environmental conditions possibly influence effectiveness of pingers or PALs, and thus bycatch rates in nets equipped with it, would have to be investigated in more detail. Although it was not possible to verify this statistically, the bycatches observed in this study could indicate that a shorter distance between two PAL devices than the currently prescribed maximum of 200 m could achieve a greater reduction potential. This could infer that a strict adherence to the maximum spacing limit may be important to emphasize to fishers when using PAL or other pinger types in any fishery.

[2] In the notation of the programming language R and the glmmTMB package, this corresponds to the model: Bycatch ~ 1 + offset(log(SoakTime)) + PAL + (1|Trip).

Table 2
Aggregated gillnet data (soak time, mesh size (stretched), net height, and string length) of vessels A–C from data selection Case 1, which includes all 778 PAL trials classified as valid. Mesh size, net height, and string length are given with mean and standard deviation, soak time with median and 25/75 quantiles owing to some extremely long soak time outliers.

Vessel	Soak time [h]			Mesh size (stretched) [mm]			Net height [m]			String length km]		
	Min.	Max.	Median, 25 & 75 % quantiles	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
A	1.99	216.83	24.27 (22.9–48.67)	110	240	167.9 ± 38.62	1.50	6	2.29 ± 1.13	0.07	2.67	1.13 ± 0.29
B	4.85	64.53	18.67 (17.33–20.08)	110	160	159.07 ± 6.43	1.45	2	1.46 ± 0.08	0.08	5.17	2.8 ± 1.18
C	2.33	70.50	23.00 (21.58–24.00)	110	150	115.11 ± 12.37	1.00	2	1.43 ± 0.18	0.03	5.29	2.02 ± 0.79

Table 3
Bycatch of harbour porpoise in strings classified as valid: date hauled, observation status, net characteristics, soak time, mean and maximum predicted windspeed, wave height during soak time of strings with observed bycatch in chronological order. Bycatch in PAL strings is in bold.

Vessel	Date hauled	Observed by EM/ observer?	PAL/ control string	PAL spacing [m]	Mesh size (stretched) [mm]	Net height [m]	String length [km]	Soak time [h]	Windspeed [m/sec (Bft)]		Wave height [m]	
									Mean	Max.	Mean	Max.
					PALv1.1							
A	26.02.15	Yes	control	–	240	2.5	1.5	51	5.8 (4)	11.3 (5)	0.5	0.9
C	11.03.15	No	control	–	110	1.5	1.4	47	4.4 (3)	8.2 (4)	0.2	0.5
A	21.04.15	Yes	control	–	240	2.5	1.6	70	4.7 (3)	8.6 (5)	0.5	1.0
A	24.04.15	Yes	control	–	240	2.5	1.2	85	5.9 (4)	11.1 (5)	0.8	1.6
A	**24.04.15**	**Yes**	**PAL**	**150**	**240**	**2.5**	**1.3**	**84**	**5.5 (3)**	**11.1 (5)**	**0.8**	**1.6**
A	28.04.15	Yes	control	–	150	1.5	1.6	18	3.4 (2)	4.5 (3)	0.1	0.2
A	30.06.15	Yes	control	–	150	1.5	0.4	23	3.9 (3	5.8 (4)	0.2	0.3
B	13.07.15	No	control	–	160	1.45	1.1	20	6.1 (4)	7.4 (4)	0.5	0.6
A	10.08.15	Yes	control	–	150	1.5	1.3	68	2.3 (2)	4.5 (3)	0.1	0.2
A	12.08.15	Yes	control	–	150	1.5	1.1	24	3.5 (2)	5.2 (3)	0.1	0.3
C	22.08.15	No	control	–	110	1.5	1.6	24	3.8 (3)	5.5 (3)	0.3	0.4
B	**01.09.15**	**No**	**PAL**	**195**	**160**	**1.45**	**2.7**	**14**	**4.5 (3)**	**6.3 (4)**	**0.3**	**0.5**
C	**25.10.15**	**No**	**PAL**	**200**	**110**	**1.5**	**2.6**	**25**	**5.6 (3)**	**6.6 (4)**	**0.2**	**0.3**
B	03.11.15	No	control	–	160	1.45	3.9	21	3.4 (2)	4.6 (3)	0.1	0.2
B	10.12.15	No	control	–	160	1.45	1.9	20	9.4 (5)	11.2 (5)	0.6	0.8
A	**01.03.16**	**Yes**	**PAL**	**210**	**240**	**3**	**1.3**	**165**	**7.4 (4)**	**10.9 (5)**	**0.4**	**0.6**
A	01.03.16	Yes	control	–	240	3	1.3	168	5.5 (3)	7.4 (4)	0.3	0.4
C	10.03.16	No	control	–	110	1.5	2.7	46	6.2 (2)	8.1 (4)	0.4	0.8
A	**31.03.16**	**Yes**	**PAL**	**210**	240	**3**	**1.4**	**217**	**3.71 (3)**	**6.2 (4)**	**0.2**	**0.2**
A	31.03.16	Yes	control	–	240	3	1.3	192	4.7 (3)	7.4 (4)	0.2	0.4
B	05.04.16	Yes	control	–	160	1.45	1.9	24	2.8 (2)	4.9 (3)	0.2	0.3
					PALv1.2							
C	18.08.16	No	control	–	130	1	1.0	24	2.2 (2)	5.0 (3)	0.1	0.3
C	18.11.16	No	control	–	130	1	1.7	23	7.3 (4)	10.2 (5)	0.4	0.6

Table 4
GLMM model results and estimated reduction rate of harbour porpoise bycatch by PAL calculated by profile likelihood for the four modelled cases (representing inclusion/exclusion of trials with 210 m PAL distance and PALv.2, respectively) with number of observations, degrees of freedom (Df), likelihood ratio tests of the hypothesis of no effect of PAL presence in the final reduced model (LRT), p-value, estimated bycatch reduction rate in the final reduced model with 95 % confidence intervals calculated from the profile likelihood.

Case	PAL spacing 210 m included	PALv.2 included	No. observations	GLMM model results			Estimated bycatch reduction rate		
				Df	LRT	P-value	Estimate	95 % conf. int.	
								Min.	Max.
1	yes	yes	2649	1	4.6464	0.0311	0.649	0.087	0.887
2	yes	no	2137	1	3.1891	0.0741	0.593	−0.088	0.871
3	no	yes	2507	1	8.2056	0.0042	0.797	0.373	0.953
4	no	no	1995	1	6.2780	0.0122	0.765	0.255	0.947

Our test of PAL as a bycatch-mitigation device was undertaken in an operational fishery, where participating fishers were allowed to follow their normal fishing routine as much as possible, provided that the pre-set experimental conditions were not violated. This included the use of

Table 5
Estimated parameters and Hessian-based standard errors in the final model for the four cases. Parameter β_0 is the intercept, β_1 is the effect of PAL presence, and $\log(\sigma_\tau)$ is the logarithm of the standard deviation of the random effect on trips. Note that confidence intervals for the effect of PAL presence reported elsewhere are based on the profile likelihood. .

Case	Parameter	Estimate	Standard error
	Intercept (β_0)	−12.5476	0.9609
1	PAL presence (β_1)	−1.0469	0.5213
	Random effect standard deviation ($\log(\sigma_\tau)$)	1.8251	0.2403
	Intercept (β_0)	−12.2934	1.0320
2	PAL presence (β_1)	−0.8986	0.5314
	Random effect standard deviation ($\log(\sigma_\tau)$)	1.7612	0.2645
	Intercept (β_0)	−12.9011	1.0325
3	PAL presence (β_1)	−1.5939	0.6403
	Random effect standard deviation ($\log(\sigma_\tau)$)	1.9529	0.2459
	Intercept (β_0)	−12.6979	1.1053
4	PAL presence (β_1)	−1.4496	0.6501
	Random effect standard deviation ($\log(\sigma_\tau)$)	1.9106	0.2674

different net types with varying mesh sizes and non-standardised setting patterns (e.g. straight, curved, or zigzag). A lower bycatch reduction effect of acoustic mitigation devices has previously been reported (Palka et al., 2008; 50–70 % depending on the time, area, and mesh size) for an operational fishery compared with a scientifically controlled test fishery with less variable conditions. It is hardly possible to compare the bycatch reduction rates of trials carried out in other operational fisheries with different gears, fishing grounds, and harbour porpoise populations. However, the mean reduction rates revealed during this study (66–80 %) are in the same range as those found in other studies (Larsen and Eigaard, 2014: 67 % in flat bottom/stony ground gillnet fishery; wreck fishery, however, 100 % reduction; Trippel et al., 1999: 77 %; Gearin et al., 2000: 85 %–97 % varying according to year; Kraus et al., 1997: 92 %; Gönener and Bilgin, 2009: 98 %).

Because PALv.1 and PALv.2 do not differ in the signal type, but only in their repetition patterns (PALv.1: one signal followed by a 20 s pause; PALv.2: 1–3 signals followed by a 4–30 s pause), we assume that there is no decrease in bycatch mitigation efficiency from PALv.1 to PALv.2. On the contrary, when modelling with data selection Case 2, excluding PALv.2 trials but including 210 m PAL spacing, the effect of PAL on bycatch rates is no longer significant ($p = 0.07$). The small number of bycatch events with PALv2, however, did not allow us to test specifically for other differences between the two PAL versions.

4.2. Factors influencing harbour porpoise bycatch during PAL testing

To avoid overfitting caused by the limited dataset, only a limited set of predictors were included in the model. Next to PAL deployment, we included string length and Vessel (representing fishing area and thus spatially different porpoise densities as well as different fishing strategies). An offset was added to normalise the differences in soak time between the strings. String length and the Vessel parameter were not found to significantly influence bycatch probability. We chose the most relevant bycatch parameter for inclusion following the result of the harbour porpoise bycatch study for the western Baltic of Kindt-Larsen et al. (2016). The bycatch probability model of Kindt-Larsen et al. (2016) also includes a measure of harbour porpoise density. These data, however, were derived from high-resolution position data from harbour porpoises tagged with satellite position transmitters and were not available for this study. Therefore, the present result, that fishing area did not influence expected harbour porpoise bycatch, should be treated with caution, because we cannot exclude the possibility that harbour porpoise densities differed considerably, at least between the fishing areas of the Danish and the two German fishers (Benke et al., 2014). However, the low effective sample size could also have masked possible differences in the effect of the different fishing strategies unique to each fishing vessel.

Although string length did not significantly influence expected bycatch in this study, other studies have found that it affects bycatch rates of harbour porpoises (Orphanides, 2009; Northridge et al., 2016). It should be noted that, in our tests, it was not possible to feed the true string length into the model because, from GPS data, we derived only the distance between start- and endpoint of each string. A relationship of string length with porpoise bycatch, therefore, could have been masked by both the small number of bycatches and constraints in data recording: Some of the strings were, in fact, not set straight and so were longer than the distance derived from GPS positions of setting start- and endpoints. This is indicated by the short minimum string lengths recorded for all three vessels (cf. Table 2) and the large variance. In fact, one of the fishers was sometimes observed setting strings in curves or even in curls and would backtrack and set the string back over itself. Therefore, the validity of the model concerning string length is reduced.

Mesh size could not be included in the model to avoid overfitting and because mesh size varied greatly across the vessels. Some mesh sizes were used only by a specific vessel. Therefore, mesh size was partly also accounted for by the Vessel model parameter, which was dropped from the final model. Bycatches occurred over the whole size spectrum of mesh sizes used: from the smallest (110 mm) to the largest (240 mm; Table 3); therefore, no clear pattern was discernible. Other studies, however, found that bycatch probability increased with larger mesh size, although it covered a larger range of 76–356 mm (Palka et al., 2008; see also Northridge et al., 2016). Ideally, future studies of harbour porpoise bycatch, with more bycatch observations, should also account for this, as well as other net characteristics and string length. Weather data were also not included in the model because of low bycatch rates, to avoid overfitting and because the weather parameters observed during soak times were within a narrow range. It seems plausible, however, that PAL effectivity (and the effectivity of other acoustic bycatch mitigation devices) could be influenced by noise from wind, waves, and other environmental sources (as proposed by Kindt-Larsen et al., 2019). Inclusion of environmental noise information in future acoustic bycatch mitigation studies could assure a more realistic appraisal of the tested device's effectivity.

Gillnet strings with defective pingers have previously been found to result in greater bycatch than strings where all pingers function correctly (Carretta and Barlow, 2011; Palka et al., 2008). Because pinger failure can never be completely avoided in a commercial fishery, we included in the analysis strings where individual PALs had failed during soak time (2.8 % of all observations), because we could not disregard the possibility that failures might have led to an increased bycatch rate. After each haul, the fishers or the observer, if present, had to check each PAL to confirm its function or to replace it. Therefore, it was not possible to follow a double-blind test design using, for instance, dummy pingers (Kraus et al., 1997; Larsen and Eigaard, 2014). But because the fishers could not intentionally select areas with higher or lower porpoise densities and bycatch probability, and were required to set the control and PAL strings in the same area, this should not have biased the results (Trippel et al., 1999).

4.3. Observer coverage

Tests of marine mammal bycatch reduction devices are often conducted with 100 % observer coverage (e.g. Gönener and Bilgin, 2009; Larsen and Eigaard, 2014). During the extensive pinger experiment of Larsen and Eigaard (2014), a bycatch of 24 North Sea harbour porpoises was recorded in only 168 days at sea, and Gönener and Bilgin (2009) observed 92 harbour porpoises taken as bycatch in their pinger experiment during 107 days at sea. In our validated dataset, 23 bycatch events (Fig. 4) were recorded during a total of 778 trips, demonstrating the much lower bycatch rates observed in our study area and fisheries. From the beginning of this project, we were aware that neither financial nor human resources would be sufficient to ensure 100 % observer coverage. From all 23 valid bycatches, 10 were self-reported and 13 were reported by REM or observer (Table 3).

4.4. PAL influence on target catch

None of the fishers reported a decrease in catch in target species when fishing with PALs (pers. comm. to observers and anonymous summary at the end of the trials). This indicates that the PALs do not influence the catchability of the target species during the trials. This is supported by more than 100 fishers deploying more than 2500 PALs in the western Baltic gillnet fishery of Schleswig Holstein since November 2017 (Till Holsten, Ostsee-Infocenter Eckernförde, pers. comm.). Cod do not react to high-intensity ultrasound with 50 kHz peak frequency (Schack et al., 2008), which is lower than the lower spectral bandwidth limit of the PAL with its low-intensity harmonics down to 60 kHz.

4.5. Long-term PAL use and possible habituation

Prior pinger sound exposure studies indicate harbour porpoise habituation (Cox et al., 2001; Culik et al., 2001; Carlström et al., 2009; Kyhn et al., 2015). The long-term bycatch study of Palka et al. (2008), however, did not find any indication of this in commercial fisheries, but their fishing vessels used various pinger types, which were pooled in the analysis. This could have masked habituation for at least some pinger types. A recent study by Kindt-Larsen et al. (2019) found that habituation appears to occur with pingers that emit only one signal type with a fixed repetition rate, not with pingers with randomised signals and repetition rates. The PALv.1 used in this study emits one F3 signal with a set pause between each signal of approximately 20 s. In comparison, PALv.2 was programmed to a variable signal repetition rate and pause duration. A comparison of PALv.1 and PALv.2 sound exposure studies of wild Belt Sea harbour porpoises using the experimental setup proposed by Kindt-Larsen et al. (2019) would allow the investigation of this with respect to a synthetic communication signal.

4.6. PAL deployment in other regions

Unclear results have been achieved so far during short-term tests of PAL in a commercial fishery in the Danish North Sea (2015 and 2016, own unpublished data) and around Iceland (ICES, 2018). In both cases, no differences in bycatch rates compared with control nets could be observed using the specific synthetic porpoise alerting signal emitted by the PALs, which was derived from the vocalisations of the Belt Sea harbour porpoise population (Clausen et al., 2011). Because different populations have different echolocation properties (Kyhn et al., 2013), it is possible that their communication signals also differ. Dialects in dolphinids, especially orcas (*Orcinus orca*) have been studied over decades (Ford, 1987) and have revealed increasing differences between pods, clans, and ecotypes. For instance, both high- and low-frequency components of North Pacific transient killer whale calls have significantly lower frequencies than those of the North Pacific resident and North Atlantic populations (Filatova et al., 2015). However, to our knowledge, possible differences in dialects have not been studied in harbour porpoises. If porpoise communication differed between populations as in dolphinids, bycatch reduction rates reported in this study using signal F3 could not be extrapolated to other regions or populations. Therefore, the signal type is the focus of other studies: Purpose-built PAL signals are currently being tested in commercial fisheries in Iceland and Bulgaria (by B. Culik), and research to reduce bycatch in these and other fisheries continues.

CRediT authorship contribution statement

Jérôme Chladek: Methodology, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing. **Boris Culik:** Conceptualization, Writing - review & editing, Funding acquisition. **Lotte Kindt-Larsen:** Formal analysis, Writing - review & editing, Resources. **Christoffer Moesgaard Albertsen:** Formal analysis, Methodology, Writing - review & editing. **Christian von Dorrien:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

Boris Culik (BC) developed and markets the PAL and holds a patent on the device (German Patent No. DE 10 2011 109 955, 2013). However, BC is not affiliated with the other institutions authoring this study, nor did he have any influence in conducting the fishery trials, recording the fishery or bycatch data, or analysing it. The other authors are not affiliated with BC or his companies F^3 and F3MT (Ltd) and 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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Part B – Fish pot

3. Alternative gear for Baltic Sea small scale fisheries

The mitigation of harbour porpoise and diving seabird bycatch requires different approaches. Furthermore, use of acoustic device covering the whole Baltic Sea could result in extensive habitat displacement for harbour porpoises (van Beest *et al.*, 2017) and would probably not mitigate seabird bycatch. Pingers as the only mitigation strategy is thus not sufficient.

Van Beest *et al.* (2017) recommend a combination of time-area closures and mandatory pinger use for western Baltic harbour porpoise conservation: closures in high-quality foraging areas and during summer and autumn, which are times of high-energy demand for harbour porpoises (lactation period). Time-area closures large enough to sufficiently reduce harbour porpoise bycatch could however have substantial consequences for the German Baltic SSF fleet, which predominantly uses gillnets (Meyer and Krumme, 2021). They would impose an important economic toll on SSF. Additional technical bycatch reduction modifications than PAL or conventional pingers are needed to avoid time-area closures to sufficiently reduce harbour porpoise bycatch.

Another option would be to develop alternative gears usable by the Baltic Sea SSF fleet (Žydelis *et al.*, 2013; Barz *et al.*, 2020; see also Brownell Jr *et al.*, 2019; O'Keefe *et al.*, 2021). In the second part of this thesis, alternative gears to gillnets are examined as another approach to mitigate bycatch. They must provide equal or better economic revenue than gillnets to be taken up by fishers. Ideally, such alternative gears should also have no or at least reduced bycatch for seabirds, for which to date no technical gillnet bycatch mitigation solution exists for the Baltic Sea.

Against this backdrop, the second part of the thesis 1) first explores the suitability of alternative gears for SSF and 2) then presents three studies aimed at improving catch efficiency and thus economic revenue of the alternative gear fish pots.

3.1 Assessment and comparison

In the following sub-chapters, alternative gears for gillnet SSF are compared and systematically assessed based on operational (i.a. versatility/flexibility, suitability for smaller vessels, handling difficulty), economic, and environmental criteria (i.a. bycatch potential, greenhouse gas emissions, bottom impact). Figure 6 provides an overview of these criteria. Information for the assessment was collated through a literature review and discussions with fishing gear technologists and professional fishers.

The two most important gear assessment criteria in this analysis are bycatch potential for harbour porpoise and diving seabirds and its catch efficiency for target species. The latter is crucial because a viable gillnet alternative imperatively needs to provide comparable catch success and thus economic revenue to gillnets (e.g. Königson *et al.*, 2015c; Ljungberg *et al.*, 2016; Meintzer *et al.*, 2017, 2018).

The assessed alternative gears include pontoon traps, longlines, jigging machines, Danish seines, and fish pots.

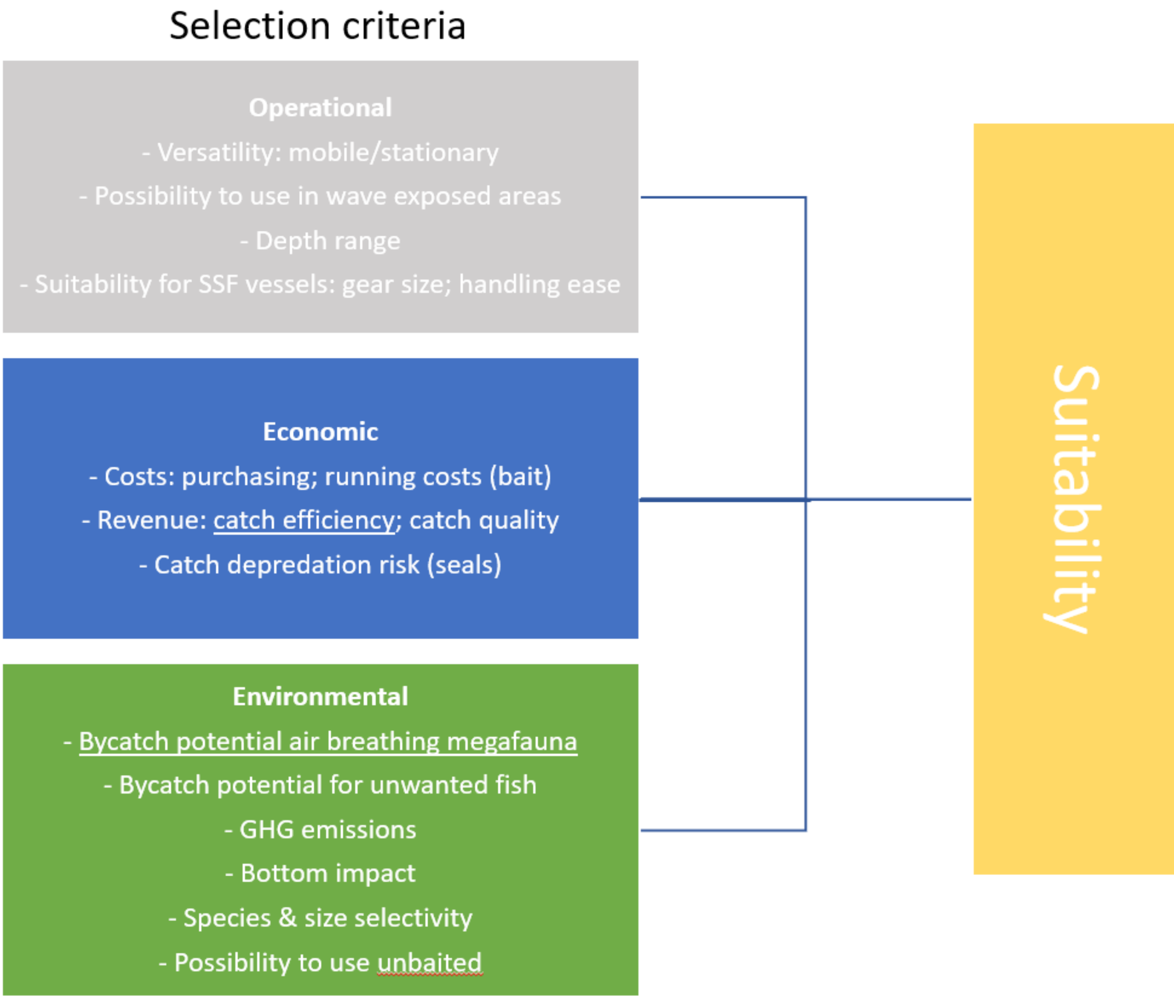

Figure 6: Selection criteria for the most suitable alternative fishing gear for Baltic Sea SSF gillnet fisheries. The two underlined criteria are the most important ones.

3.1.1 Pontoon traps

Pontoon traps are a subtype of large-scale traps. Those are stationary fishing gears made of nets that intercepts moving fish and guide them towards a so-called catch- or fish chamber (He and Inoue, 2010). The entire trap, including fish chambers, leading arms and the trap wings can be up to several hundred meters long. The catch process does not include entrapping or enmeshing the target species in the netting itself. Furthermore, traps are constructed with fish chambers which are open towards the water surface. Therefore, they have a comparably low bycatch risk for marine mammals and diving birds, with few exceptions such as young seals in the central Baltic Sea that purposely enter and depredate the fish chamber of traps with underwater net roofs blocking access to the surface (Vanhatalo *et al.*, 2014).

Pontoon traps were developed in Sweden as a sub-type of large-scale traps from which they differ in several aspects. They have a rigid fish chamber with strong netting such as Dyneema® net and an entrance closed to seals (but not fish) by a "seal exclusion device" (SED). The SED originally consist of an aluminium grid frame with wires stretched crosswise over the frame opening (Suuronen *et al.*, 2006; Hemmingsson *et al.*, 2008; Calamnius *et al.*, 2018). They were invented as a mitigation strategy against the since the 1990's continuously rising seal depredation rate in gillnet and traditional trap fisheries and later were shown to indeed minimize fish depredation risk because the fish chamber is impenetrable to seals (Suuronen *et al.*, 2004, 2006; Hemmingsson *et al.*, 2008; Vanhatalo *et al.*, 2014; Calamnius *et al.*, 2018). Fish catch is thus improved (Calamnius *et al.*, 2018). Additionally, species as well as size selection is easily adjustable (Lundin *et al.*, 2011a, 2011b, 2012, 2015) and caught fish considered as higher quality than gillnet caught fish, thus also increasing economic revenue per catch quantity (Suuronen *et al.*, 2012).

Crucial for their suitability as alternative gear to gillnets for Baltic Sea SSF, the pontoon trap fish chamber is liftable by just one fisher within few minutes (unlike traditional large-scale traps requiring at least three fishers for lifting). This is achieved by pneumatically inflating the two pontoons on which the fish chamber is mounted, and a float attached to the roof of the net chamber (Figure 7).

Figure 7: Pontoon trap with lifted fish chamber. Black netting going out to the side of the fish chamber are the trap wing nets, lead net going towards the shore indicated by floating buoys. Picture taken near Stralsund, Germany (© Thünen Institute of Baltic Sea Fisheries, Daniel Stepputtis).

This setup allows easy handling, gear moving and catch collection (Suuronen *et al.*, 2012), also for fishers working alone as is often the case for Baltic Sea SSF gillnetters. However, the pontoon trap (which includes a complete set of lead- and wing nets, fish chamber and accessories such as air compressor, hoses, and anchors) is considerably more expensive. For instance, a pontoon set acquired by the Thünen Institute in 2018 cost ~24.000 €, which is substantially more than a set of gillnets for a typical Baltic Sea SSF vessel (~3.000-4.000 € depending on type and net length).

Like for conventional large-scale traps, wing and leader nets of pontoon traps must be custom made for a particular spot (He and Inoue, 2010). The nets need to be cut to fit the bottom contour of its emplacement. Thus, pontoon traps are not as versatile as gillnets and require fishing strategies considerably different from those for gillnet fishing strategies.

Pontoon traps are not yet adapted to fish for the main target species of German Baltic SSF. Pontoon traps were developed for salmon, sea trout, and whitefish fisheries of the central Baltic Sea (Hemmingsson *et al.*, 2008). Optimization of pontoon traps for cod and herring, the main target species of German Baltic Sea gillnetters (Meyer and Krumme, 2021), was only at its beginning at the start of this thesis project.

Furthermore, pontoon traps were developed for fisheries in relatively sheltered areas such as in river mouths, often in fjord-like areas. The German Baltic Sea coast does for a large part not offer such sheltered areas. The rigid structure of pontoon fish chambers is susceptible to storms/strong sea swell because the trap wings must stay attached to the fish chamber when it is hauled. The setting depth therefore needs to be relatively shallow, where waves still reach. Appropriate emplacement areas for the pontoon along the western Baltic Sea are strongly limited compared to the gillnet fishing areas, which are relatively unsusceptible to sea swell.

Lastly, in German coastal water the large-scale traps need a permit to be operated, designated to a particular emplacement. It is somewhat doubtful that the currently limited available authorized emplacements would thus provide an alternative to gillnets to a substantial part of the current SSF gillnetters. Therefore, the pontoon trap was not chosen as focus in the search for alternative gear in this thesis.

3.1.2 Longlines and jigging machines

In this sub-chapter two hook-based angling type gears are evaluated. Longlines are a gear consisting of multiple hooks set on branches from one main leader line. Jigging machines are automatized angling machines (Figure 8). Contrary to pontoons both are not area restricted and are similarly versatile and mobile to gillnets.

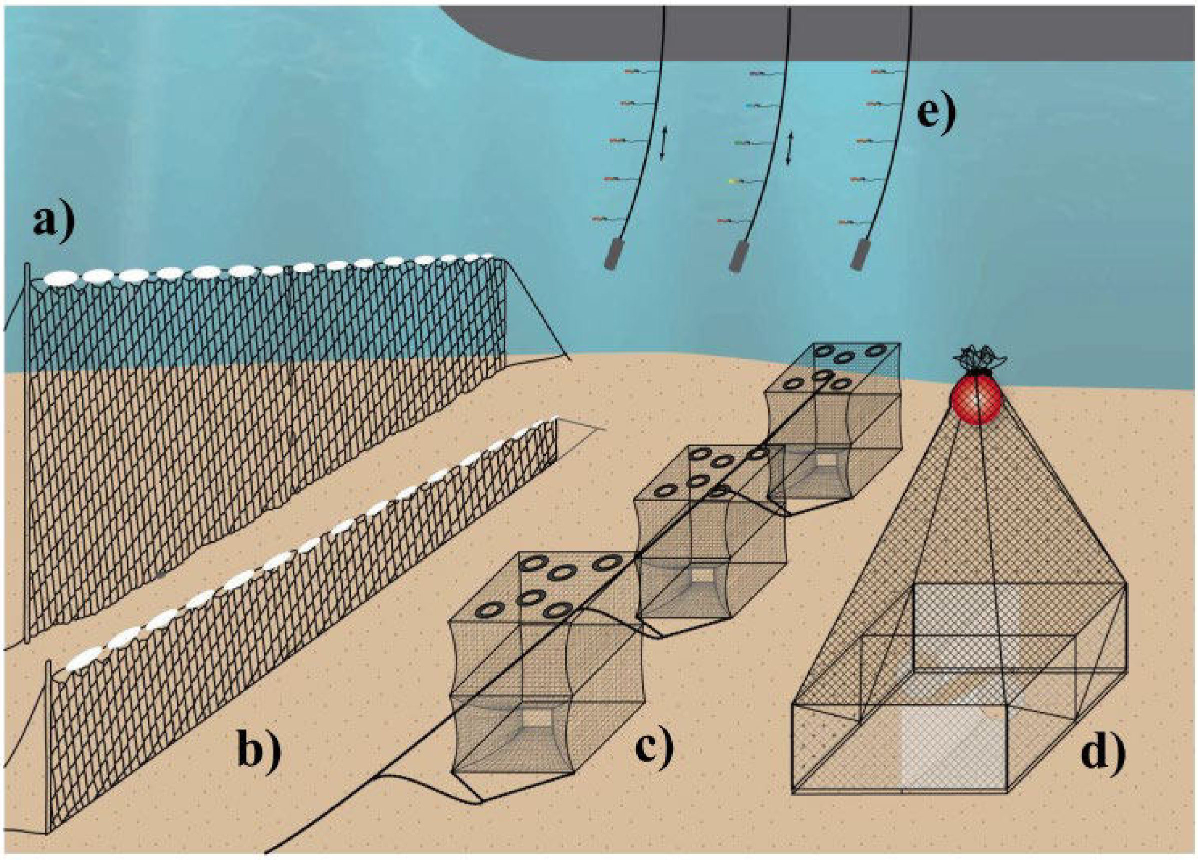

Figure 8: Schematic representation of some of the SSF fishing gear evaluated and/or tested in this thesis. a) & b) gillnets; c) & d) fish pots; e) jigging machines (Noack, 2013, reprinted with permission from © Thünen Institute of Baltic Sea Fisheries, Annemarie Schütz).

Like (pontoon) traps, longlines are considered to yield fish of higher quality than gillnets (Løkkeborg *et al.*, 2010; Suuronen *et al.*, 2012). Prior projects evaluating their potential as alternative gillnet gear however found a low catch efficiency for both gears in German waters, resulting in low-economic revenue, exacerbated by the high investment costs as well non-negligible amount of longline bird bycatch (Noack, 2013; Detloff and Koschinski, 2017). This bycatch included each one individual of the long-tailed duck (*Clangula hyemalis*) respectively the velvet scooter (*Melanitta fusca,* wintering population) during 13 fishing days (Detloff and Koschinski, 2017). Both species are classed as endangered by HELCOM (2021). Longlines thus appear not a promising alternative to gillnets, even though longline seabird bycatch risk in Baltic cod fisheries has been found to be considerably lower than with gillnets elsewhere (Žydelis *et al.*, 2013). Additionally, catch depredation from longlines by marine mammals as well as bycatch of marine mammals and birds by hook-and-line gear is reported from areas outside the Baltic Sea (Osinga and ’t Hart, 2006; Lewison *et al.*, 2014; Hamilton and Baker, 2019). Considering the rapidly increasing rates of gillnet depredation by grey seals in the Baltic Sea (Hemmingsson *et al.*, 2008; Königson *et al.*, 2010, 2015a; Varjopuro, 2011), also along the German coast (Barz *et al.*, 2020; Ferretti, 2020), longline gear thus appears even less economically promising.

Lastly, even though artificial bait for longline fishing has been explored as alternative to natural bait, their catch efficiency still does not compare to natural bait (Løkkeborg *et al.*, 2014). Thus, artificial baits have not yet been widely adopted by Baltic Sea SSF. An when bait is used in the Baltic Sea, e.g. to target European eel (*Anguilla Anguilla),* natural bait such as pieces of fresh herring are commonly used, which not only increases effort and costs to acquire the bait, but also uses fish that could (preferably) be directly used for human consumption (Suuronen *et al.*, 2012; Løkkeborg *et al.*, 2014).

Altogether, longlines and jigging machines did not appear as promising gillnet alternative and were also not chosen as focus gear in this thesis.

3.1.3 Danish seines

Danish seining (with their modifications Scottish seining and pair seining) is an active form of demersal fishing gear. It uses a small net attached to two long bridles. The bridles and the net are laid down along the bottom in a loop. Then, the net is hauled in by the two warps or bridles (Figure 9). Distinguishing the Danish seine from the trawl is primarily the absence of trawl doors. Herding of fish towards the collecting net occurs through the movements and sounds of the tensed bridles during the haul process (Suuronen *et al.*, 2012; Noack, 2017; Noack *et al.*, 2019).

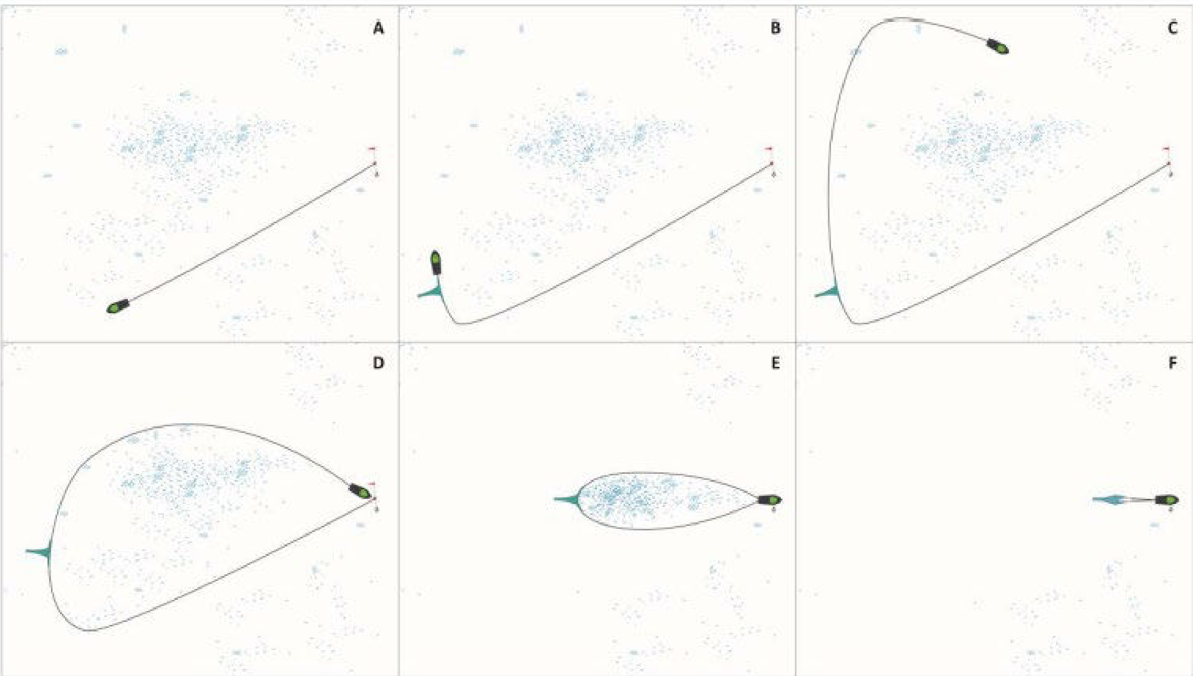

Figure 9: Phases of a Danish seine haul (i) the setting phase (A–C), ii) the herding phase (D, E), and iii) the catching phase (F)), from Noack *et al.* 2019.

Danish seining is considered more environmentally favourable than bottom trawling, especially due to the considerably lower bottom impact, as well as more cost-effective. It also catches high-quality fish due to short fishing duration. With that it could be an alternative gear to gillnets for Baltic Sea SSF vessels, pending dedicated miniaturizing development (Gabriel and Richter, 1987; Richter and Lorenzen, 1991; Noack, 2017; Noack *et al.*, 2019).

Nonetheless, at the start of the thesis project there were no small Danish seine systems available for the larger majority of smaller SSF vessels. In Germany for instance, 79% of SSF vessels are <8 m length (Meyer and Krumme, 2021). In the meantime, a new prototype "mini-Danish seine" was developed and evaluated, with promising results. But the development process is still ongoing (Larsen *et al.*, 2020a). The development process currently concentrates on the adaptation of the Danish seine system for SSF vessels, including the power system. Catch efficiency improvements can only be considered after this is accomplished. Therefore, the Danish seine was not taken into account as focus gear in this thesis.

3.1.4 Fish pots

Fish pots are passive, typically baited, stationary fishing gears. They consist of small, box- or basketlike net or grid enclosures with entrances that facilitate entry while impeding exit for target species (Thomsen *et al.*, 2010; Suuronen *et al.*, 2012; Grabowski *et al.*, 2014; Königson *et al.*, 2015a; Ljungberg *et al.*, 2016; Meintzer *et al.*, 2017) They are easily transportable and thus a flexible, versatile gear (Figure 8; Figure 10).

Figure 10: Two fish pots with funnelled entrances as illustrative example.

As gillnets, pots can be also fished from SSF vessel (Rouxel and Montevecchi, 2018), including the smallest vessels. Pots have several merits: compared to gillnets, they have as little or even less bottom impact (Thomsen *et al.*, 2010; Shester and Micheli, 2011; Suuronen *et al.*, 2012; Grabowski *et al.*, 2014), size selectivity is also easily adjustable (Ovegård *et al.*, 2011), they also have a low fuel-consumption pattern and they capture live- and thus prime quality fish, and conserve this catch quality even on long soak times, in this regard even outperforming gillnets (Suuronen *et al.*, 2012). While natural bait is often used to attract target species, unbaited pots also catch (personal observation; High and Ellis, 1973; Munro, 1974; Furevik, 1994a; Thomsen *et al.*, 2010; Sobrino *et al.*, 2011; Petetta *et al.*, 2020), so that using fish or other species fit for human consumption as bait is potentially avoidable. Additionally, small LED lights can also be used as bait, either additional to natural bait or with otherwise unbaited pots (Bryhn, 2014; Humborstad *et al.*, 2018; Utne-Palm *et al.*, 2018).

Most crucially however for the purpose of this thesis, pots have low to no bycatch potential for harbour porpoises and diving seabirds, as the risk of entanglement in the rigid net or grid pot walls or entering through the usually small pot entrances is assumedly much lower than the entanglement risk in gillnet netting (Žydelis *et al.*, 2009; Martin and Crawford, 2015). Furthermore, fish pots can easily be seal-proofed, protecting caught fish from seal depredation (Königson *et al.*, 2015b; Ljungberg *et al.*, 2016).

For these reasons, fish pots could be seen as the ideal alternative gear candidate to gillnets in the Baltic. Significant drawback however is the typically low catch efficiency of pots for finfish (Thomsen *et al.*, 2010; Suuronen *et al.*, 2012), including for cod (Furevik and Hågensen, 1997; Suuronen *et al.*, 2012; Anders *et al.*, 2017; Jørgensen *et al.*, 2017; Meintzer, 2018). Because of its otherwise positive characteristics, pots were chosen as the focus alternative gear to gillnet in this thesis.

3.2 Fish pots – development of studies

The main aim of the studies of Part B was to find possibilities to increase pot-catch efficiency for cod, the main target species of Baltic Sea gillnetters at the time this studies were conducted (Meyer and

Krumme, 2021). For this, it was necessary to develop new methods to investigate and improve fish pot catch processes.

Most pot-catch efficiency studies found that the main bottleneck of catch efficiency are fish pot entrances, which ideally should lead to easy entrance of fish approaching a pot and prohibit their subsequent escape (Thomsen *et al.*, 2010). This does relate to structural elements, such as opening size (e.g. Furevik and Løkkeborg, 1994; Carlile *et al.*, 1997) or shape (e.g. Königson *et al.*, 2015b), and to their placement on the pot (e.g. Furevik *et al.*, 2008a; Meintzer *et al.*, 2017; Hedgärde *et al.*, 2016a; see also Thomsen *et al.*, 2010). Illustrating the importance of entrances, an in-situ observation study (Meintzer *et al.*, 2017) found that only a fraction of all cod approaching a pot found its entrance. A small fraction of those cod in turn managed to pass to the pot inside. And of those, a significant part exited again before hauling. This resulted in a final catch of only 0.5% of all cod observed approaching the pot. Similar observations were also made at the Norway coast (Valdemarsen *et al.*, 1977a; Anders *et al.*, 2016) as well as the in Baltic Sea (Ljungberg *et al.*, 2016).

Therefore, the study aim of the second part of this thesis was to first improve the understanding of cod–pot entrance interactions in relation to the basic entrance parameters shape, colour, funnel presence as well as length (Paper III). Subsequently, these findings were used to develop an approach to increase fish pot retention efficiency for cod, so reducing escapement probability of cod that entered the pot, without decreasing entry probability of cod approaching the pot (Paper IV).

Since pots often are set for soak times of more than one day (e.g. Königson *et al.*, 2015a; Meintzer *et al.*, 2018; see also Thomsen *et al.*, 2010; Furevik, 1994a), including overnight, night time observations seemed warranted for the studies. A prior video-observation study had found increased cod entries into a funnelled pot illuminated by the camera light (Hedgärde *et al.*, 2016a). Considering the catch increasing effect of LED bait lights in cod pots, it was not clear if the increased entry rates at night were just an artefact of the camera illumination. Especially since the authors had reported that cod inside the pot fed on larger plankton attracted by the camera lights. These observations also indicate that light in the pot could increase cod escapement at night, thus decreasing pot-catch efficiency, especially in cases where the light fails to attract planktonic prey. Additionally, differences in cod–pot entrance interactions between illuminated pots as in prior studies and the study pot in the studies of this thesis, would contribute to understanding how cod perceive and interact with the entrances. Hence, cod–pot entrance interactions at night were investigated without using illumination visible to cod to avoid potential observation bias. For night-time observation of cod, infrared light (IR hereafter) is often used, since cod are assumed to not perceive it (e.g. Meager *et al.*, 2006; Utne-Palm *et al.*, 2018). An open-source IR-camera light was therefore first developed to carry out the observation studies of this thesis (Hermann *et al.*, 2020, Paper II).

Papers fish pot

Paper II:

HardwareX 8 (2020) e00149

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iFO (infrared Fish Observation) – An open source low-cost infrared underwater video system

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ABSTRACT

Underwater video surveillance is an important data source in marine science, e.g. for behaviour studies. Scientists commonly use water resistant ruggedized monitoring equipment, which is cost-intensive and usually limited to visible light. This has two disadvantages: the observation is limited to space and time where visible light is available or, under artificial illumination, behaviour of marine life is potentially biased. Infrared (IR) video surveillance have been used before to overcome these. It records videos at visible light and under IR-illumination. With today's efficiency of IR-LED and video technology even low-cost systems reach visibility ranges suited for many application scenarios. We describe a low-cost open-source based hardware/software system (iFO). It consists of a single-board computer controlling the camera and lamps (with high power IR-LEDs), printed circuit boards (PCB), the underwater housings and 3D-printable models to mount PCBs in the housings and the housings to standard GoPro mounts. The Linux based software includes webserver, remote control, motion detection, scheduler, video transfer, storage at external hard disk and more. A ready-to-use SD-card image is included. We use rugged underwater housings with 100 m (optional 400 m) depth ratings. Finally, we describe a typical application observing the behaviour of cod in fish pots.

Specifications table

Hardware name	*iFO- infrared Fish Observation*
Subject area	• Biological Sciences (Marine and Fishery research) • Educational Tools and Open Source Alternatives to Existing Infrastructure
Hardware type	• Underwater imaging tools • Field measurements and sensors • Electrical engineering and computer science
Open source license	*Software: MIT* *Hardware: SHL-2.0*

(*continued on next page*)

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(continued)

Cost of hardware	*1 × camera = 220 € (100 m depth rated housing),* *2 × infrared lamps = 2 × 155 € = 310 € (100 m depth rated housing)*
Source file repository	https://doi.org/10.17605/osf.io/9xuz2
Project repository	https://doi.org/10.17605/osf.io/tckpg

1. Hardware in context

We present "infrared Fish Observation" (iFO), an open-source low-cost underwater infrared (IR) video observation system using high power LEDs and low-cost CMOS camera modules. The use of IR-video surveillance at night is very common for onshore applications and therefore hardware became very efficient at low-cost. On the other hand, in marine science, the use of visible light in dark environments is mostly inappropriate to avoid bias of fish behavior. Acoustic cameras have been used for this purpose [7], but those are complex and expensive systems with low resolution compared to optical cameras. Like human eyes, many marine species, such as fish, cannot see IR-light. One major obstacle is the relative high attenuation of IR-light under water compared to visible light [2–4]. That limits this method to short-range observations. Nevertheless, IR-video surveillance have been used for underwater observations in dark environments earlier, e.g. [1,5,6,8,9]. These studies do not give detailed description of the IR systems and therefore are not reusable. Additionally, since the time of their development, technology has made great improvements. With today's effectivity of LED technology, even low-cost CMOS cameras can cover ranges of observation >2 m, suited for many application scenarios. Furthermore, single board computers like Raspberry Pi or BeagleBone are inexpensive and can be operated with freely available open source operating systems (Linux based). They are used in many different application areas and a wide range of open-source software tools are free available. This makes them ideal for quickly realizable developments of highly adaptable cost-effective systems.

2. Hardware description

As there were no affordable underwater IR systems available, we developed the open-source system iFO (infrared Fish Observation). iFO uses a consumer single-board computer (Raspberry Pi) and standard industry parts. The Raspberry Pi single-board computers have been applied for marine supervision and fish observation earlier, e.g. [20,21,22].

In our application one system consists of one camera and two lights, whereby components cost around 530€ including 100 m depth rated housings. With the reuse of existing open-source software and hardware, that were adapted to our scientific needs, we achieved a sustainable ocean monitoring system at low-cost. The system offers a webserver, a comfortable scheduler, a motion detection unit and can store internally more than one week continuous video data.

We present iFO in a typical application where we observe the behaviour of cod (Gadus morhua, L. 1758) at the entrance of different fish pots with the aim to improve the catch effectivity. It delivers 24/7 underwater video footage in a range up to 2 m at infrared illumination and much greater distances at daylight. Additionally, we use a LTE router (FritzBox 6890) with a 2 GB swappable hard disk to be used with up to four camera systems. This allows video data storage for several weeks and provides full access via VPN and LTE to the whole system in the field. It gives remotely live videos, access to the cameras' webserver for adjustment and setup, for instant download of data and to the cameras' operating system for maintenance.

2.1. Spectral sensitivity of the camera

The CMOS camera has an OV5647 [13] sensor chip, which has no IR filter. We use lenses that do not have IR filter either. As typical for colour camera sensors, the photoactive area is evenly distributed in red, green and blue filtered pixels. Its relative spectral quantum efficiency is shown in Fig. 1. Quantum efficiency (QE) is measured over a range of different wavelengths to characterize a device's efficiency at each photon energy level. It shows the fraction of emitted electrons *e* from a given number of photons illuminating the sensor. That means, e.g. a number of 100 photons of 555 nm wavelength generates 90 electrons (yellow line) on a green filtered pixel and a number of 100 photons of 850 nm wavelength generates 35 electrons (blue line) on the same pixel.

Each colour (blue, green and red) represents a third of the full active sensor area. Therefore, the total quantum efficiency of the active area for a monochromatic light at a certain wavelength can be calculated from the sum of the electrons on each coloured pixel type, e.g. for 555 nm it is the sum of 15e at blue, 90e at green and 8e at red pixel equals to 15e + 90e + 8e = 113e. It can be seen that the quantum efficiency for infrared light at 850 nm (@850 nm: 35e + 35e + 35e = 105e) is very similar to those in the visible range (@555 nm: 15e + 90e + 8e = 113e). Consequently, the camera can be used for visible light and IR-light.

The datasheet also specifies a photometric sensitivity of $\frac{680mV}{lx \cdot s}$ and a dark current value of *16 mV/s* [13] (see Table 1).

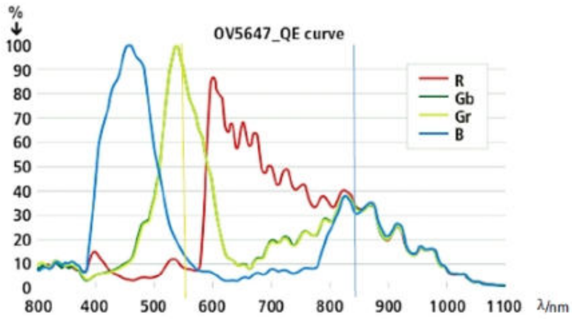


Fig. 1. Spectral quantum efficiency of the CMOS camera [14]. The sensitivity at the medium wavelength of the IR lamp (850 nm) is marked with a blue line and the sensitivity at the wavelength with the highest sensitivity of human eyes (555 nm) is marked with a yellow line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
components of iFO IR underwater observation system.

Part	Component	Type	Source	chapter
IR-server camera	Enclosure	Mechanical (from supplier)	external supplier	3.1, 3.3.1
	Single board computer	Printed circuit board	external supplier	3.3.2
	IR camera board	Printed circuit board	external supplier	3.3.3
	Real time clock	Printed circuit board	external supplier	3.3.4
	PCB IR-serverV11	Printed circuit board	Sourcefile (Eagle)	3.3.5
	Mount for PCB	Mechanical (3D printable)	Sourcefile (STL)	3.3.6
	Mount for GoPro	Mechanical (3D printable)	Sourcefile (STL)	3.2
IR-lamp	Enclosure	Mechanical (from supplier)	external supplier	3.1, 3.4.1
	PCB IR-LampV31	Printed circuit board	Sourcefile (Eagle)	3.4.2
	PCB IR-LampV32	Printed circuit board	Sourcefile (Eagle)	3.4.2
	Aluminium heat drain	Mechanical	Sourcefile (STL)	3.4.3
	Mount for GoPro	Mechanical (3D printable)	Sourcefile (STL)	3.2

2.2. Spectrum and intensity of the IR lamps

Each infrared lamp uses six Osram SFH4715AS IR-LED's [15] with a beam angle of 90°. The beam angles can be adapted by optical lenses mounted on the PCB (Table 11: no. 15, 15a). The total electrical power is $P_{el} = n \cdot U \cdot I = 6 \cdot 3.15V \cdot 1A = 18.9W$. The centroid wavelength is 850 nm with a radiant power $\phi_e = 1.530$Wper LED, resulting in ϕ_e =9.180 W per lamp. Fig. 2 shows the relative spectral intensity.

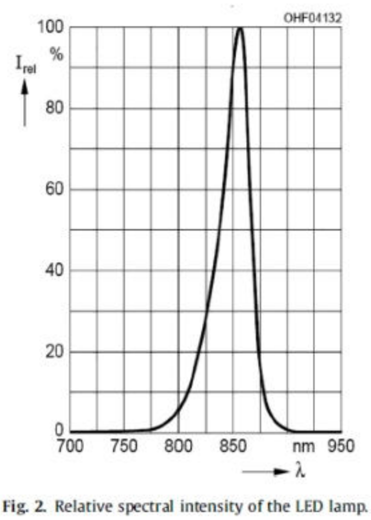


Fig. 2. Relative spectral intensity of the LED lamp.

3. Hardware components

3.1. Enclosure

The housings for the IR-server camera and the IR-lamp are taken from the Blue Robotics Inc. 3″-series. Technical details and 3D-drawings can be downloaded at [16]. We use the acrylic tube version that is depth rated to 100 m, an aluminium version rated to 400 m is also available. The end caps have through-holes for cable feed-through penetrators, whereas different types of penetrators are available [17]. The cable feed-through is sealed with marine epoxy to build a safe custom made cable confection. A detailed tutorial is given at [18].

3.2. GoPro mount for IR-lamp and IR-server

The GoPro mount (see Fig. 3 fits to the outer surface of the acrylic tube. It is tightened by a M5 × 35 mm screw (hexagon socket ISO10642) with M5 hexagon nut. We have used ABS material for 3D-printing to improve stability of the GoPro-mount under water and cold conditions. The use of standard PLA was insufficient because it became brittle in saltwater after a few weeks.

3.3. Server/Camera

In the server/camera enclosure, four printed cicuit boards (PCB) are connected to each other and tied on a 3D printable mount.

1 Raspberry Pi single-board computer [12]
2 PCB with Real time clock
3 PCB with the camera module
4 PCB 'IR-server' with voltage regulator and two output drivers.

3.3.1. Enclosure Server/Camera

For the server/camera a 298 mm acrylic tube described in chapter 3.1 is sectioned in two halfes to get enclosures for two server/cameras. For a set of two cameras the following parts (see Table 2), are needed:

Table 3 shows a distributor list for the enclosure. For sealing the cable penetrator we use potting compound (Table 8, Item15). The 100 g package can be used for about 35 cable penetrators, when all are sealed with one compound mix (within ½ an hour).

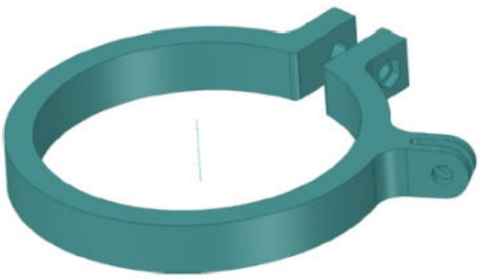


Fig. 3. 3D-printable mounting device for IR-lamp and IR-camera for GoPro mounts.

Table 2
Bill of material for a set of two IR-server/camera housings.

Item	No.	Description	Manufacturer Code	Price/€
1	1	Cast Acrylic Tube – 11.75″, 298 mm (3″)	WTE3-P-TUBE-12-R1-RP	46.00
2	4	O-Ring Flange (3")	WTE3-M-FLANGE-SEAL-R2-RP	96.00
3	2	Aluminium End Cap (3″)	WTE3-M-END-CAP-R1-RP	20.00
4	2	Clear Acrylic End Cap (3″)	WTE3-P-END-CAP-R1-RP	20.00
5	2	Enclosure Vent and Plug	VENT-ASM-R1-RP	16.00
6	4	M10 Cable Penetrator for 8 mm Cable	PENETRATOR-M-BOLT-8MM-10-25-R2-RP	20.00
Total				218.00
Total for one piece				109.00

Table 3
Distributor list for IR-server camera housings.

1:	www.bluerobotics.com	2:	www.nido.ai	3:	www.igp.de

3.3.2. *Raspberry Pi single-board computer*

The Raspberry Pi single-board computer has a CSI interface for the camera board and a 40 pin-GPIO interface used here for the PCB RTC and the PCB 'IR-server' with power converter and two output drivers (see Fig. 4).

The assembly of the PCB 'IR-server' is documented in chapter 3.3.7. The Raspberry Pi with additional PCBs and the camera PCB is fixed to a 3D-printable mount that fits into the underwater housing. The mechanical details of this mount are specified in chapter 3.3.6. The bill of material is shown in Table 4.

3.3.3. *PCB IR-camera*

The camera PCB uses the 5MP OV5647 CMOS sensor IC, which has no IR-filter. It is supplied with CSI interface and cable. The M12 S-mounted lenses are without IR-filter, either, different angles of sight are available. The bill of material is shown in Table 5.

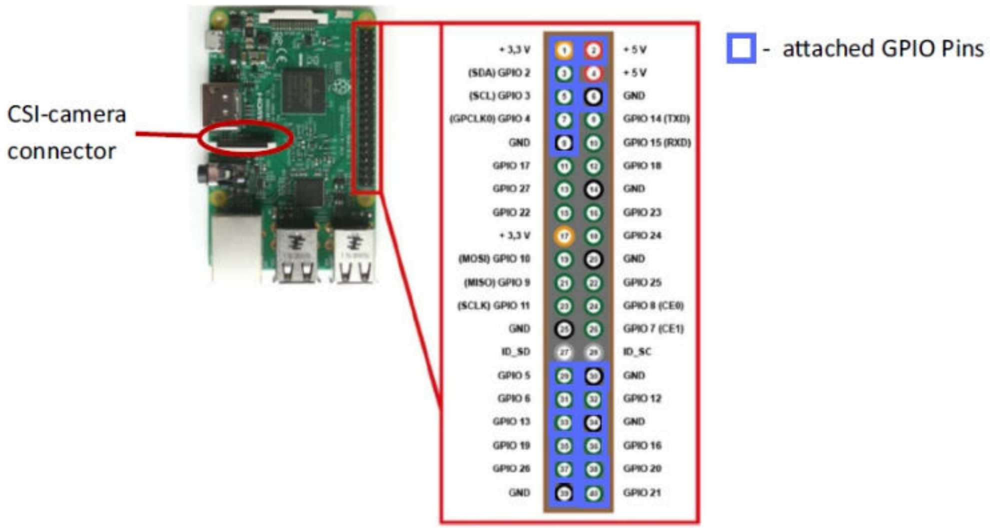


Fig. 4. RaspberryPi interfaces in use: CSI-camera connector and GPIO connector with attached pins.

Table 4
Bill of material for the Raspberry Pi.

Item	No.	Description	Distributor / Code	Manufacturer / Code	Price/€
1	2	Raspberry Pi 3 Model B+	de.rs-online.com 137-3331	Raspberry Pi 3 Model B+	58.94
2	2	Micro SD Karte, MicroSDXC 64 GB, Class 10, UHS-I U3	de.rs-online.com 174-4627	Kingston SDCR/64 GB	45.98
Total					104.92
Total for one piece					52.46

Table 5
Bill of material for IR camera PCBs.

Item	No.	Description	Distributor / Code	Manufacturer / Code	Price/€
1	2	RPi IR camera (F) (75° lens)	www.exp-tech.de EXP-R63-017	Waveshare SKU: 10299 Part:: Rpi Camera (F) UPC: 700646949915	77.20
1a	2	RPi IR camera (H) (fisheye lens)	www.exp-tech.de EXP-R63-019	Waveshare SKU: 10703 Part:: Rpi Camera (H) UPC: 799632838333	119.56
Total for one piece (75° lens)					38.60

3.3.4. PCB Real time clock

Various RTC modules are available for the Raspberry Pi. The most appropriate one is from SERTRONICS as it only uses five pins of the GPIO header at a low price. The bill of material is shown in Table 6.

3.3.5. PCB 'IR-server'

The PCB 'IR-server' is mounted via the 2 by 6-pin-socket JP1 to the GPIO pin-header of the Raspberry Pi Table 7. On the topside of the PCB, there are two pin-headers JP2 and JP4. The 4-pin I/O header JP2 is connected to the 24VDC input power and the two output drivers (O13 out and O21 out) that allow a remote control of two independent groups of lamps. In our standard applications we control the lamps by light sensors. For remote controlled lamps some modifications are necessary, which are described in chapter 3.4.5. For the standard setup, the 2-pin header JP4 delivers the 5VDC@2A power for the Raspberry Pi. It is connected via a 2-wire line with pin-sockets to the power pins of the Raspberry Pi. Fig. 5 shows the schematic and the top and bottom view of the PCB 'IR server'. Table 7 the jumper connections and Table 8 the bill of material.

Table 6
Bill of material for the real time clock.

Item	No.	Description	Distributor / Code	Manufacturer / Code	Price/€
1	2	Real Time Clock for Raspberry Pi	www.reichelt.de RPI RTC CLOCK	SERTRONICS RPI-RTC	5.50
Total for one piece					2.75

Table 7
PCB 'IR server' jumper connections.

JP1 Pin	to RPI Pin	function	Pin	to RPI Pin	function
1	40	GPIO21, Lamp2	8	33	GPIO13, Lamp1
2	39	GND	9…10	32…31	n.c.
3…6	38…35	n.c.	11	30	GND
7	34	GND	12	29	n.c.
JP2					
JP2-Pin		**to cable**			**function**
1		Lamp control 1			O13out
2		Lamp control 2			O21out
3		GND			GND
4		+24VDC in			+24VDC in
JP4					
JP4-Pin		**to RPI Pin**			**function**
1		6			GND
2		4			+5V DC

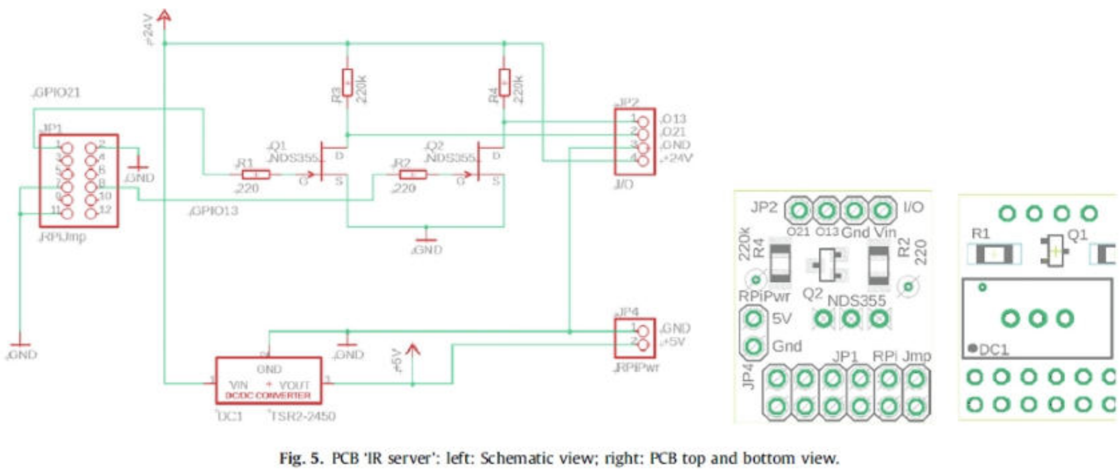


Fig. 5. PCB 'IR server': left: Schematic view; right: PCB top and bottom view.

Table 8
Bill of material for PCB 'IR-server'

Item	No.	Description	Distributor / Code	Manufacturer / Code	Price/€
1	2	Resistor SMD-1206 220kOhm 5% 0.5 W	de.rs-online.com 807–1173	TE-Connectivity CRGH1206J220K	0.058
2	2	Resisitor SMD-1206 220 Ohm 5% 0,5W	de.rs-online.com 807–1176	TE-Connectivity CRGH1206J220R	0.056
3	2	Transistor NDS355AN SOT23	de.rs-online.com 739–0167	Fairchild NDS355AN	0.54
4	1	DC/DC Converter Traco TSR2-2450 SIP3	de.rs-online.com 166–6063	Tracopower TSR2-2450	10.14
5	4/90	Pin socket 2 × 6 2.54 mm	de.rs-online.com 230–4922	Stelvio Kontek 90x2-pin 613,090,271,123	0.23
6	4/36	Pin socket 1 × 4 2.54 mm	de.rs-online.com 549–0026	E-TEC 36-pin-socket BL1-036-G-700-01	0.37
7	2/36	Pin socket 1 × 2 2.54 mm	de.rs-online.com 549–0026	E-TEC 36-pin-socket BL1-036-G-700-01	0.19
8	4/20	Pin header 1 × 4 2.54 mm	de.rs-online.com 360–6342	Molex C-Grid III 20pin 90210–0780	0.40
9	2/20	Pin header 1 x2 2.54 mm	de.rs-online.com 360–6364	Molex C-Grid III 20pin90° 90121–0780	0.18
10	4/100	Slotted screw M2 × 12 mm	de.rs-online.com 560–710	RSPRO, steel galvanized DIN84-M2x12	0.21
11	4/250	Hexagon nut M2 × 4 mm	de.rs-online.com 560–271	RSPRO, steel galvanized	0.09
12	4/100	Spacer round, Ø 6 × 3 mm, 3.2 mm drill	de.rs-online.com 102–6110	Richco 469.09.03	0.48
13	4/500	Tapping screw 2.2 × 6 mm	online-schrauben.de DIN7971-C-2,2X6,5	Steel galvanized DIN7971-C-2,2X6,5	0.24
14	4/500	Slotted screw M3 × 8 mm	online-schrauben.de DIN84-4.8-M3X8	Steel galvanized DIN84-M3x8	0.08
15	3/100	Potting compound 100 g	de.rs-online 199–1418	RS PRO Epoxid 2x50g	0.27
16	1/12	PCB IRserver_V11	www.aisler.net	PCB for playground 12pcs	1.21
Total for one piece					14.74

3.3.6. PCB mount (3D-printable)

Fig. 6 shows the 3D-printable mount that holds the Raspberry Pi with its additional PCB boards in the acrylic tube and the CMOS camera at the centre in front of the acrylic window. It is attached to the flange with four screws.

3.3.7. Assembly

For the assembly of the server/camera, the PCB of the RTC and the 'IR-server' are mounted to the GPIO header of the Raspberry Pi. The PCB 'IR-server' is connected to the Raspberry Pi GPIO-pins #29 to #40. The PCB of the RTC to the odd pin row from #1 to #9. The power supply for the Raspberry Pi is connected by a two wire cable with pin sockets between JP4 at PCB 'IR-server' and Raspberry Pi GPIO-pins #2 (+5V) and #6 (GND). All connections are marked in red in Fig. 7.

We use Raspberry Pi 3 Model B + but we also tested older versions (Pi 3 Model B and Pi 2 Model B). The camera module is without infrared filter. Different types of optics are available e.g. 160° or 75° degrees angle of view. The operating system with all necessary modules, setups and software components is written to the SD memory card. It is recommended to use 64 GB (or greater) SDXC memory card, to have enough space to locally store videos. The Raspberry Pi with the attached PCBs and the camera module are mounted to the 3D-printed mount that fits to the flange (Fig. 8).

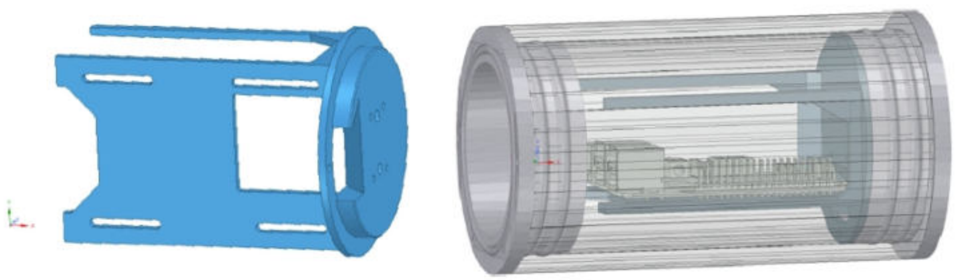


Fig. 6. Drawings of the 3D-printable mount inside the IR-server enclosure; left: PCB mount, right: schematic view of Raspberry Pi, mounted on the PCB mount inside the enclosure.

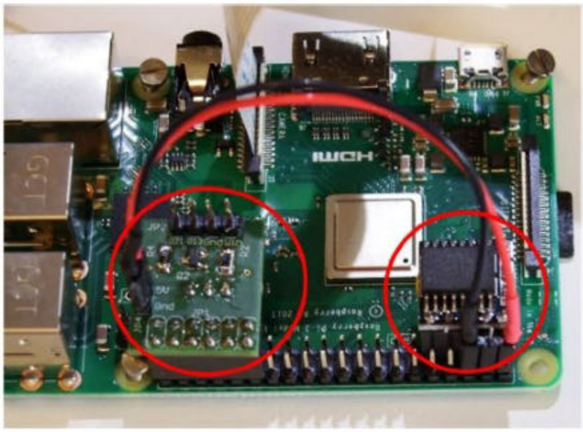


Fig. 7. PCB 'IR-server' and PCB RTC connected to the Raspberry Pi's GPIO-header.

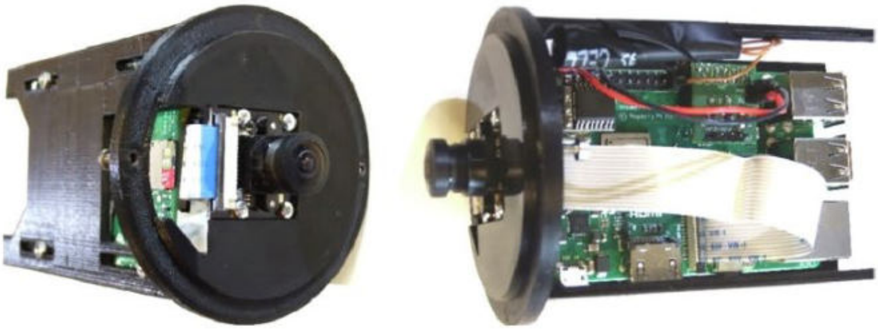


Fig. 8. Attaching the camera and the Raspberry Pi PCBs to the 3D-printed PCB mount.

The camera is mounted to the front gap with four flat head tapping screws 2.2 mm × 6 mm with the cable connector to the bottom. The Raspberry Pi is attached with four M2 × 12 mm screws (each a 3 mm spacers between the PCB and the mount) and hexagon nuts to the four slot holes on the mount. A CSI-cable connects the camera to the Raspberry Pi computer. It is inserted with the blue mark to the front at the cameras PCB and with the blue mark to the back of the Raspberry Pi (Fig. 9).

The PCB mount is fixed with four M3 × 8 mm screws to the M3 threads of the front flange. The external power has to be connected to the connector J2 at the PCB 'IR-server'. Finally, the electronics will be mounted inside the acrylic tube (enclosure) with the electrical connections tailored at the backside plate (Table 9). The underwater sealing procedure of the

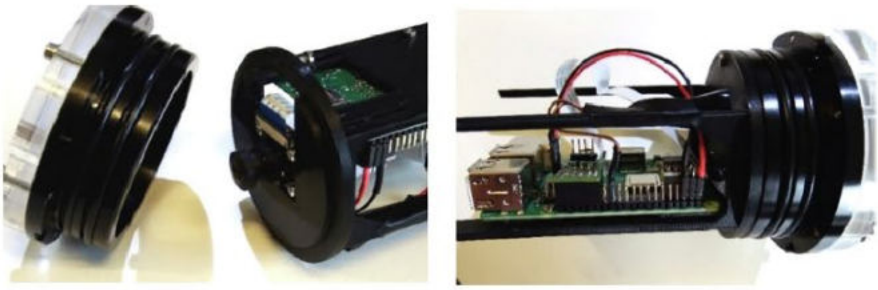


Fig. 9. Attachment of the IR-server/camera to the flange.

Table 9
Server/camera: PoE-cable configuration; the input voltage range for 24VDC is 12-36VDC.

Pin/wire	Function	colour	Pin/wire	function	Colour
1	TX+	orange/white	5	24VDCb	blue/white
2	TX-	orange	6	RX-	Green
3	RX+	green/white	7	GNDa	brown/white
4	24VDCa	blue	8	GNDb	Brown

through-hole connectors is described at [18]. The underwater cable types and cable configuration depends on the requirements of the application. As power and ethernet cable for the server/camera, we use underwater ethernet cable like [19]. After sealing, the power and data lines are assembled according to Table 9. A simple connection of the Ethernet port of the Rasperry Pi can be made by cutting a standard patch cable, dismantle the sheath and solder the four data lines (Tx+, TX-,Rx + and Rx-) to the corresponding wires of the underwater cable. The power is tranferred according to 10/100BASE-TX with PoE pinout. The four wires are soldered to a two pin socket (2x 24VDC; 2x GND) (see Fig. 10).

On the surface side, we use 9-pin WEIPU SP21 connectors to connect the underwater ethernet cable from the server/camera to the top side power and ethernet device. For easy installation we designed a 3D-printable mounting device that fits to all GoPro compatible mounts. A more detailed description with the mechanical drawings is given in chapter 3.2, Fig. 11 shows an assembled server/camera.

In summary the major assembly steps are:

1. Solder all parts to the PCBs.
2. Assemble the PCBs 'IR-server' and RTC to the RapsberyPi GPIO jumper.
3. Connect PCB 'IR-server' J4 power out to RaspberryPi GPIO jumper pins #2 (+5V) and #6 (GND) by a 2-wire line.
4. Insert the SD-card with the *iso*-image in the SD-card holder of the Raspberry PI.
5. Assemble the camera to the PCB mount.
6. Assemble the Raspberry Pi PCB to the PCB mount.
7. Connect the camera and the Raspberry Pi with a CSI-cable.
8. Assemble the PCB mount to the front flange of the enclosure.
9. Tailor the electrical connection at the backside plate to your needs and connect power in to J2 (pin #3 and #4) at the PCB 'IR-server' and the four ethernet wires to the RJ45 connector of the Raspberry Pi.

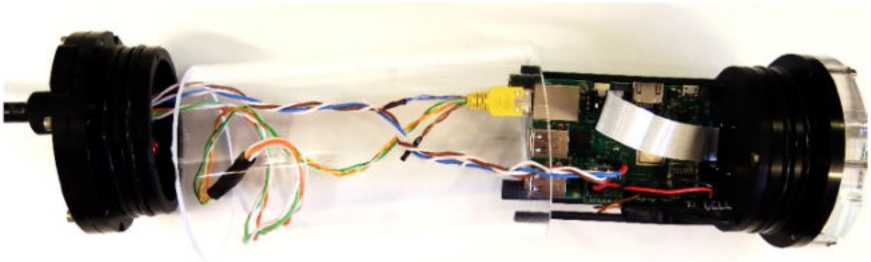


Fig. 10. Cable assembly for IR server/camera.

Fig. 11. Assembled server/camera, attached to a frame using standard GoPro-clamps.

3.4. IR lamp

3.4.1. Enclosure lamp

The housing for the IR lamp is the same as for the server/camera except, that the original tube is sectioned in four quarters of 74 mm length each. For a set of four lamps you need parts according to Table 10.

A distributor list can be found in Table 3.

For sealing the cable penetrator we use potting compound (Table 8, Item15). The 100 g package can be used for appr. 35 cable penetrators, when all are sealed with one compound mix (within ½ an hour).

3.4.2. PCB IR lamp

Two PCBs are required for each IR lamp: 'IR-lampV31' with six LEDs and 'IR-lampV32' for the LED driver. The schematics and PCBs are shown in Fig. 12 and Fig. 13.

The bill of material is given in Table 11 for four IR lamps. The six LEDs at each PCB 'IR-lampV31' are reflow soldered, while all other parts (including the SMD parts) can be also soldered manually. Both PCBs have four through holes to mount the PCBs to the M3-threads in the aluminium cooling mount. The PCB 'IR-lampV32' has 4 additional holes to mount it to the M3 threads in the flange of the underwater enclosure. When sufficient ambient light is available, e.g. during the day in shallow water, the IR illumination is not required. Therefore, there are two control options for the lamp:

1. Control by a light sensor
2. Control by the IR server/camera control signal

In our standard applications, we control the lamps by ambient light sensors (phototransistor VTT9812FH, Table 11, item 14). For a control by a light sensor, the phototransistors pins are soldered to a 3-pin socket with the anode at pin #1 and the cathode at pin #3, pin #2 is not connected. This 3-pin socket is connected to J2 at the PCB 'IR lampV32' (Fig. 13, bottom left). The setup for the control by the camera/server is described in chapter 3.4.5. The bill of material for the IR-lamps is given in Table 11.

3.4.3. Aluminium cooling mount

The two PCBs 'IR-lampV31' and 'IR-lampV32' are finally mounted to the aluminium cylinder that drains the heat from the LEDs to the aluminium flange and further to the surrounding water. The aluminium mount should have a diameter of 63.5 mm to fit best into the flange. We turned a 65 mm aluminium rod down to 63.5 mm and sawed 16 mm thick pieces from it, alternatively aluminium rods with diameters down to 60 mm can be used. The drilling were done by handcraft. There are four through holes with M3 threads to mount the PCB boards on the two sides of the cooling mount (Fig. 14).

3.4.4. Assembly

Fig. 15 shows the assembly of the PCB boards with the cooling aluminium mount from the top left to the bottom right. First, the PCB 'IR-lampV32' is mounted to the aluminium mount with four M3 × 8 mm screws and 3 mm spacers. Then the long 2-pole-pin socket of the PCB 'IR-lampV31' connected to the standard 2-pole pin header at the mounted PCB 'IR-lampV32' which is inside the 8 mm hole at the center of the aluminium mount. It is important to observe the correct polarity: LED + at 'IR-lampV32' has to be connected to LED + at 'IR-lampV31'. The PCB 'IR-lampV31' is fixed directly to the aluminium mount using four M3 × 8 mm screws. To improve heat flow, thermal conductance paste between the bottom side of the PCB and the aluminium mount can be used. Finally, the block with the PCB boards and the aluminium mount is inserted into the flange and fixed with four M3 × 8 mm screws. Thermal conductance paste between the lateral area of the aluminium and the flange would increase heat flow even further.

The backside plate of the enclosure with its the electrical connections can be tailored to specific needs. The underwater sealing procedure of the through-hole connectors is described at [18]. Underwater cable types and cable configuration depend on the requirements of the application. In our application, we use 3-wire water resistant DIN VDE 0276 NYY-J 3x1,5mm^2 cable and 3-pin WEIPU SP21 connectors to connect the lamps to the top side surface unit. After sealing, the power

Table 10
Bill of material for the underwater housing (4 pieces).

Item	No.	Description	Manufacturer Code	Price/€
1	1	Cast Acrylic Tube – 11.75", 298 mm (3")	WTE3-P-TUBE-12-R1-RP	46.00
2	8	O-Ring Flange (3"	WTE3-M-FLANGE-SEAL-R2-RP	192.00
3	4	Aluminium End Cap (3" Series)	WTE3-M-END-CAP-R1-RP	40.00
4	4	Clear Acrylic End Cap (3" Series)	WTE3-P-END-CAP-R1-RP	40.00
5	4	Enclosure Vent and Plug	VENT-ASM-R1-RP	32.00
6	4	M10 Cable Penetrator for 8 mm Cable	PENETRATOR-M-BOLT-8MM-10-25-R2-RP	20.00
Total				370.00
Total for one lamp				92.50

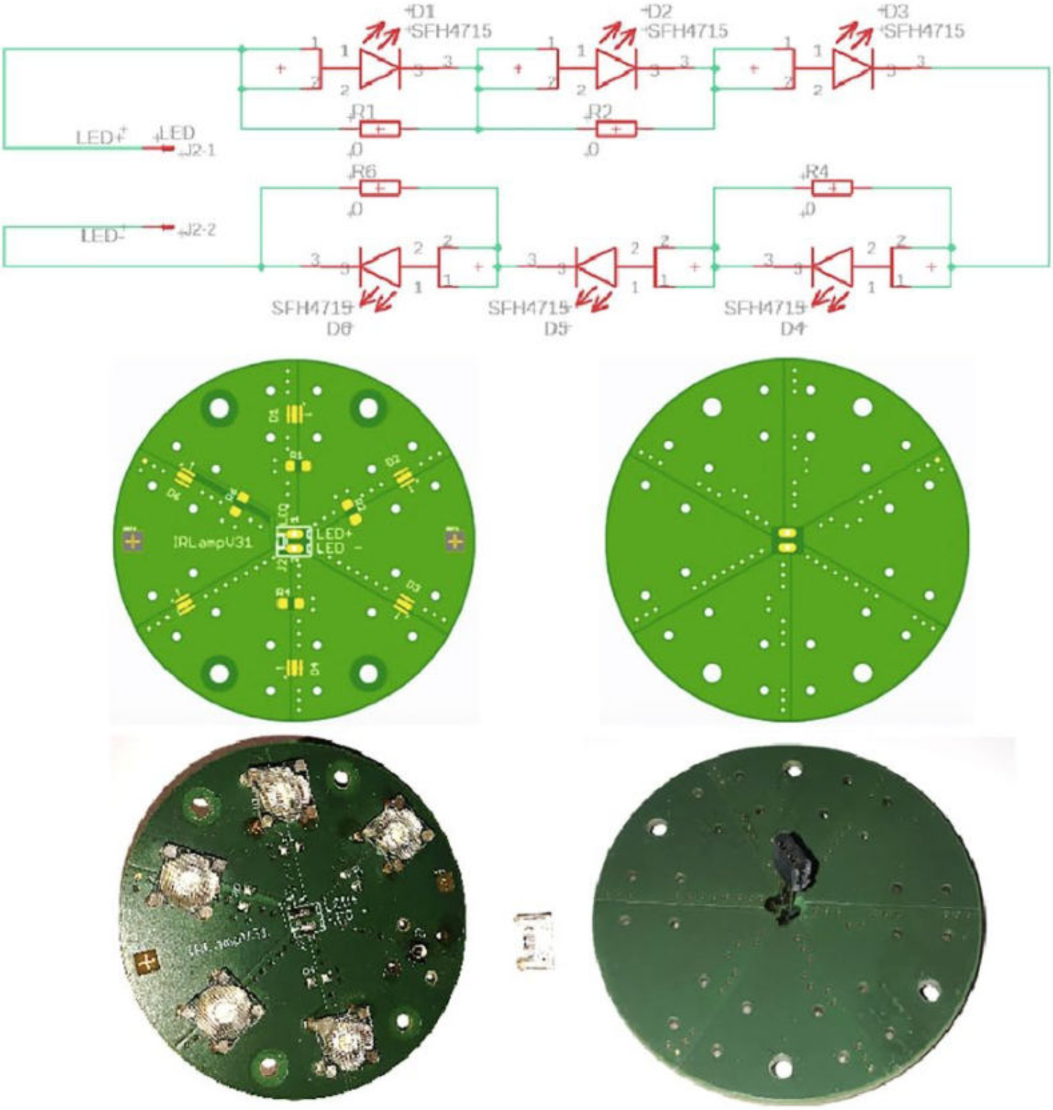


Fig. 12. PCB IR-lampV31: Top: Circuit diagram; Mid: PCB layout in top and bottom view; Bottom assembled PCB with optional lens assembly (left), long pin-socket at bottom side (right).

and data lines are assembled according to Table 12. The two power wires are soldered to a 2-pin socket, which is connected to J1 of the PCB 'IR-lampV32' with respect to the correct polarity. There are two options to control the lamps: by an ambient light sensor (standard) and remotely from the server/camera (optional) (see Fig. 16).

For easy installation we designed a 3D-printable mount for the IR lamp that fits to GoPro compatible clamps. A more detailed description with the mechanical drawings is given in chapter 3.2. Fig. 17 shows an assembled IR-lamp mounted to a frame.

Major assembly steps are:

1 Soldering all parts to the PCBs 'IR-lampV31' and 'IR-lampV32'.
2 Glueing optical lenses to the PCB 'IR-lampV31' (optional).
3 Assembling the PCB 'IR-lampV32' to the aluminium mount with spacers.

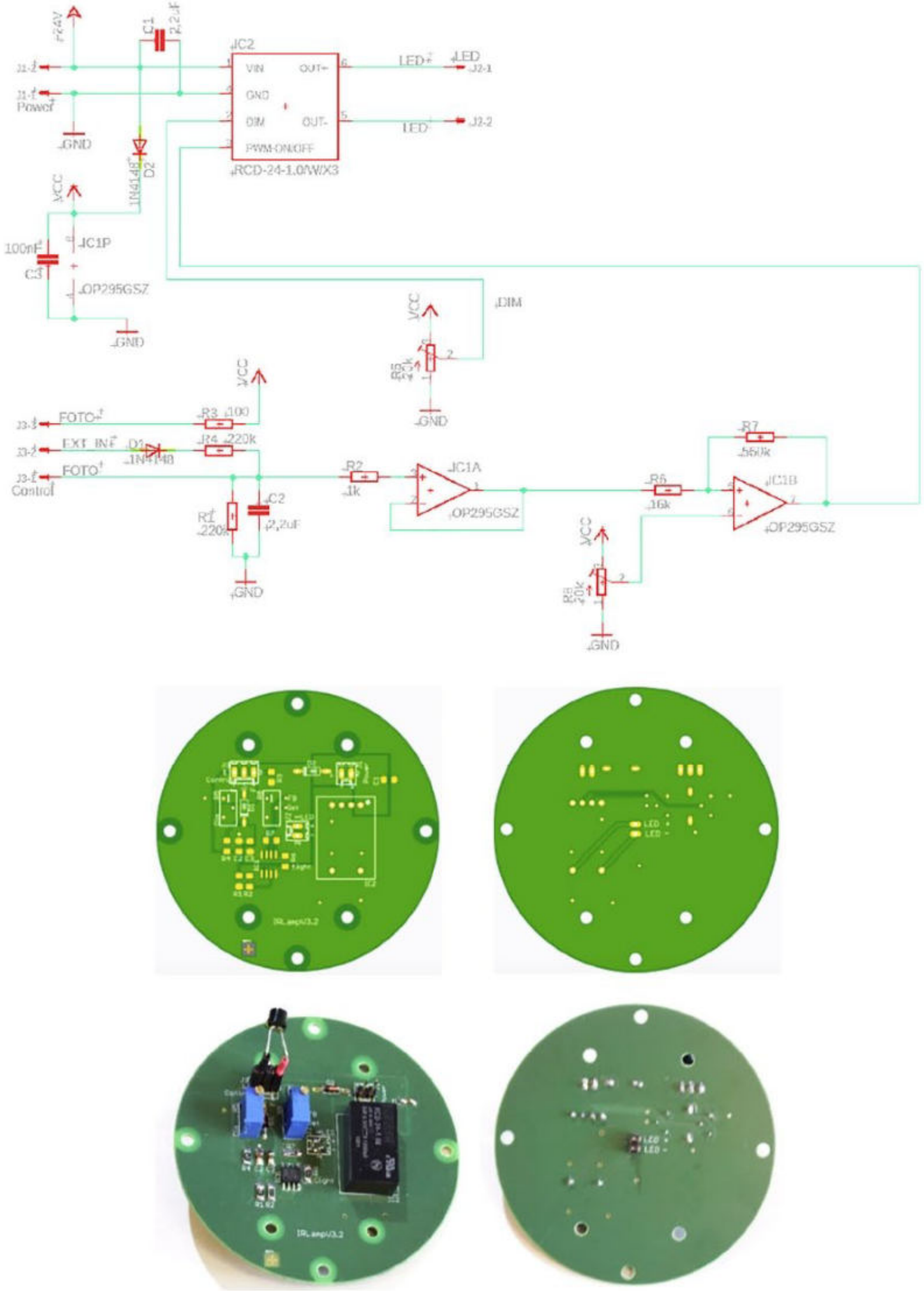


Fig. 13. PCB 'IR-lampV32': Top: Circuit diagram; Mid: top and bottom view; Bottom: assembled PCB top and bottom view.

Table 11
Bill of material for the two PCBs of IR-Lamp (4 pieces each).

Item	No.	Description	Distributor / Code	Manufacturer / Code	Price/€
1	8	Capacitor SMD-3216 2,2uF/100 V	de.rs-online.com 136–4335	AVX SMD MLCC X7R 12061C225KAT2A	2.40
2	4	Recom LED-Treiber IC, 31 W, PCB 6-Pin	de.rs-online.com 668–9870	Recom RCD-24-1.0	44.48
3	8	OpAmp OP295GSZ SOIC8	de.rs-online.com 523–0284	AnalogDevices OP295GSZ	33.28
4	8	Diode 1 N4148	de.rs-online.com 739–0290	Schaltdiode 1N4148TA, 100 V 400 mA DO-35 2-Pin	0.88
5	8	Resistor SMD-1206 220kOhm 5% 0.5 W	de.rs-online.com 807–1173	TE-Connectivity CRGH1206J220K	0.24
6	4	Resistor SMD-1206 100Ohm 5% 0.5 W	de.rs-online.com 807–1104	TE-Connectivity CRGH1206J100R	0.12
7	4	Resistor SMD-1206 15kOhm 5% 0.5 W	de.rs-online.com 807–1132	TE-Connectivity CRGH1206J15K	0.12
8	4	Resistor SMD-1206 560kOhm 5% 0.5 W	de.rs-online.com 807–1255	TE-Connectivity CRGH1206J560K	0.12
9	20/36	Pin socket 1 × 2 2.54 mm	de.rs-online.com 549–0026	E-TEC 36-pin-socket BL1-036-G-700-01	1.87
10	8/20	Pin socket 1 × 2 2.54 mm long	de.rs-online.com 217–609	HARWIN 20-pin-socket D01B99520-42	0.83
11	28/36	Pin header 1 × 4 2.54 mm	de.rs-online.com 360–6342	Molex C-Grid III 20pin 90210–0780	1.55
12	4	Trimmpoti 3296Y 10kOhm 10% 1/2W	de.rs-online.com 522–0079	Bourns 25 Gang THT 3296Y-1-103LF	9.24
13	24	Osram Oslon Black LED ± 45° SFH4715S	de.rs-online.com 758–7646	OSRAM SFH4715S, 3 Pin	76.08
14	4	Phototransistor VTT9812FH	www.digikey.de VTT9812FH-ND	Excelitas Technologies	4.08
15*	24	OSRAM lens 10 mm med. spot frosted, 30°	www.lumitronix.com 60,387	Carclo SKU 60,387	26.88
15a*	24	OSRAM lens 10 mm plain tight, 20°	www.lumitronix.com 60,386	Carclo SKU 60,386	26.88
16	48/500	Slotted screw M3 × 8 mm	online-schrauben.de DIN84-4.8-M3X8	Steel galvanized DIN84-M3x8	0.96
17	16/100	Spacer round, Ø 6 × 3 mm, 3.2 mm drill	de.rs-online.com 102–6110	Richco 469.09.03	1.91
18	6/100	Potting compound 100 g	de.rs-online.com 199–1418	RS PRO Epoxid 2 × 50 g	0.54
19	4/12	PCB IRlamp_V31	www.aisler.net	PCB for playground 12 pcs	19.40
20	4/12	PCB IRlamp_V32	www.aisler.net	PCB for playground 12 pcs	25.88
21	1	Aluminium rod diameter 65, 63.5 or 60 mm, length 70 mm			
Total					250.86
Total for 1 piece					62.71

* Optional: depending on the application, different type of LED lenses can be used.

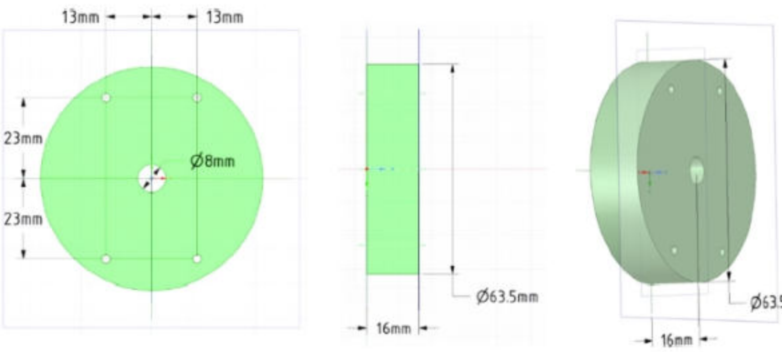


Fig. 14. Drawing of the aluminium cooling mount for the two PCBs 'IR-lampV31' and 'IR-lampV32'.

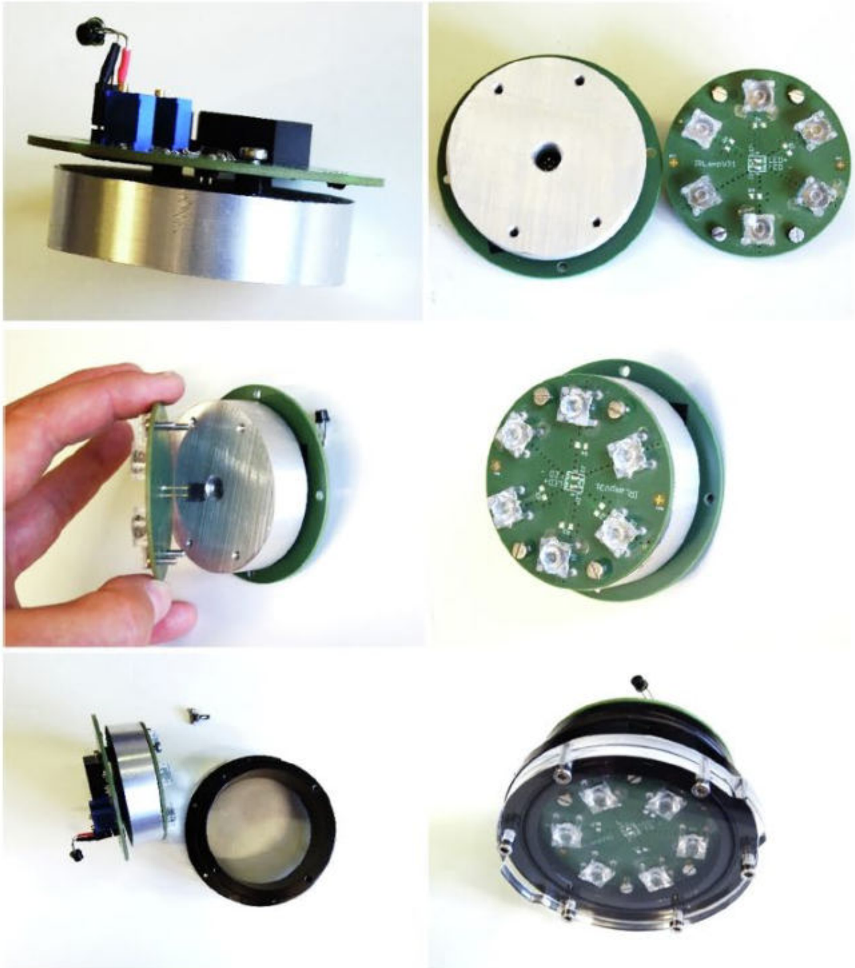


Fig. 15. Assembly of the aluminium mount and the PCBs to the flange of the enclosure.

Table 12
IR-lamp: cable configuration (*for server/camera controlled lamp, see chapter 3.4.5).

Pin/wire	Function	colour	connect to
1	+24VDC	brown	IR-lampV32, J1, pin 1
2	Control	yellow/green	IR-lampV32, J2, pin 2*
3	GND	blue	IR-lampV32, J1, pin 2

4 Assembling the PCB 'IR-lampV31' to the aluminium mount with respect to the polarity of LED+ and LED- connectors, heat conducting paste can be used.
5 Assembling the mount with its devices to the front flange of the enclosure.
6 Tailor the the electrical connection at the backside plate to your needs and connect the power to J1 at the PCBs 'IR-lampV32'.

3.4.5. PCB IR lamp under server/camera control

In our standard applications we control the lamps by ambient light sensors. For a remote control by server/cameras the cable setup is different and another cable type is needed. It either has two more wires for the lamp control, e.g. a underwater data cable with shielded 5 × twisted pairs (Table 13, Item 1) or one twisted pair with a greater cross-sectional area for power

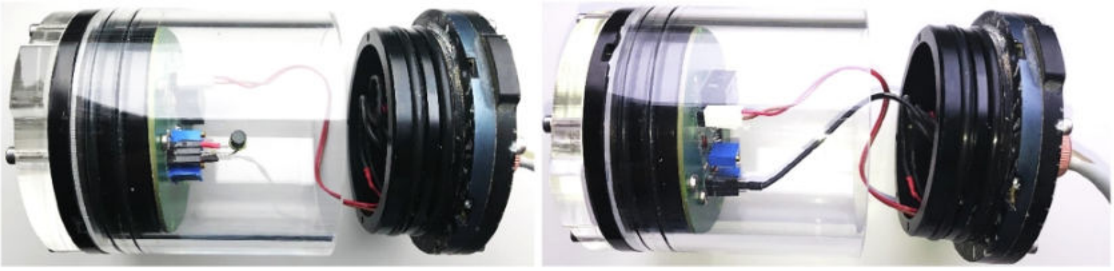


Fig. 16. Cable assembly for IR lamp (left: ambient light control, right: Server/camera control).

Fig. 17. Assembled IR lamp with 3D-printed mount attached to a frame using standard GoPro-clamps.

Table 13
Cable types for server/camera remote operation of the lamps.

Item	No.	Description	Distributor / Code	Manufacturer / Code	Price/€
1	100 m	Helukabel 21037 Datenkabel LiYCY 5 × 2 × 0.25 mm^2 Grau	www.conrad.de 1931447 – 62	AVX SMD MLCC X7R 12061C225KAT2A	144.04
2	1 m	SubConn PUR Cable P3TSP22#/1TSP18#	www.bornhoeft.de P3TSP22#/ 1TSP18#	SubConn PUR Cable P3TSP22#/ 1TSP18#	–

supply (Table 13, Item 2). It this case, the power supply is connected via the thicker twisted pair and the remaining twisted pair can be used for the two control lines.

For the remote control setup, the four twisted pairs for Ethernet are connected as described in Table 9. The two wires of the remaining twisted cable pair are connected to the lamp control outputs at J2 on PCB 'IRserverV11'. Each of these wires can control a group up to six lamps. Therefore, the power-in-wires and the lamp control output wires are soldered to a 4-pin socket ordered as shown for JP2 in Table 7. This 4 pin-socket is connected to J2 on PCB 'IRServerV11' in the correct orientation. And, as in the standard setup, the 2-pin header JP4 is connected via a 2-wire line with pin-sockets to the power pins of the Raspberry Pi (GPIO jumper pins #2 (+5V) and #6 (GND)). Fig. 18 shows a wiring diagram.

In the surface unit, the control wires from the IR server/camera cable are connected to the control wire of cable to the lamps they should control. Two groups of lamps ('Lamp control 1' or 'Lamp control 2) can be controlled by one server/camera. They are controlled by the GPIO Pins GPIO13 and GPIO21. It can be done by simple bash scripts, which can be accessed in the webservers scheduler or other LinuxOS scheduler (e.g. crontab).

For the remote control setup also the IR lamp wiring is modified. At first, the ambient light sensor is removed. The control signal wire (Table 12) from the underwater cable is soldered to a 3-pin socket at pin #2, while pin #1 and pin #3 are not connected. This 3-pin socket is connected to J2 at the PCB 'IR- lampV32' (Fig. 16, right). As in standard configuration, the two power wires are soldered to a 2-pin socket, which is connected to J1 (see Figs. 17 and 18).

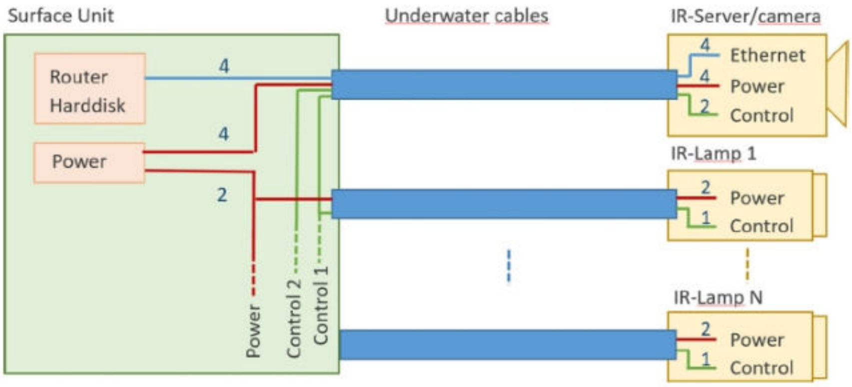


Fig. 18. Wiring diagram for the remote lamp control in a surface unit.

4. Software

The server/camera uses a Linux Debian OS without graphical XServer. The open source software RPi-Cam-Control [10,11], provide a webserver which gives access to settings for camera and motion detection, as well as to basic system settings, like restart, power down or user defined functions (Fig. 19). Additionally, a live video stream and a comfortable scheduler are available, that can also start user defined scripts. A full documentation can be found at [12]. All software is packed as .iso image.

4.1. Setup the SD card image and access the server

The software for the server/camera is pre installed on the image file, that can be written to the SD-card using command "*dd*" under a LinuxOS or using the software Rufus (https://rufus.ie) under WinOS.

This SD-card has to be inserted into the Raspberry Pi before powering the server/camera. Two network connections are predefined, which can be modified after the first connection:

1. Ethernet connection: Static IP Adress: 192.168.178.6 Gateway 192.168.178.1
2. Wifi Connection: SSID: NKServer, Password: 3790 0606 0721 2004 9114 with DHCP enabled

The predefined connections were configured with the network command line interface "*nmcli*". Both make it easy to install the cameras immediately on any FritzBox either directly wired or via Wifi, when the Wifi connection of the router is setup as predefined in the server/camera above. For a login the following credentials are valid:

Hostname: IRServer3 **User:** pi **Password:** irserver **Static IP:** 192.168.178.6

The server/camera is remote accessible via three protocols at its IP address:

1. via HTTP through the webserver interface,
2. via SSH connection to the Linux OS or
3. via SCP for file or video transfer from the camera to the remote system.

Fig. 19. Screenshot of RPi-Cam-Control-Webfrontend on a mobile device.

5. Use case with remote access via surface unit

In our specific use case, we wanted to improve fish pots for cod (*Gadus morhua*, L. 1758), especially the design of the pot entrance. Therefore, we needed a video surveillance system to observe cod behaviour in relation to different entrance designs – during day and night for several months.

The requirements were:

- observation at day and night
- minimum observation range: 2 m
- video data storage for several months
- fast swappable data disk
- motion detection
- remotely accessible
- webserver with live stream

In this use case the fish traps are located in shallow water (below 10 m depth) but we use the system also for applications in deeper waters (see specifications). A combination of two iFO systems is installed in the field (each with one camera and two IR-lamps). Both connected to an LTE router (FritzBox6890) with a swappable network attached storage (NAS) hard disk (Fig. 20).

This allows continuous video data storage for several weeks and delivers full remote access via VPN and LTE to the underwater iFO systems. They are remotely accessible for live video streams, setup and administration, for video file downloads and maintenance (see Figs. 21 and 22).

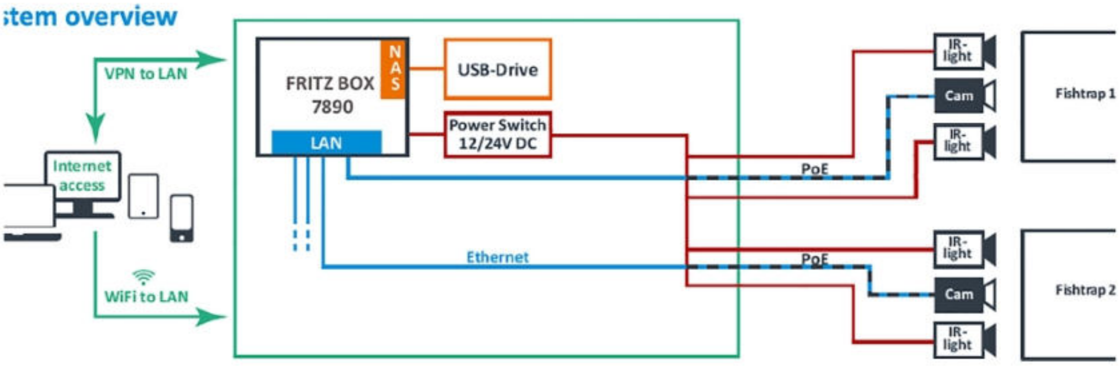
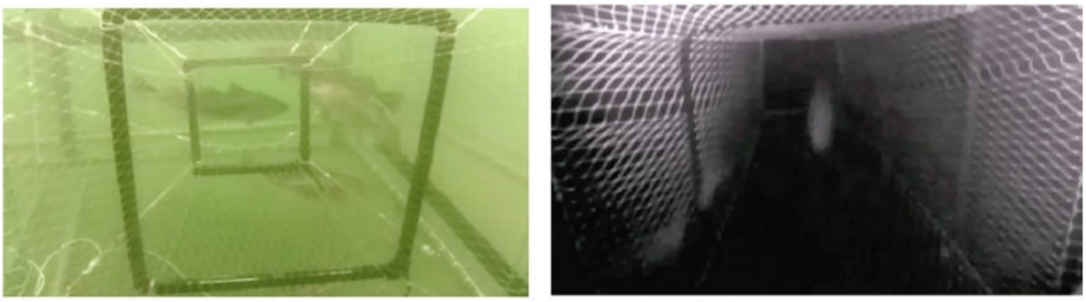


Fig. 20. System overview of the remotely accessible system in the field.



daytime video still showing cod in the trap

nighttime video still showing a cod leaving the trap

Fig. 21. Daytime and nighttime video stills at the entrance of fish pots.

Fig. 22. Surface unit of system in the field with LTE-router (FritzBox, NAS, plugs and wires; lid opened).

6. Summary and outlook

In this document, we present iFO, an open source low-budget underwater infrared video observation system with full documentation and sources to easily reproduce this. We briefly outlined one typical field of application, but we also use this system for other observation tasks, e.g. in fish tanks and off-shore. Of course, the system can be used in other environments and purposes as well: e.g. in harsh environments with the current underwater enclosures or in other environments with adapted ones. As a next step, we will derive a practical method from this work to estimate the underwater range of vision for infrared camera and light systems in general.

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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Using an innovative net-pen-based observation method to assess and compare fish pot-entrance catch efficiency for Atlantic cod (*Gadus morhua*)

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ABSTRACT

In many places, gillnet fishing is considered a conservation threat for air-breathing marine species. Fish pots represent an alternative to gillnetting; however, due to their low catch efficiency pots are rarely taken up by commercial fisheries. To improve pot efficiency for Atlantic cod (*Gadus morhua*), we used a novel enclosure to observe cod interacting with pot entrances, and investigated several entrance design parameters, including funnel colour, entrance funnel presence, length and entrance form. We demonstrate that the key factor for entrance passage is to give cod an unobstructed view of the inside or outside when they try to enter or exit the pot, respectively. Funnel colour (colours tested: white, green and transparent) influences entrance passage rates, with significantly higher entrance passage rates for the transparent funnel. Funnel presence increases the entrance encounter rate by enlarging the outer opening of the entrance. It decreases exit rates by deflecting cod away from the inner entrance opening and by reducing the area in which the exit is perceptible to cod inside the pot. Increasing funnel length further reduces this area and may deter cod by the longer passage length. This is the first study to observe cod–pot interactions day and night using an infrared camera, revealing a pronounced diurnal pattern with few nocturnal entrance passages, suggesting that cod–pot interactions are primarily guided by vision. The findings underline the importance of funnels and reveals promising avenues for their further improvement, e.g., by using transparent fish retention devices. The new pen-based method is superior in several ways to conventional field-pot catch-rate comparisons: It allows identification of differences in catch efficiency and describes the underlying cod behavioural mechanism leading to these differences. Thus, it allows targeted, efficient and iterative cod-pot catch-efficiency enhancements.

1. Introduction

Worldwide, fishery bycatch threatens several taxa of marine birds, mammals and turtles (e.g., Lewison et al., 2014; Read et al., 2006; Wiedenfeld et al., 2015). Although gillnets have limited effect on the benthic environment (Grabowski et al., 2014) and may be adjusted to target specific species and size classes of fish (Suuronen et al., 2012), gillnet fishing is often associated with substantial bycatches of birds, mammals and turtles (Gilman, 2015; Northridge et al., 2016; Žydelis et al., 2013). Many of these are endangered and protected under diverse national and international laws and regulations, e.g., the European Union (EU) Habitats and Species Directive (CEC, 1992). Furthermore, gillnets are susceptible to catch depredation by marine mammals, making the economic viability of gillnet fisheries difficult in some places (e.g., Buscaino et al., 2009; Geraci et al., 2019; Königson et al., 2015b).

To address these issues, alternative gears are discussed for many fisheries around the world (Žydelis et al., 2013), e.g., the Baltic SSF fisheries (ASCOBANS, 2016). Fish pots are passive, easily transportable, typically baited, stationary fishing gears consisting of small, net enclosures with entrances that facilitate entry while impeding exit for target species (Königson et al., 2015a; Ljungberg et al., 2016; Meintzer et al., 2017; Thomsen et al., 2010). The negative environmental impacts of fish pots are relatively inconsequential (Grabowski et al., 2014; Ovegård et al., 2011; Shester and Micheli, 2011; Suuronen et al., 2012; Thomsen

Abbreviations: FOV, field of view; FRD, fish retention device; IR, infrared; PIT, passive integrated transponders; RFID, Radio-frequency identification.

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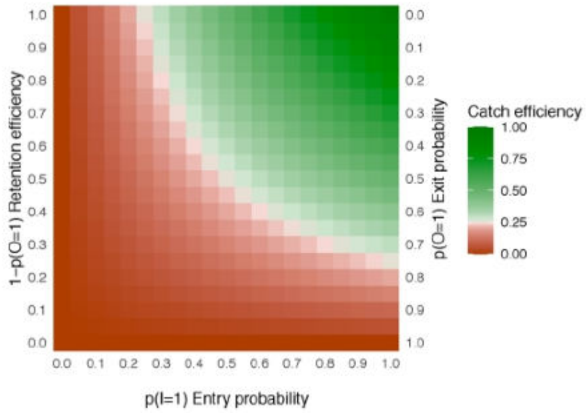

Fig. 1. Schematic representation of the dependence of pot-catch efficiency on access and escape probability of pot entrances.

et al., 2010). Importantly, pots have low to no bycatch potential for harbour porpoises (*Phocoena phocoena*) and seabirds, because the risk of entanglement or accidental catch in the pots is assumedly lower than with gillnets (Martin and Crawford, 2015; Žydelis et al., 2009). Additionally, seal-proof pot designs are available to protect the fish inside the pot from depredation (Königson et al., 2015b; Ljungberg et al., 2016). Also, pots allow the catch to be collected alive, increasing catch quality and maximising survival rates for unwanted bycatch (Furevik, 1994; Humborstad et al., 2016; Ovegård et al., 2011; Suuronen et al., 2012). However, catch rates of pots are still low in many fisheries, including pot fisheries for Atlantic cod (*Gadus morhua*; henceforth termed cod) in the Baltic Sea (Anders et al., 2017; Jørgensen et al., 2017; Suuronen et al., 2012), prompting many studies in recent decades to improve pot design and thereby improving catch efficiency (e.g., Bjordal and Furevik, 1988; Carlile et al., 1997; Furevik et al., 2008; Furevik and Løkkeborg, 1994; Jørgensen et al., 2017; Ovegård et al., 2011). Studies have revealed that only a small number of the cod approaching a pot find the entrance and manage to enter the pot (e.g., Meintzer et al., 2017; Valdemarsen et al., 1977). Such findings indicate that pot entrances are catchability bottlenecks (Furevik, 1994; Thomsen et al., 2010). Key performance characteristics include 'perceptibility' (how probable are fish to find the entrance), 'attractivity' (how probable are fish to attempt entering through the located entrance), 'ease of access' (how probable are fish to then successfully pass the entrance), and 'retention capacity' (how probable are fish to remain inside the pot), determined by the entrances' position in the pot (Furevik et al., 2008; Hedgärde et al., 2016; Thomsen et al., 2010), as well as by their design (Furevik, 1994; Furevik and Løkkeborg, 1994; Ljungberg et al., 2016; Olsen, 2014). Pot entrances are typically funnel shaped (Furevik, 1994), with the funnel design strongly influencing catch efficiency (e.g., Furevik and Løkkeborg, 1994; Ljungberg et al., 2016). Examples of relevant design aspects of the funnel are opening size (e.g., Carlile et al., 1997; Furevik and Løkkeborg, 1994), shape (Königson et al., 2015b), angle (Carlile et al., 1997; Ljungberg et al., 2016), and material (High and Ellis, 1973). A thorough understanding of the fish–gear interaction is essential to improving catch efficiency (He, 2010). For fish pots, this is difficult to investigate with catch-per-unit-effort metrics, i.e., the number of fish in a pot after hauling, which do not provide direct information regarding the sequence of fish–pot interaction, including the crucial relationship between entry- and exits rates, causing the observed differences in catch efficiency between different pot designs (Furevik and Løkkeborg, 1994; Hedgärde et al., 2016). Pot catch efficiency is thus a function of entry probability and exit probability (see Fig. 1 for a schematic catch efficiency illustration). Consequently, observational studies of fish–pot interactions, particularly using *in situ* video, have shed light on the basic principles of fish-pot catch efficiency (e.g., Hedgärde et al., 2016; Ljungberg et al., 2016; Meintzer et al., 2017; Renchen et al., 2012).

Table 1
Catch date and gear for experimental cod. Please note that 'Total number of caught cod' is the total number of cod caught, of which only a fraction were included in the experiment. 'In experiment' is the number of the caught cod included in the experiments.

Fishing gear	Date caught	Total number caught cod
Fish pot	27.11.2018	48
Bottom trawl	05.12.2018	67
Bottom trawl	15.01.2019	100
Bottom trawl	12.02.2019	156
Fish pot/hook& line	11.04.2019	26
	Sum	*544*
	In experiment	*152*

The explanatory power of field observational studies, however, is limited, because this approach does not include controlling the intrinsic (e.g. fish hunger) and extrinsic (e.g. fish density, temperature) parameters that affect pot catch rates (e.g., Stoner, 2004, 2003; Stoner and Ottmar, 2004; Stoner and Sturm, 2004). Therefore, we developed a novel method for faster, more efficient and direct comparison of pot design in the controllable environment of a net pen. To determine optimal cod-pot design parameters, we address the following questions:

(1) How does the diel period affect cod–gear interaction? So far, video studies of cod interaction with pots have been conducted either only by day (Anders et al., 2016, 2017; Ljungberg et al., 2016; Meintzer et al., 2017) or during the day and at night under strong artificial lighting (Hedgärde et al., 2016) in the spectral visual range of cod (Bowmaker, 1990). Therefore, these studies have limited explanatory power for a general description of the diurnal pattern of cod–pot interactions, which could influence cod-pot catch efficiency. Therefore, we used an infrared camera system (IR) to observe cod during the day and at night.
(2) How do entrance design parameters affect cod entry and exit rates? First, we studied the effect of funnel colour, because the colour of fishing gear is important in shaping cod–gear interaction, and thus catch success (Arimoto et al., 2010). Colour influences the perceptibility of the entrance by determining its visibility and its contrast to the background and other parts of the pot. Then, we tested the effect of funnel presence and length, because the findings concerning the effect of funnel length on entry and exit probabilities have been inconclusive so far (Li et al., 2006a, 2006b; Walsh and Hiscock, 2005). Finally, we studied the effect of entrance shape by studying cod interactions with a narrow funnel entrance. Such entrances are commonly used in some fisheries (Furevik and Løkkeborg, 1994; Li et al., 2006b, 2006a), although results for cod are limited (Furevik and Løkkeborg, 1994; He and Winger, 2010).
(3) How does cod social behaviour affect entrance interaction? Cod entrance probability into pots is influenced by social foraging behaviour (Anders et al., 2017; Hedgärde et al., 2016). We investigated if leader–follower dynamics (e.g., Björnsson et al., 2018; Millot et al., 2012) modify pot-entrance interactions.

2. Material and methods

Experiments were conducted during December 2018 and March–April 2019 in the sporting marina of Rostock-Warnemünde, Germany (Fig. A1, 54°10′52.7″N 12°05′18.0″E).

2.1. Cod used in experiments

A total of 544 cod were caught using bottom trawl, fish pot, or hook and line and of these 152 were included in the experiment (Table 1). To minimise cod stress and exhaustion, fishing depth was shallower than 20

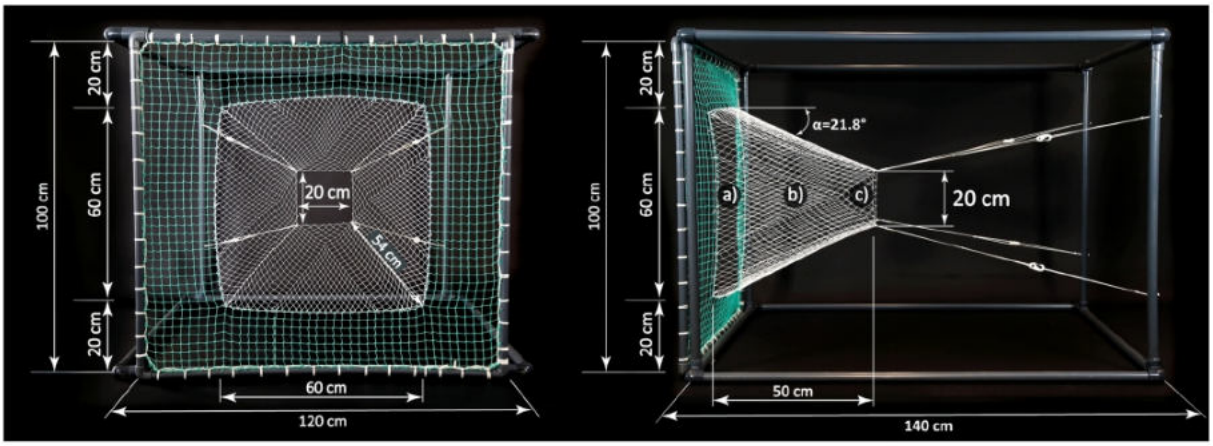

Fig. 2. Control entrance (white PA funnel, 25 mm mesh size, 60 × 60 cm outer opening and 20 × 20 cm inner opening, L 50 cm) used for experiments. Left front, right side view. The nomenclature used for parts of a cod entrance is indicated on the side view: (a) outer opening; (b) funnel; (c) inner opening. The single opening of the 'No funnel' entrance is also referred to as 'Inner opening' in the analysis. Illustration of all other entrance types is available in the appendix.

m, and trawl haul duration was limited to 30 min. Most cod were caught off the coast of Rostock-Warnemünde near the location of the experiment and transported in a fish tank with constant seawater supply to the holding net pen the same day. All cod were transferred to the holding net pen (see below) the same day they were caught and had at least 4 days acclimation time before inclusion in an experimental trial. Cod were fed *ad libitum* with thawed and cut herring (*Clupea harengus*) once a week. Before they were included in an experiment, cod were not fed for at least a week, because elevated hunger levels in fish are linked to greater motivation to enter fish pots (Thomsen et al., 2010; Ljungberg et al., 2020; Ovegård et al., 2012). Because the motivation of cod to enter pots is socially mediated (Anders et al., 2017) and cod pots are usually encountered by more than one cod during their soak time (e.g., Anders et al., 2016; Hedgärde et al., 2016; Ljungberg et al., 2016), groups of eight cod were used in each trial. Because cod are cannibalistic (e.g., Hardie and Hutchings, 2011) and to avoid social stress, cod groups in trials were within a similar length range (30–39 cm, 40–49 cm and 50–59 cm). Since cod possess complex learning strategies and long-term memory (Meager et al., 2018), only naïve cod were used and cod were not re-used in subsequent trials.

2.2. Experimental setup

Two identical net pens (dimensions 3 × 3 × 3 m = 27 m^3; Mieske, 1998; see Fig. A2) were used; one was used for experimental treatments, the other for holding the fish before experiments. An experimental pot (W 250 cm; D 140 cm; H 100 cm) with two side-by-side entrances was constructed and positioned inside the net pen (Figs. A3 and A4). The pot frame was made of standard PVC tubes and had green PE netting (Polyethylene, 25 mm bar length). Fish pot entrances were mounted on (120 × 100 cm) PVC-tube frames and could be exchanged. We used a funnel as baseline entrance type for indirect comparisons (white PA (Polyamide) netting, L 50 cm, 60 × 60 cm outer opening and 20 × 20 cm inner opening; Fig. 2; hereafter 'control entrance'). The control entrance and all test funnels had a 25 mm mesh bar length. The general design of the funnels was based on the two-chambered cod pot developed by Furevik et al. (2008) and used in several pot studies (e.g., Bryhn et al., 2014; Jørgensen et al., 2017; Ovegård et al., 2011). Because we were limited in size by the space available in the net pen, we used a square opening design instead of the rectangular opening used by Furevik et al. (2008).

Movements were not limited inside the pot, and cod could freely move from one entrance to the other. Olfactory bait (e.g. cut herring) could not be used, as it typically rapidly loses most of its effectiveness after 1.5 h (Løkkeborg, 1990; Westerberg and Westerberg, 2011). Furthermore, olfactory bait plumes are current dependent (Løkkeborg, 1998, 1990; Vabø et al., 2004), thus possibly introducing a side bias where the experimental cod prefer one entrance side to the other. To provide a long-lasting attractant to lure the cod into the pot, we placed a green fishing bait light (model "Deep water fishing light", 523 nm peak wave length, intensity 124 μW, Manufacturer Artisan fisheries consultants, Spain; Bryhn et al., 2014; Utne-Palm et al., 2018) at mid-pot height in the pot centre, in equal distance to both entrances. Data were collected in paired trials, each experimental trial consisting of a test entrance set in the pot together with the control entrance. To avoid possible bias caused by cod side preferences, at least two replicates were conducted for each comparison, while switching the side of entrance types between replicates. For each trial of a particular test

Table 2
Description of pot entrances included in the experiments. Each modified entrance type was compared with the 'White funnel' control entrance. Illustrations of entrance types can be found in Fig. 2 (control entrance) and Fig. A5 (control and all other entrance types). Abbreviations: PA = Polyamide; PE = Polyethylene; d = diameter.

Name	Twine type	Mesh size [mm]	Outer opening dimension [cm]	Funnel length [cm]	Inner opening dimension [cm]	Parameter tested
White funnel (control entrance)	*PA white multifilament d =0.9 mm*	*25*	*60 × 60*	*50*	*20 × 20*	*Control*
Green funnel	PE green multifilament d = 1.2 mm	25	60 × 60	50	20 × 20	Funnel colour
Transp. funnel	PA transparent monofilament d =0.5 mm	25	60 × 60	50	20 × 20	
No funnel	–	–	–	–	20 × 20	Funnel length
Long funnel	PA white multifilament d =0.9 mm	25	60 × 60	75	20 × 20	
Narrow funnel	PA white multifilament d =0.9 mm	25	60 × 60	50	Height: 20 cm & Width: 2.5 cm	Funnel shape

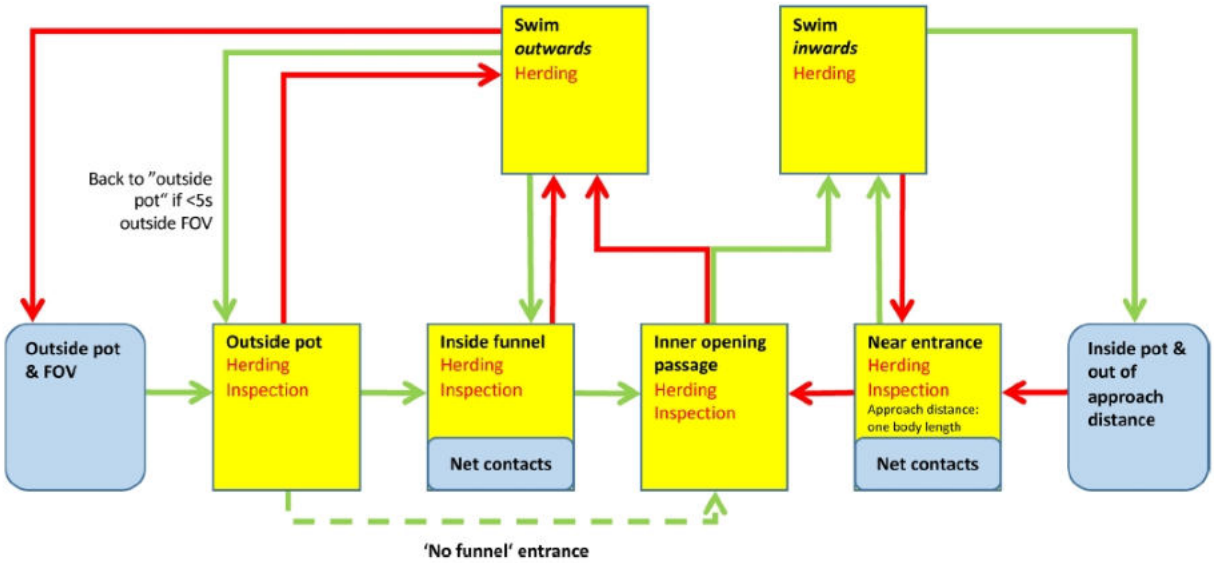

Fig. 3. Behavioural flow diagram of pot-interaction event chains. Blue boxes: point events (no duration); yellow boxes: state events (with duration); black: event type name; red: event modifier; green arrows: movements from the outside inwards; dashed green arrow: movement for 'no funnel' entrance; red arrows: from inside the pot outwards. Definition of event modifier: 'Herding' is defined as one or more fish following the swimming path of a leader cod; 'Inspection' indicates that a cod is inspecting structural elements during the event (see text for explanation). On the outside, an event chain starts or ends when a cod enters or leaves the camera field of view (FOV) outside the pot (event 'Outside pot and FOV'). On the inside, an event starts or ends when a cod approaches the inner entrance opening to within one body length or increases its distance from it to more than one body length. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

entrance–control entrance combination, eight cod of the same length classes were randomly fetched and set into the experimental pen. After at least 15 min acclimation time the pot was then lowered into the net pen, indicating the start of the experiment. Each trial was conducted from ∿14:00 to 13:30 the following day. Water temperature ranged from 4.0 °C to 5.0 °C in December 2018 trials and from 3.5 °C to 10.0 °C at the end of the experiment on 28. April 2019.

2.3. Tested entrance types

To test the influence of funnel colour, length and shape, we used pot entrances, differing from the control entrance by only one design parameter (Table 2; pictures included in appendix (Fig. A5)).

2.4. Fish observation

2.4.1. Infrared (IR) camera system

To study fish, including cod, in darkness without influencing their behaviour, IR light is often used (e.g., Meager et al., 2006; Utne-Palm et al., 2018). Therefore, we developed an infrared (IR) lamp and camera system, 'infrared Fish Observation' (iFO; Hermann et al., 2020) to observe cod day and night in this study. The system can record videos at visible as well as IR light and has a minimum observation range of 1.8 m, video data storage capacities for several weeks, a rapidly swappable datadisk, and remote access connection through a webserver with live stream. In this study, we used two iFO systems, each with one camera and two IR lamps (Figs. A3 and A4; centroid frequency 850 nm).

2.4.2. Radio-frequency identification (RFID) of cod

Cod were implanted with passive integrated transponders (PIT tags; 32 mm long half-duplex; manufactured by Oregon RFID, Oregon, USA; animal welfare permit 7221.3–1-009/18 of the Agency for agriculture, food safety and fishery of the Federal State Mecklenburg-West Pomerania in Germany), and each entrance was equipped with two radio-frequency identification (RFID) antennae (Figs. A3 and A4). However, owing to technical difficulties, we refrained from analysing these data. Nevertheless, they were used to improve the manual analysis of the video recordings (see below) by allowing us to pinpoint periods of increased entrance interaction before detailed video analysis and by helping us to disaggregate event timings when several cod interacted simultaneously with an entrance.

2.5. Behavioural analysis

To provide a comprehensive description of the event chain of cod interacting with the pot entrances, we constructed a detailed ethogram and a behavioural flow diagram (Fig. 3; Table 3), adapting prior behavioural analysis approaches (Anders et al., 2016; Ljungberg et al., 2016; Meintzer et al., 2017; Santos et al., 2020). Most behavioural units were mutually exclusive events with quantifiable duration. The exception was the brief (<1 s) touching of entrance structures that occurred when individuals were inside the funnel or near the inner entrance opening (event 'net contacts'). These contacts could be directed, inquisitive touches, usually during the day, or inadvertent bumps with the entrance when trying to pass, most often at night. Additionally, inspection and herding (leader–follower) events were also logged, with 'herding' defined as one or more fish following the swimming path of a leader cod. Inspection of the different structural entrance elements involved reduced swimming speed, contorted swimming paths to approach different parts of the entrance, gaze directed not ahead of their swimming path but directed at the entrance/funnel and sometimes targeted net contacts. Cod leaving the camera field of view (FOV) for <5 s were considered staying within the same event. Videos were analysed with the software BORIS (Behavioural Observation Research Interactive Software) version v. 7.9.7 (Friard and Gamba, 2016). Each trial was fully analysed by one observer.

2.6. Statistical analysis

The pot-entrance catch-efficiency metric is a function of entry and

Table 3

Behavioural ethogram of cod interactions with pot entrances illustrated in the behavioural flow diagram (Fig. 3). For "Starting point" and "Endpoint", "*Inwards*" describes a cod swimming *towards* the pot inside while "*Outwards*" describes a cod swimming towards the pot exterior.

Event	Event type	Description	Starting point	Endpoint	Event modifier*
Outside pot	State	Cod is outside the pot entrance, gaze directed at entrance.	*Inwards:* Cod enters FOV (event chain begins). *Outwards:* When two-thirds of body length has passed outer entrance opening and cod does not directly leave FOV (previous event: 'Swim outwards').	*Inwards:* Tip of cod snout passes outer entrance opening (next event: 'Inside funnel' or 'Inner opening passage' if 'No funnel' entrance). *Outwards:* Cod turns and starts to swim outwards (next event: 'Swim outwards').	Herding, Inspection
Inside funnel	State	Cod is inside the funnel (excluding direct outward swimming) *Note: Does not apply to 'No funnel' entrance.*	*Inwards:* Tip of cod snout passes outer entrance opening (previous event: 'Outside pot'). *Outwards:* Cod aborts swimming outwards (previous event: 'Swim outwards').	*Inwards:* Tip of cod snout passes inner entrance opening (next event: 'Inner opening passage'). *Outwards:* Cod turns and starts to swim outwards (next event: 'Swim outwards').	Herding, Inspection
Swim *outwards*	State	Cod swims towards pot outside (outside inner opening).	*Inwards:* Cod turns and starts to swim outwards (previous event: 'Outside pot' or 'Inside Funnel'). *Outwards:* Two-thirds of cod passed entrance inner opening and cod starts swimming outwards (previous event: 'Inner opening passage').	*Inwards:* Cod swims backwards or turns >90° towards pot inside (next event: 'Outside pot' or 'Inside funnel'). *Outwards:* Cod leaves FOV outside the pot (end of event chain).	Herding
Inner opening passage	State	Cod passes inner opening of entrance in either direction.	*Inwards:* Cod snout enters inner opening (previous event: 'Inside funnel' or 'Outside pot' for 'No funnel' entrance). *Outwards:* Cod snout enters inner opening (previous event: 'Near entrance').	*Inwards:* Two-thirds of cod body length passes the inner opening towards inside of pot (next event: 'Swim inwards'). *Outwards:* Two-thirds of cod body length passes the inner opening towards outside pot (next event: 'Swim outwards').	Herding, Inspection
Near entrance	State	Inside pot, when (a) cod is within one body length of inner opening, (b) its gaze is towards the inner opening, (c) swimming path deviation towards inner opening, usually concurrent with an abrupt prior deceleration.	*Inwards:* Cod aborts inward swimming and turns back towards inner opening (previous event: 'Swim inwards'). *Outwards:* Cod approaches opening to within one body length, attention directed towards opening (begin of event chain).	*Inwards:* Cod turns away from entrance (next event: 'Swim inwards'). *Outwards:* Cod snout enters inner opening (next event: 'Inner opening passage').	Herding, Inspection
Swim *inwards*	State	Cod swims towards pot inside (inside pot).	*Inwards:* Cod starts swimming towards pot inside (previous event: 'Inner opening passage'). *Outwards:* Cod aborts inner opening approach and turns towards pot inside (previous event: 'Near entrance').	*Inwards:* Cod is more than one body length away from entrance/funnel inner opening (end of event chain). *If cod re-approaches the opening to within one body length in <5 s, it is still considered in the same event pass.* *Outwards:* Cod turns back again towards opening (next event: 'Near entrance').	Herding
Net contacts	Point	Cod touches entrance netting with snout.	–	–	–

*Event modifiers: *Herding:* Cod exhibit a behavioural pattern involving one leader and one or more followers.
Inspection: Cod in event is visually inspecting any parts of the entrance. Inspection is discernible from the eye movement as well as the body position that cod dynamically adjust to inspect their point of interest.

Table 4
Overview of entry and exit numbers of all trials conducted by different entrance types (Test) compared with 'White funnel' entrance (Control); 'Position control' indicates on which pot side the control entrance was situated. Total entries, respectively, exits through test/control entrances. Cod mean length given with standard deviation.

Tested entrance	Trial number	Position control	Entries		Exits		Cod mean length [cm]
			Control	Test	Control	Test	
Green funnel	1	Left	4	3	0	2	43.3 ± 1.4
Green funnel	2	Right	3	12	2	5	44.8 ± 2.9
Green funnel	3	Right	14	7	9	5	44.8 ± 2.2
Green funnel	4	Right	9	17	6	13	36.5 ± 1.7
Green funnel	5	Right	22	7	15	7	43.1 ± 2.8
Green funnel	6	Left	12	12	6	11	35.6 ± 2.4
		Sum	64	58	38	43	
Transparent funnel	7	Left	3	6	0	2	36.4 ± 2.8
Transparent funnel	8	Right	1	3	0	2	37.0 ± 2.6
Transparent funnel	9	Right	10	3	3	3	44.5 ± 2.3
Transparent funnel	10	Left	6	21	1	19	37.1 ± 1.3
Transparent funnel	11	Left	10	1	2	1	44.4 ± 2.3
Transparent funnel	12	Right	14	31	3	33	54.9 ± 3.1
		Sum	44	65	9	60	
No funnel	13	Left	17	15	0	24	44.5 ± 3.2
No funnel	14	Right	34	65	2	91	35.3 ± 2.3
No funnel	15	Left	115	17	9	111	34.5 ± 3.4
		Sum	166	97	11	226	
Long funnel	16	Right	4	6	2	0	36.3 ± 1.7
Long funnel	17	Left	37	37	66	0	53.3 ± 2.0
		Sum	41	43	68	0	
Narrow funnel	18	Right	11	2	6	0	41.3 ± 1.1
Narrow funnel	19	Left	7	1	0	0	36.5 ± 1.7
		Sum	18	3	6	0	

exit/retention probability (Fig. 1). 'Entry' is defined as the passage of a cod from outside the pot to inside the pot; 'exit' is defined as the passage of a cod from inside the pot to outside the pot. For each entry or exit event, a cod could choose either the test or the control entrance, respectively. Therefore, observed entries and exits for each experiment were treated as paired (control entrance vs. test entrance) comparison data. To address the study's research topics, we used two different methods.

Using the first method, we compared the number of successful entries and exits of both entrance types, using a generalised linear model (GLM). A successful entry or exit is defined as an event chain starting outside the pot and ending inside the pot, or vice versa. In an exploratory data analysis, potential covariables on entrance interactions were evaluated to determine if they could have influenced the entrance interactions and should be included in the analysis. The following were chosen for inclusion: (1) To account for possible side preference, the side of the control entrance was included as a blocking factor in the full model. (2) Although most entrance interactions occurred during the day, we also included 'day period' in the full model with two states: 'day' (time between sunrise and sunset) and 'night' to reflect possible differences in diurnal entrance/exit patterns. Day period information (sunset, sunrise, civil dawn, civil dusk) was acquired using R suncalc package (Thieurmel and Elmarhraoui, 2019). Time is in local time (CET = UTC + 1 h). For each pairwise comparison, the entryand exit proportion was modelled as follows:

Being I/O, the binary variable expressing the entrance used by the observed fish to enter (I) or exit (O) the pot (0 = control, 1 = test), and X a three-dimensional vector including the model intersect, and the dummy variables representing side where the test is positioned (0 = left, 1 = right) and day period (0 = day, 1= night), then $p(X) = p(\gamma = 1|X)$ is the expected probability of either entry or exit in the test, conditioned to side and day period. A $p(X)$ of 0.5 indicates no difference between test and control entrance, while values less than 0.5 indicate lower entry or exit rates for the test entrance than for the control entrance. The product of both probabilities ($p(I = 1) * p(O = 1) = 0.25$) would then express equal catch efficiencies between control and the paired test entrance. Following the same argumentation, unequal catch efficiency resulting in values greater than 0.25 would indicate higher catch efficiency of the test entrance relative to the control, while values below 0.25 would indicate the opposite. The binary GLM applied expresses $p(X)$ as:

$$\log(p(X)/(1 - p(X)) = \beta_0 + \beta_1 * side + \beta_2 * dayperiod \quad (1)$$

On the right hand model side, the coefficient β_0 is the model intercept, and β_1 and β_2 quantify the potential effect of side and day period on entry and exit probability in the test entrance. The models were fitted with the statistical software R (3.6.3, R Core Team, 2020). In addition to Model (1), all possible simpler models were calculated, and the final model selected from the candidates via AIC (Akaike, 1973). To calculate the isolated entrance effect on the catch entry and exit from the final models with more than one covariate, we used the r contrast.sum() function to access the intercept value contrasted with the other covariates. The GLM analysis is a coarse first approach that allows the inference of strong differences between the control and the test entrance. This, however, does not reveal the underlying mechanism leading to possible differences in interaction and does not allow the incorporation of the information provided by aborted atempts at entry or exit.

Therefore, we used the second method to determine at which point in the event chain control- and test-entrance types provoked different reactions by the interacting cod. We adapted and applied a hierarchical tree classification method of Santos et al., 2020). The individual event chains of cod entrance interactions were pooled for each experiment and across replicates. These event chains were then arranged in an inverted tree-like structure with the root containing the total number of observations on top. Each behavioural node in the level immediately below the root contained counts of observed entry/exit events, either in the test or control entrance. After this first level, different event chains were encompassed in one branch up to the parent node, where they differed. At this point, the event chains split into branches. Then, each one could once again contain several event chains that separated at lower event levels, creating the tree. The terminal leaves at the end of each event chain represented the final fate of the observed cod 'Inside pot' or 'Outside pot.' Based on the information contained in the tree, the marginal probability (MP) for a given behavioural event to happen is calculated as:

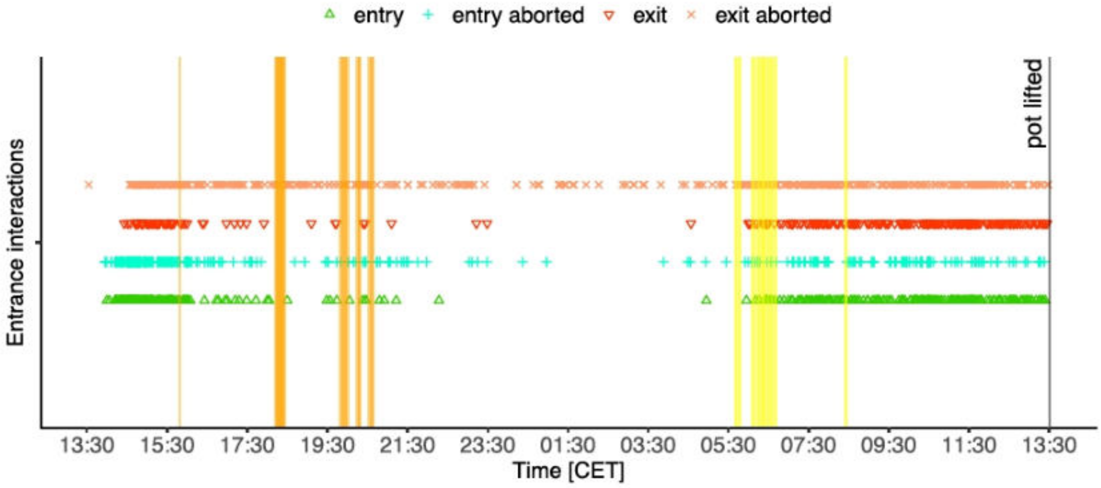

Fig. 4. Gantt chart of entry, aborted entry, exit, and aborted exit events of all trials with entrances including funnels (16 trials). Orange vertical lines indicate sunset; yellow vertical line indicate sunrise. All vertical lines have identical thickness, but trials on consecutive days appear as thicker lines. Pots were always lifted at 13:30 h, except for one replicate where the pot was lifted at 13:56 h. Start times varied between 13:35 and 15:57 h. The Gant chart for each of the experiments included here can be found in the appendix (Figs. A6–A9). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

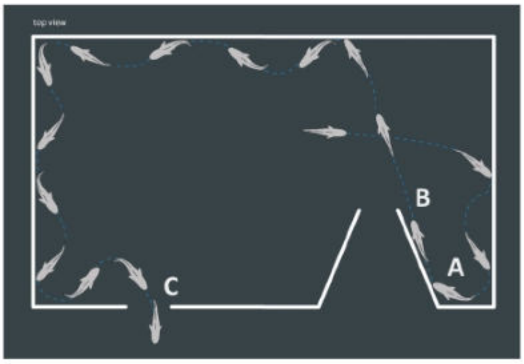

Fig. 5. Net-wall-guided search pattern at twilight; left side without funnel and right pot side with funnel.

$$MP = P(N_i) = \frac{N_i}{Root} \quad (2)$$

where N_i is the number of cod performing the event i (node i), and $Root$ is the total number of observed interactions. Similarly, the conditional probability (CP) that an event i could happen, given the MP of its parent link k in the level immediately above, is:

$$CP = P(N_i|N_k) = \frac{N_i}{N_k} \quad (3)$$

Trees were constructed for each experiment once for entrance interactions starting at the pot outside and once starting at the pot inside. To account for behavioural variability that occurs naturally between and within experimental replicates, we adapted and applied a double bootstrap method often used in trawl selectivity studies (Millar, 1993). Each iteration of the bootstrap produces an artificial tree after resampling experimental replicates and observations within the resampled replicates. This procedure was repeated B = 1000 times, leading to 1000 artificial trees, allowing calculation of 95 % Efron-percentile Confidence Intervals associated with the average probabilities (Eqs. 2 and 3) from the empirical tree (Santos et al., *in press*; 2016). The resulting trees were inspected for differences in event-chain flows and event links of both main entrance branches, based on MP and CP. Little or no CI overlap between the same event-chain links of both entrance types indicated significant differences.

3. Results

In total, we analysed 19 trials with a total duration of 435.0 h (Table 4 and Table A1). In rare cases, the video cameras stopped recording for short periods (seconds to minutes). For instances when the video cameras stopped recording, the periods were excluded from analysis for both entrances within the trial.

3.1. Diurnal activity pattern

Throughout all trials, we observed a pronounced activity decrease at night (Fig. 4). In the first hours after starting each trial, cod interacted intensively with the entrances. This activity decreased towards the evening, after which almost no nightly interaction with the entrances occurred. Most of the few nightly interactions are approaches to the entrances from the inside (shown as aborted exits in Fig. 4).

The IR-camera system did not illuminate the whole pot inside. Cod moved less during morning and evening twilight, and almost no movement occurred during the night proper. Cod inside the pot appeared to follow a net-wall-guided search pattern where they swam along the net wall and frequently touched it with the snout or pectoral fins. When swimming into a pot corner, or against the funnel, fish usually turned to the side away from the net wall and then continued swimming (Fig. 5A). When the cod thus passed the inner opening of the funnel (Fig. 5B), they would continue towards the pot wall opposite and not exit through the inner opening. In contrast, the 'No funnel' entrance lacked this deflection mechanism (Fig. 5C). Here, cod exited notably more during twilight ('No funnel' exits = 36, control entrance exits = 2; Fig. 6). For night and twilight entries, there was no strong difference between both entrances, with fewer entries through the 'No funnel' (entries = 15, control entrance entries = 19).

Starting around civil dawn, cod activity increased, swimming actively throughout the pot. But for all entrances, except the 'No funnel' (Fig. 6), cod started passing the entrances again only shortly after sunrise, and the highest entrance-passage rates were observed in the period

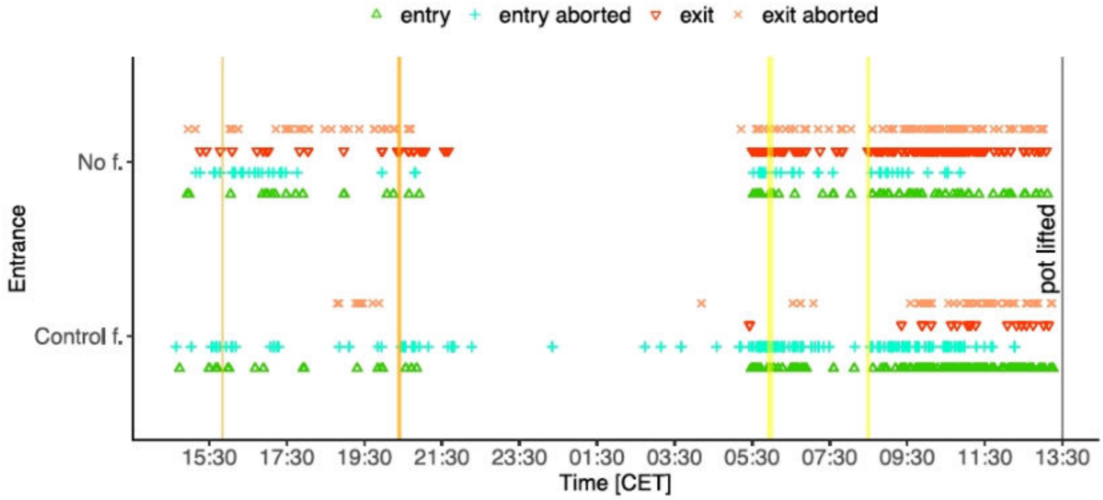

Fig. 6. Gantt chart of entry, aborted entry, exit, and aborted exit events in the 'No funnel' experiments (three replicates). Orange and yellow vertical lines indicate sunset and sunrise, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5
GLM parameters of all experiment final models. 'Test entrance' indicates the experiment, 'Model' indicates if the model is for the entries or the exits of the experiment, 'Side' and 'Day period' are the covariates, 'D. o. f.' are the model degrees of freedom, and p(I/O = 1) indicates the probability that an entry or exit occurred through the test entrance. Note that *, **, and *** denote that the Wald-test *p*-value is <0.05, <0.01, and <0.001, respectively. Significant values in are bold. N/I stands for 'Not included' in the final model.

Test entrance	Model	Intercept	Side	Day period	Deviance	D. o. f.	p(I/O = 1)
Green funnel	Entries	−0.098 ± 0.181	N/I	N/I	168.83	121	0.48 (0.39–00.56)
	Exits	1.022 ± 0.587	0.405 ± 0.281	−0.769 ± 0.564	107.20	78	0.74 (0.47–0.90)
Transparent funnel	Entries	**0.390* ±.195**	N/I	N/I	147.03	108	0.60 (0.50–0.68)
	Exits	**1.897*** ±.357**	N/I	N/I	53.44	68	0.87 (0.77–0.93)
No funnel	Entries	**−0.385** ±0.145**	**−1.033*** ±0.145**	N/I	289.26	261	0.41 (0.34–0.47)
	Exits	**3.263*** ±0.397**	−0.555 ± 0.397	N/I	86.65	235	0.96 (0.92–0.98)
Long funnel	Entries	0.048 ± 0.218	N/I	N/I	116.40	83	0.51 (0.41–0.62)
	Exits	No exits through 'long funnel'					
Narrow funnel	Entries	**−1.792** ±0.624**	N/I	N/I	17.23	20	0.14 (0.05–0.36)
	Exits	No exits through 'long funnel'					

after sunrise.

3.2. *Funnel colour effect on catch efficiency*

3.2.1. *Green funnel*

Six replicates were conducted for the comparison of the 'White funnel' (control entrance) with the 'Green funnel' (Table 4). The final model for the expected probability to enter through the 'Green funnel' included only the intercept, indicating that side and day period had no influence on the entry (Table 5). Entry rate $p(I = 1)$ was 0.48, so very similar to the control entrance. As both main branches are almost identical, the behavioural event-chain tree underlines this pattern (Fig. 7).

The final exit model included side and day period (Table 5), with a higher, but not significant, exit rate through the 'Green funnel' ($p(O = 1) = 0.74$). The behavioural event-chain tree reveals that this was possibly because more cod approached the 'Green funnel' inner opening (Fig. 8). However, the CI of the first level nodes as well as of the following nodes overlap, indicating no significant difference. Therefore, the observed difference is at least partly the result of a side effect and more nightly exits through the 'Green funnel' (night exits: 'Green funnel' n = 5, control n = 1).

3.2.2. *Transparent funnel*

Six replicates were conducted to compare the 'White funnel' (control entrance) with the 'Transparent funnel' (Table 4). The final models included only the intercept (Table 5). Cod passed more often through the 'Transparent funnel,' with the difference between entries ($p(I = 1) = 0.60$) being weaker than for the exits ($p(O = 1) = 0.87$). The higher entry probability through the 'Transparent funnel' is driven mainly by a higher, but non-significant, interaction rate with this entrance (Fig. 9). Furthermore, more, cod entered the transparent funnel, with little CI overlap. In all, 30 out of 36 contacts in the 'Transparent funnel' were accidental when cod tried to pass into the pot through the transparent netting, whereas only six net contacts were deliberate tactile probing contacts. In contrast, only five funnel netting contacts in the control entrance were accidental, whereas six were deliberate probing contacts. This difference indicates that cod did not always perceive the 'Transparent funnel' or at least did not perceive it as an obstacle.

For exit events, there were fewer interactions in total, but more aborted exit attempts were observed for the 'White funnel' (control), resulting in strong differences in exit probabilities (Fig. 10).

3.3. *Funnel length*

3.3.1. *No funnel*

Three replicates of the comparison between 'No funnel' and 'White funnel' (control) entrance were conducted (Table 4). Both selected models included the side covariate (Table 5). The probability of entering through the 'No funnel' entrance was only 0.41 $p(I = 1)$, whereas exits

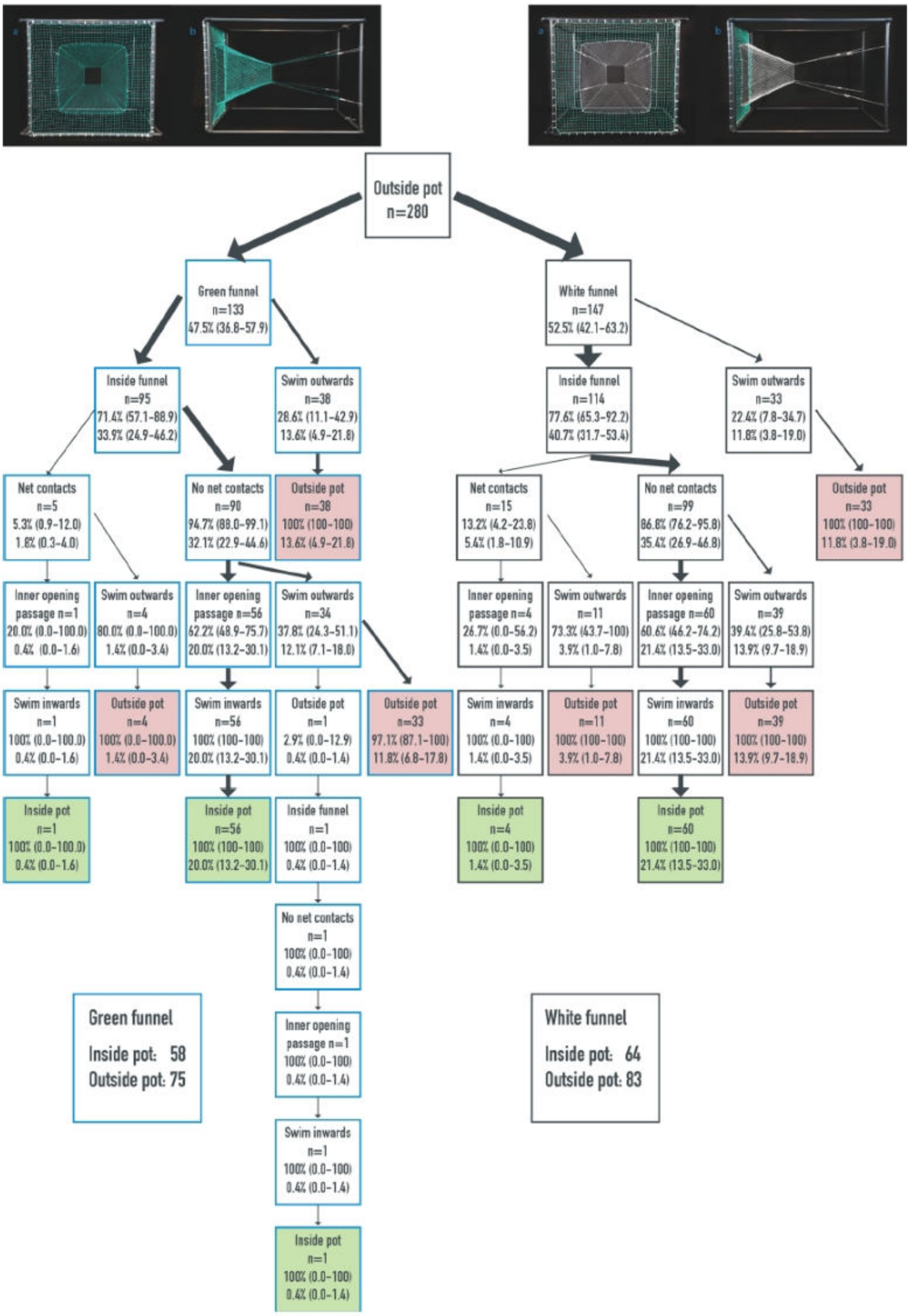

Fig. 7. Behavioural event-chain tree comparing the 'Green funnel' (Test) with the 'White funnel' (Control) for cod interactions with pot entrances starting outside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point of the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

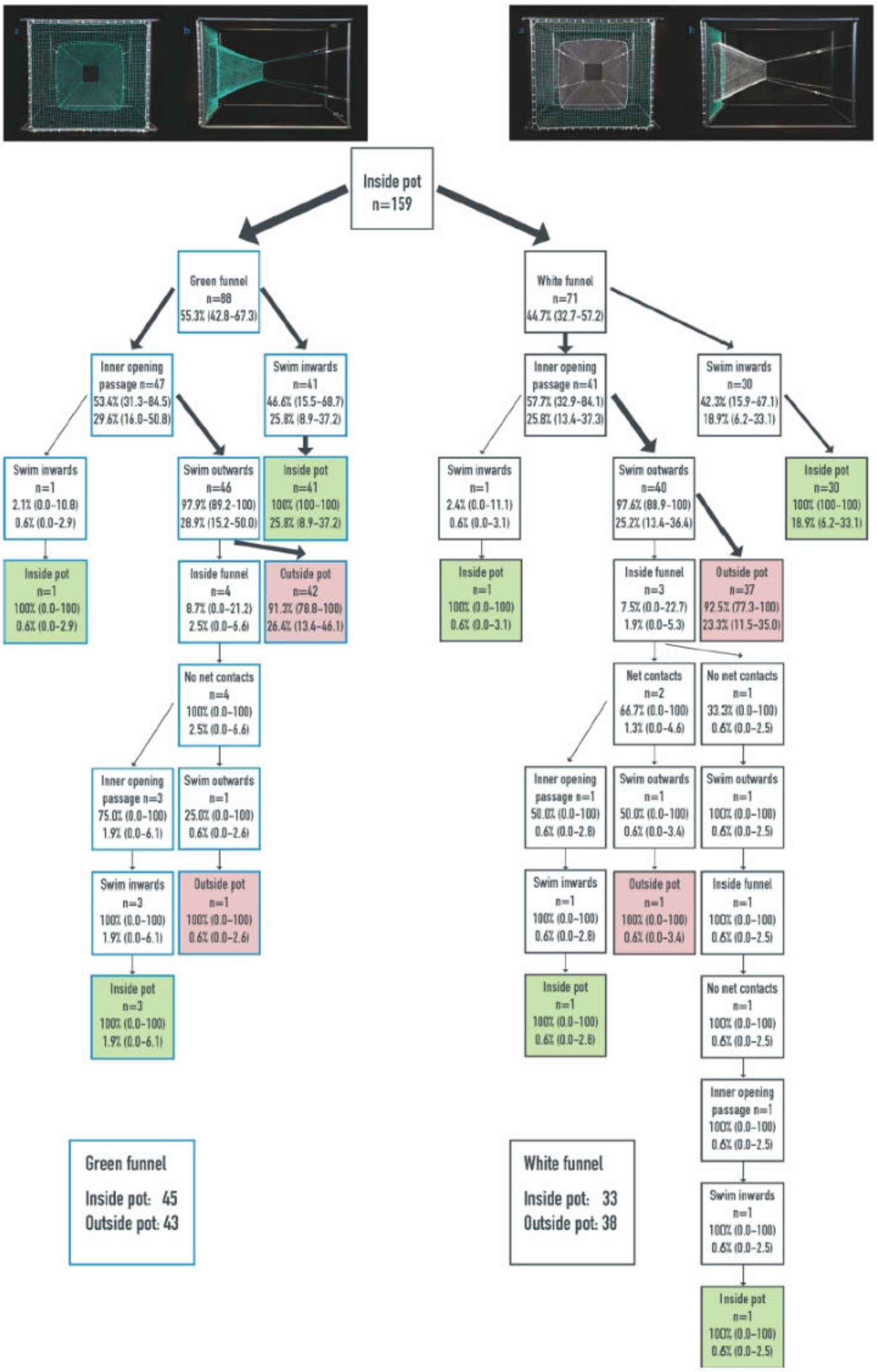

Fig. 8. Behavioural event-chain tree comparing the 'Green funnel' (Test) with the 'White funnel' (Control) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point in the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

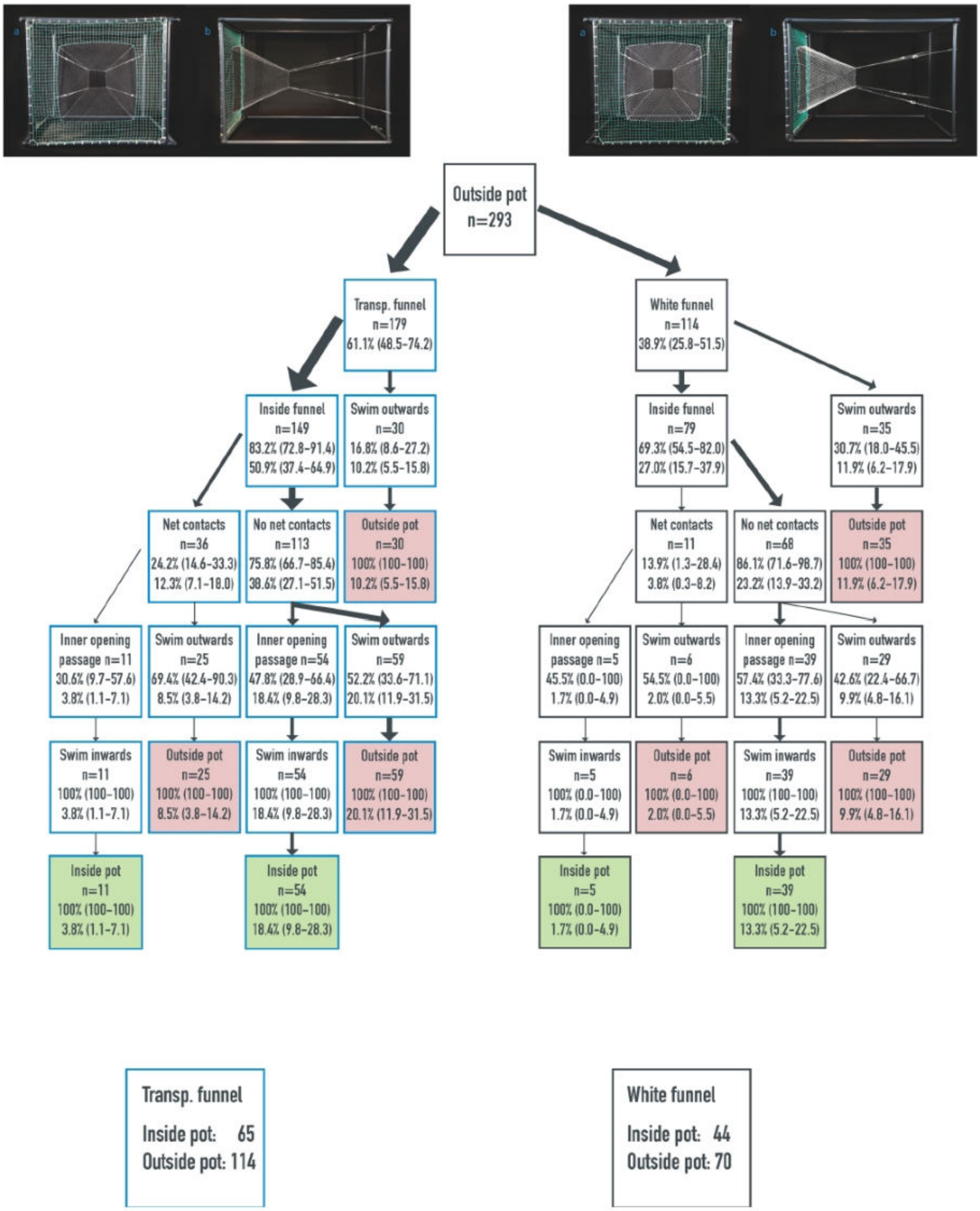

Fig. 9. Behavioural event-chain tree comparing the 'Transparent funnel' (Test) with the 'White funnel' (Control) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point in the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

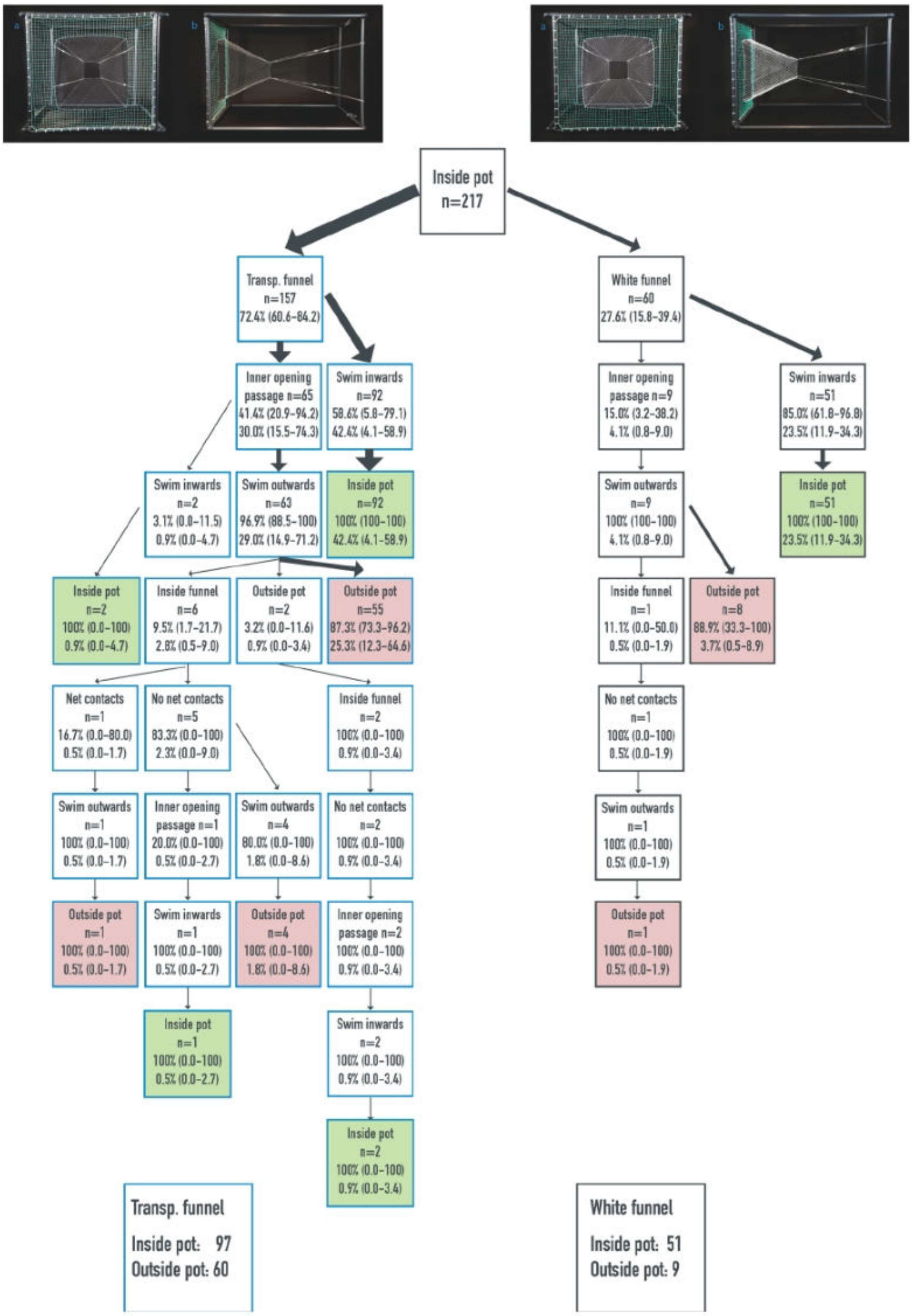

Fig. 10. Behavioural event-chain tree comparing the 'Transparent funnel' (Test) with the 'White funnel' (Control) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point in the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

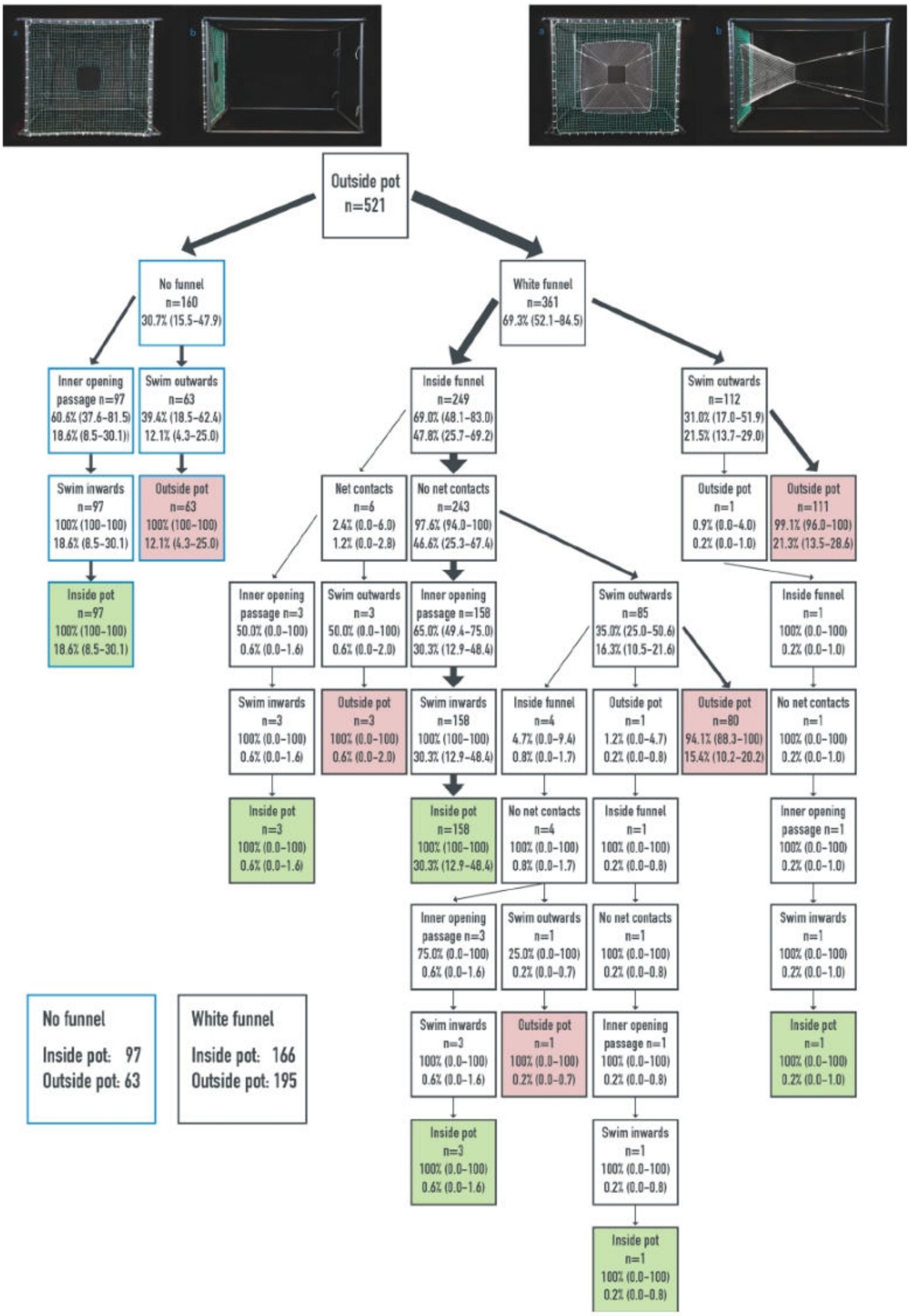

Fig. 11. Behavioural event-chain tree comparing the 'No funnel' (Test) with the 'White funnel' (Control) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point in the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

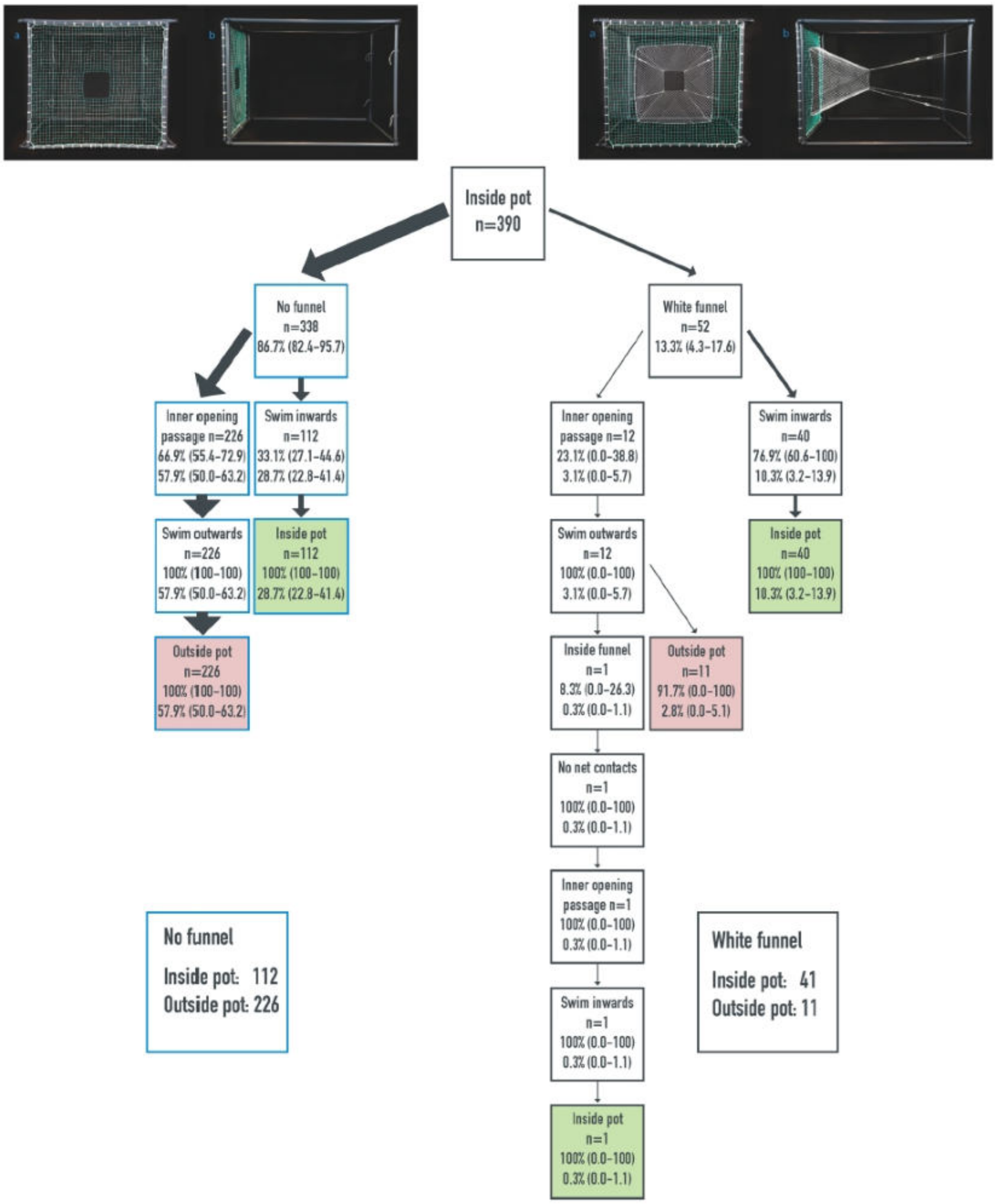

Fig. 12. Behavioural event-chain tree comparing the 'No funnel' (Test) with the 'White funnel' (Control) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point in the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

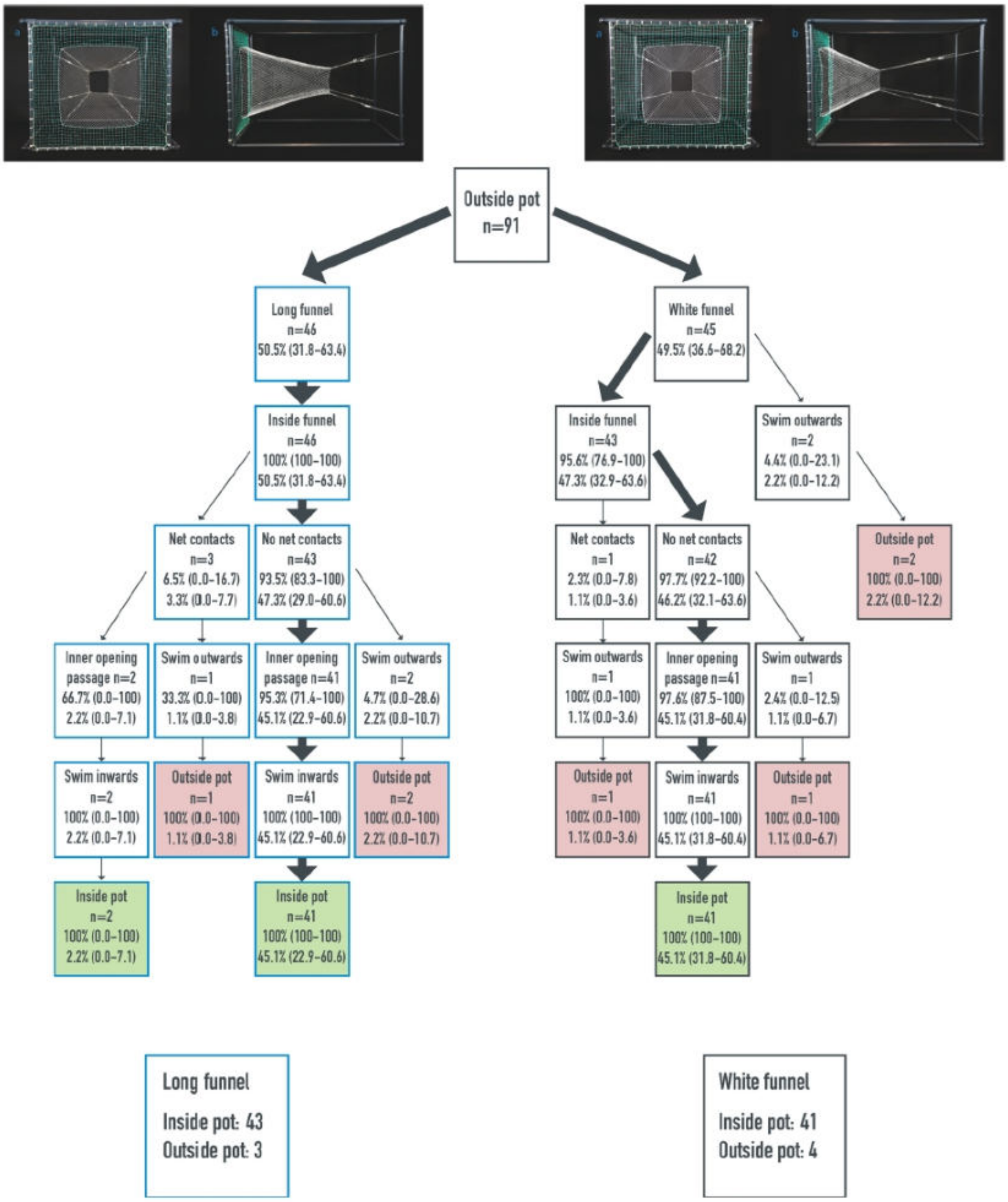

Fig. 13. Behavioural event-chain tree comparing the 'Long funnel' (Test) with the 'White funnel' (Control) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point in the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

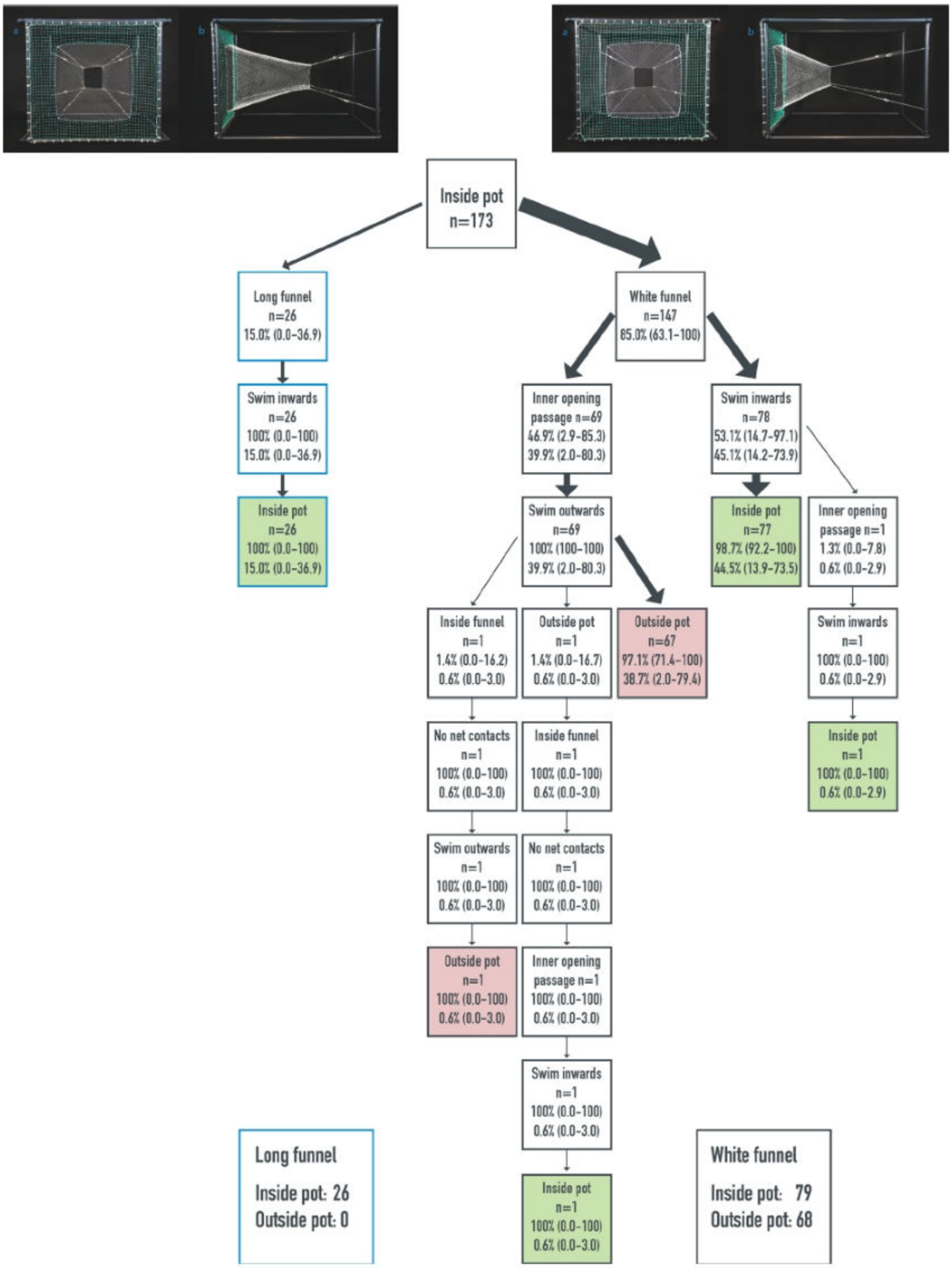

Fig. 14. Behavioural event-chain tree comparing the 'Long funnel' (Test) with the 'White funnel' (Control) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point in the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

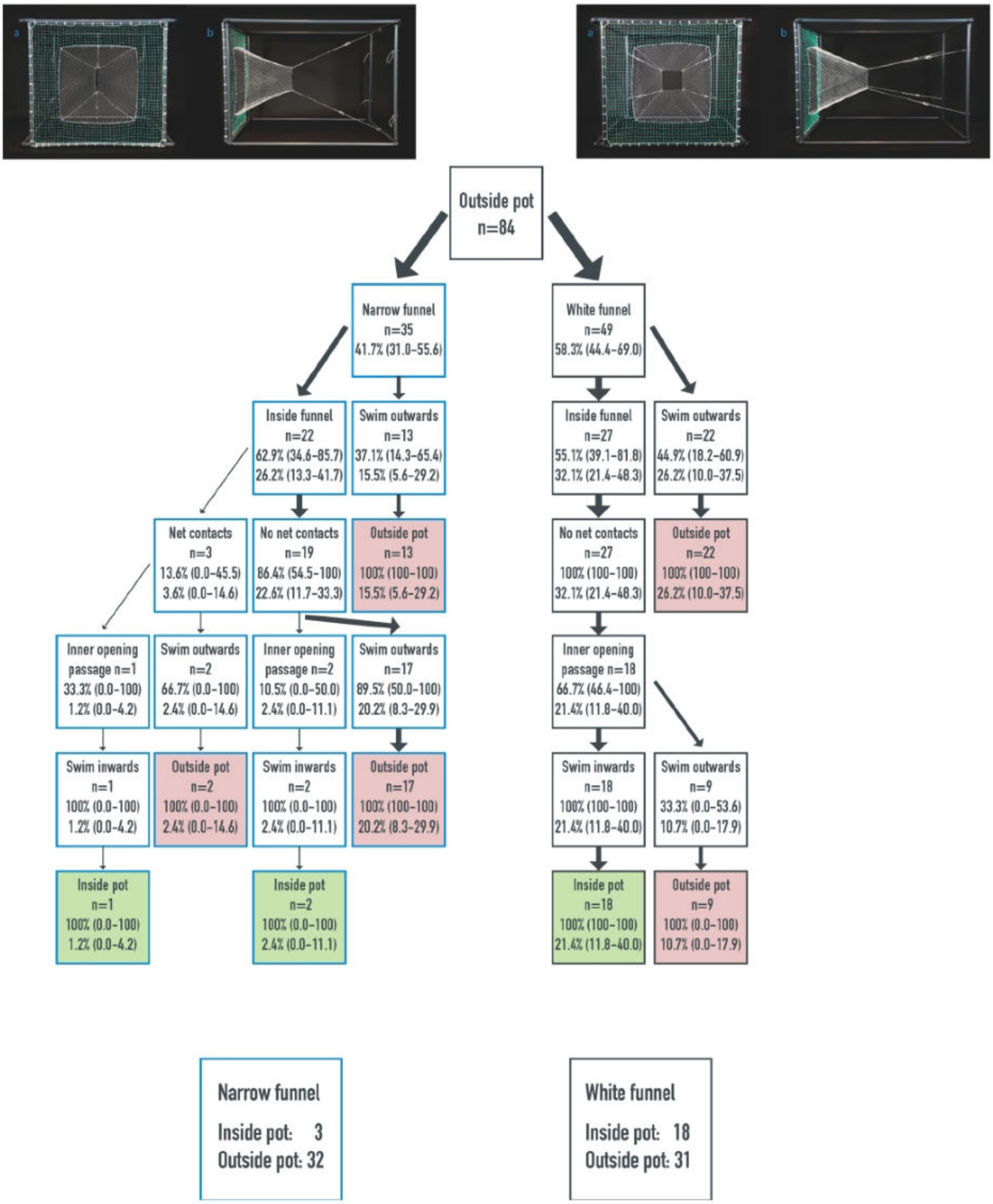

Fig. 15. Behavioural event-chain tree comparing the 'Narrow funnel' (Test) with the 'White funnel' (Control) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point in the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

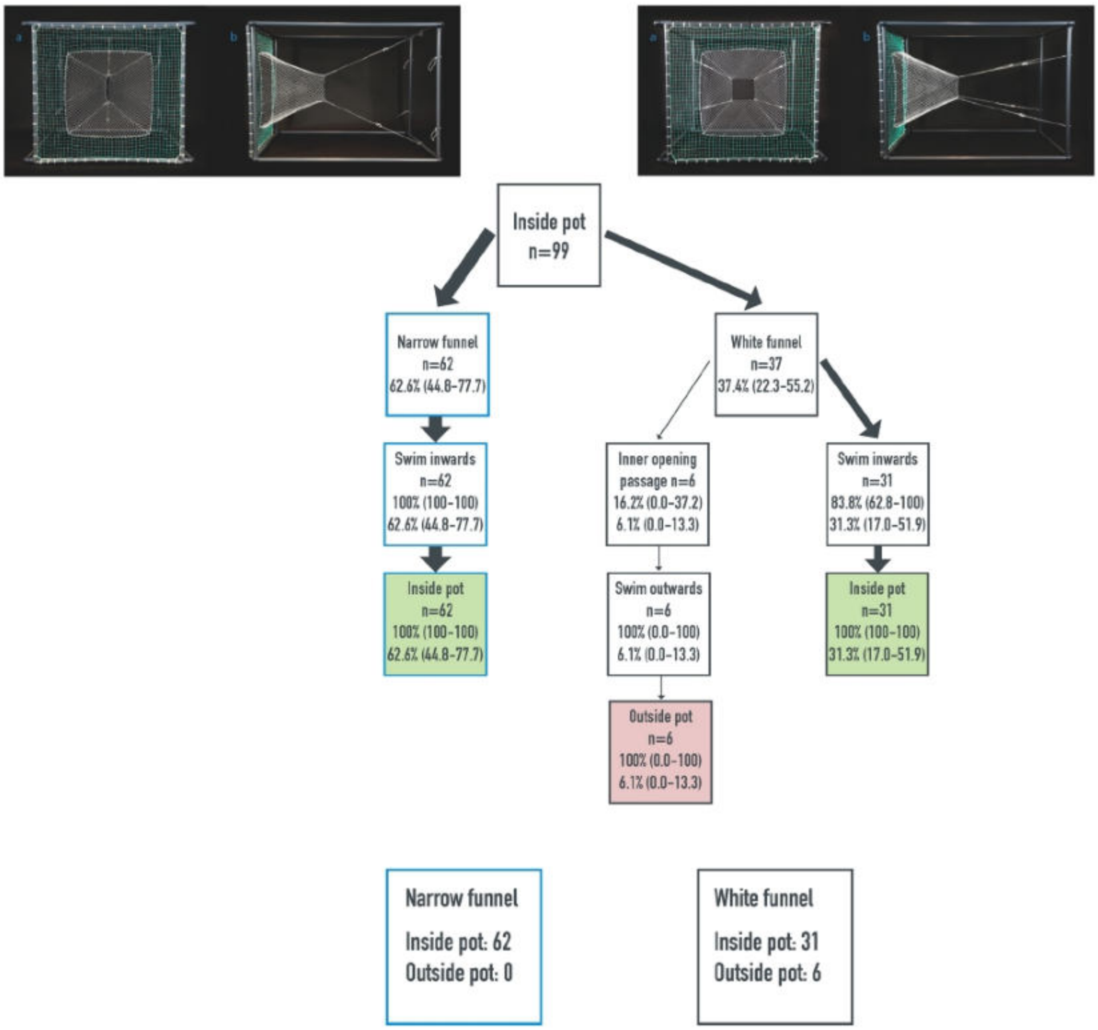

Fig. 16. Behavioural event-chain tree comparing the 'Narrow funnel' (Test) with the 'White funnel' (Control) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line gives the event type name; the second line gives number of times this event was observed at this point in the event chain; the third line gives the marginal probabilities (MP), related to the total number of interactions; and the last line gives the conditional probabilities (CP), related to the number of interaction in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

occurred almost exclusively through the 'No funnel' ($p(O = 1) = 0.95$). The behavioural event-chain tree for cod interactions starting outside the pot demonstrates that cod interacted significantly more often with the 'White funnel' control than with the 'No funnel' entrance (first level nodes in Fig. 11). However, of the cod approaching either entrance, the proportions aborting the entry attempt were similar (event chains 'Swim outwards' in Fig. 11). Nonetheless, a portion of the cod entering the control funnel aborted their entry attempt inside the funnel, reducing the entry efficiency of the control entrance at this point. Therefore, the lower entrance probability of the 'No funnel' entrance found by the GLM is caused by fewer cod encountering the 'No funnel' entrance. Inside the pot, significantly more cod interacted with the 'No funnel' than with the control entrance (Fig. 12). Only 13.3 % of the interactions were observed at the control entrance. Furthermore, significantly more cod interacting with the 'No funnel' entrance exited through it (66.9 %), whereas only 23.1 % of cod interacting with the control entrance passed it to the outside. Therefore, the 'No funnel' entrance has a significantly lower cod retention capability.

3.3.2. *Long funnel*

Two replicates of the comparison between the 'Long funnel' (75 cm) and 'White funnel' (50 cm; control) entrances were conducted (Table 4). No significant differences in the entry probabilities were observed ($p(I = 1) = 0.51$; Table 5). The almost identical behavioural event-chain tree branches support this observation (Fig. 13). In contrast, cod exited only through the control entrance, indicating that escapement through the 'Long funnel' is not the option preferred by cod. This is also apparent in the behavioural event-chain tree for inside interactions: Cod strongly preferred interacting with the control entrance; only 15.0 % of all inside pot interactions occurred at the 'Long funnel' entrance, with no CI overlap (Fig. 14). Furthermore, all interactions at the 'Long funnel' inner opening were aborted exit attempts, whereas 46.9 % of cod interactions at the control entrance ended with a successful passage towards the pot outside.

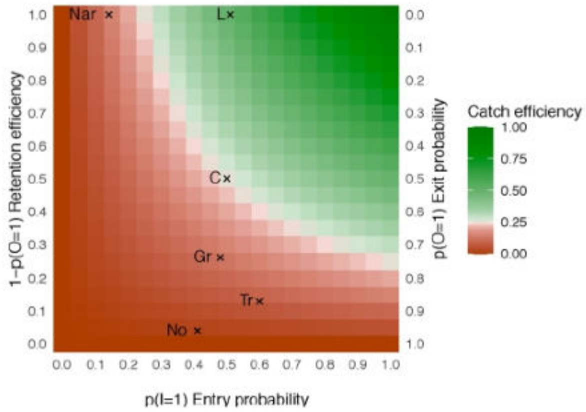

Fig. 17. Comparison of catch efficiency for pot-entrance types in catch efficiency matrix. 'C' = the control entrance; 'Gr' = 'Green funnel'; 'Tr' = 'Transparent funnel'; 'No' = 'No funnel'; 'L' = 'Long funnel'; 'Nar' = 'Narrow funnel'.

3.4. *Funnel shape: narrow*

Two replicates of the 'Narrow funnel' control entrance comparison were conducted (Table 4). Cod entered significantly more often through the control entrance and did not exit through the 'Narrow funnel'. The final model for entries includes neither side nor day period (Table 5). The low entry probability through the 'Narrow funnel' $p(I = 1) = 0.14$, and the fact that no cod exited through it, reveal a clear preference for the control entrance for entering as well exiting. The behavioural tree (Fig. 15) reveals that the significantly lower entry rate through the 'Narrow funnel' is not because fewer cod interacted with it, but because most cod turn around inside the funnel, just before the narrow inner opening. Although there were no exits through the 'Narrow funnel' entrance – vs. six exits through the control entrance (Table 4) – the number of interactions at the 'Narrow funnel' entrance was considerably larger (62.2 %) than at the control entrance, with little CI overlap (Fig. 16).

3.4.1. *Comparison of all entrances*

Because the final catch efficiency of pots is determined by the relationship between pot entry and exit rates, we directly compare all entrance types in a two-dimensional graph (Fig. 17), based on the expected probability of either entry $p(I = 1)$ and exit $p(O = 1)$ or retention $(1 - p(O = 1))$ in the test entrance. A catch efficiency of 0.25 indicates no difference between a test entrance and the reference control entrance, while a higher value indicates a higher catch efficiency than the control entrance and vice-versa (see chapter 2.6 "Statistical analysis"). The 'Green funnel' entrance performed worse than the control entrance because of a higher exit probability. Although the 'Transparent funnel' performed better for entries than the 'White funnel' entrance did, the overall catch efficiency was lower owing to the low retention capacity of this entrance. The 'No funnel' entrance is considerably less efficient than the control entrance, because it had fewer entries and more exits. Crucially, the exits were almost all exclusively through the 'No funnel' entrance. The 'Long funnel' entrance is considerably more efficient than the control entrance, because it does not differ in entry rate, whereas no exits occurred through the long funnel entrance. Although no cod exited the 'Narrow funnel' entrance, it was less efficient than the control entrance because significantly fewer cod entered through it.

3.5. *Entrance inspections and herding*

3.5.1. *Entrance inspections*

Cod inspected the entrances in 96.8 % of all interactions, revealing that cod are attentive to the structural entrance elements and pass entrances with caution. Event duration of all successful and unsuccessful passages by not-inspecting cod (8.7 ± 4.0 s), was significantly shorter than for inspecting cod (15.4 ± 16.3 s; Shapiro–Wilk test for normality of all event durations $W = 0.543$, $p < 0.001$; Wilcoxon test $W = 2312$, $p < 0.001$).

3.5.2. *Herding*

Herding events were rare, with only 8.4 % of (attempted) entries (n = 1464) and 4.5 % of (attempted) exits (n = 1156). Event duration of cod in herding events (7.8 ± 7.4 s) was significantly shorter than cod interacting alone with the entrances (15.7 ± 16.4; Wilcoxon test $W = 16658$, $p < 0.001$), indicating that cod in herding events moved faster, and so the speed of the lead cod triggered movements of the following cod.

4. Discussion

In this study, we successfully developed and applied a novel method to study the interaction between cod and pot entrances. The crucial relationship between pot entry and exit rates (Furevik and Løkkeborg, 1994; Hedgärde et al., 2016) was investigated for different funnel designs and allowed us to describe *how* and infer *why* cod interact differently with various entrances, which could not have been carried out with traditional catch comparison experiments. This study reveals that different entrances have strong effects on cod behaviour and so on the pot's catch efficiency. This understanding of behaviour is essential to improving pot design. In addition, it is the first study where cod–pot interactions were observed at night without strong lighting in the visible spectral range of cod, thus avoiding influencing behaviour.

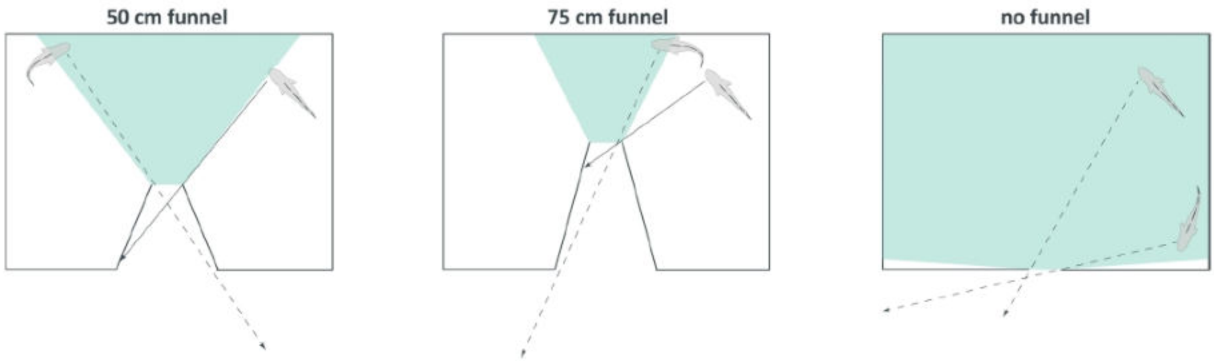

Fig. 18. Schematic illustration of area inside a fish pot with outside view through the funnel, depending on funnel length.

4.1. Diurnal entrance interactions are primarily vision-based

The activity pattern of cod follows a diurnal rhythm with reduced activity at night (e.g., Løkkeborg and Fernö, 1999), regulated by ambient light levels (Meager et al., 2005, 2010, 2018; Meager and Batty, 2007; Monk et al., 2006). The present study revealed that this also applies to interactions with pots, including slow movements of cod and almost no entrance passages at night. The rapid onset of entries and exits around dawn indicates that cod primarily use vision to locate and navigate through funnel entrances. This is corroborated by the fact that, in 96.8 % of all observed entrance interactions, cod visually inspected the entrances, whereas only 3.4 % of the interactions were accompanied by tactile probing. This tactile probing seems to be more relevant to the net-wall-guided search pattern during low light conditions, which results in more escapements through the 'No funnel' entrance than through funnel entrances, because funnels deflect fish away from the exit. Based on these findings, the increased nightly catch and entrance rates of illuminated cod pots (Bryhn et al., 2014; Hedgärde et al., 2016; Humborstad et al., 2018) could thus not only be the result of light attraction, but also the result of the illumination of the entrances, which allow cod to visually perceive and navigate through them into the pot. In contrast, the low-intensity lights might limit the visual dark adaptation of cod inside the pot without compensating with sufficient illumination to perceive the entrance netting clearly. Low-intensity lights could thus reduce their ability to exit the pot through the entrances. This could represent additional mechanisms explaining how lights increase pot-catch success.

4.2. Funnel colour

Funnel colour influenced cod passage through pot entrances. The results of the 'Transparent funnel' and the 'Green funnel' experiments underline the importance of colour and thus of cod vision in cod–pot entrance interactions. The white funnel of the control entrance resulted in a visibly strong contrast between the funnel, the background, and the green netting of the pot housing. For entries, the 'Green funnel' entrance performed similarly to the white control entrance with no differences found. However, the GLM model revealed a higher, but not significantly different, exit rate through the 'Green funnel', mostly the result of more exits during dusk and dawn, when some light was still available for orientation. Because the coastal waters at the site of the experiment had a green hue, the contrast between ambient light and green funnel netting seemed to appear lower than the white control funnel netting. Cod searching for an exit during twilight could thus have been drawn more towards the green funnel, which possibly appeared less conspicuous against the background, creating the appearance of an unobstructed passage. This would fit with previous findings that the visual stimulus of different netting colours against the background influences fish–gear interactions (summarised by Arimoto et al., 2010). The contrast between the 'Transparent funnel' and the background appears even more reduced. There were more passages through the 'Transparent funnel', indicating that cod searching for passage were attracted to it. Furthermore, many cod accidentally swam into the transparent funnel netting, indicating that they had problems perceiving it. Therefore, we propose that for cod to approach an entrance, they need to perceive it as an open passage into or out of the pot. This aligns well with the observation that cod and other fish species often fail to enter pots because they fail to locate pot entrances (e.g., Anders et al., 2016; Meintzer et al., 2017; Rose et al., 2005). Because the' Transparent funnel' exit probability was higher than the entry probability, the control entrance (and by transposition also the 'Green funnel' entrance) had better catch efficiency (Fig. 17). Nevertheless, the increased entry probability through the 'Transparent funnel', and the larger number of behavioural interactions with it, indicate development potential. For example, equipping transparent funnels with fish retention devices (FRD; Carlile et al., 1997; High and Ellis, 1973), which allow entry but not exit, could improve catch efficiency, provided the FRD does not disproportionally decrease the entry rate. Therefore, FRDs should also be transparent. Alternatively, the high exit rates of transparent funnels could be countered by including a second catch chamber situated above the first catch chamber as in the widely used Norwegian floated pot (Furevik et al., 2008). Lastly, these results also align with a recent two-year cod pot catch comparison study in Newfoundland and Labrador waters where the pots with transparent funnel netting outperformed the pot types with white funnel netting (Meintzer et al. 2018).

4.3. Funnel length

The results of the 'No funnel' and the 'Long funnel' entrance experiments highlight the importance of funnels for catch efficiency. The lower entry and higher exit rates through the 'No funnel' entrance, resulting in relatively poor catch efficiency of all tested entrance types, demonstrate that funnels are crucial to cod pots, congruent with a previous field-pot-entrance video study (Ljungberg et al., 2016). Significantly fewer cod approached the 'No funnel' entrance from the outside. Therefore, cod searching for a way into the pot had a greater chance of encountering the control entrance, probably because its outer opening area is nine times larger than the 'No funnel' entrance. The funnel colour experiments indicate that a clear unobstructed view of the pot outside is important for enticing cod inside the pot to approach the entrance. Although the view of the pot's outside is limited in most positions inside the pots with funnel entrances, it is mostly unobstructed for the 'No funnel' entrance (Fig. 18), thus attracting cod to it. Additionally, this is reinforced by the observed net-wall-guided search behaviour at twilight. The increase in funnel length resulted in greater catch efficiency, because significantly fewer cod approached the 'Long funnel' from inside and none exited through it. This could also be because the pot area, from which the pot exterior is visible through the 'Long funnel', is smaller than the control entrance with shorter funnel length (Fig. 18). Nevertheless, there were 26 aborted inside approaches to the 'Long funnel' inner opening. This indicates that the funnel length itself also has an exit-impeding effect. These findings may further explain the larger catch taken in larger pots (e.g., Bagdonas et al., 2012; Furevik and Løkkeborg, 1994; Hedgärde et al., 2016; Munro, 1974), because larger pots can accommodate longer funnels and have more space in the pot without unobstructed view of the outside through the funnels. The positive effect, however, can be expected to have a tipping point when the funnel is so long that cod searching along the back net wall find the funnel inner opening in their nearfield and exit through it, and when the pot inside is too far away for cod outside the pot to be enticed to enter.

4.4. Funnel shape: narrow funnel

Although no cod exited through the 'Narrow funnel' entrance, its catch efficiency was relatively poor, because it had almost no entries. The low entry rate was caused by more cod aborting entry attempts inside the funnel, which supports previous findings that cod do not like to pass through narrow entrances (Pol et al., 2010). Narrow funnel entrances for cod potting are thus not advisable.

4.5. The influence of social behaviour on entrance interactions

In addition to basic design parameters of the entrances, social behaviour influenced entrance interactions. The significantly higher speed of cod in leader–follower events indicates that the speed of the leader cod cues other cod to follow the leader. This fits with a previous study that reveals that leaders of cod shoals arriving at a feeding station have the highest arrival speed and are able to train naïve cod (Björnsson et al., 2018). Also, the decision of cod to enter a pot is often socially mediated (Anders et al., 2017; Hedgärde et al., 2016) and generally, cod rely on social cues when foraging (Meager et al., 2018).

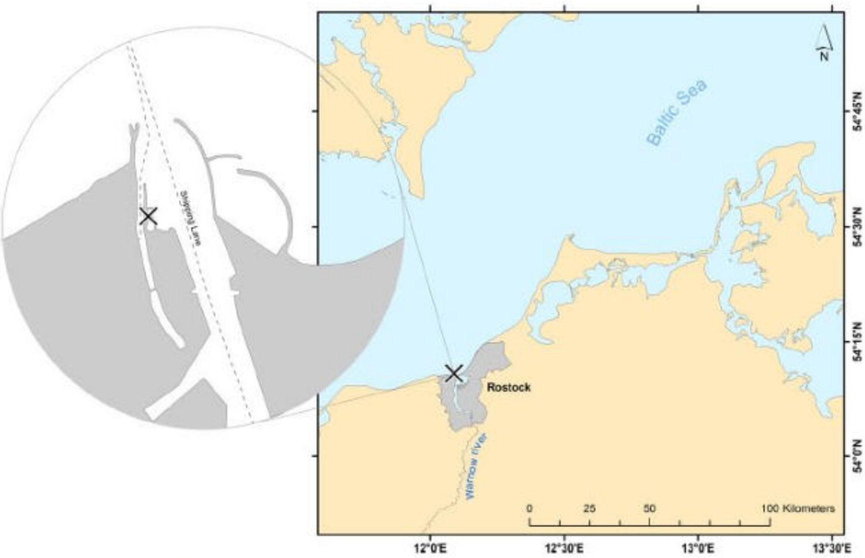

Fig. A1. The experiment's location in sporting marina Rostock-Warnemünde, Germany.

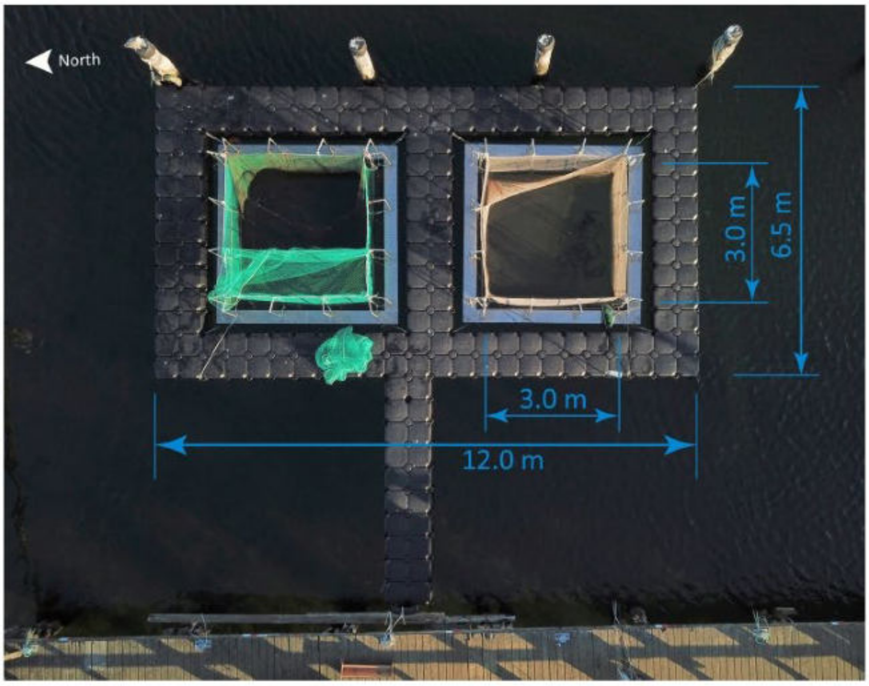

Fig. A2. Net-pen facility in Rostock-Warnemünde, Germany. Aerial view. The right net pen (south) is the experimental net pen; on the left (north) is the holding pen.

4.6. Conclusion and outlook

The findings presented here lead to the following recommendations on entrance design and cod-pot fishing strategy: Increasing funnel length may reduce exit rates (but bearing in mind a potential turnaround point). Funnels should be set into the pot to minimise the area inside the pot from which the pot outside can be seen through the inner funnel opening. Transparent funnel netting allows for higher entry rates, but is recommended mainly when FRDs are attached to an entrance (Carlile et al., 1997; Furevik, 1994; High and Ellis, 1973; Munro, 1974), or a second catch chamber (Furevik, 1994; Furevik et al., 2008) is added to the pot design to mitigate the increased exit probability through the transparent funnel. Ideal setting time of the day of pots equipped with olfactory bait is at dawn, because olfactory bait rapidly loses its attractive capacity after only 1.5 h soak time (Løkkeborg, 1990; Westerberg and Westerberg, 2011). This assures a strong attraction at the time of the day with highest cod-pot entry rates. Furthermore, the strong effects of entrances observed in this study and the detailed insights gained demonstrate the efficiency of the net-pen-based approach to studying cod–pot interactions. Furthermore, the bootstrap-based,

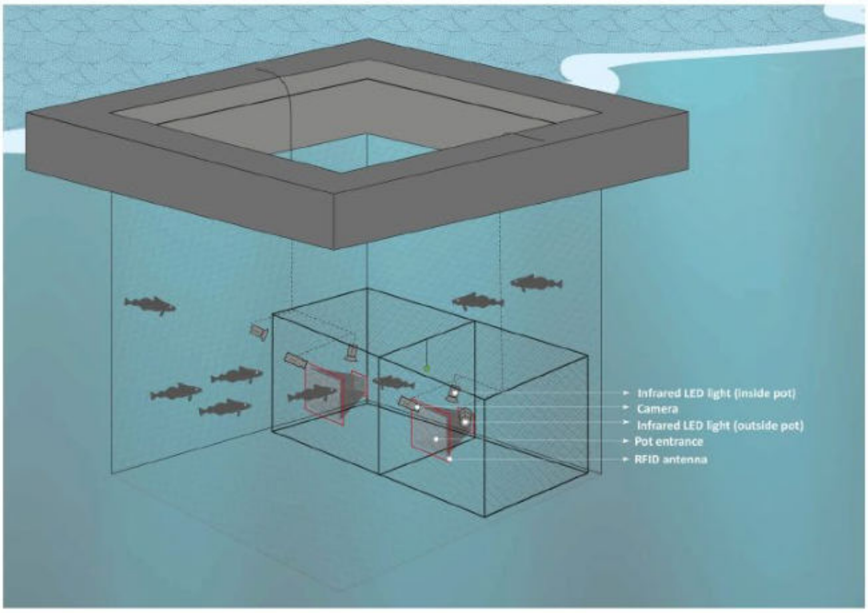

Fig. A3. Schematic representation of the experimental setup. An experimental pot with two exchangeable entrances is lowered into a 3 × 3 × 3 m net pen. Cod inside the pot are free to swim from one entrance to the other. For observation, an IR-camera system (one camera and one IR light before the entrance, one IR light inside the pot above the inner opening of the funnel), and two RFID antennae are mounted at each entrance. Note: Owing to technical difficulties, RFID data could not be used in the data analysis.

Fig. A4. Experimental pot with two exchangeable entrances. Two IR cameras (1) in front of each funnel entrance and two IR lights (2) on each entrance side (one inside above the funnel inner opening, the other outside next to the IR cameras). Black frames around funnels are RFID antennae (3). Note: Owing to technical difficulties, RFID data could not be used in the data analysis.

behavioural-tree method allows the interaction process to be 'dissected' and the cause of the observed differences to be identified. In this study, we used this approach to investigate the effect of different entrance designs on the entry and exit behaviour of cod. Other pot design parameters, such as FRDs, pot size and shape (e.g., Hedgärde et al., 2016), or entrance opening size and shape (e.g., Königson et al., 2015b; Ljungberg et al., 2016) can also influence the catch efficiency of pots, and should be investigated using this method. Based on such experiments, optimised pot designs can be efficiently developed, and their ultimate catch efficiency can be subsequently tested in field trials.

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CRediT authorship contribution statement

Jérôme Chladek: Conceptualization, Methodology, Validation,

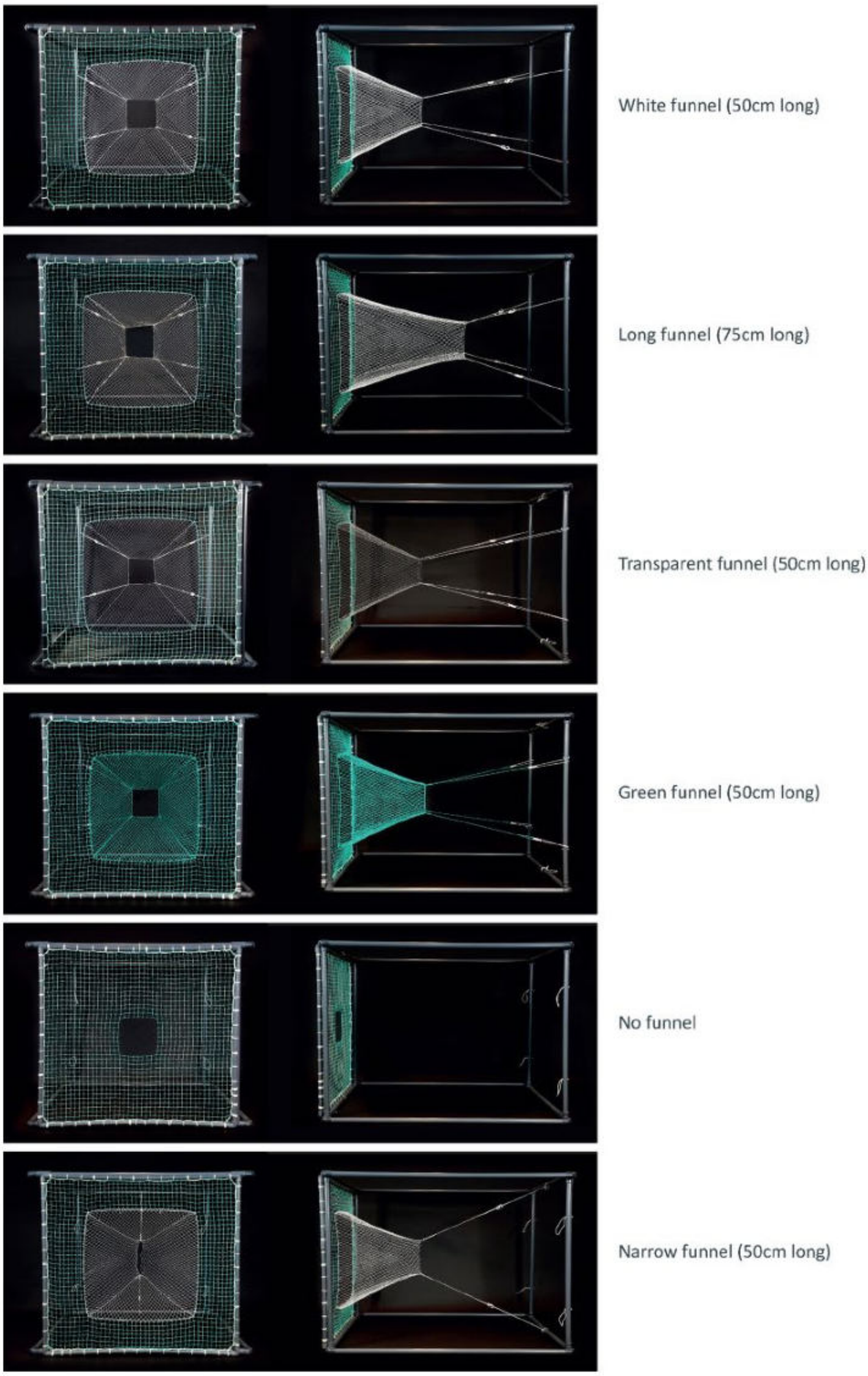

Fig. A5. Front and side views of all experimental entrances.

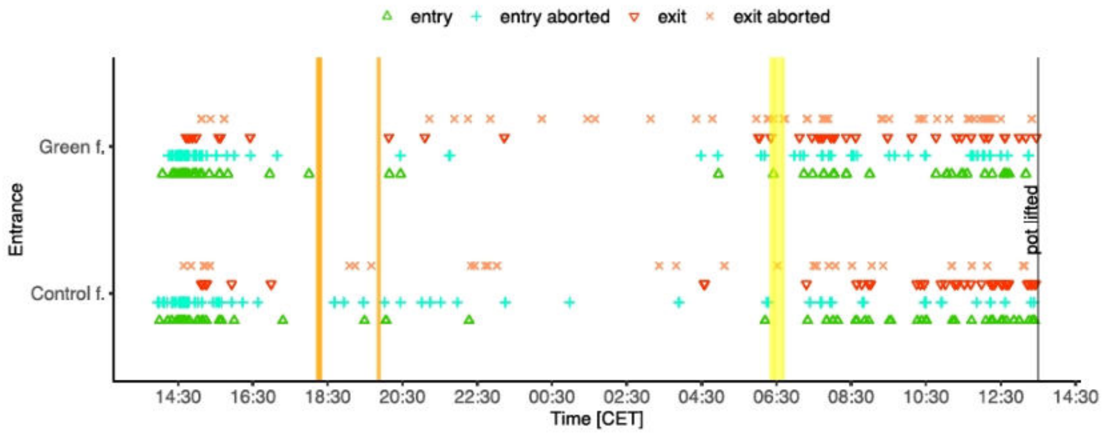

Fig. A6. Gant chart of entry, aborted entry, exit and aborted exit events of all 'Green funnel' experiments with entrances including funnels (six trials). Vertical lines indicate sunset, sunrise times, and time pot lifted respectively.

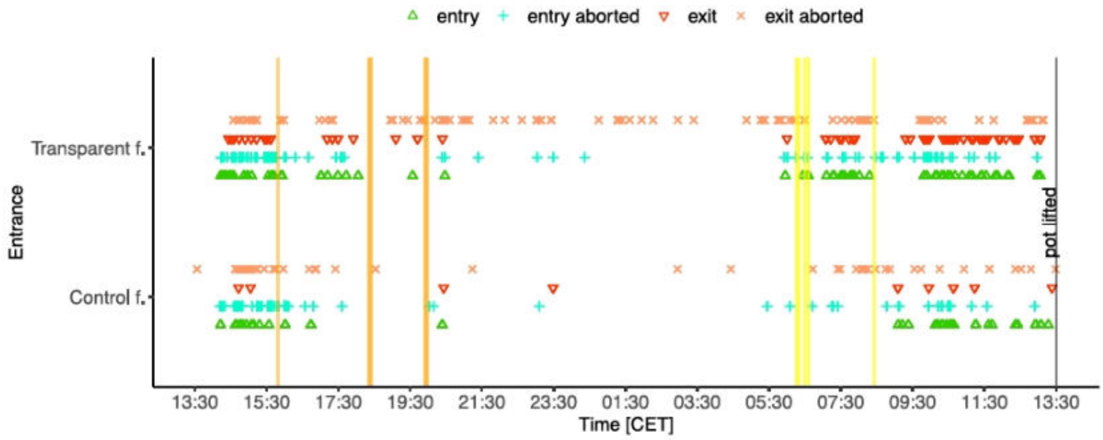

Fig. A7. Gant chart of entry, aborted entry, exit and aborted exit events of all 'Transparent funnel' experiments with entrances including funnels (six trials). Vertical lines indicate sunset, sunrise times, and time pot lifted, respectively.

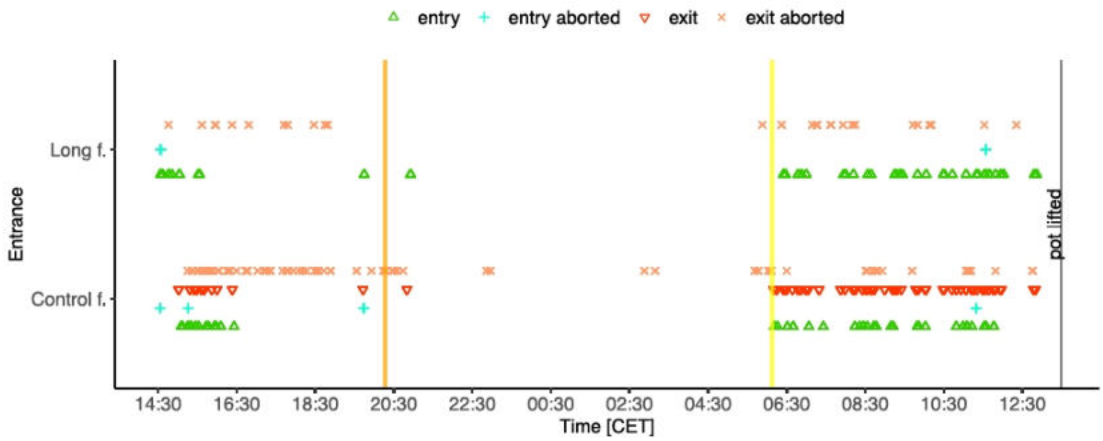

Fig. A8. Gant chart of entry, aborted entry, exit and aborted exit events of all 'Long funnel' experiments with entrances including funnels (two trials). Vertical lines indicate sunset, sunrise times, and time pot lifted, respectively.

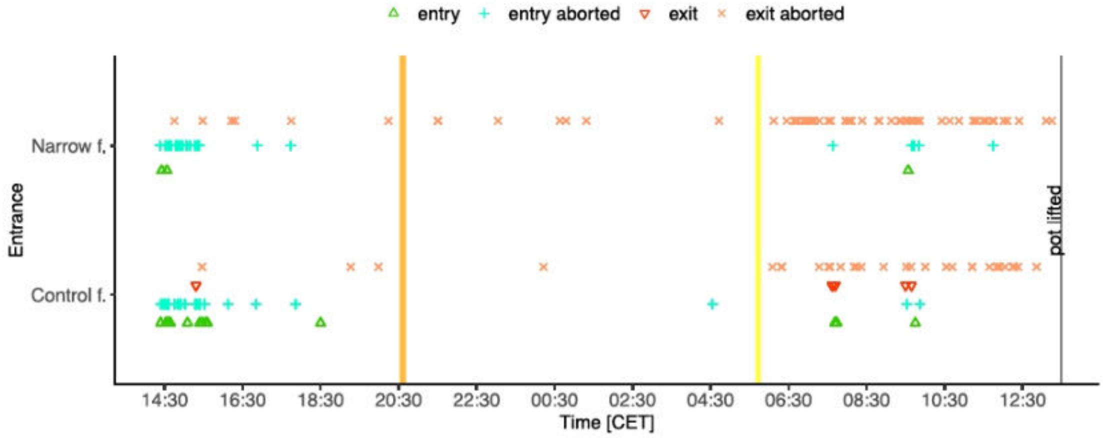

Fig. A9. Gant chart of entry, aborted entry, exit and aborted exit events of all 'Narrow funnel' experiments with entrances including funnels (two trials). Vertical lines indicate sunset, sunrise times, and time pot lifted, respectively.

Table A1
Overview of all trials conducted for different entrance types (Test) compared with 'White funnel' entrance (Control): Start, end times and total duration of all entrance experiments. Time gaps equals the total duration of gaps in video recordings. End time is the time when the experimental pot was lifted.

Tested entrance	Start time	End time (pot lifted)	Duration [hh:mm]	Time gaps [hh:mm]
Green funnel	14.03.2019 15:27	15.03.2019 13:28	22:01	00:16
Green funnel	15.03.2019 14:27	16.03.2019 13:42	23:15	00:10
Green funnel	16.03.2019 14:11	17.03.2019 13:32	23:21	00:14
Green funnel	17.03.2019 14:02	18.03.2019 13:28	23:26	00:32
Green funnel	03.04.2019 14:15	04.04.2019 13:29	23:14	00:20
Green funnel	04.04.2019 14:15	05.04.2019 13:30	23:13	00:24
Transparent funnel	14.12.2018 15:57	15.12.2018 13:56	21:58	00:15
Transparent funnel	18.03.2019 15:04	19.03.2019 13:29	22:26	00:13
Transparent funnel	19.03.2019 15:28	20.03.2019 13:29	22:01	00:18
Transparent funnel	20.03.2019 14:10	21.03.2019 13:31	23:21	00:24
Transparent funnel	05.04.2019 14:24	06.04.2019 13:29	23:05	00:09
Transparent funnel	07.04.2019 14:03	08.04.2019 13:30	23:27	00:38
No funnel	19.12.2018 14:52	20.12.2018 13:15	22:23	00:15
No funnel	20.04.2019 14:07	21.04.2019 13:30	23:22	00:07
No funnel	21.04.2019 14:28	22.04.2019 13:29	23:01	02:15
Long funnel	16.04.2019 14:34	17.04.2019 13:32	22:58	00:56
Long funnel	17.04.2019 14:43	18.04.2019 13:11	22:28	00:13
Narrow funnel	26.04.2019 14:21	27.04.2019 13:27	23:06	00:14
Narrow funnel	28.04.2019 14:22	29.04.2019 13:27	23:04	00:30

Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Daniel Stepputtis:** Conceptualization, Investigation, Methodology, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition, Writing - review & editing. **Andreas Hermann:** Investigation, Methodology, Software, Writing - review & editing. **Isabella M.F. Kratzer:** Conceptualization, Investigation, Visualization, Writing - review & editing. **Peter Ljungberg:** Conceptualization, Methodology, Visualization, Writing - review & editing. **Paco Rodriguez-Tress:** Investigation, Methodology, Formal analysis, Visualization, Writing - review & editing. **Juan Santos:** Methodology, Formal analysis, Writing - review & editing. **Jon C. Svendsen:** Methodology, Resources, Writing - review & editing.

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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Appendix

Table A2
GLM entries and exit GLM AICs of all tested entrance experiments. Models in bold selected by lowest AIC.

Test entrance	Direction	Model	AIC
Green funnel	Entries	$\boldsymbol{\eta X = \beta_0}$	170.83
		$\eta X = \beta_0 + \beta_1 * side$	172.82
		$\eta X = \beta_0 + \beta_2 * dayperiod$	172.77
		$\eta X = \beta_0 + \beta_1 * side + \beta_2 * dayperiod$	174.75
	Exits	$\eta X = \beta_0$	113.98
		$\eta X = \beta_0 + \beta_1 * side$	113.58
		$\eta X = \beta_0 + \beta_2 * dayperiod$	113.37
		$\boldsymbol{\eta X = \beta_0 + \beta_1 * side + \beta_2 * dayperiod}$	113.20
Transparent funnel	Entries	$\boldsymbol{\eta X = \beta_0}$	149.03
		$\eta X = \beta_0 + \beta_1 * side$	151.03
		$\eta X = \beta_0 + \beta_2 * dayperiod$	151.01
		$\eta X = \beta_0 + \beta_1 * side + \beta_2 * dayperiod$	153.01
	Exits	$\boldsymbol{\eta X = \beta_0}$	55.44
		$\eta X = \beta_0 + \beta_1 * side$	57.40
		$\eta X = \beta_0 + \beta_2 * dayperiod$	55.59
		$\eta X = \beta_0 + \beta_1 * side + \beta_2 * dayperiod$	57.48
No funnel	Entries	$\eta X = \beta_0$	348.28
		$\boldsymbol{\eta X = \beta_0 + \beta_1 * side}$	293.26
		$\eta X = \beta_0 + \beta_2 * dayperiod$	349.42
		$\eta X = \beta_0 + \beta_1 * side + \beta_2 * dayperiod$	293.80
	Exits	$\eta X = \beta_0$	91.02
		$\boldsymbol{\eta X = \beta_0 + \beta_1 * side}$	90.65
		$\eta X = \beta_0 + \beta_2 * dayperiod$	92.99
		$\eta X = \beta_0 + \beta_1 * side + \beta_2 * dayperiod$	92.57
Long funnel	Entries	$\boldsymbol{\eta X = \beta_0}$	118.4
		$\eta X = \beta_0 + \beta_1 * side$	120.05
		$\eta X = \beta_0 + \beta_2 * dayperiod$	119.05
		$\eta X = \beta_0 + \beta_1 * side + \beta_2 * dayperiod$	120.65
	Exits	No exits through 'Long funnel'	–
Narrow funnel	Entries	$\boldsymbol{\eta X = \beta_0}$	19.22
		$\eta X = \beta_0 + \beta_1 * side$	21.19
		$\eta X = \beta_0 + \beta_2 * dayperiod$	no entries at night
		$\eta X = \beta_0 + \beta_1 * side + \beta_2 * dayperiod$	no entries at night
	Exits	No exits through 'Narrow funnel'	–

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Paper IV:

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Development and testing of fish-retention devices for pots: transparent triggers significantly increase catch efficiency for Atlantic cod (*Gadus morhua*)

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Fish pots have lower catch efficiency than gillnets and trawls and, therefore, are rarely used for catching Atlantic cod (*Gadus morhua*) and similar species. Fish-retention devices (FRDs), non-return devices that permit fish to enter the pot while impeding exit, reduce the pot exit rate and therefore can increase catches. Conventional FRDs, however, also reduce entry rate and may not improve catches. To increase pot-catch efficiency, we developed and tested a new trigger-type FRD, made of transparent acrylic glass, which we named acrylic fingers (AFs). AFs are almost invisible underwater and offer little resistance to entering cod. We compared AFs with Neptune fingers (NFs), a conventional trigger-type FRD with a distinct visual outline, by observing cod entry and exit rates through both trigger types rigged to a pot in a net pen. Both trigger types significantly reduced exit rates compared with a funnel without triggers; however, NFs also reduced entry rates by visually deterring cod. Specifically, AFs have higher entry-to-exit ratios and therefore improve catch efficiency. Combining AFs with funnels further increased catch efficiency. Thus, transparent acrylic triggers present a promising new approach to increasing pot-catch efficiency and may increase the uptake of the cod pot, an environmentally low-impact gear.

Keywords: catch efficiency, fish–gear interaction , fish pots, fish-retention device, passive fishing gear, pot entry-to-exit ratio

Introduction

Fishing affects marine ecosystems in many ways, including overfishing, impacts on the benthic environment, bycatch, and ghost fishing through lost or discarded fishing gear (e.g. Gilman *et al.*, 2005, 2006; Suuronen *et al.*, 2012; Žydelis *et al.*, 2013; Grabowski *et al.*, 2014; Lewison *et al.*, 2014; Gilman, 2015). Fish pots, relatively small, easily transported, and typically boxlike fishing gears, have a comparatively small environmental impact (Thomsen *et al.*, 2010; Shester and Micheli, 2011; Suuronen *et al.*, 2012; Grabowski *et al.*, 2014), an easily adjustable target-species size selectivity (Ovegård *et al.*, 2011), and they deliver the catch alive and so in prime quality (Furevik, 1994; Thomsen *et al.*, 2010; Suuronen *et al.*, 2012; Humborstad *et al.*, 2016). Therefore, increasing gear switch towards pots could reduce fishery-related environmental impacts and thus contribute to objectives including ensuring sustainability of fisheries, as set out in Goal 14 of the United Nation's Sustainable Development Goals [UN (United Nations), 2015], or more specifically in the European Common Fisheries Policy's Basic Regulation [EP (European Parliament) and EU Council (Council of the European Union), 2013]. To date, low pot-catch efficiency for many fish species, e.g. Atlantic cod, limits the use of fish pots in most fisheries (Furevik and Hågensen, 1997; Suuronen et al., 2012; Anders et al., 2017a; Jørgensen et al., 2017; Meintzer et al., 2018). To increase the use of fish pots, their catch efficiency must be improved. Efficiency depends greatly on the pot entry and exits ratios, which are influenced in turn by the entrance design. An approach to reducing exits involves equipping pot entrances with fish-retention devices (FRDs; e.g. Carlile et al., 1997). One type of FRD has semi-rigid, finger-like structures made of metal or plastic, so-called triggers. Fish coming from outside can push inside with little effort, but not vice versa, because the fingers impede exiting. Triggers are used in Atlantic cod pot fishing in Newfoundland (Meintzer et al., 2018). They were shown to increase the pot-catch rate up to 17-fold for Pacific cod (*Gadus microcephalus*; Carlile et al., 1997). Later studies of trigger-equipped pots in fisheries targeting Atlantic cod, however, have reported lower catch rates, with the observation that cod turn around towards the pot exterior right in front of the triggers (Olsen, 2014; Meintzer et al., 2017, 2018). This results in disproportionally fewer entries, resulting in reduced catch efficiency. All trigger types studied present a distinct visual outline to approaching cod. A recent study observing cod interaction with different entrance types in a net pen revealed increased cod passage rates (entry and exit) through transparent funnels, which apparently appear like a large unobstructed passage to approaching cod (Chladek et al., 2020). This indicates that cod primarily use vision to assess an entrance. Lightweight transparent triggers offer little resistance to entering cod and are less perceptible or possibly imperceptible to the cod until they touch it. These qualities could harness the triggers' exit-blocking properties without decreasing entries.

In this study, we designed, assessed, and compared a new transparent trigger type with commercially available, non-transparent triggers. The transparent trigger FRD is made of transparent acrylic glass, which has a refractive index for visible light similar to seawater (Malitson, 1965; Austin and Halikas, 1976), making it almost invisible underwater. Also, because its density resembles seawater, an acrylic trigger finger can easily be pushed inwards by entering cod, offering little resistance. The transparency and low resistance to entering fish are thus what sets this acrylic trigger concept apart from prior conventional trigger types and could potentially improve pot catchability. As conventional triggers, we tested "Neptune fingers" (NFs; Neptune Marine Products, USA). They have been found to increase the pot-catch rate for Pacific cod (Carlile et al., 1997) but have not been evaluated for Atlantic cod. This study aimed to assess whether not the transparent triggers FRDs and NFs improve Atlantic cod pot-catch efficiency. Furthermore, we assessed whether the use of triggers renders funnels obsolete, or if a combination of the two elements improves fish pot-catch efficiency.

Material and methods

Experiments were conducted during April–May 2019 in the sporting marina of Rostock-Warnemünde, Germany (Supplementary Figure S1; 54°10′52.7″N 12°05′18.0″E). Cod were caught off the coast of Rostock-Warnemünde, near the location of the experiments, using bottom trawl, fish pot, or hook and line. To minimize stress and exhaustion for the cod, fishing depths were always shallower than 20 m and trawl haul duration was limited to 30 min. Cod were fed *ad libitum* with thawed and cut herring (*Clupea harengus*) once a week. Before experiments, cod were not fed for at least a week, as elevated hunger levels of fish often elevate motivation to enter fish pots (Thomsen et al., 2010; Ovegård et al., 2011, 2012; Ljungberg et al., 2016). Because the motivation of cod to enter pots is socially mediated (Anders et al., 2017a) and because cod pots are usually encountered by more than one cod (e.g. Anders et al., 2017b; Hedgärde et al., 2016; Ljungberg et al., 2016), groups of eight cod, or in one trial seven cod, were used in each trial. Because cod are cannibalistic (e.g. Hardie and Hutchings, 2011), and to avoid social stress, individuals in the groups were of similar length ranges (30–39, 40–49, or 50–59 cm). Cod were kept at least 3 days in the holding net pen before inclusion in an experimental trial. Water temperature ranged from 5.5°C from the beginning of the experiment on 14 March to 13.0° at the end of the experiment on 25 May.

Set-up of the experiment

Two identical net pens ($3\ m \times 3\ m \times 3\ m = 27\ m^3$; Mieske, 1998; see Supplementary Figure S2) were used: one for experimental treatments and the other for holding the fish before experiments. An experimental pot (W 250 cm × D 140 cm × H 100 cm) with two side-by-side entrances was constructed and positioned inside the net pen (Supplementary Figures S3 and S4). It was made of standard polyvinyl chloride (PVC) tubes and green PE netting (polyethylene, 25-mm bar length). Fish pot entrances were mounted on PVC-tube frames (120 cm × 100 cm) and could be interchanged. We used a funnel as the baseline entrance type for indirect comparison of trigger performance [white multifilament polyamide (PA) netting of 0.9 mm twine diameter, 50 cm long, with a 60 cm × 60 cm outer opening and a 20 cm × 20 cm inner opening; Figure 1 upper part; hereafter termed "Fun" entrance]. The funnel had 25 mm mesh bar lengths. The general design was based on the two-chambered cod pot developed by Furevik et al. (2008) and used in several pot studies (e.g. Ovegård et al., 2011; Bryhn et al., 2014; Jørgensen et al., 2017).

Because the space available in the net pen was limited, we used a square opening design instead of the rectangular opening used by Furevik et al. (2008). To isolate the trigger effect from the funnel effect and to investigate if funnels are still needed when triggers are used, we also conducted experiments with the triggers attached to a simple 20 cm × 20 cm opening in the pot net wall (Figure 1, lower part).

Movement was not limited inside the pot, and cod could move freely from one entrance to the other. To provide a long-lasting attractant to lure cod into the pot, we used a green fishing bait light typically used for pots and longlines (Bryhn et al., 2014), hung in the middle of the pot in equal distance to both entrances (Supplementary Figure S3). Data were collected in paired trials, each experimental trial consisting of two different entrances set together into the pot. To avoid possible bias resulting from cod side preferences, at least two replicates were conducted for each comparison, while switching the side of entrance types. Each individual trial was conducted from ~14:00 to 13:30 the following day. For each trial, the cod were first set into the experimental pen and then the pot was lowered into the net pen, starting the experiment. In total, 18 trials were conducted.

FRDs

The transparent triggers, named acrylic fingers (AFs hereafter), were constructed from 3-mm-thick acrylic glass, 266-mm long, laser cut to size. They had pinholes in their head by which they were threaded onto a 2.5 mm-diameter aluminium rod. Fourteen

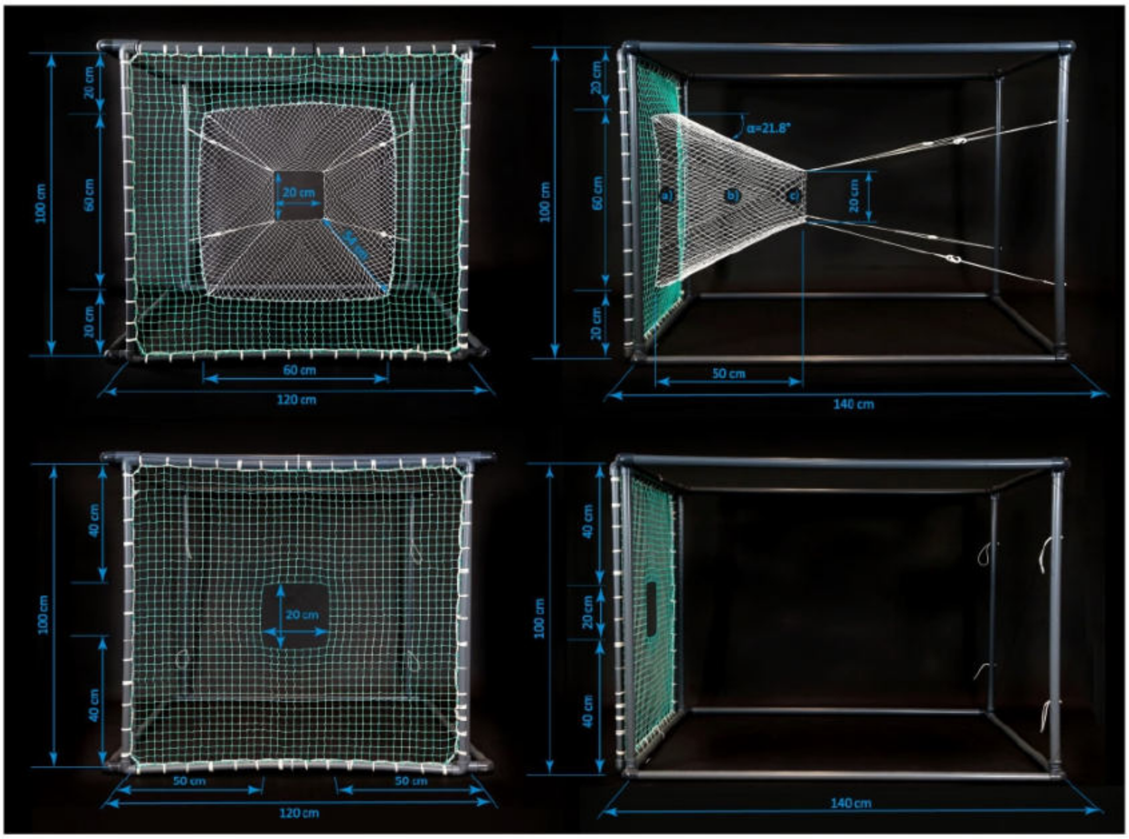

Figure 1. Above: "Fun" entrance (white PA funnel, 25-mm bar width, a 60 cm × 60 cm outer opening and a 20 cm × 20 cm inner opening, length 50 cm) used for experiments. Left: front view; right: side view. The nomenclature describing the parts of a cod entrance is indicated on the upper side view: (a) outer opening; (b) funnel; and (c) inner opening. Below: "No funnel" entrance ("NoFun"). Left: front view; right: side view. Its single opening is also referred to as "Inner opening" in the analysis.

round washers in the same material and thickness as the fingers' heads were spaced at 42-mm intervals on either sides of each finger. We chose a relatively large diameter for the head and washers to increase the fingers' side stability. We oriented the AF inter-finger space width to the 45-mm inter-finger space of the NF (described below), setting it 3-mm smaller because the AFs are less rigid than the NFs. Furthermore, this is between the 40- and 45-mm pot selection windows mesh size that Ovegård *et al.* (2011) reported as having a L_{50} of 32 and 38 cod total length and therefore was adequate to meet the 35-cm cod minimum conservation reference size (MCRS) for cod in the Baltic Sea. Assembled AF triggers had five fingers (Figure 2). Three additional washers were set at the outside of the two outer fingers. The AF's total width was 201 mm. A cable tie on each end fixed washers and fingers in place while allowing them to turn up and down, which could then be attached to the pot entrance with a further zip tie pair (see below). The AFs were almost imperceptible underwater (Figure 2). They were longer than the NoFun entrance height. Because the AF fingertips were hanging inside the pot, they could only be lifted towards the pot inside. In water, the weight of the AF was reduced and cod could easily lift the fingers when entering the pot.

Parts for the NF triggers were sourced from the manufacturer Neptune marine products (US, http://neptunemarineproducts.com/). The NF we tested was held together by two black "7-in end pieces" on each side and a red "regular finger unit" above and below. The regular finger units were angled towards each other so that their fingertips were almost touching (Figure 2), according to the manufacturer's instructions. The space between two fingers of the regular finger unit was 45 mm. The inner width of the NF frame was 19.5 cm. Both types of assembled trigger units were attached to the entrances with thin white cable ties. The NoFun entrances equipped with the NF and AF triggers are hereafter referred to as NoFun + NF and NoFun + AF, respectively. The Fun entrances equipped with NF and AF triggers are hereafter referred to as Fun + NF and Fun + AF, respectively.

Fish observation

Infra-red camera system

To observe cod at night without influencing their behaviour, we used an infra-red (IR) lamp and camera system, known as IR Fish Observation (iFO; Hermann *et al.*, 2020). The system can record videos at visible and IR light and has a minimum

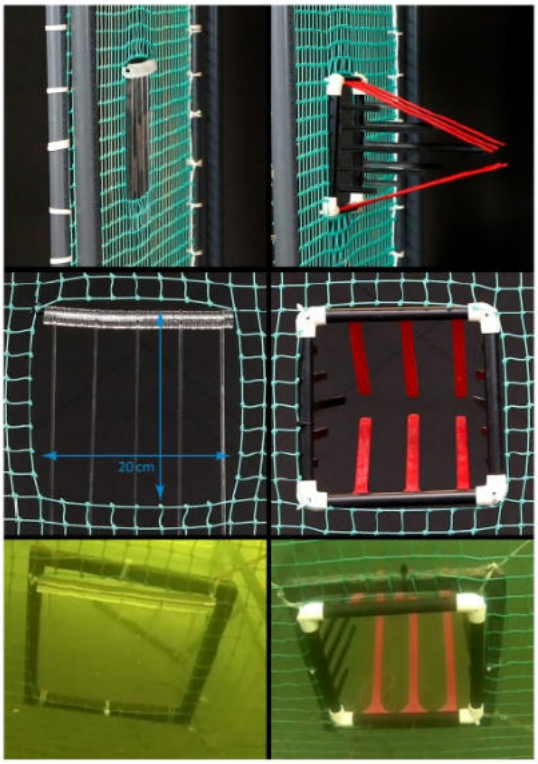

Figure 2. AFs (left) and NFs (right) attached to the NoFun entrance. First row side view in air, second row front view in air, and last row front view underwater. For photos of triggers attached to the Fun entrance, see Supplementary Figure S5.

observation range of 1.8 m, sufficient video data storage capacities for several weeks, a rapidly swappable datadisk, and remote access connection through a webserver with live stream. In this study, we used two iFO systems, each with one camera and two IR lamps (Supplementary Figures S3 and S4; centroid frequency 850 nm). IR light is often used to study fish in darkness, including cod (e.g. Meager *et al.*, 2006; Utne-Palm *et al.*, 2018).

Radio-frequency identification of cod

Cod were implanted with passive integrated transponders in their abdominal cavity (PIT tags; 32-mm long half-duplex; manufactured by Oregon RFID, Oregon, USA; permit 7221.3-1-009/18 of the Agency for agriculture, food safety and fishery of the Federal State Mecklenburg-West Pomerania in Germany), and each entrance was equipped with two radio-frequency identification (RFID) antennae (Supplementary Figures S3 and S4). However, owing to technical difficulties, we refrained from analysing these data. Nevertheless, they were used to improve the manual analysis of the video recordings (see below) by allowing us to pinpoint periods of increased entrance interaction before detailed video analysis and by helping us to disaggregate event timings when several cod interacted simultaneously with an entrance.

Behavioural analysis

To provide a comprehensive description of the event chain of cod interacting with the pot entrances, we constructed a detailed ethogram and a behavioural flow diagram (Figure 3 and Table 1), adapting prior behavioural analysis approaches (Ljungberg *et al.*, 2016; Anders *et al.*, 2017b; Meintzer *et al.*, 2017; Santos *et al.*, 2020). Most behavioural units were mutually exclusive events with quantifiable duration. The exception was the brief (<1 s) touching of entrance structures, occurring when inside the funnel or near the inner entrance opening (events "net contact" or "FRD contacts"). These contacts could be directed inquisitive touches, usually during the day, or inadvertent bumping into the entrance when trying to pass, most often at night. Cod leaving the camera field of view (FOV) for <5 s was considered staying within the same event. Videos were analysed with the software Behavioural Observation Research Interactive Software version v. 7.9.7 (Friard and Gamba, 2016). Each trial was fully analysed by one observer. Example video scenes were compiled in a short illustrational video, accessible here: https://vimeo.com/433971235.

Statistical analysis

The pot-entrance catch-efficiency metric is a function of entry and exit/retention probability. "Entry" is defined as the passage of a cod from outside the pot to inside the pot; "exit" is defined as the passage of a cod from inside the pot to outside the pot. For each entry or exit event, a cod could choose either of the two entrances. Therefore, entries or exits observed in each experiment were treated as paired comparison data; for each experiment, one entrance was defined as "control", and the other was defined as "test". In experiments that compared the Fun entrance with the trigger-equipped funnel, the Fun entrance was defined as control and the trigger entrances as test. In experiments that compared two trigger entrances, one of the AF entrances was defined as control and the other one as test. To address the research topics of the study, we used two different methods: first, a generalized linear model (GLM) and, second, a hierarchical tree classification method.

Using the first method, we compared the number of successful entries and exits of both entrance types, using GLM. A successful entry or exit is defined as a successful entrance passage by a cod starting outside the pot and ending inside the pot, or vice versa. An exploratory data analysis found no clear relationships between variables measured during the experiments and the probability of entry/exit in either test or control. Both entrance sides of the pot could be subjected to different physical conditions (e.g. currents or illumination) that might influence the entrance choice of a cod trying to enter or exit the pot, therefore confounding the effect of the entrance design itself. To balance this potential side effect, "side" was included in the model as a blocking factor. Initially, we also considered including "day period" in the full model with the two states: "day" (the time between sunrise and sunset) and "night" to reflect possible differences in diurnal entrance/exit patterns. Day period information (sunset, sunrise, civil dawn, civil dusk) was acquired using R suncalc package (Thieurmel and Elmarhraoui, 2019). Because there were almost no entries or exits at night, however, we only included side as a covariate. For each pairwise comparison, the entry and exit proportion was modelled as follows:

Being I/O, the binary variable expressing the entrance used by the observed fish to enter (I) or exit (O) the pot ($0 = \text{control}$, $1 = \text{test}$), and X a three-dimensional vector including the model intersect, and the dummy variable representing side where the

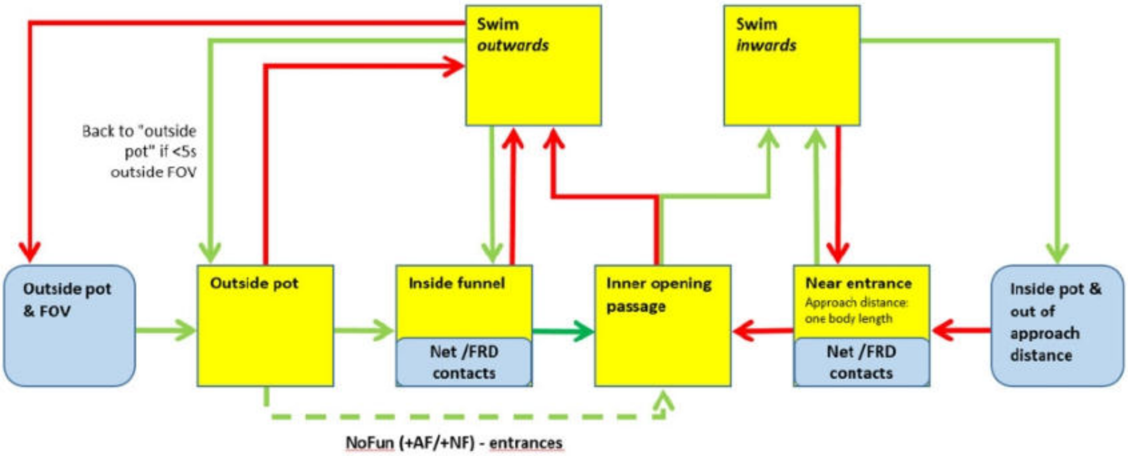

Figure 3. Behavioural flow diagram of pot-interaction event chains. Blue boxes: point events (no duration); yellow boxes: state events (with duration); bold: event type name; red: event modifier; green arrows: movements from the outside inwards; dashed green arrow: movement for NoFun + AF/NoFun + NF (both without funnel); red arrows: from inside the pot outwards. On the outside, an event chain starts or ends when a cod enters or leaves the camera FOV outside the pot (event "Outside pot & FOV"). On the inside, an event starts or ends when a cod approaches the inner entrance opening to within one body length or increases its distance from it to more than one body length.

test is positioned (0 = left, 1 = right), then $p(X) = p(\gamma = 1 \vee X)$ is the expected probability of either entry or exit through the test, conditioned to side. A $p(X)$ of 0.5 indicates no difference between test and control entrance; values <0.5 indicate lower entry or exit rates for the test entrance than for the control entrance. The binary GLM applied expresses $p(X)$ as:

$$\log(p(X)/(1 - p(X))) = \beta_0 + \beta_1 \times \text{side}. \quad (1)$$

On the right model side, the coefficient β_0 is the model intercept and β_1 quantifies the potential effect of side on entry and exit probability through the test entrance. The models were fitted with the statistical software R (3.6.3, R Core Team, 2020). In addition to model (1), the second model, without side was calculated and the final model selected from the two candidates using AIC (Akaike, 1973). If the side effect was kept in the model, its effect was assessed using the sum-to-zero contrast available for GLM models in the statistical analysis program R. In general, pot efficiency, and more particularly pot-entrance efficiency, depends on the ratio between fish-entry and -exit rates (Furevik, 1994; Hedgärde *et al.*, 2016). Therefore, the product of $p(I)$ and $p(O)$ can be interpreted as a metric of catch efficiency of the test entrance relative to the control entrance. Assuming that the relative probabilities of entry or exit through the test or control are the same [$p(I) = 0.5$ and $p(O) = 0.5$], then the relative catch efficiency calculated for the test entrance should not be significantly different from 0.25. Because the calculations involve two antagonist selective processes, improvements in relative catch efficiency need to be interpreted by considering the trade-offs between $p(I)$ and $p(O)$. To allow for indirect catch-efficiency comparisons between the trigger types, the GLM-calculated entry and exit probabilities of the comparisons between the trigger and the Fun entrance were plotted against each other.

The GLM analysis is a coarse first approach to quantifying entry and exit probabilities of the test entrance relative to the control entrance. However, this does not reveal the underlying mechanism leading to possible differences in interaction and does not allow the incorporation of the information provided by aborted entry or exit attempts. Therefore, using the second statistical method, we investigated at which point in the event chain do control and test entrance types provoke different reactions from the interacting cod. We adapted and applied the hierarchical tree classification method of Santos *et al.* (2020). The individual event chains of cod–entrance interactions are pooled for each experiment and across replicates. These event chains are then arranged in an inverted tree-like structure with the root containing the total number of observations on top. The behavioural nodes in the level immediately below the root each contain the number of observed entry/exit events, either in the test or the control entrance. After this first level, different event chains were encompassed in one branch up to the parent node where they differed. At this point, the event chains split into branches, when each one could once again contain several event chains that separated at lower event levels, creating the tree. The terminal leaves at the end of each event chain represented the final fate of the observed cod "Inside pot" or "Outside pot". Based on the information contained in the tree, the marginal probability (MP) for a given behavioural event to happen is calculated as:

$$\text{MP} = P(N_i) = \frac{N_i}{Root}, \quad (2)$$

where N_i is the number of cod performing the event i (node i) and *Root* is the total number of observed interactions. Similarly, the conditional probability (CP) that an event i could happen, given that the parent node k in the level immediately above happened, is:

$$\text{CP} = P(N_i|\ N_k) = \frac{N_i}{N_k}. \quad (3)$$

Table 1. Behavioural ethogram of cod interactions with pot entrances illustrated in the behavioural flow diagram (Figure 3).

Event	Event type	Description	Starting point	Endpoint
Outside pot	State	Cod is outside the pot entrance, gaze directed towards entrance.	*Inwards*: Cod enters FOV (begin event chain). *Outwards*: When two-thirds of body length has passed outer entrance opening and cod does not directly leave FOV (previous event: "Swim outwards").	*Inwards*: Tip of cod snout passes outer entrance opening (next event: "Inside funnel" or "Inner opening passage" if "No funnel" entrance). *Outwards*: Cod turns and starts to swim outwards (next event: "Swim outwards").
Inside funnel	State	Cod is inside the funnel (excluding direct outward swimming). *Note: Does not apply to "No funnel" (NoFun) entrance.*	*Inwards*: Tip of cod snout passes outer entrance opening (previous event: "Outside pot"). *Outwards*: Cod aborts swimming outwards (previous event: "Swim outwards").	*Inwards*: Tip of cod snout passes inner entrance opening (next event "Inner opening passage"). *Outwards*: Cod turns and starts to swim outwards (next event: "Swim outwards").
Inner opening passage	State	Cod passes inner opening of entrance in either direction.	*Inwards*: Cod snout enters inner opening (previous event: "Inside funnel" or "Outside pot" for NoFun entrance). *Outwards*: Cod snout enters inner opening (previous event: "Near entrance").	*Inwards*: Two-thirds of cod body length passes the inner opening towards inside of pot (next event: "Swim inwards"). *Outwards*: Two-thirds of cod body length passes the inner opening towards outside pot (next event: "Swim outwards").
Swim *inwards*	State	Cod swims towards pot inside (inside pot).	*Inwards*: Cod starts swimming towards pot inside (previous event: "Inner opening passage"). *Outwards*: Cod aborts inner opening approach and turns towards pot inside (previous event: "Near entrance").	*Inwards*: Cod is more than one body length away from entrance/ funnel inner opening (end of event chain). *If cod re-approaches the opening to within one body length in <5 sec., it is still considered in the same event pass.* *Outwards*: Cod turns back again towards opening (next event: "Near entrance").
Near entrance	State	Inside pot, when (i) cod is within one body length of inner opening, (ii) its gaze is towards the inner opening, and (iii) swimming path deviation towards inner opening, usually concurrent with an abrupt prior deceleration.	*Inwards*: Cod aborts inward swimming and turns back towards inner opening (previous event: "Swim inwards"). *Outwards*: Cod approaches opening to within one body length, attention directed towards opening (begin of event chain).	*Inwards*: Cod turns away from entrance (next event: "Swim inwards"). *Outwards*: Cod snout enters inner opening (next event: "Inner opening passage").
Swim *outwards*	State	Cod swims towards pot outside (outside inner opening).	*Inwards*: Cod turns and starts to swim outwards (previous event: "Outside pot" or "Inside Funnel"). *Outwards*: Two-thirds of cod passed entrance inner opening and cod starts swimming outwards (previous event: "Inner opening passage").	*Inwards*: Cod swims backwards or turns >90° towards pot inside (next event "Outside pot" or "Inside funnel"). *Outwards*: Cod leaves FOV outside the pot (end of event chain).
Net/FRD contacts	Point	Cod touches entrance netting or triggers with snout.	–	–

For "Starting point" and "Endpoint", "*Inwards*" describes a cod swimming *towards* the pot inside while "*Outwards*" describes a cod swimming towards the pot exterior.

Trees were constructed for each experiment, once for entrance interactions starting outside the pot and once starting inside the pot. To account for behavioural variability that occurs naturally between and within experimental replicates, we adapted and applied a double bootstrap method often used in trawl selectivity studies (Millar, 1993). Each iteration of the bootstrap produces an artificial tree after resampling experimental replicates and observations within the resampled replicates. This procedure was repeated $B=1000$ times, leading to 1000 artificial trees, allowing calculation of 95% Efron-percentile confidence intervals associated with the average probabilities [(2) and (3)] from the empirical tree (Santos *et al.*, 2016; 2020). The resulting trees were inspected for differences in event-chain flows and event links of both main entrance branches, based on MP and CP. No *CI* overlap between the same event-chain links of both entrance types was interpreted as significant differences.

Results

In total, we analysed 18 trials with a total duration of 407.19 h (Supplementary Table S1). Sometimes, the video cameras failed and stopped recording for short periods (seconds to minutes). To avoid bias caused by camera failure on one of the two entrances, those periods were excluded from the analysis of both entrances. Most entrance passages occurred during day (204 of all 221 observed entries and 90 of all observed 96 exits). In the first two experiments, we compared triggered entrances with the Fun entrance, representative of a basic funnelled entrance without triggers. In the last three experiments, we compared the AF and NF triggers directly (Table 2).

Comparison of triggers with funnel entrance

Fun entrance vs. Fun + AFs entrance

Five replicates were conducted of the experiment comparing the Fun entrance (control) with the Fun + AF entrance (test; Table 2). The final model for the entries included only the non-significant intercept, indicating that there was no side effect on entry probabilities (Table 3). Entry rate $p(I = 1)$ of the Fun + AF entrance was 0.45 (0.33–0.57), similar to the Fun entrance (0.5). Although there were more approaches to the Fun entrance, *CIs* overlap, and the proportions of cod entering either funnel were almost identical, as were the final proportions of cod passing the entrance to the pot inside. This revealed that cod moved through both entrances equally, explaining the absence of a trigger effect on entrance probabilities (Figure 4).

All 28 observed exits were through the Fun entrance and significantly more cod approached the Fun from inside (Figure 5).

Fun entrance vs. Fun + NFs entrance

Five replicates were conducted of the experiment comparing the Fun entrance with the Fun + NF entrance (Table 2). Significantly more cod entered through the Fun than the Fun + NF entrance, the final model for the entries included only the highly significant negative intercept, $p(I = 1)$, which was 0.20 (0.11–0.34; Table 3). No significant differences between the proportions of cod approaching and entering either funnel were observed (Figure 6). Thus, there was a difference in the number of entries because significantly more of the cod that entered the Fun entrance passed the inner opening towards the pot inside than those that entered the trigger-equipped funnel. This only applies to interactions without net contacts; there were too few interactions with net contacts to allow for conclusions.

Significantly more of inside entrance approaches were to the Fun entrance (Figure 7). All 13 exits were through the Fun entrance and all approaches to the triggers were aborted exit attempts. One cod managed to pass from inside the pot through the NF into the funnel but then turned around again and passed them a second time back towards the pot inside. This occurred at night. It appears that the cod was not able to orient itself in the dark and passed through the NF by chance after hitting it from above while swimming. After passing the triggers, it bounced chaotically into the funnel netting, appearing as if it was trying to push through it and finally was deflected back towards the NF and then passing it back into the pot.

Comparison of catch efficiencies

Although no exits occurred through both trigger types, only the Fun + AF entrance (catch efficiency = 0.446) performed better than the Fun control entrance, because almost no cod entered the pot through the NF (Figure 8; catch efficiency Fun + NF = 0.204). Both trigger types were rarely touched in attempted entries and exits, indicating that triggers are inspected primarily visually and that the NF deterring effect is visual.

Direct trigger entrance comparisons

Fun + AFs vs. no funnel + AFs entrance

We compared the Fun + AF and the NoFun + AF entrances in three replicates, with the Fun + AF entrance set as control $[p(I/O = 0)]$ for GLM. The final model included the intercept and the side covariate; as in one of the trials, no cod entered through the NoFun + AF entrance. Therefore, we classified this as a perfect separation (Allison, 2008) by the side covariate and proceeded to describe the calculated entry probabilities with the model excluding the side covariate, although its AIC was higher. We consider this a not ideal, albeit adequate, procedure to calculate the resulting test entry probability, considering that, in all other experiments, the side covariate was not included in the AIC-selected models, indicating that there was no side effect. This model returned a significantly lower entry probability through the NoFun + AF [0.29 (0.20–0.41); Table 3]. The behavioural event-chain tree of outside interactions (Figure 9) reveals that the higher entry rate of Fun + AF entrance resulted from significantly more interactions with it. For both entrances, the number of cod that had approached the NoFun + AF entrance and then passed it towards inside (event type "Inside opening passage") is similar.

Cod exited almost exclusively through the NoFun + AF entrance. The final exit model included only the significant intercept; the probability that an exit occurred through the NoFun + AF entrance $[p(O = 1)]$ was 0.90 (0.66–0.99). This was caused by significantly more of the entrance interactions from the inside occurring with the NoFun + AF entrance (Figure 10). The result of this experiment, where both entrances were equipped with the same triggers, demonstrates that combining triggers with a funnel considerably increases catch efficiency by increasing entrance contact probability of cod approaching the pot from outside (= increase in entry probability) and decreasing contact probability for cod inside the pot (= decrease in exit probability). This also fits with the low number of inside interactions with either triggered funnel in the Fun + AF vs. Fun + NF experiment.

In contrast to the other experiments including the AF, cod were able to pass them towards the outside. In the first two trials, the length distribution of the cod was 320–390 and 300–360 mm, respectively. Those cod were small enough to pass between two fingers without touching them. The cod in the third trial, however, were between 400 and 430 mm; those cod were not able to pass between the fingers without touching them. We observed that cod were able push through two adjacent AF fingers because the distance between two fingers was too large and/or the fingers were not rigid enough or not assembled tightly enough to resist sideways bending or displacement by cod pushing against them.

Fun + AFs vs. Fun + NFs entrance

The Fun + AF and the Fun + NF were compared in two replicates. The Fun + AF entrance was set as control $(p(I/O = 0))$ for the GLM. The entries' final model included only the significant negative intercept; the probability for entry through Fun + NF entrance $(p(I = 1))$ was 0.15 (0.04–0.45; Table 3), revealing a clear preference of the cod to enter the pot through the AF-equipped entrance. The behavioural event tree, however, did not mirror this result; there was no significant difference in the number of cod approaching or passing either entrance (Figure 11).

Table 2. Overview of the number of entries and exits for all trials conducted for different entrance type combinations.

Exp.	Control	Test	Position control	Cod length group [cm]	Entries		Exits	
					Control	Test	Control	Test
1	Fun	Fun + AF	Left	40–49	2	6	0	0
	Fun	Fun + AF	Left	50–59	14	5	10	0
	Fun	Fun + AF	Left	50–59	8	6	8	0
	Fun	Fun + AF	Right	40–49	7	9	9	0
	Fun	Fun + AF	Right	30–39	5	3	1	0
					36	29	28	0
2	Fun	Fun + NF	Right	40–49	9	0	2	0
	Fun	Fun + NF	Left	40–49	13	1	6	0
	Fun	Fun + NF	Left	40–49	5	3	0	0
	Fun	Fun + NF	Right	30–39	6	2	2	0
	Fun	Fun + NF	Right	40–49	6	4	3	0
					39	10	13	0
3	Fun + AF	NoFun + AF	Left	30–39	18	4	0	13
	Fun + AF	NoFun + AF	Right	30–39	11	0	1	2
	Fun + AF	NoFun + AF	Left	40–49	20	16	1	31
					49	20	2	46
4	Fun + AF	Fun + NF	Right	30–39	7	1	0	0
	Fun + AF	Fun + NF	Left	30–39	4	1	0	0
					11	2	0	0
5	NoFun + AF	NoFun + NF	Left	30–39	7	1	0	0
	NoFun + AF	NoFun + NF	Right	30–39	6	1	5	0
	NoFun + AF	NoFun + NF	Right	30–39	9	1	2	0
					22	3	7	0

By definition, the Fun entrance without triggers was the control entrance when one of the two tested entrances was equipped with a trigger. In trials comparing Fun entrances with triggered entrances, the Fun entrance was defined as control. In trials where both entrances were equipped with triggers, an entrance equipped with the AF triggers was defined as "Control". "Position control" describes the pot side on which the control entrance was situated. The number of entries and exits trough test/control entrances is given.

Table 3. GLM parameters of all final experiment models.

Exp.	Entrance control	Entrance test	Replicates	Model	*n* control	*n* test	Intercept	Side	Dev.	*df*	*p*(*I*/*O* = 1)	Notes
1	Fun	Fun + AF	5	Entries	36	29	−0.216	N/I	89.35	64	0.45 (0.33–0.57)	–
				Exits	28	0	No exits through triggers	–	–	–	0	–
2	Fun	Fun + NF	5	Entries	39	10	**−1.361*****	N/I	49.59	48	0.20 (0.11–0.34)	–
				Exits	13	0	No exits through triggers	–	–	–	0	–
3	Fun + AF	NoFun + AF	3	Entries	49	20	−9.604	8.96	74.73	67	0.0001 (0–NaN)	Entries model without "side" added
				Entries	*49*	*20*	***−0.896**** **	*N/I*	*83.079*	*68*	*0.29 (0.20–0.41)*	
				Exits	2	46	**2.239****	1.55	13.41	46	0.90 (0.66–0.99)	–
4	Fun + AF	Fun + NF	2	Entries	11	2	**−1.705***	N/I	11.16	12	0.15 (0.04–0.45)	–
				Exits	0	0	No exits through either triggers	–	–	–	–	–
5	NoFun + AF	NoFun + NF	3	Entries	22	3	**−1.992****	N/I	18.35	24	0.12 (0.04–0.31)	–
				Exits	7	0	Only 7 exits through AF	–	–	–	0	–

See "Material and methods" section for the meaning of entrance abbreviations. Exp. = experiment number, "Dev." = model deviance; "*df*" = degrees of freedom; $p(I/O = 1)$ = resulting probability that an entry or exit occurred through the entrance defined as test; *, **, and *** = the Wald test *p*-value is <0.05, <0.01, and <0.001, respectively. Significant values are in bold. N/I = "not included" in the final model. Please note that, for the experiment Fun + AF vs. NoFun + AF, the selected entries model included the "Side" covariate owing to a perfect separation by the side covariate. Therefore, the model without the side covariate added is in italics.

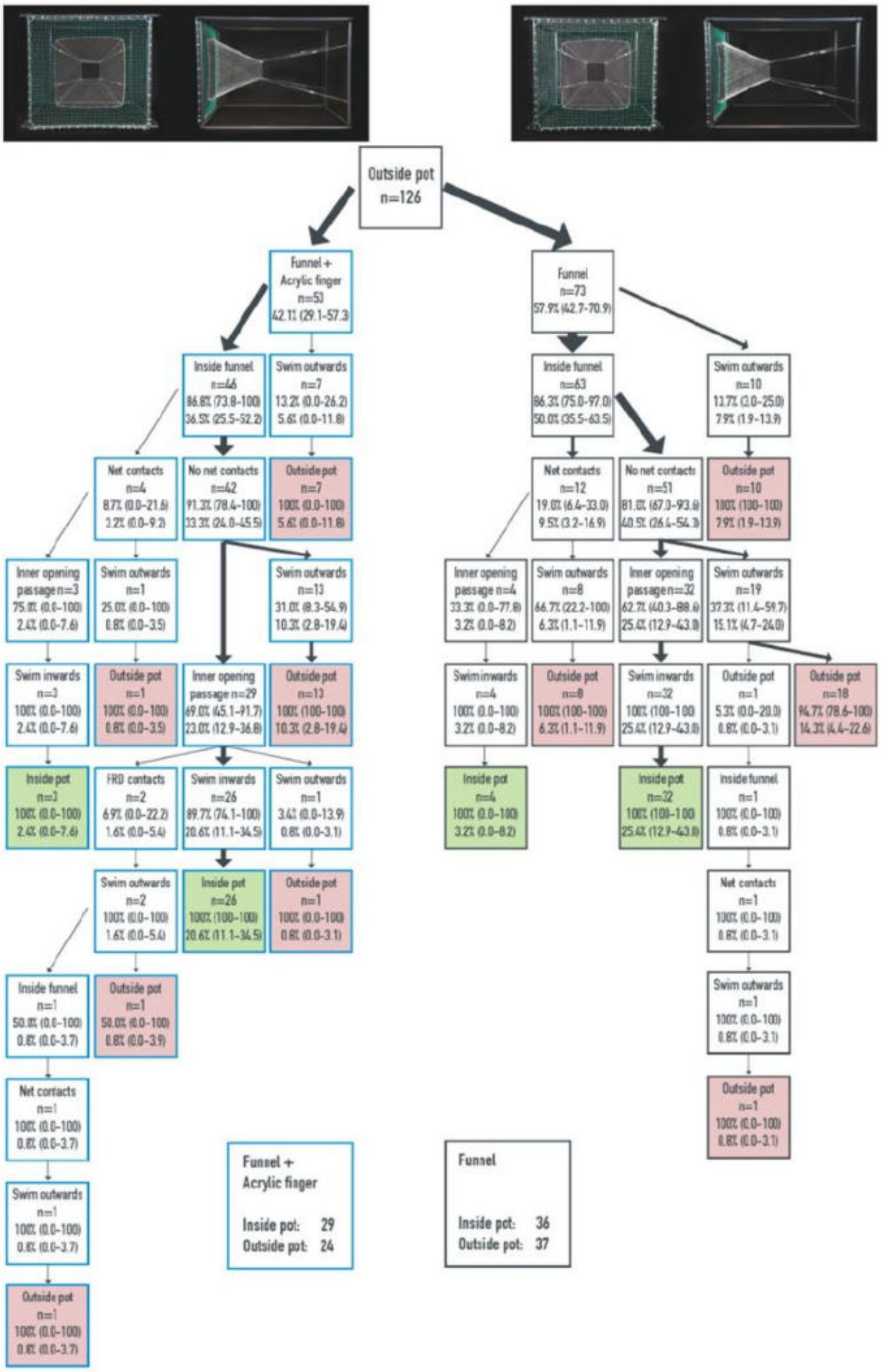

Figure 4. Behavioural event-chain tree comparing the Fun entrance (control) with the Fun + AF entrance (test) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

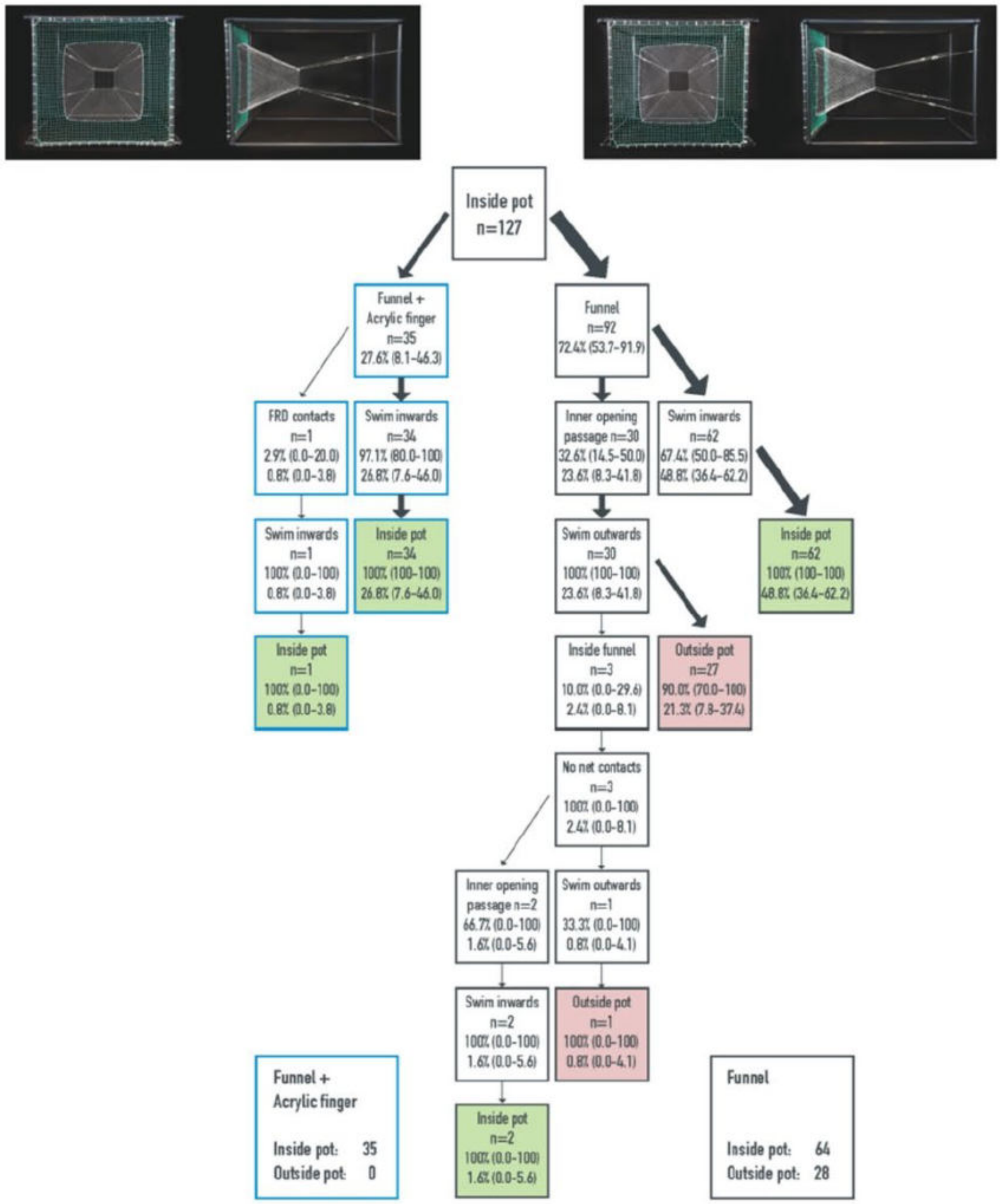

Figure 5. Behavioural event-chain tree comparing the Fun entrance (control) with the Fun + AF entrance (test) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

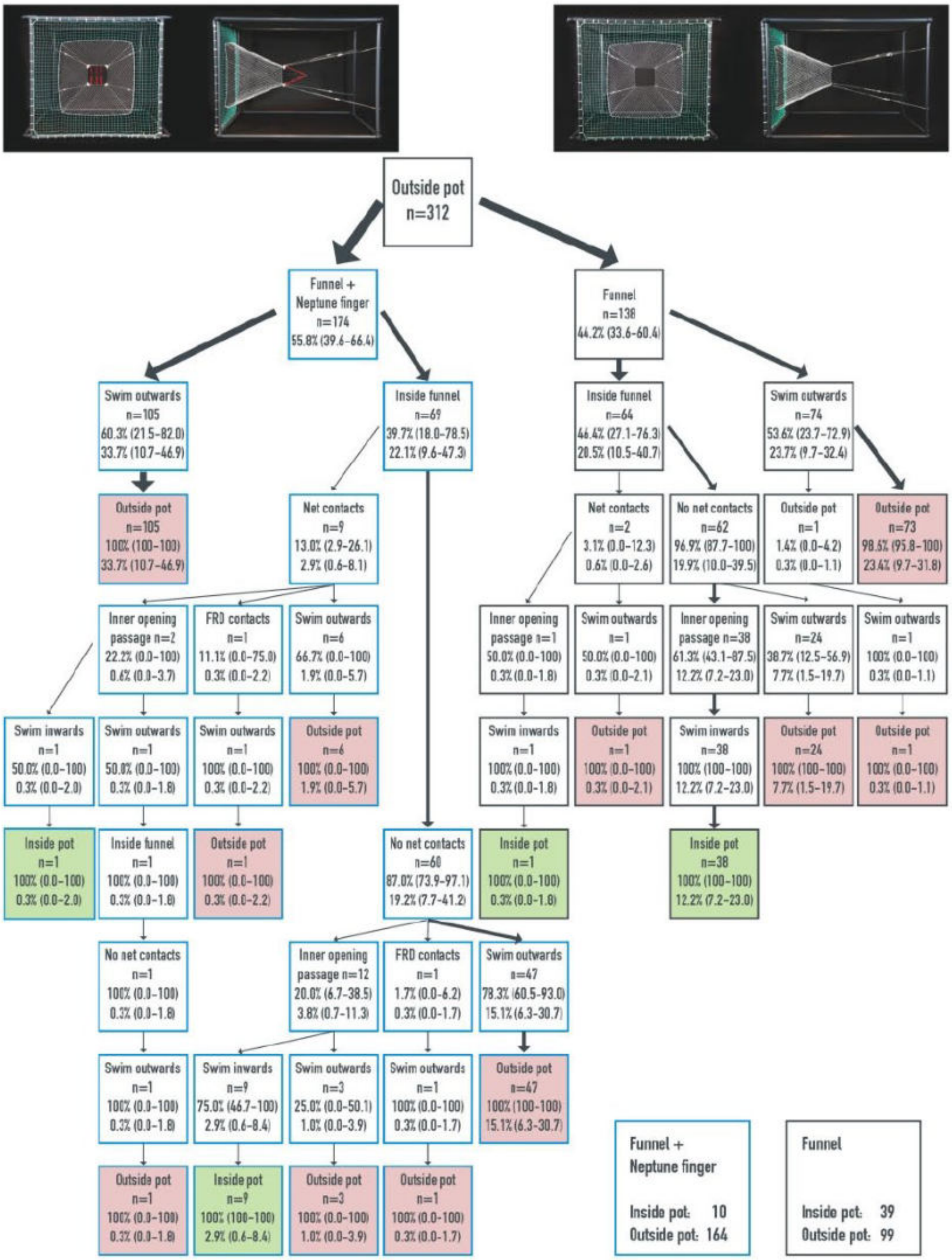

Figure 6. Behavioural event-chain tree comparing the Fun entrance (control) with the Fun + NF entrance (test) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

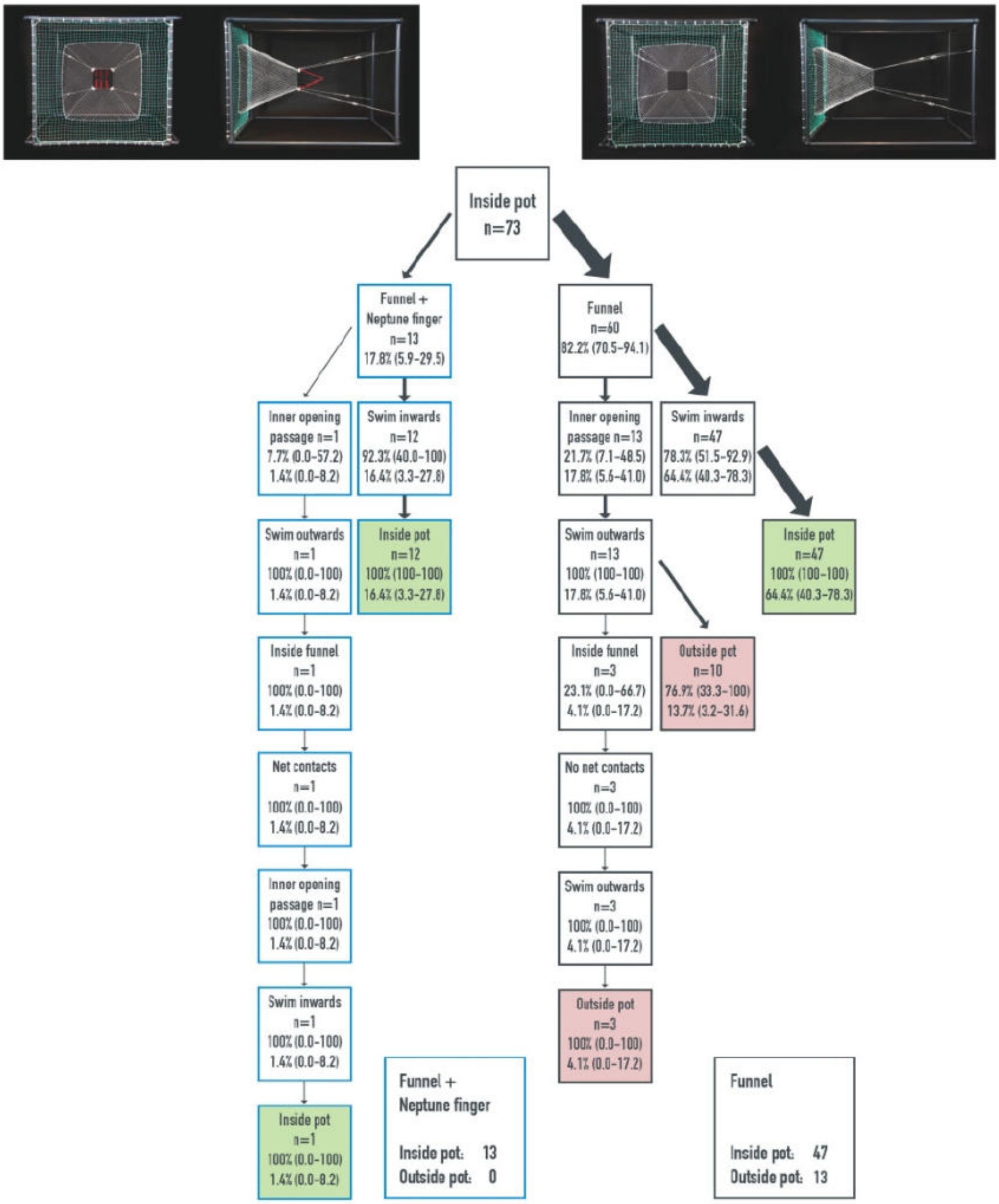

Figure 7. Behavioural event chain tree comparing the Fun entrance (control) with the Fun + NF entrance (test) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

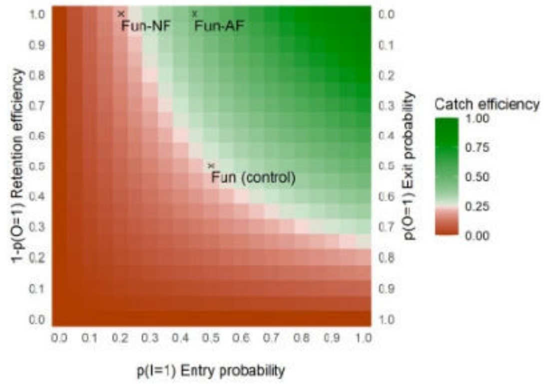

Figure 8. Catch efficiency comparison from experiments comparing the Fun entrance (control) with the Fun + AF and Fun + NF entrances (test).

This, however, could be the result of the low sample size of only 13 pot entries in total. This small number of entries resulted from both trigger types blocking the cod from exiting. In the second trial of this experiment, the last of all trials conducted in the study, only five of the seven cod in the experiment entered the pot.

Both trigger-equipped openings were approached from the inside nine times (Figure 12). This number of inside interactions is markedly smaller than in the experiments comparing one trigger type with the Fun entrance without trigger. Notwithstanding the small approach numbers, significantly fewer cod approached the Fun + NF from inside.

No funnel + AFs vs. no funnel + NFs entrance

We compared the NoFun + AF and the NoFun + NF entrances in two replicates. The NoFun + AF was set as control $[p(I/O = 0)]$. The final entry model included only the intercept. There were significantly fewer entries through the NoFun + NF [0.12 (0.04–0.31); Table 3]. The behavioural analysis tree reveals that this was caused by significantly fewer approaches to the NoFun + NF (Figure 13). There were no exits through the NoFun + NF and seven exits through the AF. All cod in this experiment were in the 30–39-cm length class. All cod exiting through the NoFun + AF seemed able to pass between two fingers without touching them. Nonetheless, 88.5% (66.6–97.6%) of all inside approaches to the NoFun + AF were aborted, indicating that the NoFun + AF still had an exit-impeding effect (Figure 14).

Discussion

The study of this innovative new trigger concept, named AFs, revealed an AF exit-impeding effect while avoiding the drawback of other FRDs, which may deter fish owing to their distinct visual outline and the physical resistance other FRDs present to fish entering the pot. We compared the AFs with commercially available NFs and demonstrated that cod avoid passing the NFs, indicating that NFs have a strong deterring effect on exits and on entries. Adding NFs to a funnel reduced catch efficiency from 0.250 to 0.204, whereas adding AFs to the same funnel entrance almost doubled catch efficiency to 0.446. Therefore, AFs might support the uptake of the environmentally favourable fish pots in fisheries. The low inside approach number of cod to either entrance of the Fun + AF vs. Fun + NF experiment indicates that the passage of a trigger-equipped entrance, necessitating physical contact with the trigger, is a deterring process, inhibiting subsequent re-approaches to the trigger-equipped entrances. Notwithstanding the generally small approach numbers to either entrance in this experiment, significantly fewer cod approached the Fun + NF from inside, also reflecting the deterrent effect of the NF observed in the prior experiments.

FRDs are typically described as reducing escape rates but inevitably also reducing entry rates (e.g. Munro, 1972; High and Ellis, 1973; Furevik and Løkkeborg, 1994; Olsen, 2014). In contrast, we found no evidence that AFs reduced fish-entry rates. To our knowledge, the present study is the first to demonstrate an FRD that does not significantly decrease entry rates compared with the same entrance without an FRD. The AFs performed significantly better than the NFs in direct comparisons. Nonetheless, cod exited through the AF entrances in five of the 13 trials. Four of the trials with exiting cod involved the smallest cod length class (30–39 cm), and cod were able to pass between two fingers. This is not necessarily a negative result because providing a pot-escapement opportunity for small cod increases fishing efficiency for larger cod (Ovegård *et al.*, 2011) in addition to reducing the bycatch of cod smaller than MCRS. However, in one trial, larger cod (40–49 cm; i.e. larger than MCRS) also exited through the AF entrance by physically pushing two adjacent fingers sideways, which demonstrates further improvement potential. Possible improvements include: reducing inter-finger width, increasing the AFs' thickness to reduce their flexibility, and stiffening the fingers to prevent wobbling. The AFs could be further integrated into a holding frame by fixing brackets to the inner bottom side into which the AF's fingertips could be held in place when lowered, preventing lateral movement of the fingers. Therefore, the AF, as well as other trigger-type FRDs, could also be used as selection devices, expanding the selection options of pots by using them in conjunction with selection windows. Moreover, selection windows could be replaced by size-selective triggers, which could increase pot versatility. Changing the target species and/or size would then require only changing the trigger configuration (e.g. more or less inter-finger width of triggers) or the pot entrance, and without additionally changing the selection window.

The use of both funnels and triggers synergistically improved pot-catch efficiency: only two of the 55 exits through AFs were through the AFs attached to the white funnel. All others took place through AFs attached to the NoFun opening. In experiment 4, Fun + AF performed significantly better for entries and for exits than the NoFun + AF entrance. This was the result of a significantly higher approach probability of cod to the Fun + AF from outside and a significantly lower approach probability for cod inside the pot. Considering that many cod do not enter a pot because they fail to find the entrance (e.g. Hedgärde *et al.*, 2016; Meintzer *et al.*, 2017), this funnel effect could be the result of the outer opening size being nine times larger than the NoFun opening, thus increasing contact probability for approaching cod.

The deterring effect of NFs appears to be caused by its distinct visual outline. Nevertheless, the shape of both FRDs also differed (AFs are curtain shaped, similar to a cat door, whereas the NFs are funnel shaped), which may also influence catch efficiency.

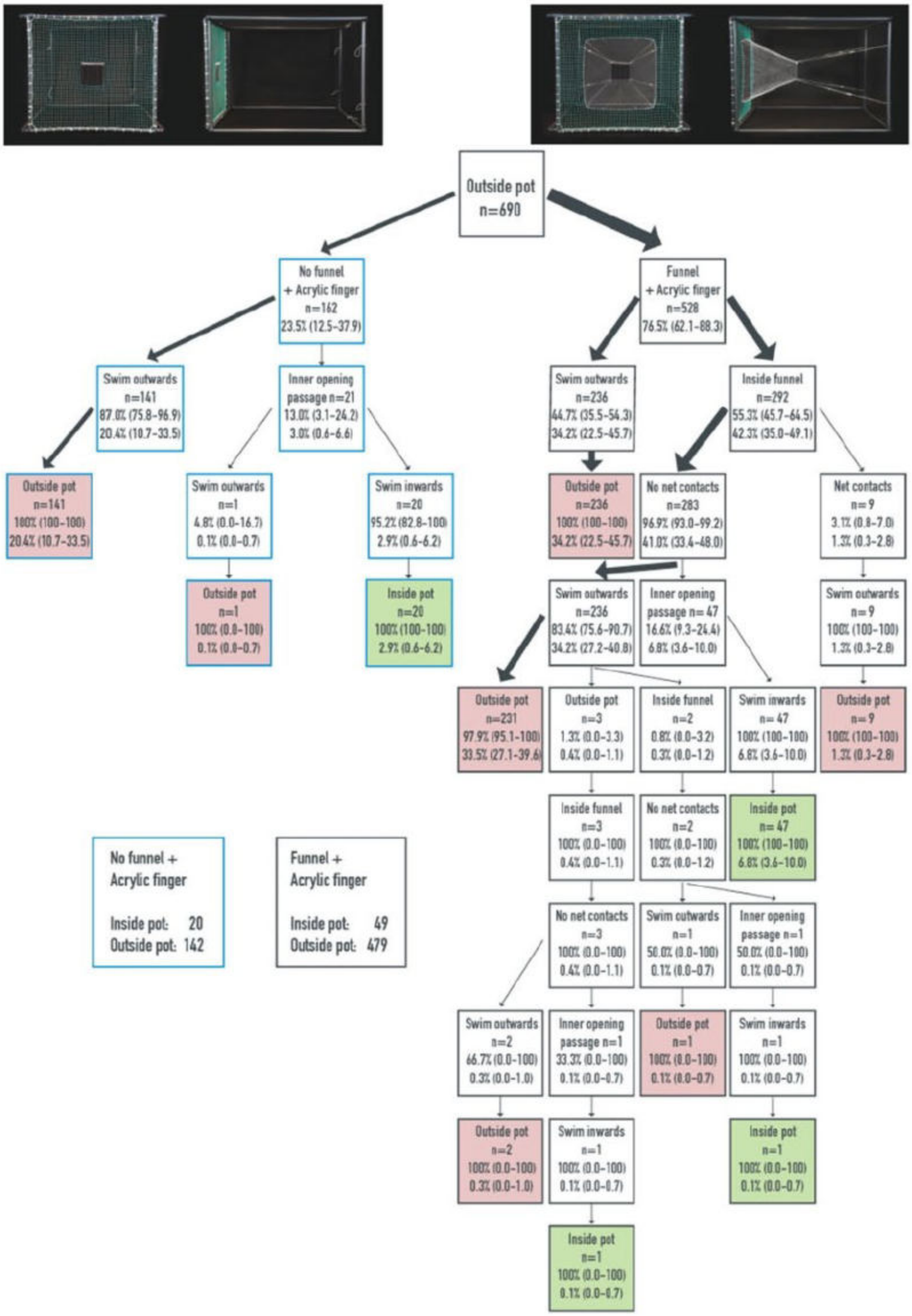

Figure 9. Behavioural event-chain tree comparing the Fun + AF entrance (control) with the NoFun + AF entrance (test) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

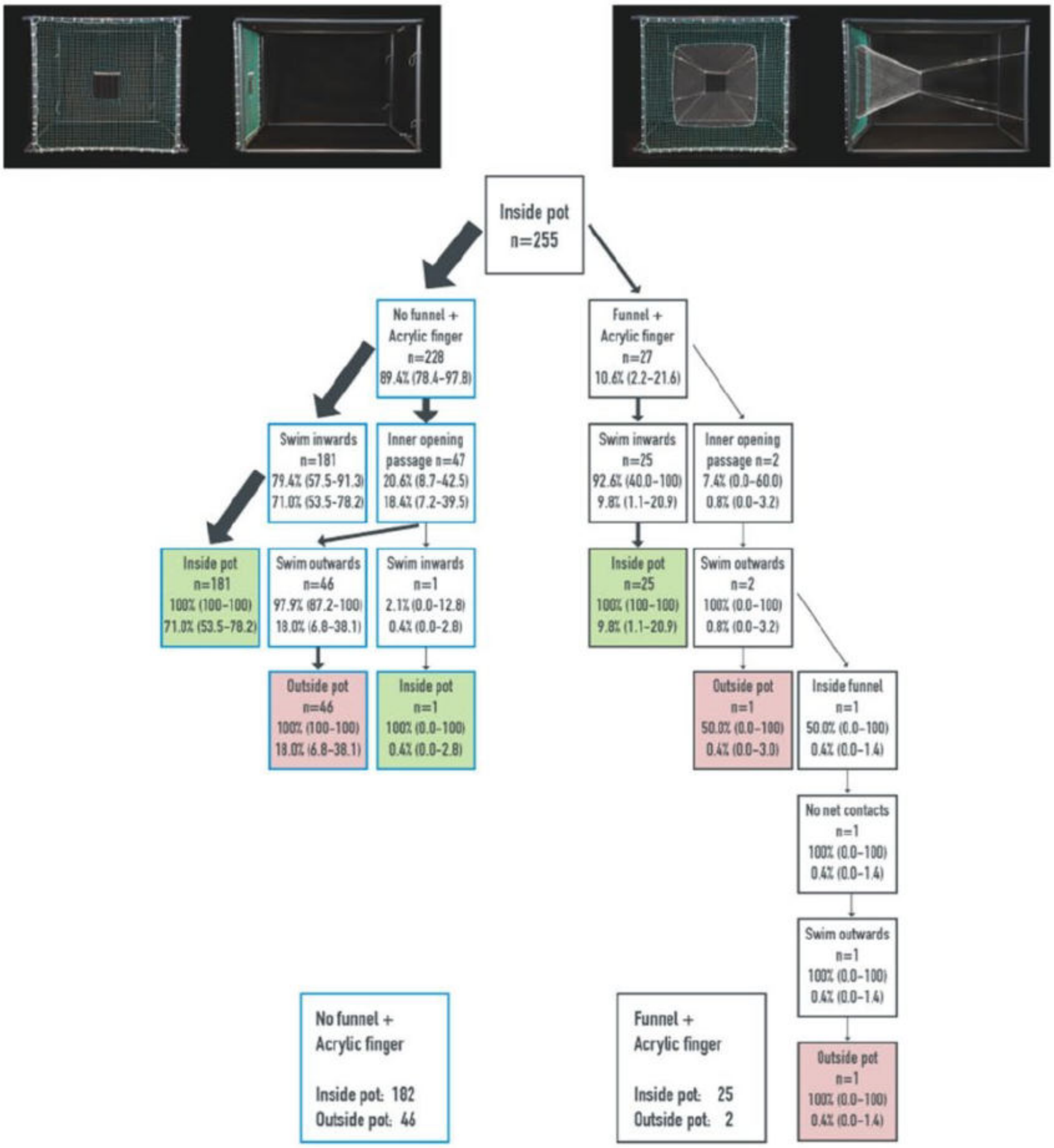

Figure 10. Behavioural event-chain tree comparing the Fun + AF entrance (control) with the NoFun + AF entrance (test) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

However, cod rarely touched either trigger before either passing or turning around, indicating that a possible shape effect is probably limited. The only NF passage from the inside was observed at night, when a cod apparently swam inadvertently into a gap between two fingers. Before bumping back into the triggers and passing it again towards the pot inside, it moved chaotically inside the funnel, bumping several times into the netting. This is in line with observations of cod interacting with steel pot triggers: most of the cod turning away from the triggers did so without touching the triggers (Olsen, 2014). Trigger detection and

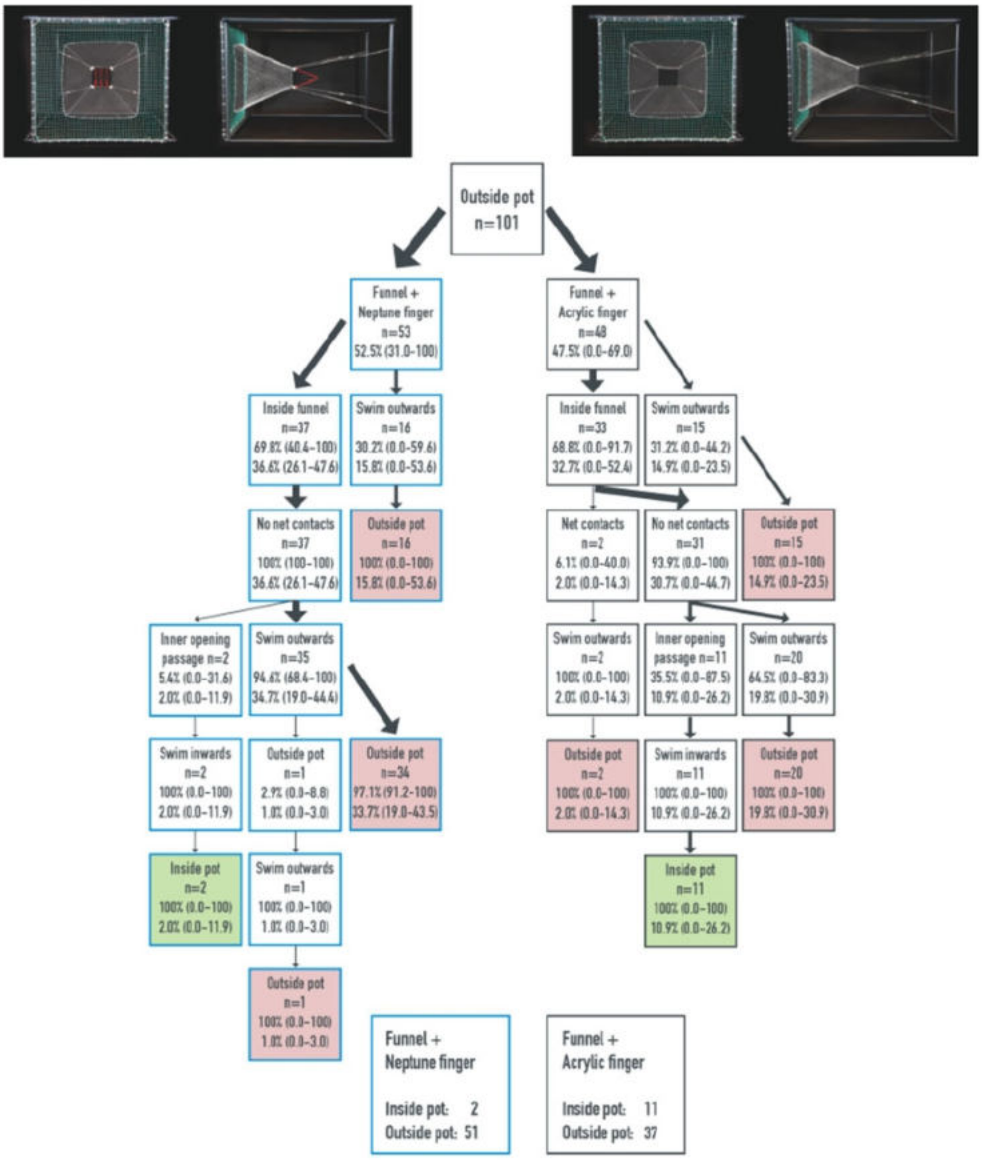

Figure 11. Behavioural event-chain tree comparing the Fun + AF entrance (control) with the Fun + NF entrance (test) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

inspection are thus primarily visually mediated. In contrast to the NFs, the AFs work because of their inconspicuousness by not affecting approach probability to the entrance while still physically blocking exits.

Carlile's *et al.* (1997) findings could indicate that Pacific cod are less reluctant to pass entrances that they have to push through physically. However, the mean size of Pacific cod fished in the different pot types ranged from 58.7 to 62.3 cm, considerably larger than the Atlantic cod in this study. Possibly, larger Atlantic cod could also be less reluctant to enter NFs because large cod have been observed to be less hesitant to contact and push steel triggers inwards to enter a pot (Olsen, 2014). It seems plausible that larger cod would be even less deterred by transparent AF. In addition, they would increase visibility of the pot inside, including

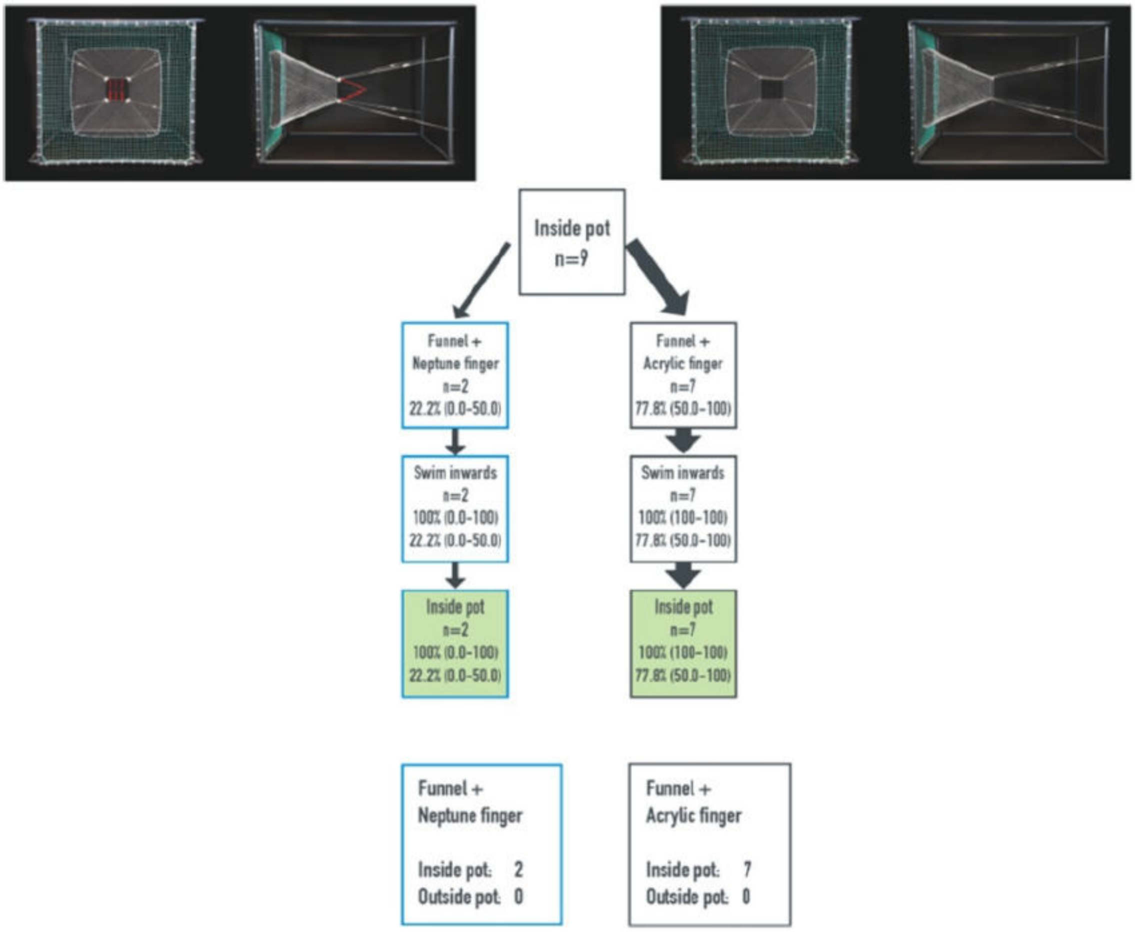

Figure 12. Behavioural event-chain tree comparing the Fun + AF entrance (control) with the Fun + NF entrance (test) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

the pot bait, usually hung in front of the entrance (e.g. Furevik *et al.*, 2008; Meintzer *et al.*, 2017), which could be even more important when a bait light is used (Bryhn *et al.*, 2014; Humborstad *et al.*, 2018).

In addition to the necessary improvements described above, the AFs probably need further testing and development cycles. This study's tests were short and in a controlled environment. The construction of AFs is not as robust as that of the commercially field-tested NFs and probably will not sustain prolonged fishing under demanding commercial fishing conditions. Because the AFs' near invisibility underwater is the result of its favourable refractive index, algal overgrowth and scratches accumulating on its surface could reduce its effectiveness over time. Technological improvement in these areas could increase long-term AF effectiveness. In any case, AFs will have to be cleaned or replaced after a certain time. Prolonged field tests, best under the conditions of commercial fisheries, are thus warranted. Another study using the same experimental set-up found that cod movement through funnels increases when transparent funnel netting is used instead of white netting (Chladek *et al.*, 2020). Therefore, AF effectiveness could be increased further by using transparent funnel netting. Furthermore, we tested only one kind of transparent trigger; other transparent trigger types could be just as, or even more, efficient. In summary, AFs or other transparent triggers can improve cod pot-catch rates considerably and they have great development potential for even larger increases in catch efficiency, furthering the uptake of pots.

Supplementary data

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

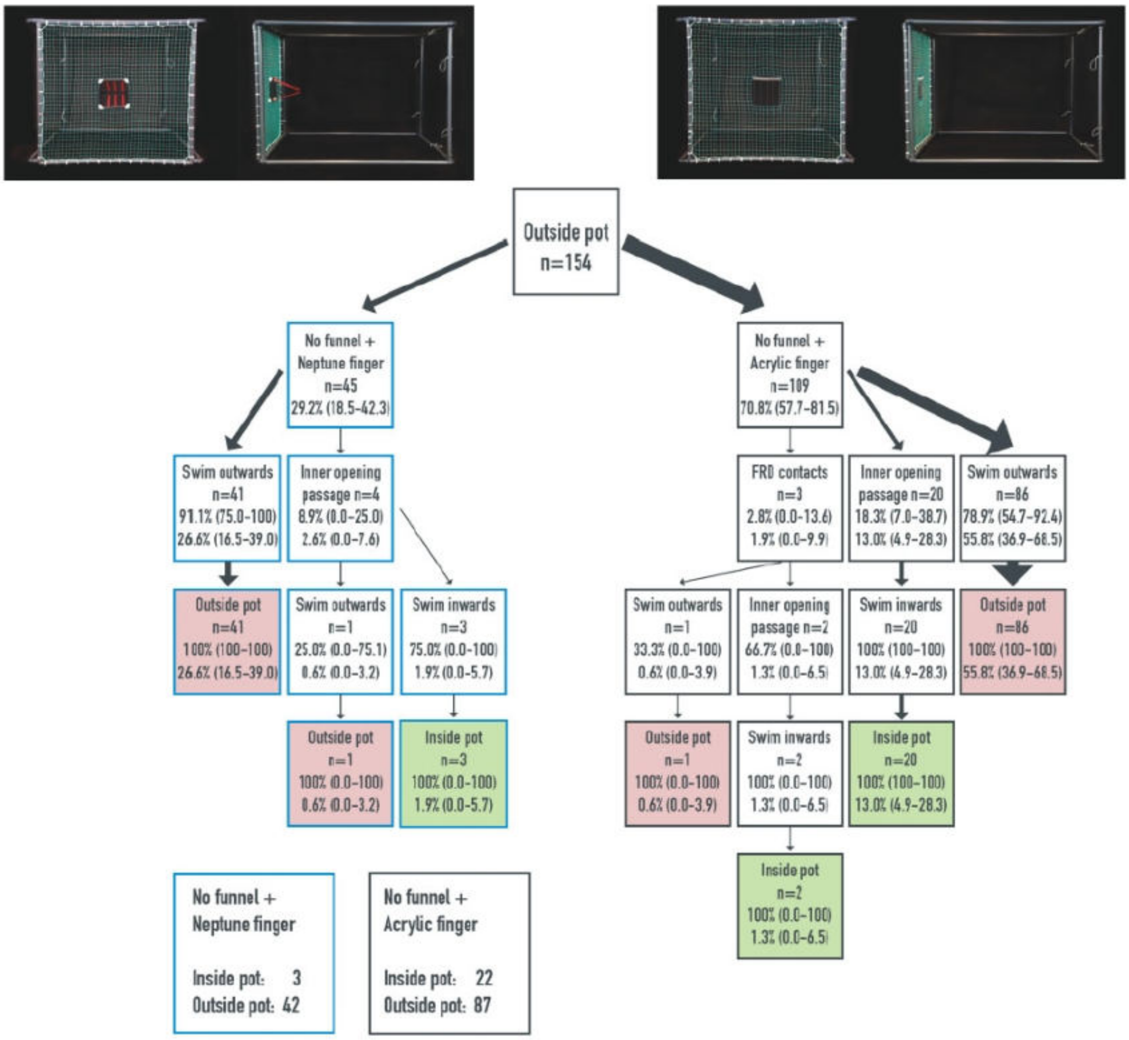

Figure 13. Behavioural event-chain tree comparing the NoFun + AF entrance (control) with the NoFun + NF entrance (test) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

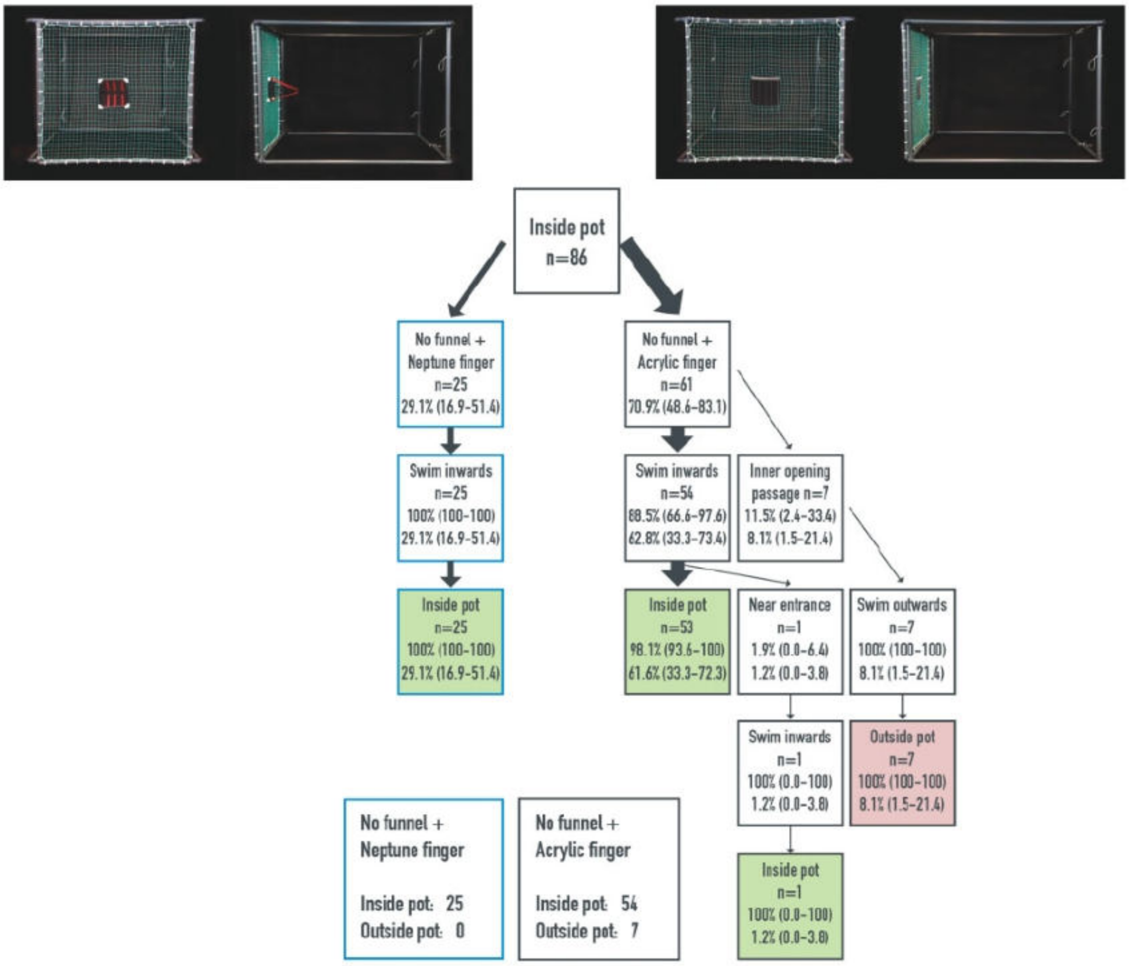

Figure 14. Behavioural event-chain tree comparing the NoFun + AF entrance (control) with the NoFun + NF entrance (test) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed at this point in the event chain; the third line = the MP related to the total number of interactions; the last line = the CP related to the number of interactions in the parent link (the link above a respective link). Confidence intervals are based on 1000 bootstrap iterations. The thickness of each arrow is representative of the MP the arrow is pointing to.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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Handling editor: Michael Pol

General discussion

In this chapter the thesis's findings are discussed. First, its key contributions are laid out. This is followed by a more in-depth discussion of Part A, the PAL study, and of Part B, the fish pot studies. Each of these in-depth discussions lays out future research possibilities resulting from the findings presented. In the final chapter "Conclusion and outlook", the relevance of the thesis is exemplified by setting out its contributions to planned or ongoing scientific research efforts and reflecting it in the context of the current regulatory discussion by EU Baltic Sea riparian states on harbour porpoise bycatch mitigation.

3.3 Key contributions of Papers I, II, III and IV

It will likely not be a single method or technology solving the problem of harbour porpoises and diving seabird bycatch. It will rather be a combination of measures (e.g., Northridge *et al.*, 2016; Brownell Jr *et al.*, 2019; Barz *et al.*, 2020). In line with such a "toolbox" thinking, two different bycatch reduction approaches were pursued in this thesis: gillnet modification and alternative gear development.

<u>Part A: PAL significantly reduces harbour porpoise bycatch</u>

In the first part of this thesis, the PAL as a new kind of pinger, using biologically relevant acoustic signals to warn western Baltic harbour porpoises of gillnet presence, was tested. This study proved that the PAL significantly reduces their bycatch risk in gillnet fisheries.

The study found indications that PAL efficiency is dependent on a sufficiently short distance between two PAL devices along a gillnet string. Four of the five recorded harbour porpoise bycatches were in strings with distances between PAL >195 m. Therefore, PAL efficiency could possibly be increased by limiting the distance between subsequent PAL to less than the currently 200 m prescribed in the EU for high frequency pingers (EC, 2020). Considering similar findings of increased efficacy at shorter intervals for conventional pingers (Kindt-Larsen *et al.*, 2019), this finding is possibly applicable to all pinger types.

In addition, the PAL study was, to the authors knowledge, the first bycatch mitigation study with acoustic devices also incorporating environmental data such as wind speed and wave height during string deployment. Their possible influence on bycatch probability could not be directly tested by modelling to avoid overfitting. The absence of strong wind speed and wave height differences between bycatches in control- and PAL strings nevertheless indicates that weather does not strongly influence the PAL efficiency. Nonetheless, a possible influence could not be ruled out with the study. This approach merits to be taken up in further similar studies.

The PAL study could by design not investigate, if such biologically relevant signals are in any way preferable to the artificial "noise" of conventional pingers. Still, the proven effectiveness of the PAL has in a wider perspective important global implication: it shows that acoustic signals proper to the targeted cetacean species can reduce their bycatch – with a possibly different effect mechanism than conventional pingers.

<u>Part B: Fish pot improvements</u>

In the second part of the thesis, another "tool" of the bycatch mitigation toolbox was investigated: alternative fishing gears to gillnets. In a first step, an in-depth assessment of different alternative fishing gears was undertaken, leading to fish pots to be chosen as the most promising alternative to gillnets to be investigated further.

In a second step, a detailed literature review was undertaken to identify means for cod pot-catch efficiency improvements. The aim was to a) identify the pot fishing elements (structural, strategic, and operational) that keep their fishing efficiency low and b) develop a method to efficiently improve these elements. Here, fish pot entrances were identified as the main bottleneck of their catch efficiency (see Furevik, 1994a; as well as Thomsen *et al.*, 2010 for an overview). Entrances were thus set as the focus of the following studies.

Next, a method to improve entrances efficiently was developed. Its inception resulted from the observation made during the review that the numerous field catch comparison studies of different cod pot (entrance) types often did not deliver conclusive explanations for the causes of catch differences (Bjordal and Furevik, 1988; Furevik and Løkkeborg, 1994; Furevik *et al.*, 2008a; Bagdonas *et al.*, 2012; Ljungberg *et al.*, 2016; Meintzer *et al.*, 2018). The reason was that these studies did not collect any information about how the target species interacted with the experimental gear. This information is however essential for efficient fishing gear development (Løkkeborg *et al.*, 1993; He, 2010). Approaching fish characteristics and states such as sex, hunger level, fitness or maturity are furthermore not controllable in field catch comparisons, and often not identifiable. Equally, environmental parameters such as turbidity, water temperature, or prey availability are difficult to control. These characteristics and parameters however can modify fish susceptibility to gear (e.g. Stoner, 2003, 2004; Stoner and Ottmar, 2004; Stoner and Sturm, 2004). And compared pot types often had multiple structural differences in several different parameters, impeding sound deductions as to why one pot type outperforms another (e.g. Furevik and Løkkeborg, 1994; Meintzer *et al.*, 2018).

The results of pot field catch comparisons are thus difficult to interpret in relation to the catch *process* because these variables also significantly affect pot (as well as other passive gear) catch rates. To avoid these issues, a new net pen-based observation method was developed in this thesis to rapidly compare fish interactions with different entrance parameters and identifying optimized entrance parameters to increase pot catch rates (Figure 11 and Figure 12).

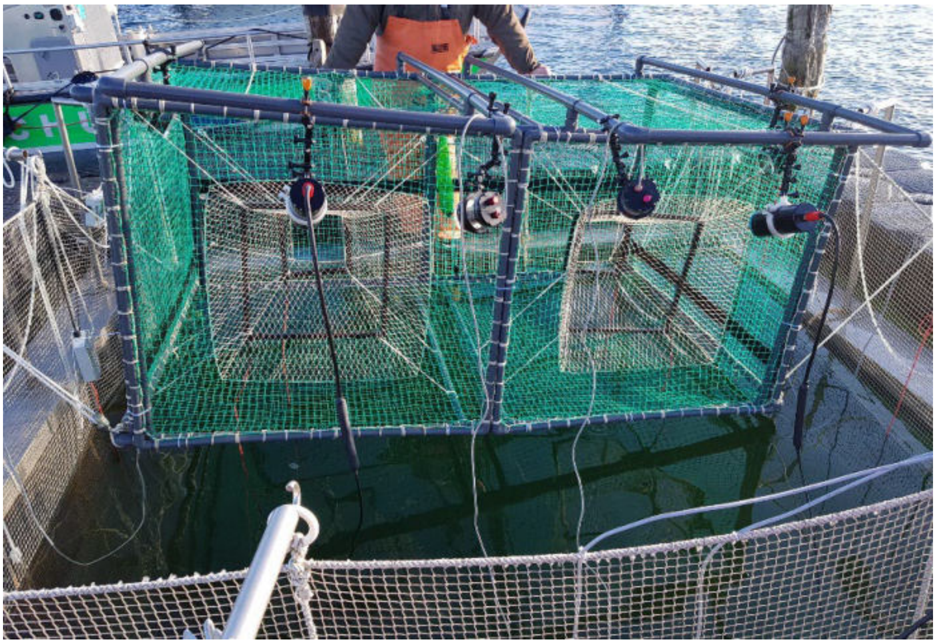

Figure 11: Setup for the net pen-based observation method developed in this thesis at the study location in Warnemünde, Rostock (Germany). With green netting: the experimental pot. Hanging on the frame going out from the pot roof and pointing at the two pot entrances each an infrared light and camera.

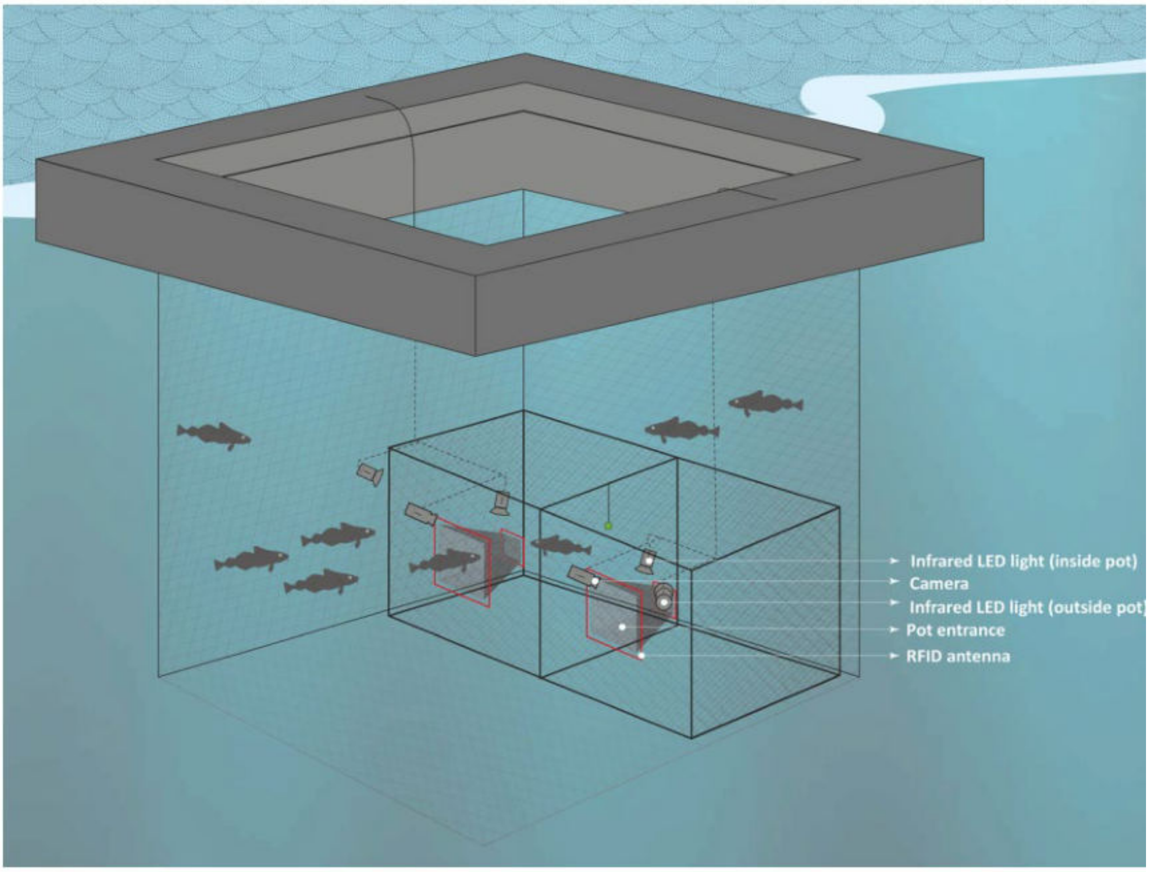

Figure 12: Schematic representation of the net pen-based observation method.

IR-sensitive camera system for day- and night-time observations

The newly developed IR- capable camera system allowed unobtrusive nightly observation of cod–pot interactions (Paper II). Its development was the result of several considerations: 1) Cod pots are usually soaked for several days (e.g. Thomsen *et al.*, 2010; Königson *et al.*, 2015a); 2) including pot illumination increases catch rates (Bryhn, 2014; Humborstad *et al.*, 2018); 3) cod also forage at night (Løkkeborg and Fernö, 1999); and 4) before, cod–pot interactions were only observed at night under strong artificial lighting (Hedgärde *et al.*, 2016a). The IR-system permitted for the first elucidating the marked differences between cod–pot interactions at night and at day (Paper III).

Cod diurnal entrance passage differences and importance of vision for entrance interactions revealed

Cod seldomly passed the experimental pot's entrances at night, most passages occurred during the day. This new understanding is crucial for shaping cod pot fishing strategies. It is especially important when fishing with pots baited with natural bait such as cut herring, as these rapidly lose their attractive capacity after less than just two hours soak time (Løkkeborg, 1990; Westerberg and Westerberg, 2011). Setting pots baited with natural bait in the middle of the night would lead to cod attracted to the pot not being able to enter it before the bait's attractive capacity expires.

The finding of diurnal entrance passage differences, coupled with the observation of the cod–pot entrance interactions, revealed that cod primarily rely on vision to find and navigate through pot entrances (Paper IIIC:\Users\JuJ\Desktop\PhD manuscript\Development - Paper IV). This is corroborated by the observed reluctance of cod to pass conventional triggers with strong visual outline (Paper IV). This understanding is essential for any further efforts on cod pot entrance innovation, and it facilitates innovating any cod pot part. More broadly speaking, it helps furthering the innovation of any similar entrapping passive gear such as large-scale traps, pound nets or fishing weirs. This significance of cod visual navigation through pot entrances fits with studies showing that large piscivorous fish such as cod orient visually (Løkkeborg and Fernö, 1999; Utne-Palm, 2002; Meager and Batty, 2007; Hedgärde *et al.*, 2016a; Meager *et al.*, 2018). It indicates that cod pot catch rates could be reduced in times of high turbidity when cod will be hindered finding and navigating cod pot entrances. This new understanding of diurnal entrance passage differences and the importance of vision for cod for interactions with entrances is useful for developing cod pot fishing strategies.

Net pen-based observation method developed

Concerning future cod pot-catch efficiency improvement efforts, the study of Paper III and IV demonstrated that cod pot-catch efficiency studies can benefit from using the net pen-based observation method. The method includes a detailed behavioural ethogram quantifiably 'dissecting' cod interactions with the entrance at different locations outside the pot in front of the entrance – inside the entrance – and at the entrance end inside the pot. The method includes a package of several statistical procedures, which used together allow directly comparing catch efficiency of different entrances and allow illustrating *how* and *why* cod interact differently with these entrances using the resulting behavioural flow diagram. This diagram permits to visually pinpoint the causes for differences observed between compared entrances. The behavioural flow diagram also supports conceptualizing entrance improvements based on the differences.

With the net pen-based observation method, the relationship between pot entry- and exit rate, one of the main factors affecting cod pot-catch efficiency, was effectively investigated. This could not have been achieved with conventional catch comparison field studies. The study elucidated the drastic effect that basic cod pot entrance parameters such as funnel length or colour have on cod–pot interactions and thus pot catch efficiency. Importantly, the results of Papers III and IV were accomplished with a high degree of accuracy, as the usage of a baseline control funnel, from which each tested entrance only differed in one aspect such as colour or length, allows to attribute the cause of the observed differences to just this one aspect.

Innovative fish retention device "Acrylic fingers" developed

The new pot triggers developed in Paper IV, the "Acrylic fingers" (AF) are the first cod pot trigger that reduced cod exit rates without reducing entry rates. Their addition to a funnel almost doubles its catch efficiency. This is a significant improvement in comparison to prior cod pot triggers developed. So far, these have always been found to in parallel reduce entry rates (e.g. Munro, 1972; High and Ellis, 1973; Furevik and Løkkeborg, 1994; Olsen, 2014). Lastly, the AF could also be used as an easily adjustable and straightforward way to implement an escape window to decrease bycatch of cod under the cod minimum conservation reference size ("MCRS", in the Baltic Sea 35 cm) and simultaneously increase catch efficiency for cod over MCRS (Ovegård *et al.*, 2011). The easy adjustability of the interfinger-width would additionally increase the versatility of the pots equipped with AF, for example to optimize entrances for more than just one target species ("multispecies entrances").

Conclusions on the findings made with net pen-based observation method

In summary, the net pen-based observation studies (Papers II, III, and IV) did not only deliver a quantified catch efficiency comparison between different entrances, but additionally also revealed the underlying mechanisms leading to these observed differences. Thus, they delivered important insights on how cod interact with pot entrances, how this is interaction is influenced by entrance parameters and how these insights can be used to increase pot-catch efficiency. Moreover, further avenues for cod pot catch increases were laid out through them.

Specific recommendations for cod-pot design and -fishing strategy developed

Additionally, the fish pot studies of this thesis led to several important, immediately implementable recommendations for cod pot fishing (presented in order of importance):

- Funnels are crucial for cod pot-catch efficiency, use them!
- The longer the funnel, the higher its catch efficiency (a tipping point with increasing funnel length, after which the entrance probability is reduced again, has however to be assumed).
- Place funnels in the pot so that the pot area from which the pot outside can be seen through the inner funnel opening is smallest.
- Avoid narrow entrance openings.
- Use transparent funnels (funnels made of transparent netting material) combined with an efficient catch retention mechanism such as the developed AF.
- Avoid conspicuous fish-retention devices with distinct visual outline.
- Set pots baited with olfactory bait at dawn or latest two hours before dusk in order to lure cod at the time of maximum bait attractive capacity and while it can still see enough to find and pass the entrance.
- Considering the importance of vision for cod for interacting with pot entrances, cod pot fishing efficiency is likely reduced in periods of elevated turbidity, such as after strong rains in coastal waters. Preferably set cod pots in periods of low turbidity and avoid periods of elevated turbidity.

In conclusion, not only have the results of the two presented net pen-based observation studies provided direct recommendations how to increase cod pot-catch efficiency, they also have provided a method to rapidly and efficiently study further pot fishing parameters. Therefore, the stepwise net pen-based observation method to study cod–pot interaction is recommendable for pot-catch efficiency studies.

Concerning the overarching goal of the second part of this thesis – increasing cod pot-catch efficiency to further their uptake as alternative to gillnets – these two fish pot development studies (Papers III and IV) are important steps towards economic competitiveness of cod pots via gillnets.

Future prospects

Cod pots have been shown to be economically competitive to gillnets in the Baltic Sea for some parts of the year (Königson *et al.*, 2015a). They were also shown to outcompete gillnets in catch efficiency in Labrador, Canada (Nguyen and Morris, 2021). Therefore, the “catchability gap” appears to be surmountable in the medium term. Further research for closing this gap should build on the findings presented here.

Economic competitiveness of fish pots as alternative passive gear is progressed by the findings of these studies. The developed methods and techniques of experimental setup and statistical analysis will further contribute to this goal. They could be used to investigate the influence of a multitude of parameters influencing fishing with passive entrapping gear (including pots, weirs, and traps) for cod as well as other species. This includes different structural- (e.g. size, shape, floating/bottom standing), fish state (e.g. size, hunger state, fitness), or abiotic parameters (e.g. temperature, current direction/strength, light conditions) as well as social effects (e.g. leader-follower dynamics).

3.4 Further considerations on PAL

PAL–replication for other porpoise (sub-)populations / other cetaceans

The PAL is effective in reducing western Baltic harbour porpoise bycatch and is similar to the efficiency of conventional pingers, but not necessarily higher (e.g., Gönener and Bilgin, 2009, who achieved a 98% bycatch reduction with pingers; Paper I). Bycatch reduction efficiency is also dependent on operational factors. For instance, in a pinger test in Danish gillnet fisheries, bycatch reduction was 67% in normal flat bottom set gillnets but 100% for gillnets set on wrecks (Larsen and Eigaard, 2014), using the same pinger type. This could explain the different bycatch mitigation effect level measured for the PAL and for conventional pingers. Nevertheless, this difference could also result from actual differences between the effect mechanisms of PAL and conventional pingers. While the PAL is theorized to function by alerting approaching harbour porpoises (Culik *et al.*, 2015; Chladek *et al.*, 2020), pingers are assumed to work by deterrence (e.g. Dawson *et al.*, 2013).

The existence of an genuine difference between the two pinger types is indicated by the inconclusive results of PAL influence on harbour porpoise bycatch rates in the North Sea (2015 and 2016, own unpublished data) and even more the results of a test around Iceland (ICES, 2018). During the latter study, eleven out of twelve harbour porpoises caught in the PAL strings were large adult males, while the gender ratio was more balanced in the control string bycaught harbour porpoises (seven males vs. four females). For pingers, no comparatively strong regional differences in the bycatch mitigation effect on individuals of the same species are known.

Several harbour porpoise populations have been recognized to differ in their echolocation properties (Kyhn *et al.*, 2013; Dähne *et al.*, 2020). Furthermore, some well-studied cetacean species are known to exhibit population distinct dialects (Winn *et al.*, 1981; Helweg *et al.*, 1996; Rendell and Whitehead, 2005; Filatova *et al.*, 2015b, 2015a; Wellard, 2018; see also Würsig, 2019). Therefore, the differing results from these PAL bycatch studies could indicate that also harbour porpoise populations exhibit distinct dialects. Concluding, this seems to confirm that the PAL effect mechanism is indeed different from the determent mechanism of conventional pingers, warranting more studies.

If confirmed, such a distinct effect mechanism would open new bycatch mitigation avenues, for the western Baltic harbour porpoise, as well as other harbour porpoise (sub-)populations and other cetacean species. Using proper communication signals for bycatch reduction would then be a worthwhile option to consider for any cetacean species.

PAL – suitability of other communication signals

If the PAL effect mechanism is indeed different from pingers' effect mechanism, other harbour porpoise communication signals could be as good or even better in mitigating their bycatch.

The PAL F3 signal was isolated from a study describing in total 14 click trains recorded during aggressive interactions. It was compared to two other signals, another click train observed in the study as well as a generalized version of all of the aggressive click trains recorded in this study (Clausen *et al.*, 2011; Culik *et al.*, 2015). Therefore, studies appear worthwhile to identify further harbour porpoise communication signals and evaluate their effectiveness for bycatch reduction.

Within such studies, focusing on the identification of signals that harbour porpoises vocalize to warn each other of danger, would seem to be more appropriate than identification of further aggressive signals. Recent observations of harbour porpoises, described as neophobic and shy (e.g. Dawson *et al.*, 2013; Teilmann and Sveegaard, 2019) staying for extended periods in the vicinity of a set gillnet (Maeda *et al.*, 2021) indicate that they possibly do not perceive gillnets as danger. Using a warning sound instead of an aggressive signal for the PAL (which can be programmed to produce other sounds than the F3 signal) could for this reason be more appropriate. Porpoises receiving such a warning signal could understand that an unspecified threat is near the emitter. With the F3 signal however, it can be assumed that receiving porpoises would expect an aggressive conspecific at the emitter. Thus, using a generalized warning signal appears more conducive to effectively reduce bycatch than the F3 signal.

A recent study reported that porpoises can hunt collaboratively with role specialization and active coordinating communication (Ortiz *et al.*, 2021). Other studies revealed that harbour porpoises are in acoustic communication contact much more than previously thought (Sørensen *et al.*, 2018; Teilmann and Sveegaard, 2019; Macaulay, 2020). These findings imply a larger acoustic repertoire of harbour porpoises, including dedicated warning signals. Studies to identify and decipher further communicative signals, especially warning signals, could be designed similar to the harbour porpoise communication study from Clausen *et al.* (2011). For this, at least a pair of trained porpoises (e.g. such as the ones from Elmegaard *et al.*, 2019) would be needed in order to have one emitter and one receiver of a warning signal.

As stated before, such studies should always be undertaken for the respective (sub-)population whose bycatch is to be mitigated. Such communication studies on other harbour porpoise (sub-)populations, using the same standardized experimental setup and method, could also shed more light on (possible) communication differences between them.

The PAL was developed and proven to incite harbour porpoises to increase their distance to gillnets where those are attached to. It was also developed to elicit acoustic investigation of the sound source (Culik *et al.*, 2015), meaning in direction of the PAL-carrying gillnet. Following this approach in future investigations for bycatch mitigating signals, it would be advisable to study their effect on the echolocation intensity of receiving harbour porpoises.

In any regards, all further identified signals would need to be tested in commercial fisheries with harbour porpoise bycatch from the (sub-)population the tested communication signals stem from. The PAL study (Paper I) delivered a methodological "blueprint" for this.

Possible influences on the effective range of the PAL signal: spacing distance and ambient noise

PAL does not *eliminate* harbour porpoise bycatch risk, as five harbour porpoise bycatch events were observed in PAL-equipped gillnets. Four of the bycatches in PAL-equipped gillnets occurred in gillnets with ≥195 m spacing in between PAL. Two of them were with 210 m spacing, the maximum PAL distance in the study. Furthermore, these bycatch events occurred after soak periods with maximum windspeeds between 4 and 5 Bft. No indications were found that weather strongly influences PAL bycatch. Harbour porpoises bycatch events in control strings however occurred also at lower windspeeds. Maximum windspeed of control bycatch events was 3 Bft. This indicates that increasing windspeed decreases PAL (and possibly also pinger) efficiency, especially at higher PAL spacings.

It must be noted though, that soak times with higher observed wind speeds >5 Bft were rarely recorded during the PAL study. Fishers avoid setting gillnets when high swell and/or strong wind conditions are predicted in order to avoid net loss or damages (Andersen *et al.*, 2012).

The indications of reduced efficiency of PAL with larger inter-device spacing and higher windspeeds are in line with prior findings: weather conditions influence background noise levels and thus cetacean auditory resolution (e.g. Richardson *et al.*, 1995). For instance, the detection distance of the F3 signal by a harbour porpoise oriented towards the emitting PAL prototype has been modelled as 670 m in conditions of 0 Bft and no rain, and as only 280 m with 7 Bft and strong rain (Culik *et al.*, 2015). Additionally, pinger efficiency was found to be negatively dependent on the pinger spacing along the gillnet string (Palka *et al.*, 2008; Larsen *et al.*, 2013). It is also reduced by ambient noise, depending on weather conditions (Kindt-Larsen *et al.*, 2019). Lastly, harbour porpoise bycatch risk in the Celtic Sea has been found to significantly increase during neap tides. They increase tidal current strengths and thus noise levels which influence gillnet acoustic detectability (Tregenza *et al.*, 1997).

A dedicated study to elucidate how weather and sea state conditions affect pinger efficiency has yet to be undertaken in a commercial fisheries trial (but see also Omeyer *et al.*, 2020 for a PAM study with i.a. inconclusive results concerning wind speed effect on porpoise detection probability near an active pinger). Possibly, the approach in the PAL study, to incorporate meteorological data from meteorological services could be used to retroactively perform such investigation with pinger bycatch mitigation studies already performed (e.g. Larsen and Eigaard, 2014). Provided GPS setting location and soak times are incorporated, such datasets could be linked with weather service databases to access the weather conditions prevailing during the soak times of the pingered and unpingered gillnets. Such studies could be additionally complemented by studies of how harbour porpoises adapt their behaviour and habitat use in rough sea conditions. These should be undertaken with the use of passive acoustic detection (PAM)- schemes (e.g. Macaulay, 2020), as visual detection schemes (e.g. Isojunno *et al.*, 2012) are only possible under calm sea conditions.

Possible habituation and habitat exclusion after long-term PAL use

Long-term pinger bycatch studies did not report evidence of habituation (Palka *et al.*, 2008; Carretta and Barlow, 2011b). Like conventional pingers, PAL could nonetheless lead to habituation of harbour porpoise to the PAL signal over time (pinger concern I; Cox *et al.*, 2001; Culik *et al.*, 2001; Carlström *et al.*, 2009; Kyhn *et al.*, 2015). Habitation to the PAL signal would lead to harbour porpoises less reacting to it and reduction of its bycatch mitigating effect. Harbour porpoises would then again approach nets to such a short distance where they would be in risk of entanglement (Dawson *et al.*, 2013; Larsen and Eigaard, 2014; Kindt-Larsen *et al.*, 2019).

Some lower degree of habituation would however even be beneficial. Harbour porpoise would not be largely displaced but keep sufficient distance to PAL-equipped nets. This would decrease possible habitat displacement (pinger concern III; van Beest *et al.*, 2017; Kindt-Larsen *et al.*, 2019).

Culik *et al.* (2015) found that harbour porpoise increase their distance to an active PAL slightly by only 32 m. This study was undertaken in a comparatively narrow and highly trafficked Little Belt. Thus, it can only conditionally be compared to displacement distance by conventional pingers studied elsewhere in less restricted areas. Nonetheless, the comparatively short displacement distance in comparison to conventional pingers (Cox *et al.*, 2001: 208 m; Culik *et al.*, 2001: 380 m; Carlström *et al.*, 2009: 300 m), indicates a possibly lower displacement risk by the PAL.

This consideration is in line with the findings of a limited study assessing possible habitat displacement by the PAL. It was undertaken at the German Baltic coastal waters of Schleswig-Holstein in an area with in total 1145 PAL distributed to gillnet vessels active in that areas. Following a Before-After-Control-Impact ("BACI") study design, harbour porpoise densities estimated from flight transects were compared to periods before 2018, the year when these PAL were distributed to the gillnet fishers. No indications of harbour porpoise density displacement away from the area was found. The authors rather report a possible porpoise density increase in the area compared to the period before the PAL were in use (Nehls *et al.*, 2020).

Potential habituation and habitat displacement remain an important aspect for research to confidently assure a constant PAL bycatch mitigation effect. Additionally, studies are required to better understand, if using species or (sub-)population proper signals is generally advantageous to pinger sounds. Further studies could elucidate if the reinforcement of the PAL's biological significance (Culik and Conrad, 2013; Culik *et al.*, 2015) really prevents excessive habituation. Moreover, it has been shown that using pingers with several, randomized alternating signals mitigates habituation risk (Kindt-Larsen *et al.*, 2019). Therefore, identifying further (sub-)population proper signals and implementing them as a set in the PAL could decrease habituation risk to the PAL.

<u>Gillnet setting patterns: possible influence on bycatch probability and pinger effectiveness</u>

During the PAL commercial fisheries test, fishers did not always set their gillnet strings in a straight line. A variety of different, intentional setting patterns, such as zigzag or curved were observed. The most extreme variant observed was a "criss-cross" pattern, for which fishers would repeatedly backtrack in loops during setting, thus crossing the gillnet string over itself. An example is the blue line illustrated in Figure 13.

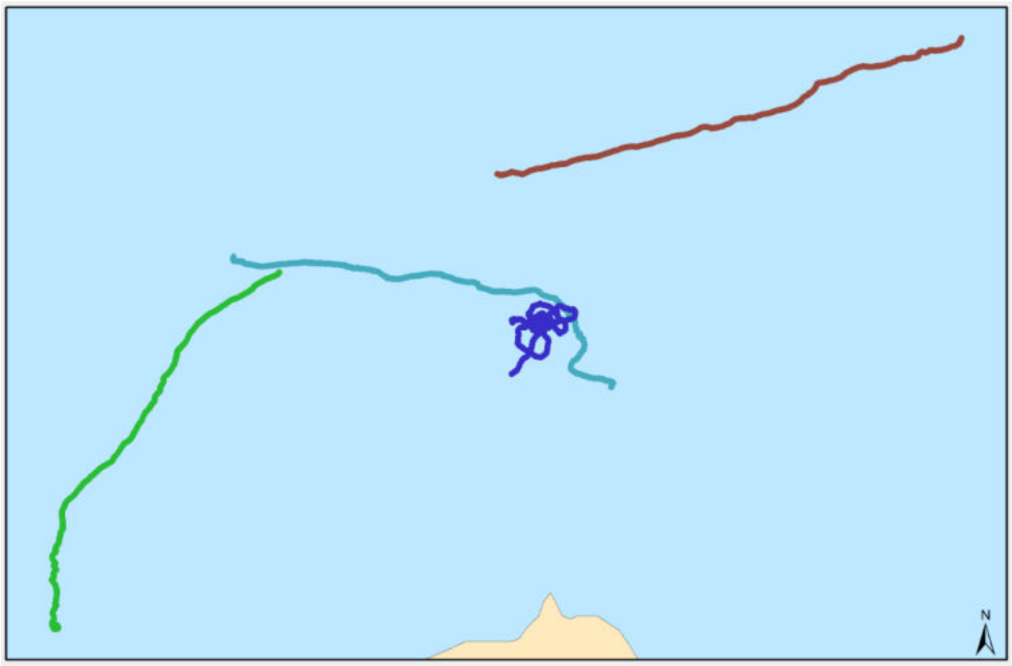

Figure 13: GPS tracks extracted from REM data of four different gillnet string set during one fishing trip of the PAL study. The dark blue track is from a gillnet string where the fisher backtracked in loops during setting, thus crossing the string repeatedly over itself and over the adjacent turquoise coloured track ("criss-cross" pattern).

While the occurrence of non-straight gillnet setting patterns has been described elsewhere (e.g. Sala *et al.*, 2018; Dias *et al.*, 2020), a study of the possible influence on harbour porpoise gillnet bycatch as well as on pinger efficiency is so far owing. It was not possible to conduct such an analysis in the PAL study since we did not know the setting patterns for all set strings. A harbour porpoise bycatch study by Larsen and Eigaard (2014) however indicates an influence on pinger efficiency of gillnet setting pattern. The study indirectly incorporated the influence of gillnet setting patterns by disaggregating gillnets set in the so-called wreck fishery and the fishery on flat bottom/stony ground. In the wreck fishery, several gillnet strings are often set in close proximity of few meters (Vinther, 1999), so not necessarily straight and possibly overlapping. In the flat bottom/stony ground fishery, longer, single gillnets are set straight on the ground. The authors observed the highest bycatch rate in unpingered strings on the wreck fishery (also reported by Vinther, 1999). The bycatch was reduced by 100% by pinger usage. In the flat bottom/stony ground fishery with straight set gillnets however, the bycatch rate was comparatively lower but only reduced by 67% through pingers. Furthermore, differing distances between pingers strongly influences bycatch mitigation efficiency (e.g. Larsen *et al.*, 2013) and setting pingered gillnets in any form other than in a line will reduce the distance between subsequent pingers.

An influence of the setting pattern on pinger efficacity can additionally be expected because pingers can have non-spherical sound propagation (Shapiro *et al.*, 2009). For example, the PAL has an approximate 90° cone behind its air-filled housing to where the signal is not emitted (Culik *et al.*, 2015).

Summing up, it is possible that gillnet setting pattern influences pinger efficiency. Future studies could investigate to what extent gillnet setting pattern influences gillnet bycatch risk and pinger bycatch efficiency. This would advance the acoustic bycatch mitigation technology as well as contribute to the understanding as to how and why bycatch occurs.

Combination of the PAL with pearl net

A technology to increase the acoustic visibility of gillnets for harbour porpoise by adding small acrylic glass spheres in the gillnet is under development (Kratzer *et al.*, 2020, 2021, 2022). The aim is to increase harbour porpoise awareness of the net as an obstacle and with that decrease their bycatch risk. A first commercial fisheries trial of this so-called "Pearl net" at the Turkish Black Sea coast yielded inconclusive results due to limited bycatch numbers (Kratzer *et al.*, 2021). Therefore, more studies are currently undertaken (Project: Gillnet modifications to reduce bycatch (PEARLNET_OP)), respectively in the starting phase (Project: STELLA II).

If a bycatch reduction effect of the Pearl net can be confirmed, combining it with acoustic devices such as the PAL or pingers could lead to a higher bycatch reduction than either of the Pearl net or the device alone. A combination PAL-Pearl net could be even more effective than the combination pinger-Pearl net, as PAL increases acoustic activity of approaching harbour porpoises by 10% (Culik *et al.*, 2015) while pingers possibly reduce acoustic activity (Cox *et al.*, 2001; Culik *et al.*, 2001; Teilmann *et al.*, 2006; Carlström *et al.*, 2009; Hardy *et al.*, 2012). The PAL would thus increase the chance of early detection of the Pearl net. Lastly, following the theory of Dawson *et al.* (1998), combining PAL and Pearl net could open up the possibility that harbour porpoises could learn to associate the PAL signal with Pearl net presence.

3.5 Further considerations on the fish pot studies

Observational fish pot studies: net pen-based observation method vs. in-situ observations?

The set of methods developed in this thesis to study fish pots (net pen-based day-&night-time observation system; entrance interaction ethogram; combined statistic approach of Generalized linear model & hierarchical tree classification) allowed the detailed "dissection" of the entrance interaction process, thus permitting pinpointing accurately the differences between the compared entrances. The development of this study built on prior cod pot gear development studies, in which cod were observed interacting with pots (Valdemarsen *et al.*, 1977a; Bagdonas *et al.*, 2012; Anders *et al.*, 2016; Hedgärde *et al.*, 2016a; Ljungberg *et al.*, 2016; Anders *et al.*, 2017; Meintzer *et al.*, 2017). Those were all conducted in-situ. This approach has the advantage of well reflecting actual commercial fisheries conditions. At the same time, it has the following constraints:

- Cod exhibit complex learning capacities, long-term memory and the ability to learn from conspecifics (Björnsson *et al.*, 2018a; Meager *et al.*, 2018), and the capacity to use social cues when foraging (Meager *et al.*, 2018). Specifically, cod have been shown to modify their approach to fish pots depending on social cues such as conspecific size or leader-follower dynamics (Anders *et al.*, 2017; Paper III). With an increased understanding of these effects, pot catch efficiency could be increased. However, investigating them in field trials is however difficult because fish that leave and then re-enter the camera field-of-view cannot be distinguished from newly arriving fish.
- Fish size can only be assessed in a coarse way, e.g. by roughly categorising arriving fish in two lengths classes by comparing them to pot structural elements (e.g. Anders *et al.*, 2017). Newer technological approaches could solve this problem in future research, such as using stereo-camera technology to obtain 3D-footage (e.g. Mallet and Pelletier, 2014; Neuswanger *et al.*, 2016; Cundy *et al.*, 2017; Sheehan *et al.*, 2020). Another possibility could be the use of acoustic cameras to measure fish size (e.g. Rose *et al.*, 2005). They, however, have a lower resolution than video cameras and no recording possibility of fish body colour and shading, which complicates species identification. Likewise, this technology does not allow to record and analyse gaze and behaviour in detail of fish interacting with the pot. This complicates understanding which structural elements are inspected by the fish (Paper III). Moreover, these methods inevitably increase experimental setup complexity, equipment handling time, and duration of video-data post-processing. Investigating the effect of fish size on fish–pot interactions will overall remain difficult with in-situ studies.
- As with field catch comparisons, approaching fish characteristics and states such as sex, hunger level, or maturity are not controllable and often not identifiable during in-situ observations. Environmental parameters such as turbidity, water temperature or prey availability are also difficult to control. These characteristics and parameters however can modify fish susceptibility to gear (e.g. Løkkeborg *et al.*, 1993; Stoner, 2003, 2004). Some, like turbidity, can even inhibit data collection.
- Most importantly, the presence of the study target species is not controllable and difficult to assess in field pot studies. This factor is especially problematic when the target species abundance is low. It gets most difficult when target species abundance is projected to stay low for an extended period of time, as is actually the case for both stocks of Baltic Sea cod (Sguotti *et al.*, 2019; ICES, 2021a, 2021b; Möllmann *et al.*, 2021).

The net pen-based observation method can potentially overcome all the above-mentioned drawbacks of in-situ observational studies (Løkkeborg *et al.*, 1993; Stoner, 2003). It corresponds to an early recommendation for passive gear development that behavioural studies should generally be the first step of gear development efforts (Løkkeborg *et al.*, 1993). Using the method presented here as the first step in gear development will accelerate (cod) pot gear development. It will moreover add to the knowledge about target species–pot interactions.

Crucially, the method allows to rapidly identify the most promising pot modifications from a set of tested modifications. And it allows revealing the underlying effect mechanism causing the observed performance differences. Based on this understanding, it permits rapid conceptualisation of further promising modifications to be evaluated in an iterative approach. This is well illustrated by the development of the AF (Paper IV). They were conceptualized based on the findings of Paper III that cod primarily use vision to navigate entrances and that an unobstructed view into the pot increases pot entrance passage.

Pot improvement candidates found this way should however be validated in field tests, best by field observations combined with catch comparisons (Hedgärde *et al.*, 2016b; see also Løkkeborg *et al.*, 1993 for a comparison of ex-situ and in-situ gear development studies). This would assure that these modifications work as intended. And it would reveal possible unknown effects absent in the controlled net pen environment.

Catch comparison tests would additionally enable quantifying the catch rate influence of the modification and examine their persistency over time. For example, the positive effect of the AF is expected to wear off after some time of use, as the AFs' near invisibility underwater is the result of its favourable refractive index, algal overgrowth and scratches accumulating on its surface could reduce their transparency and thus their effectiveness over time (Paper III). With catch comparisons this could be quantified and a cleaning/replacement interval recommendation for the AF formulated.

Ideally, such subsequent field observational studies should use an IR light capable camera with long run times of a least 24 h to be able to register possible diurnal interaction differences. For this, the IR camera system developed for the studies presented here (Paper II) can be used. And the behavioural analysis workflow described here can also be used to analyse cod–pot interactions in the field.

Possible improvements of the net pen-based observation method

The net pen study setup included a Radio-Frequency Identification (RFID)-setup. The initial aim was to explore the possibility of individual differences between cod individuals in interactions with the cod pot (entrances). The setup did however not work as expected. Cod behaviour analyses on an individual level were not possible. Future studies could nevertheless avoid the technical problems of this study and use RFID technology to investigate differences in pot interactions between cod individuals. For example to investigate differences in cod–pot interactions along the shy-boldness and/or the proactive-reactive continuum (Meager *et al.*, 2018).

A simpler, non-technical solution could be to always include just one cod individual in each experimental replicate. This however does not seem to be advisable for most possible research questions. It would considerably increase the required experimental effort to collect sufficient data. And it would not be feasible to simultaneously investigate the influence of social effects on pot catchability, such as size-dependent attraction or repulsion (Anders *et al.*, 2017), leader-follower dynamics (Björnsson *et al.*, 2018a; Paper III), or the role of inter-specific competition on bait locating (Stoner and Ottmar, 2004) and thus pot-entering motivation. Individual fish can exhibit behavioural plasticity modulated by the presence of conspecifics when interacting with fishing gear (e.g. Stoner and Ottmar, 2004; Anders *et al.*, 2017). Conclusion drawn from observing individual fish interacting with fishing gear can thus be erroneous, particularly for pot fishing, which in their soak time can attract a large number of fish simultaneously (e.g. Ljungberg *et al.*, 2016; Meintzer *et al.*, 2017).

The net pen-based observation study setup would benefit from including a reliable method for individual fish identification. Either through an optimized RFID setup or through an alternative method. An alternative to RFID would avoid having to place RFID-antennas around the experimental fish pot entrances, influencing their appearance. For example, cod could be individually marked by colour-coded external markings (e.g., spaghetti tags). As an added benefit exterior markings would be less invasive than the implanted RFID tag, increasing fish welfare and reducing experimental effort. External markings would be further advantageous, because when several RFID tags enter a RFID detection field simultaneously all tags reciprocally block their detection. If external markings with colour codes are used, it should however be ensured that the colour code is identifiable under IR illumination. Further identification options can be obtained by alternating the placement of the external markings on the observed cod; e.g., left or right fish flank, or using more than one spaghetti tag per fish.

For the duration of the pot experiments conducted during this thesis, the net pen was hanging in the waters of the Warnemünde yacht harbour (Rostock, Germany). While this allowed to investigate the influence of diurnal effects, environmental parameters such as salinity, light regime, or temperature are dictated by the conditions present there. The strong influence of environmental parameters on pot and other passive gears' catch efficiency is evidenced by a large number of studies (see among others the following reviews: Furevik, 1994a; He, 2010; Løkkeborg *et al.*, 2014). The current understanding in this regard could however miss important influences of environmental parameters on cod–pot interactions and pot cod catchability (Königson *et al.*, 2015a). To enhance this understanding, the study setup could be installed in an aquarium tank where environmental parameters can be controlled.

With such a tank-based behavioural pot study, the role of bottom structural complexity (e.g. High and AJ, 1970; Luckhurst and Ward, 1987; Königson *et al.*, 2015a) on pot catchability could also be investigated. More specifically, it could be studied if cod respond differently to the same pot design parameters in standardized low- and high complexity habitats. For this, experimental trials with rocks placed on the tank bottom (representing a high-complexity habitat) and without (representing a low-complexity habitat) could be compared.

Using the net pen-based observation method for further cod pot parameter improvements

Other influencing parameters could be investigated with the net pen-based observation method described here, next to environmental parameters as described above. For instance:

In Paper III, it was shown that the longer the funnel, the better its catchability. This funnel length effect, however, can be expected to reach a tipping point. Once the funnel is so long that cod searching for an exit along the back net wall find the funnel inner opening in their immediate vicinity, exit rates can be expected to increase. Also, at a certain increased funnel length, cod entry probability could be reduced because the inner opening would be too far away for pot at the funnel entrance. Thus, a "too long" funnel could then again have a reduced cod retention capability compared to a slightly shorter funnel. The findings in Paper III and Paper IV indicate that cod primarily use vision to find and navigate through a pot entrance from both sides (i.e. into and out of the pot). Therefore, a funnel length threshold might exist. Beyond this threshold, the pot inner would appear too far away for cod outside the pot to pass the funnel. Further studies investigating how funnel length can be in relation to the backward pot wall and for an optimal funnel length thus appear promising.

Cod–entrance interactions in high turbidity: Considering the finding that cod principally rely on vision to navigate pot entrances and that cod are known to also forage in highly turbid waters (e.g. Meager and Batty, 2007), future research could focus on how cod interact with pot entrances in highly turbid waters. Such findings could facilitate optimizing cod pot entrances for fishing in such waters, and better understanding how cod interact with pot entrances generally and thus to also optimize cod pot entrances in non-turbid waters.

Combining AF with "transparent funnels": In Paper III the highest number of passages through any of the tested funnels was observed for the funnel made of transparent netting. This, combined with the other indications of Paper III for cod visual navigation, led to the development of the transparent AF in Paper IV. These were found to significantly reduce cod exit rates. However, because transparent funnels not only had the highest entry- but also a high exit rate compared to the other tested funnels, they were not the most catch efficient. Adding AF to transparent funnels should negate this drawback.

Therefore, such a combination has the potential for a highly catch efficient cod pot entrance. Quantifying its catch efficiency and investigating further improvements of such an entrance should best be undertaken with the net pen-based observation method.

Studying social effects on pot catch efficiency: In Paper III, the net pen-based observation method also allowed to shed light on variables influencing pot interactions other than differing pot entrances. Herding events, i.a. when several cod interacted jointly with a pot entrance, were significantly shorter than entrance interactions in which single cod interacted with the entrances. This indicates that the speed of the leading cod initiating the interaction in herding events is what triggers other cod to follow. This observation of a social effect on cod–pot entrance interaction fits with similar observations of social effects mediating cod interactions with their environment in tanks or net pens (e.g. Nilsson *et al.*, 2008b, 2008a, 2012; Nilsson and Torgersen, 2010; Millot *et al.*, 2012; Björnsson *et al.*, 2018b). Together with prior in-situ studies of cod interacting with cod pots (Anders *et al.*, 2017) or of other fish interacting with typical longline or fish pot bait (Stoner and Ottmar, 2004), this finding underscores the importance of studying social effects in catch efficiency studies (see also He, 2010). The net pen based approach would allow analysing these effects more closely, because fish with certain characteristics can be chosen for experiments. Furthermore, individuals in experimental groups can be marked and distinguished throughout an experiment.

In the here presented studies, the net pen-based observation method was used to study the effect several entrance parameters on cod–pot entrance interactions. These parameters included funnel netting colour; funnel presence and -length; entrance form; and presence of FRDs. In further studies, the net pen-based observation method could also be used to optimize prior cod pot developments, including the following:

Opening size and shape: The size of an entrance opening is a central aspect of any fish pot, as the larger an entrance opening, the easier a fish can find and pass the entrance (e.g. Bagdonas *et al.*, 2012). This goes in both directions, though, for entries as well as exits. An optimal entrance opening size, depending on target species (size) as well as entrance type, is the size where catch efficiency (ratio between entry- and exit probability) is maximised (e.g. Munro, 1972; Carlile *et al.*, 1997). In a field cod pot catch comparison of different entrances in the Baltic Sea, the most catch efficient entrances had an opening size more closely fitting the oval cross section of cod compared to the other, less-performing cod pot entrances (Königson *et al.*, 2015b). Using these findings as a starting point, research on cod pot entrances optimizations concerning opening size and shape, could also be undertaken with the net pen-based observation method. Such studies could also include AF as modifications of the examined entrance types.

Optimizing seal exclusion devices: As stated above in chapter 1.3, seal depredation of gillnets (pinger concern IV) is, next to the bycatch of harbour porpoises and seabirds, one of the severe and continuously increasing problems in Baltic Sea gillnet fisheries (e.g. Königson *et al.*, 2015a; Ljungberg *et al.*, 2016). Cod pot entrances are one of the “weak points” through which grey seals can gain access to fish caught in the pot. Therefore, cod pot entrances developed for use in the Baltic Sea should be seal proofed by addition of so-called “seal exclusion devices” (Königson *et al.*, 2015b; Hedgärde *et al.*, 2016b). Such barriers need to be rigid and able to resist the considerable force of adult male grey seals, which have been shown to “specialize” in fish pot raiding in the Baltic Sea (Königson, 2013). Most cod pot seal exclusion devices change appearance as well as rigidity of cod pot entrances and have been shown to influence cod pot catchability (Königson *et al.*, 2015b). The net pen-based observation method could in this regard not only be used to optimize cod pot entrance, but also to optimize seal exclusion devices. For instance, the two steel-framed devices that eliminated seal bycatch and increased pot-catch efficiency in a study by Königson *et al.* (2015b), could be combined with the AF developed in Paper IV.

Funnel shape: The funnels tested in Paper III were all straight, vertically- and horizontally symmetrical funnels. Other funnel shapes are however known to be employed around the world. So-called “horse-neck funnels” for instance, used in Caribbean fisheries (e.g. Luckhurst and Ward, 1987; Whitelaw *et al.*, 1991) are initially straight funnels that have a downward turn at the inner end. Another non-symmetrical funnel type used in western Australia has a part of its rigid net wall tapering towards the pot inner terminating in a vertical slit of the height of the trap, much higher than wide (Whitelaw *et al.*, 1991). A large variety of other funnel shapes, designed to catch a multitude of species, especially from pots of traditional fisheries, are also known (e.g. Furevik, 1994a; Thomsen *et al.*, 2010).

Pot volume: Cod pot volume has been found to positively influence the pots’ catch rate (Furevik and Løkkeborg, 1994; Hedgärde *et al.*, 2016b). This is a phenomenon also described for other target species (Munro, 1974). The net pen-based observation method could be used to examine this more closely. Also considering the indications found in Paper III that cod pot exit rate is influenced by the entrance funnel length. It appears possible that those two catch efficiency influencing factors are interconnected by one underlying mechanism. This could be the ratio between the area in which cod in the pot can see the unobstructed exit through the entrance in their proximity and the rest of the pot in which the outside is physically blocked by pot netting or too far away. If this is confirmed, it could be used to increase catch rates.

Second catch chamber (“parlour pot”): One of the most widely used cod pot design is the “Norwegian cod pot”, developed by Furevik *et al.* (2008a). Its main innovations are a second catch chamber and addition of floats to lift it above bottom to avoid crustacean bycatch and maintaining the entrance oriented down current. The second catch chamber is situated above the first catch chamber and accessible by a slit in the dividing net “floor”. Two-chamber pots, or “parlour pots”, where a second catch chamber is horizontally placed behind the first catch chamber, have also been developed before for cod as well as for other target species (e.g. Munro, 1983; Bjordal and Furevik, 1988; Furevik and Løkkeborg, 1994; Thomsen *et al.*, 2010).

Size selection: Cod pot bycatch of non-target species and undersized cod is not a pressing development issue as cod pots usually deliver their catch alive and in good condition (Furevik, 1994b; Suuronen and Erickson, 2010; Thomsen *et al.*, 2010; Suuronen *et al.*, 2012; Humborstad *et al.*, 2018) and size selection is easily adjustable by using so-called “selection windows”. These are net panels with larger mesh size than the regular pot wall through which smaller fish can escape (Thomsen *et al.*, 2010; Ovegård *et al.*, 2011). For Baltic cod, ideal mesh size for catching sized cod and releasing undersized cod has been described before, with indications that the selection windows also increased catch efficiency (Ovegård *et al.*, 2011). Nonetheless, further pot development issues for Baltic cod potting could be addressed by developing further selection possibilities. For instance, for releasing flatfish, or for releasing cod of all sizes when targeting flatfish.

Flatfish optimized entrances: Both Baltic Sea cod stocks are currently in unfavourable conditions, leading to low cod abundance and limited cod catch opportunities (ICES, 2021b, 2021a). Total Allowable Catch recommended by the International Council for the Exploration of the Sea (ICES) for both Baltic cod stocks decreased constantly in the last years (ICES, 2020a, 2021a). Simultaneously, Baltic Sea flatfish stocks are in increasingly good conditions (e.g. ICES, 2021c, 2021d, 2021e). Using the net pen-based observation method to identify pot modifications for flatfish pot catch improvements would therefore contribute to assuring alternative catch opportunities to cod for Baltic Sea SSF. Ex-situ behavioural flatfish gear studies have been successfully conducted in the past (e.g. Stoner, 2003; Ryer and Barnett, 2006; Soetaert *et al.*, 2016). Preliminary observations of flounder (*Platichthys flesus*) and plaice (*Pleuronecta platessa*) at the experimental pot used for the studies of Papers III and IV revealed that these flatfish interact differently with pot entrances than cod. For instance, flatfish were observed laying down on the upper or lower horizontal panels of the entrance funnels. Using the here presented method to optimize pot entrances for Baltic flatfish fisheries thus seems promising.

Taking this concept further, since the AF by itself block fish from exiting, the recommendation to best adapt the entrance shape to the target species cross-section in order to reduce exit probability (Königson *et al.*, 2015b), is reduced and entrances could not just be optimized for targeting flatfish, but possibly also to target roundfish (other than cod), thus creating multispecies pot entrances. Such multispecies entrances are already in development and a first prototype build (personal communication D. Stepputtis, Thünen Institute of Baltic Sea Fisheries 03.04.2022).

In such development studies for multispecies pots for species other than cod, a secondary goal could be to optimize the entrance for reducing cod interactions with them to avoid their catch. This could be helpful for Baltic cod stocks protection.

Combining cod pot innovations of this thesis with other catch improving innovations

Cod pots have been shown to be similarly catch efficient as gillnets in the Baltic Sea for some parts of the year (Königson *et al.*, 2015a). The current catch efficiency gap between pot and gillnet catch efficiency is thus surmountable. The results of the pot studies of this thesis shorten it considerably. Combining the findings of this thesis with prior cod pot innovations could further improve cod pot catch success. For instance, an approach to increase the perceptibility of pot entrances and thus the cod entry rate is the use of floated single-entrance baited pots. As cod follow the bait plume upstream due to positive rheotaxis (Valdemarsen *et al.*, 1977b; Løkkeborg *et al.*, 1989; Furevik, 1994a; Løkkeborg, 1998), they automatically encounter the pot entrances, which are always oriented downstream due to alignment of the pot with the current. This results in higher catches of floated single-entrance baited pots compared to bottom-set baited pots where entrances are not automatically facing downstream (Furevik *et al.*, 2008b; Jørgensen *et al.*, 2017). Using transparent funnels + AF on such floated pots probably will increase their catch rates even more.

Strong LED lights considerably increase cod pot catch rates by attracting cod prey, which in turn attracts cod into the pot (Humborstad *et al.*, 2018; Utne-Palm *et al.*, 2018). Based on the findings of Paper III, the cod pot catch rate increased found by Humborstad *et al.* (2018), could also partly be due to the cod being able to perceive and navigate through the pot entrances. This positive attractive effect of the light could to some extent however be diminished. Cod which entered an illuminated pot could be more able to find their way back out of the pot due to the illuminated entrance. The AF (Paper IV) would limit or possibly eliminate this possibility. Therefore, for cod pots soaking over night, combining strong LED lights together with transparent funnels plus AF could possibly maximize cod pot-catch efficiency.

3.6 Conclusion and outlook

The PAL has been shown to effectively reduce bycatch of the western Baltic harbour porpoise. Since 2017 it is in use by over 100 SSF vessels on the German Baltic coast of the federal state Schleswig-Holstein (Paper I). No indications for detrimental habitat exclusion have been found so far (Nehls *et al.*, 2020). The PAL development, test, and subsequent implementation in this SSF fishery thus is a success. Therefore, the PAL concept to use biologically relevant acoustic signals instead of pinger artificial noise with no biological relevance for harbour porpoises, can be considered comparably efficient to conventional pingers.

Nevertheless, no other acoustic alerting devices using signals based on actual vocalizations by the concerned cetacean species is currently in development. This is likely due to the difficulty of accomplishing the obligate first step in such a development process: access to captive individuals of this species is necessary to conduct observations of individuals interacting, including click communication recording. Such studies could however be undertaken in the future. The more such acoustic devices are developed for other cetacean species or harbour porpoise populations, the more the possible advantages theorized by the PAL developers could be elucidated (see sub-chapter 2.1). This could lead to further innovations in gillnet cetacean bycatch mitigations, even if the PAL concept should later be found to be less efficient compared to conventional pingers.

Some of the open questions concerning the PAL effect mechanism, will possibly be answered by a recently started follow-up PAL study (Project: PAL use in German waters - Current efficiency and mode of operation"). Primary project goal is to assess the long-term persistence of PAL's bycatch mitigation efficiency (habituation). Further objective is to assess other possible unintended effects on harbour porpoises. This follow-up study not only highlights the actuality of the harbour porpoise bycatch issue in the Baltic Sea, but also the importance of the first part of this thesis. The findings of Paper I are highly relevant for this study.

In the second part of this thesis, an innovative net pen-based observation method was developed and successfully utilized for cod pot development, leading to specific cod pot design as well as pot fishing strategies improvements. It remains to be seen how those recommendations are taken up and refined even further. They, however, offer significant advances in cod pot-catch efficiency improvements and lay out options for further improvements, both structurally and in terms of fishing strategies. The fishing strategy recommendations (e.g., if bait is used, best set the pots at dawn, when cod entrance interactions peak) can immediately be implemented to increase cod pot catch.

The most innovative cod pot structural improvement developed in the second part of the thesis are the AF. However, some cod in the study of Paper IV were able to exit through the AF. While this was mostly by cod below MCRS, few larger cod were able to pass the AF equipped entrances by pushing two adjacent AF to the side, showing further mechanical improvement potential for the fingers. Structural AF adjustments to inhibit exiting by larger cod should be researched using the net pen-based observation method. Possible AF adjustment include reducing inter-finger width, increasing the AF' thickness and thus reducing their flexibility or stiffening the AF by other means (e.g., using a more rigid acrylic). Another approach could be to set AF into a holding frame with brackets fixating the AF tips when lowered. This could prevent AF sideways movement when cod push against them from the pot inside. Linked to this is a need for improving AF's robustness considering the demanding commercial fishing conditions as well as inevitable scratching and algal overgrowth. These effects could increase AF visibility after a certain time of use, hence reducing their efficiency. Addressing these wear effects could be addressed by material optimization, and by fishing operation optimization. An automated pot set&retrieve system for instance, such as in Alaskan Pacific cod pot fisheries (Thomsen *et al.*, 2010), including an automated AF cleaning mechanism could reduce handling time as well as the AF's endurance.

Summarizing, the cod pot catch studies of this thesis will improve cod pot-catch efficiency in the short term and even more in the medium- to long-term, pending further research building up on the findings of the studies as well on the developed net pen-based observation method. Considering the recent increased number of fish pot publications with cod (e.g. Anders *et al.*, 2016, 2017; Hedgärde *et al.*, 2016b; Ljungberg *et al.*, 2016; Humborstad *et al.*, 2018; Meintzer *et al.*, 2018; Utne-Palm *et al.*, 2018) or other finfish target species (see Petetta *et al.*, 2020 and references therein), an uptake of this method in the near future seems conceivable.

Furthermore, the scientific relevance of the fish pot studies of this thesis is exemplified in a recently started follow-up research project. One principal component of this new project is the direct continuation of the fish pot studies (personal communication D. Stepputtis, Thünen Institute of Baltic Sea Fisheries 03.04.2022).

Lastly, the high political relevance of the fish pot studies is reflected by the recent developments of the harbour porpoise bycatch issue in the Baltic Sea: In 2020, ICES answered a request by the European Commission concerning possible emergency measures to protect the endangered Baltic proper harbour porpoise sub-population (ICES, 2020b). The ICES report makes concrete and far-reaching mitigation recommendations, comprising a mixture of permanent and temporal fisheries closures inside Central Baltic protected areas and gillnet pinger obligations outside of protected areas. The regional fisheries policy group of EU Baltic Sea Member States (“BALTFISH”) delivered a Joint Recommendation to the European Commission for harbour porpoise protection with fisheries closure inside protected areas. These were based on the measures recommended by ICES. However, the plans for complementary pinger implementation outside protected areas recommended by ICES have currently stalled. In an unexpected turn of events, the Defence Ministries of BALTFISH member states have voiced serious concerns over the effect of large-scale acoustic mitigation devices (pingers as well as the PAL) implementation on these countries’ marine defensive capacities. In consequence, pingers as well as the PAL could be ruled out as mitigation measures. This would again increase the need to develop new or improved alternative gears for SSF gillnet vessels – as done in this thesis – to reduce harbour porpoise bycatch.

4. Literature of introduction and of general discussion

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Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift mit dem Titel „Fishing gear technology to mitigate harbour porpoise and seabird bycatch in the Baltic Sea: Gillnet modifications and alternative fishing gear fish pot“ selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare, on oath, that I have written the present dissertation „Fishing gear technology to mitigate harbour porpoise and seabird bycatch in the Baltic Sea: Gillnet modifications and alternative fishing gear fish pot“ by my own and have not used other than the acknowledged resources and aids.

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