




## Original Article

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

Jérôme Chladek <sup>1\*</sup>, Daniel Stepputtis<sup>1</sup>, Andreas Hermann<sup>1</sup>, Peter Ljungberg <sup>2</sup>,  
Paco Rodriguez-Tress<sup>1</sup>, Juan Santos <sup>1</sup>, and Jon Christian Svendsen<sup>3</sup>

<sup>1</sup>Fisheries and Survey Technology, Thünen Institute of Baltic Sea Fisheries, Alter Hafen Süd 2, Rostock 18069, Germany

<sup>2</sup>Institute of Coastal Research, Department of Aquatic Resources, Swedish University of Agricultural Sciences, Kustlaboratoriet, Turistgatan 5, Lysekil 453 30, Sweden

<sup>3</sup>Section for Coastal Ecology, Technical University of Denmark, National Institute of Aquatic Resources (DTU Aqua), Lyngby 2800, Denmark

\*Corresponding author: tel: +49 381 66099 102; e-mail: [chladek-sc@posteo.de](mailto:chladek-sc@posteo.de).

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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 Hågenesen, 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°C at the end of the experiment on 25 May.

## Set-up of the experiment

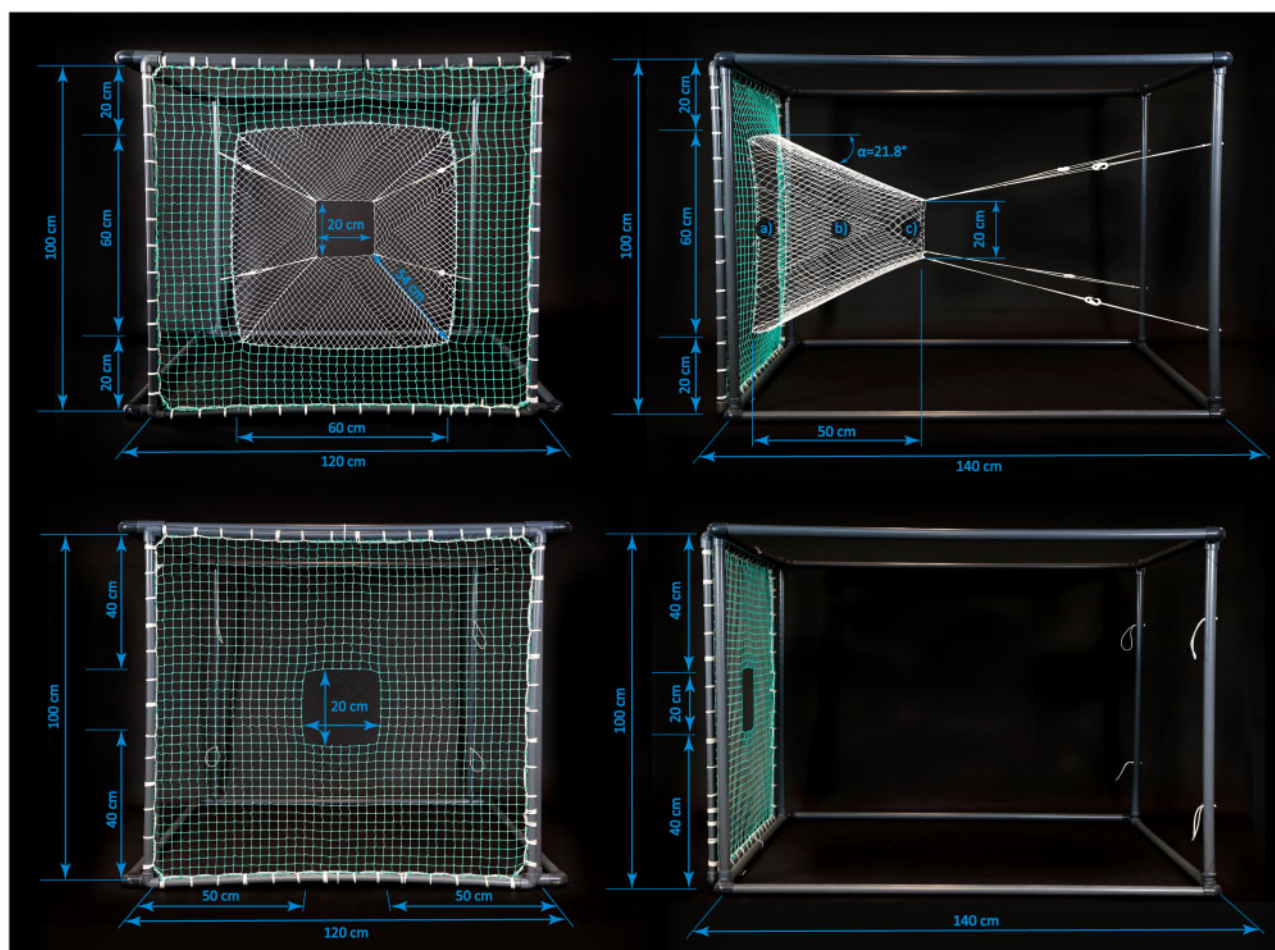
Two identical net pens (3 m × 3 m × 3 m = 27 m<sup>3</sup>; Mieske, 1998; see Supplementary Figure S2) were used: one for experimental treatments and the other for holding the fish before experiments. An experimental pot (W 250 cm × D 140 cm × H 100 cm) with two side-by-side entrances was constructed 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.

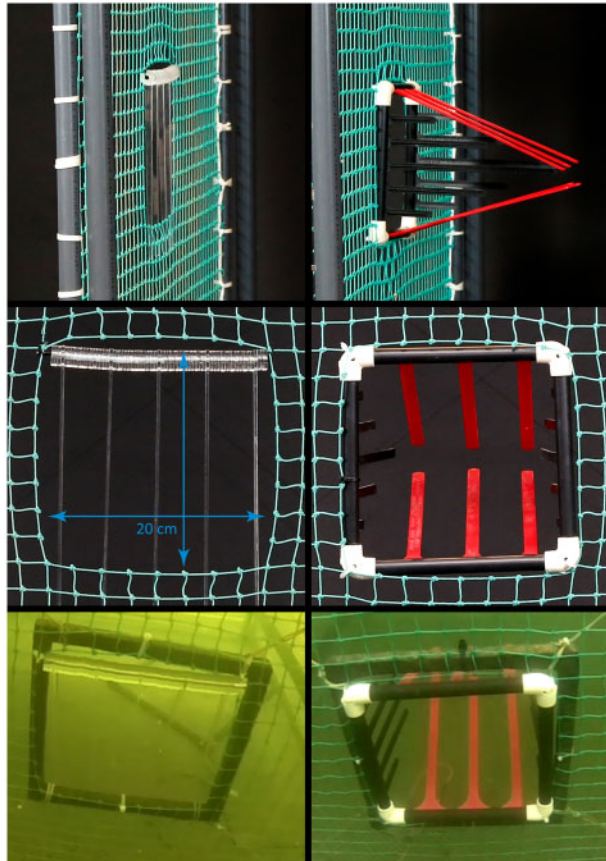
round washers in the same material and thickness as the fingers’ heads were spaced at 42-mm intervals on either sides of each finger. We chose a relatively large diameter for the head and washers to increase the fingers’ side stability. We oriented the AF inter-finger space width to the 45-mm inter-finger 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://neptonmarineproducts.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

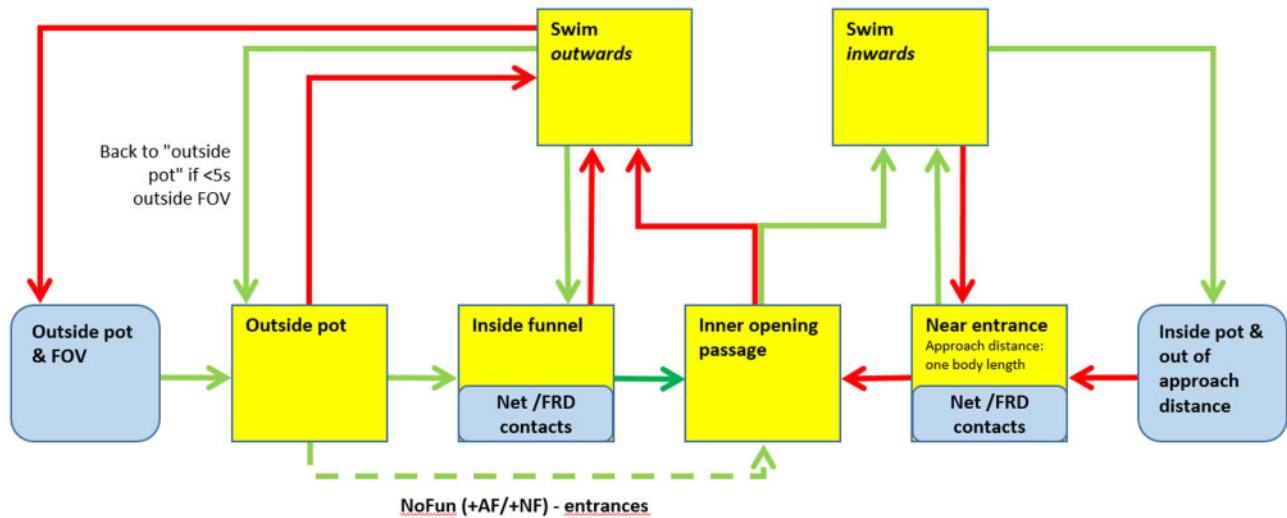
To provide a comprehensive description of the event chain of cod interacting with the pot entrances, we constructed a detailed ethogram and a behavioural flow diagram ([Figure 3](#) and [Table 1](#)), adapting prior behavioural analysis approaches ([Ljungberg et al., 2016](#); [Anders et al., 2017b](#); [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 ([Thieurmél 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 = control, 1 = test), and  $X$  a three-dimensional vector including the model intercept, 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  $\beta_0$  is the model intercept and  $\beta_1$  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:

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

where  $N_i$  is the number of cod performing the event  $i$  (node  $i$ ) and  $\text{Root}$  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.	<i>Inwards:</i> Cod enters FOV (begin event chain). <i>Outwards:</i> When two-thirds of body length has passed outer entrance opening and cod does not directly leave FOV (previous event: "Swim outwards").	<i>Inwards:</i> Tip of cod snout passes outer entrance opening (next event: "Inside funnel" or "Inner opening passage" if "No funnel" entrance). <i>Outwards:</i> Cod turns and starts to swim outwards (next event: "Swim outwards").
Inside funnel	State	Cod is inside the funnel (excluding direct outward swimming). <i>Note: Does not apply to "No funnel" (NoFun) entrance.</i>	<i>Inwards:</i> Tip of cod snout passes outer entrance opening (previous event: "Outside pot"). <i>Outwards:</i> Cod aborts swimming outwards (previous event: "Swim outwards").	<i>Inwards:</i> Tip of cod snout passes inner entrance opening (next event "Inner opening passage"). <i>Outwards:</i> Cod turns and starts to swim outwards (next event: "Swim outwards").
Inner opening passage	State	Cod passes inner opening of entrance in either direction.	<i>Inwards:</i> Cod snout enters inner opening (previous event: "Inside funnel" or "Outside pot" for NoFun entrance). <i>Outwards:</i> Cod snout enters inner opening (previous event: "Near entrance").	<i>Inwards:</i> Two-thirds of cod body length passes the inner opening towards inside of pot (next event: "Swim inwards"). <i>Outwards:</i> 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).	<i>Inwards:</i> Cod starts swimming towards pot inside (previous event: "Inner opening passage"). <i>Outwards:</i> Cod aborts inner opening approach and turns towards pot inside (previous event: "Near entrance").	<i>Inwards:</i> Cod is more than one body length away from entrance/ funnel inner opening (end of event chain). <i>If cod re-approaches the opening to within one body length in &lt;5 sec., it is still considered in the same event pass.</i> <i>Outwards:</i> 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.	<i>Inwards:</i> Cod aborts inward swimming and turns back towards inner opening (previous event: "Swim inwards"). <i>Outwards:</i> Cod approaches opening to within one body length, attention directed towards opening (begin of event chain).	<i>Inwards:</i> Cod turns away from entrance (next event: "Swim inwards"). <i>Outwards:</i> Cod snout enters inner opening (next event: "Inner opening passage").
Swim outwards	State	Cod swims towards pot outside (outside inner opening).	<i>Inwards:</i> Cod turns and starts to swim outwards (previous event: "Outside pot" or "Inside Funnel"). <i>Outwards:</i> Two-thirds of cod passed entrance inner opening and cod starts swimming outwards (previous event: "Inner opening passage").	<i>Inwards:</i> Cod swims backwards or turns >90° towards pot inside (next event "Outside pot" or "Inside funnel"). <i>Outwards:</i> 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.

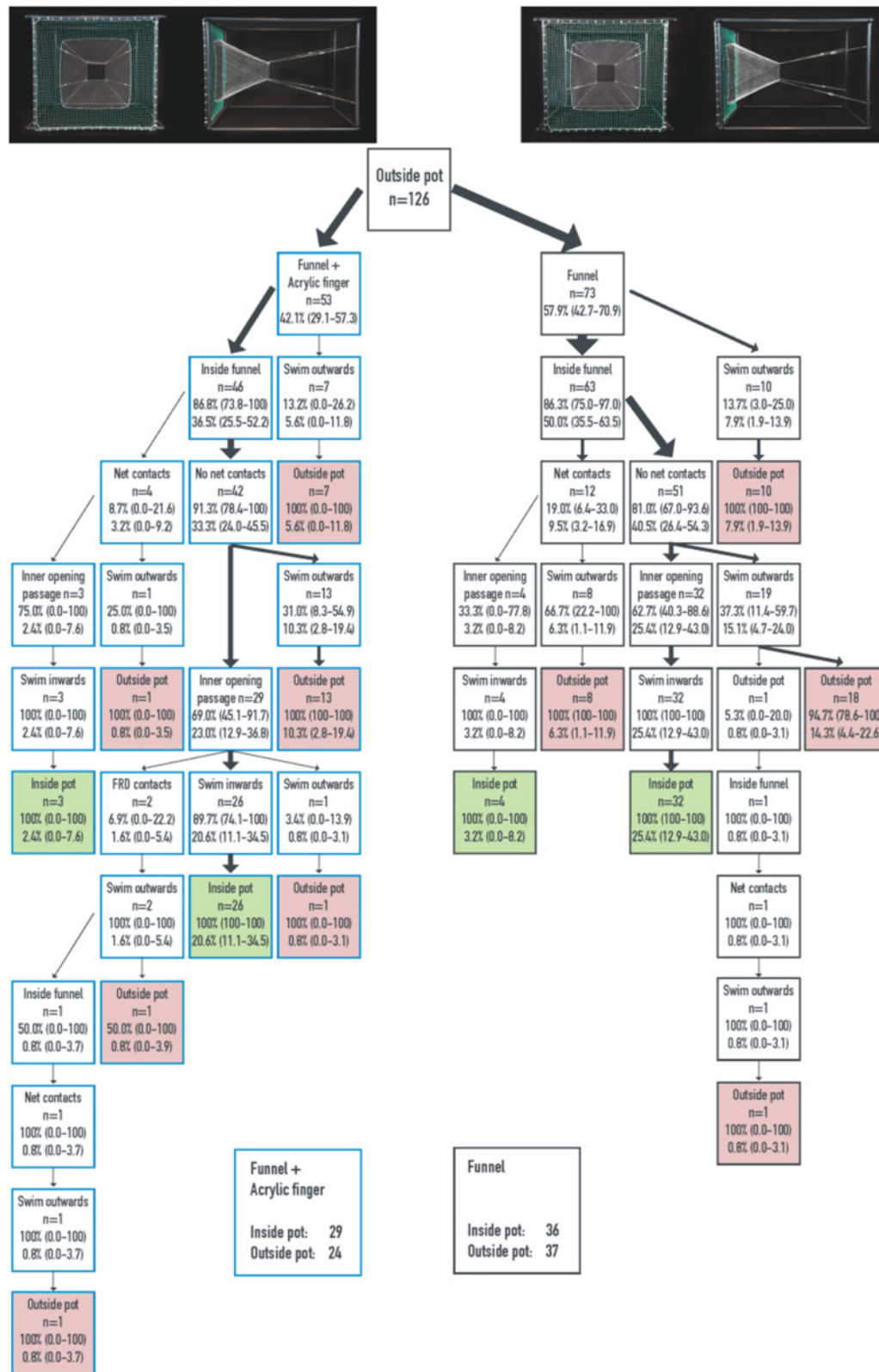
Exp.	Control	Test	Position control	Cod length group [cm]	Entries		Exits	
					Control	Test	Control	Test
1	Fun	Fun + AF	Left	40–49	2	6	0	0
	Fun	Fun + AF	Left	50–59	14	5	10	0
	Fun	Fun + AF	Left	50–59	8	6	8	0
	Fun	Fun + AF	Right	40–49	7	9	9	0
	Fun	Fun + AF	Right	30–39	5	3	1	0
					36	29	28	0
2	Fun	Fun + 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 through test/control entrances is given.

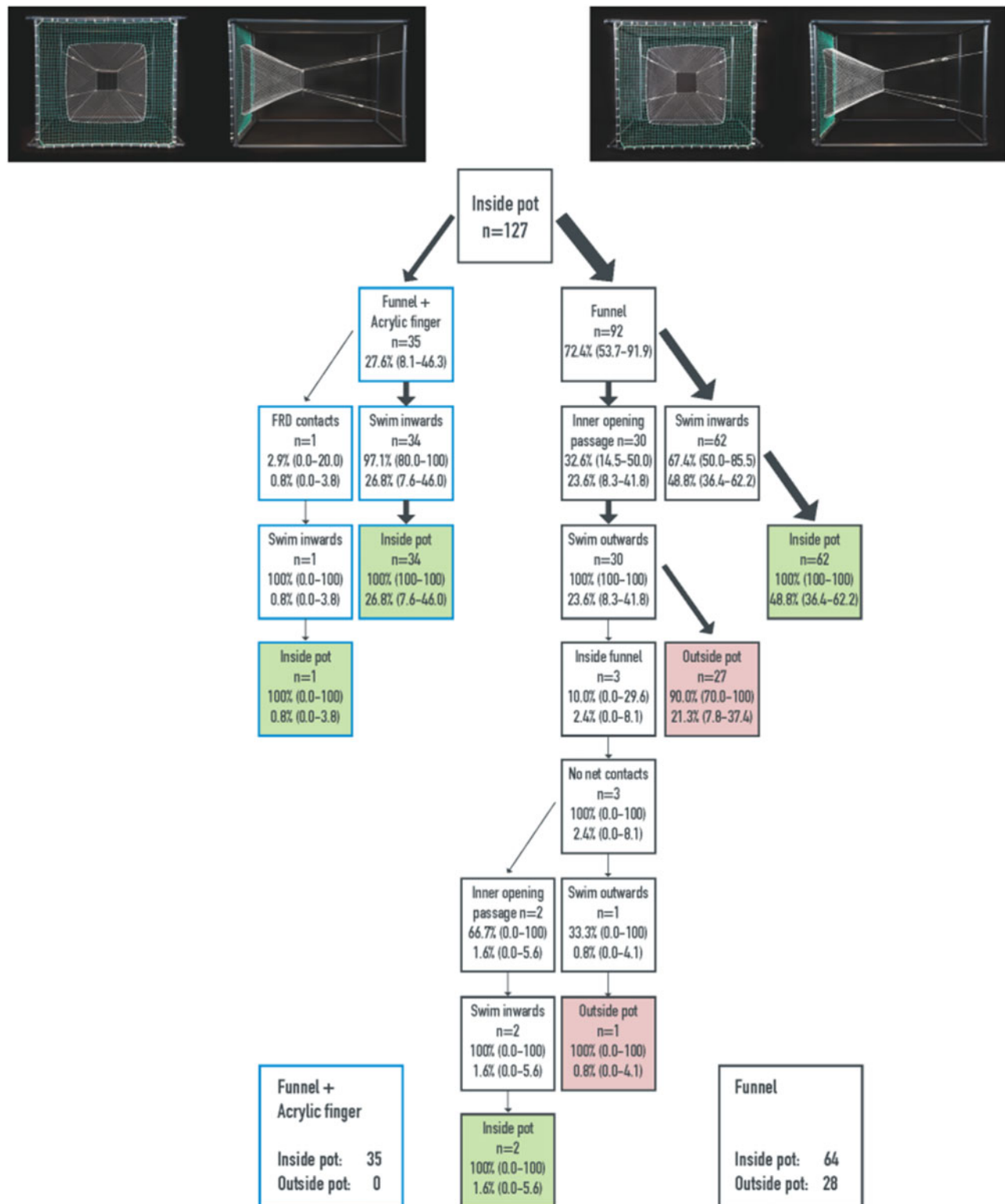
**Table 3.** GLM parameters of all final experiment models.

Exp.	Entrance control	Entrance test	Replicates	Model	<i>n</i> control	<i>n</i> test	Intercept	Side	Dev.	<i>df</i>	<i>p</i> ( <i>I/O</i> = 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	<b>−1.361***</b>	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
				<i>Entries</i>	49	20	<b>−0.896***</b>	N/I	83.079	68	0.29 (0.20–0.41)	–
4	Fun + AF	Fun + NF	2	Exits	2	46	<b>2.239**</b>	1.55	13.41	46	0.90 (0.66–0.99)	–
				Entries	11	2	<b>−1.705*</b>	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	<b>−1.992**</b>	N/I	18.35	24	0.12 (0.04–0.31)	–
				Exits	7	0	Only 7 exits through AF	–	–	–	0	–

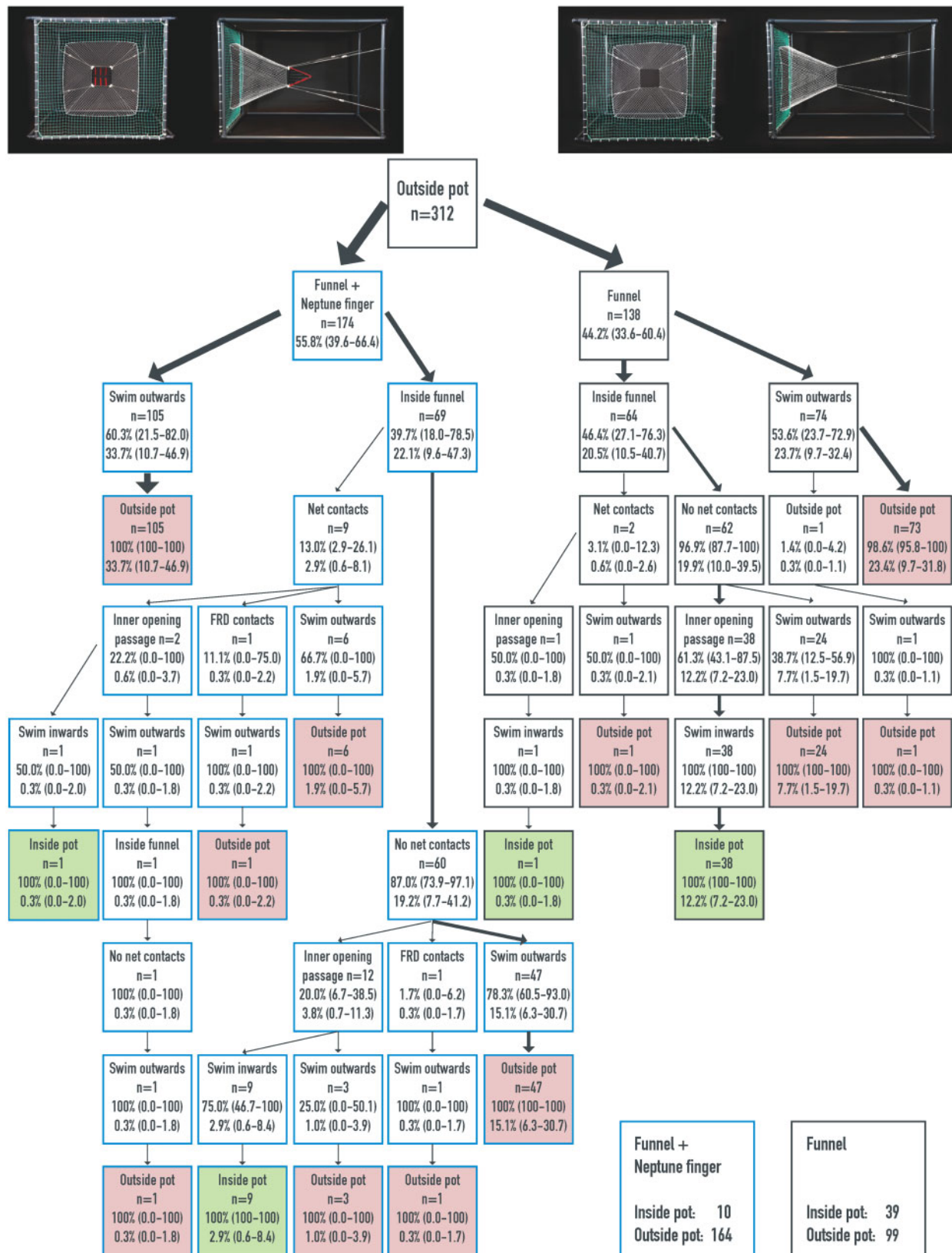
See “Material and methods” section for the meaning of entrance abbreviations. Exp. = experiment number, “Dev.” = model deviance; “*df*” = degrees of freedom; *p*(*I/O* = 1) = resulting probability that an entry or exit occurred through the entrance defined as test; \*, \*\*, and \*\*\* = the Wald test *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.



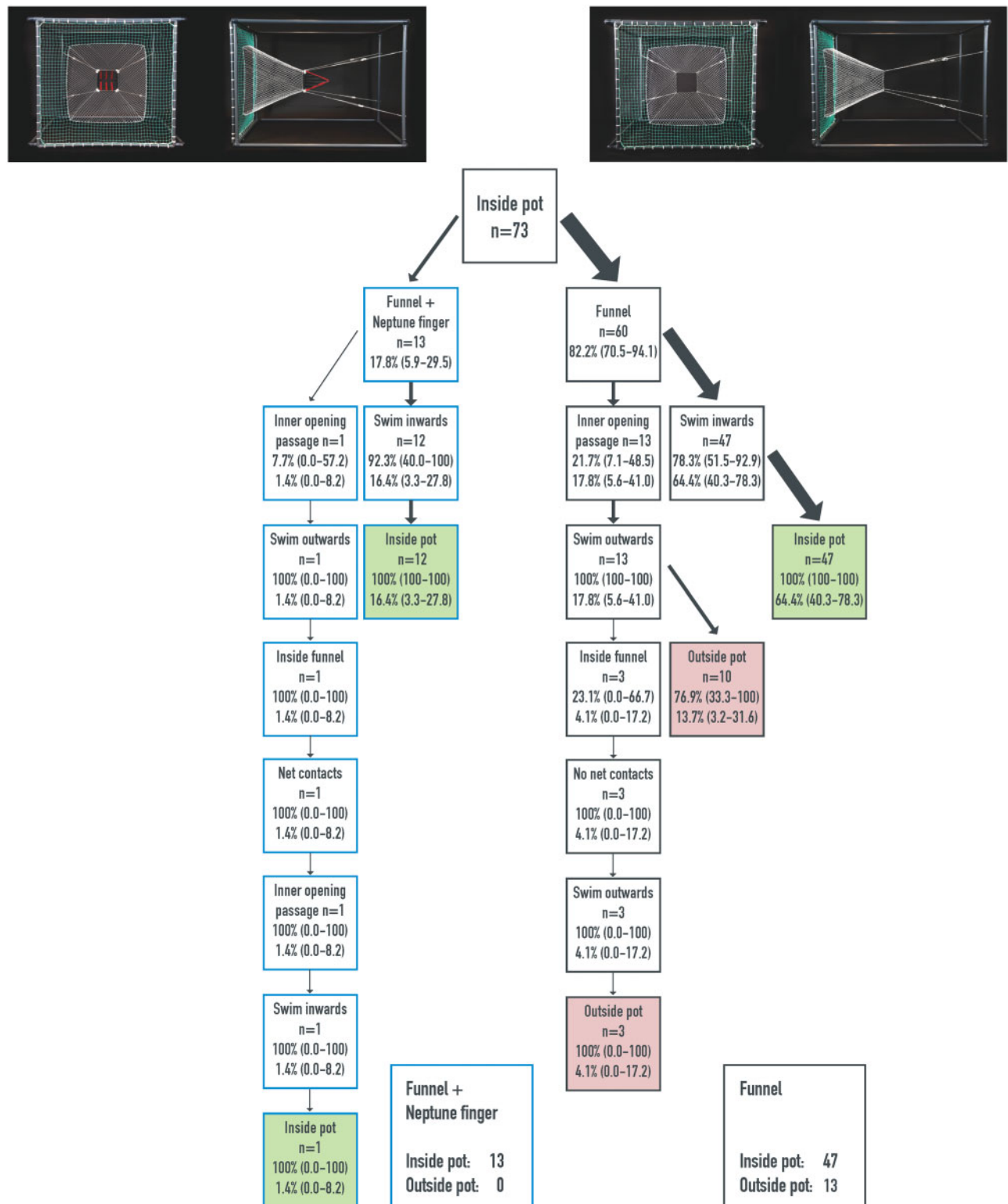
**Figure 4.** Behavioural event-chain tree comparing the Fun entrance (control) with the Fun + AF entrance (test) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed 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.



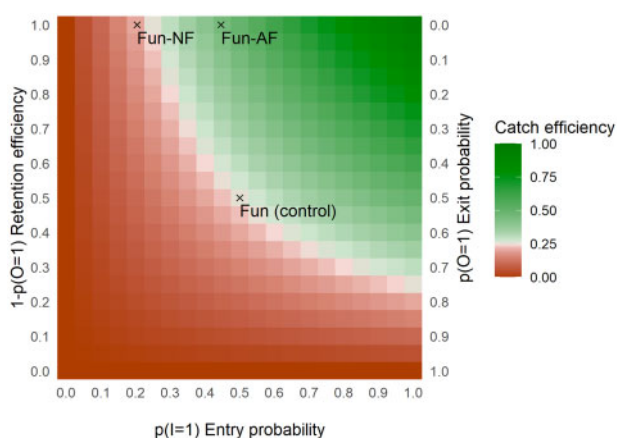
**Figure 5.** Behavioural event-chain tree comparing the Fun entrance (control) with the Fun + AF entrance (test) for interactions of cod with pot entrances starting inside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed 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

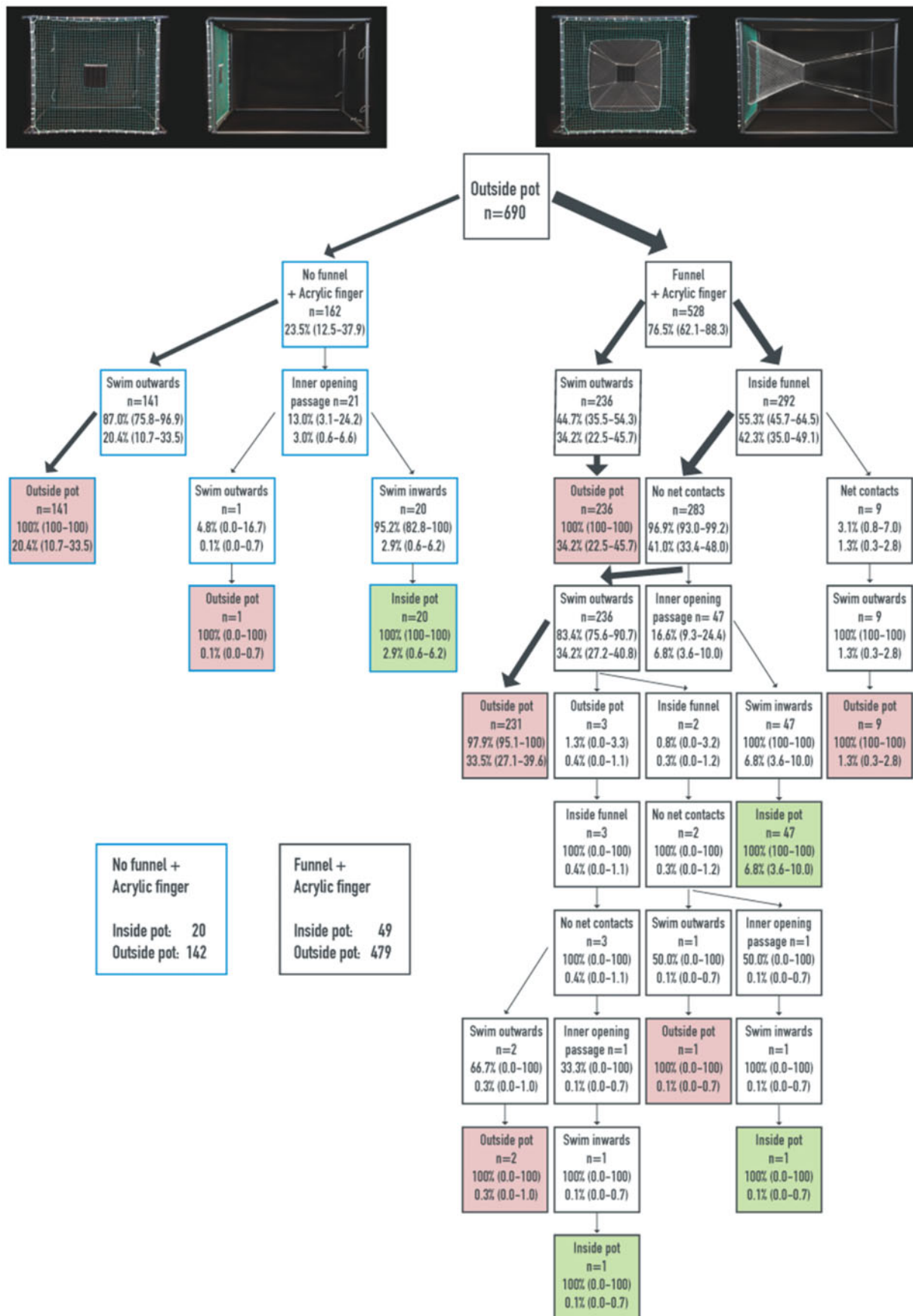
The study of this innovative new trigger concept, named AFs, revealed an AF exit-impeding effect while avoiding the drawback of other FRDs, which may deter fish owing to their distinct visual outline and the physical resistance other FRDs present to fish entering the pot. We compared the AFs with commercially 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.

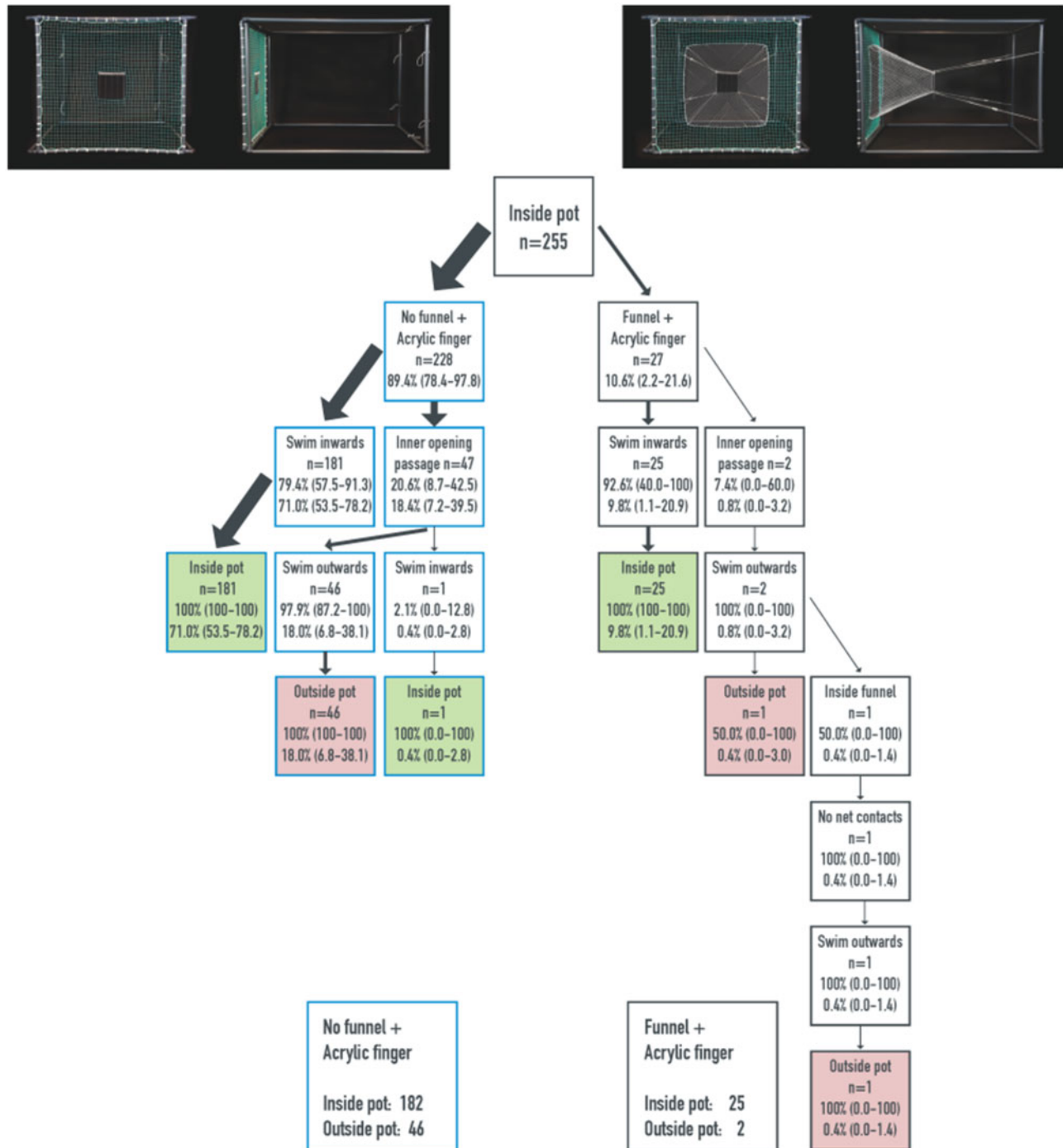
FRDs are typically described as reducing escape rates but inevitably also reducing entry rates (e.g. Munro, 1972; High and Ellis, 1973; Furevik and Løkkeborg, 1994; Olsen, 2014). In contrast, we found no evidence that AFs reduced fish-entry rates. To our knowledge, the present study is the first to demonstrate 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-escape 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.



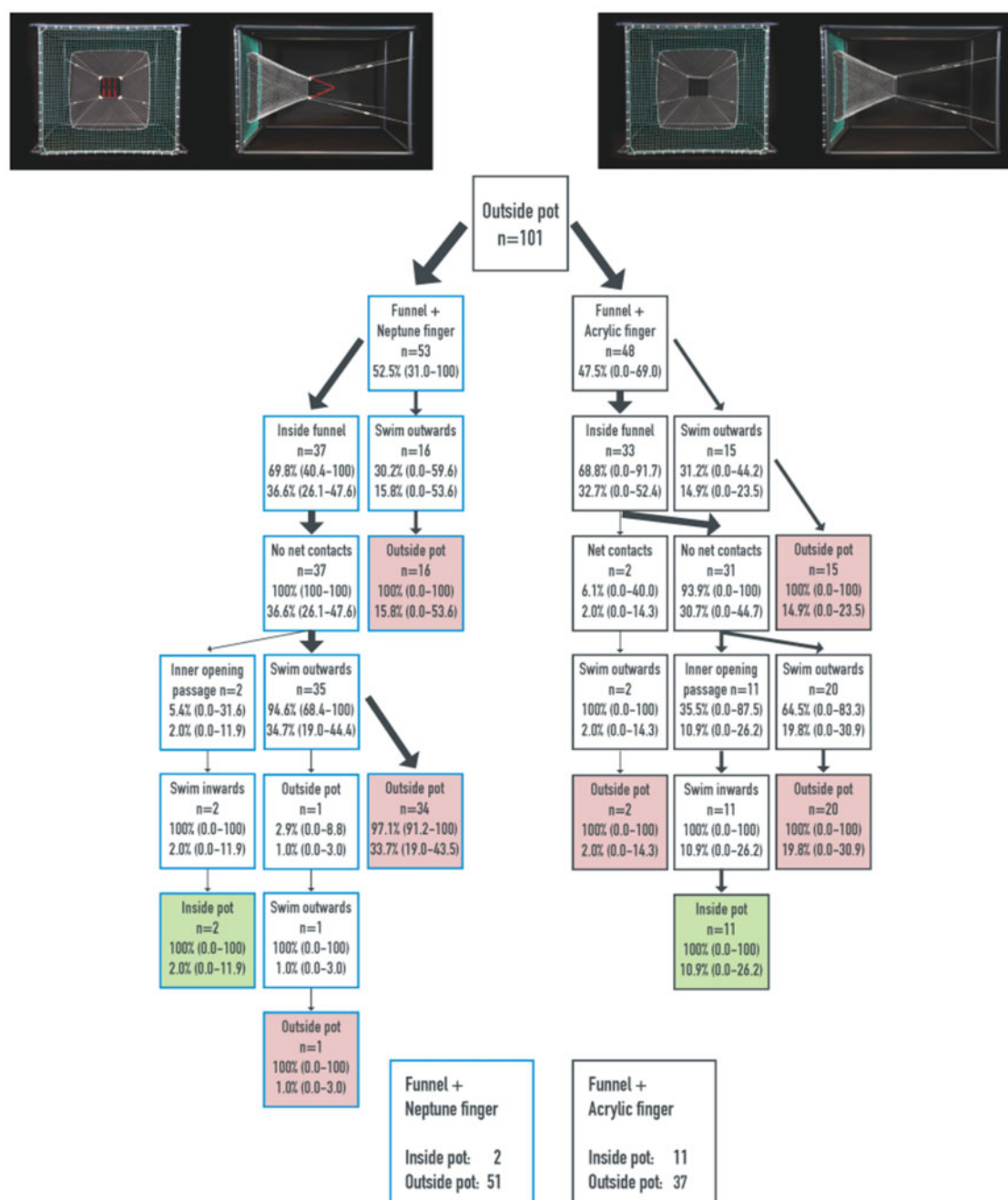
**Figure 9.** Behavioural event-chain tree comparing the Fun + AF entrance (control) with the NoFun + AF entrance (test) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed 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

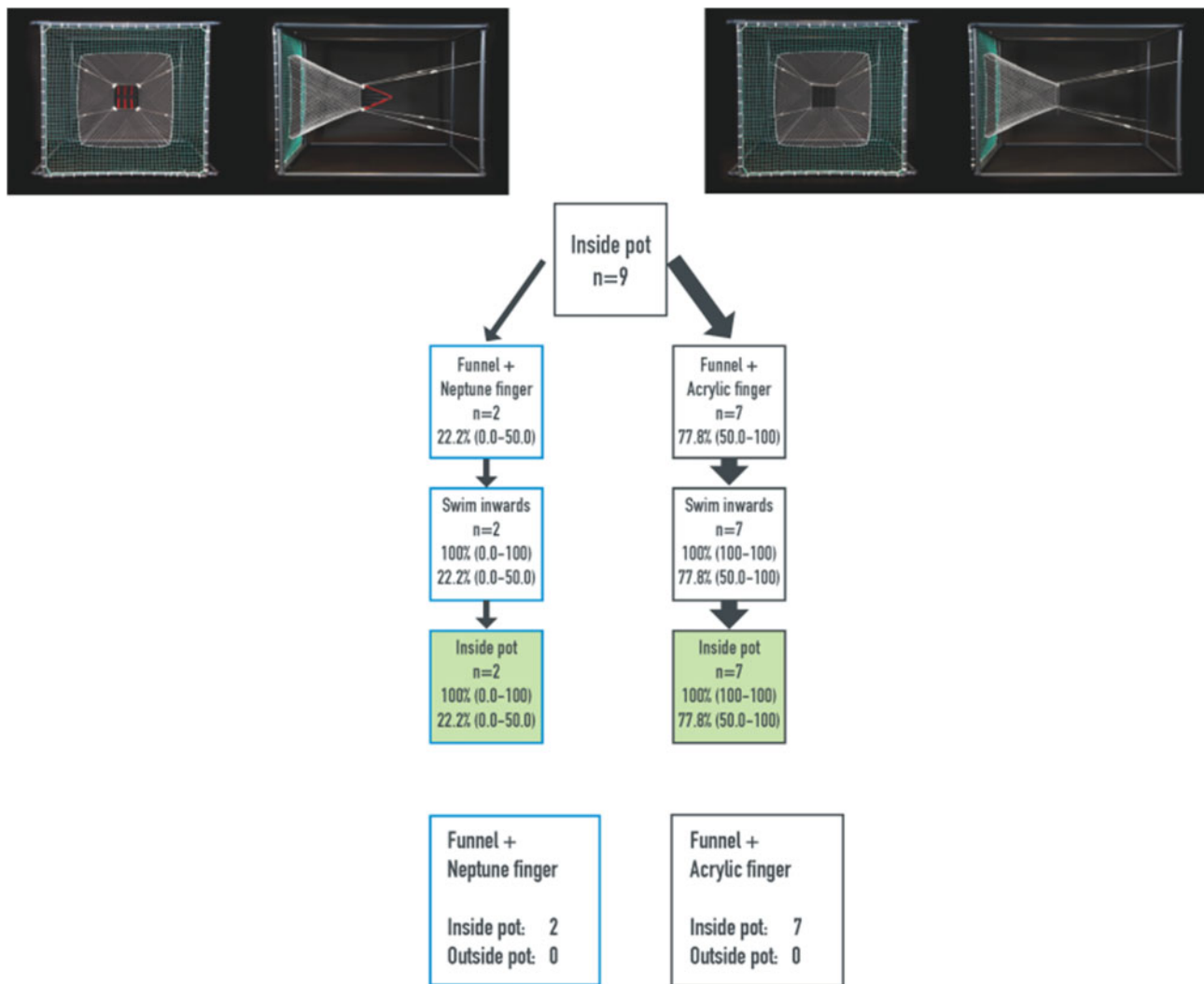


**Figure 11.** Behavioural event-chain tree comparing the Fun + AF entrance (control) with the Fun + NF entrance (test) for interactions of cod with pot entrances starting outside. Each box represents an event type; the first line = event type name; the second line = number of times this event was observed 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 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.

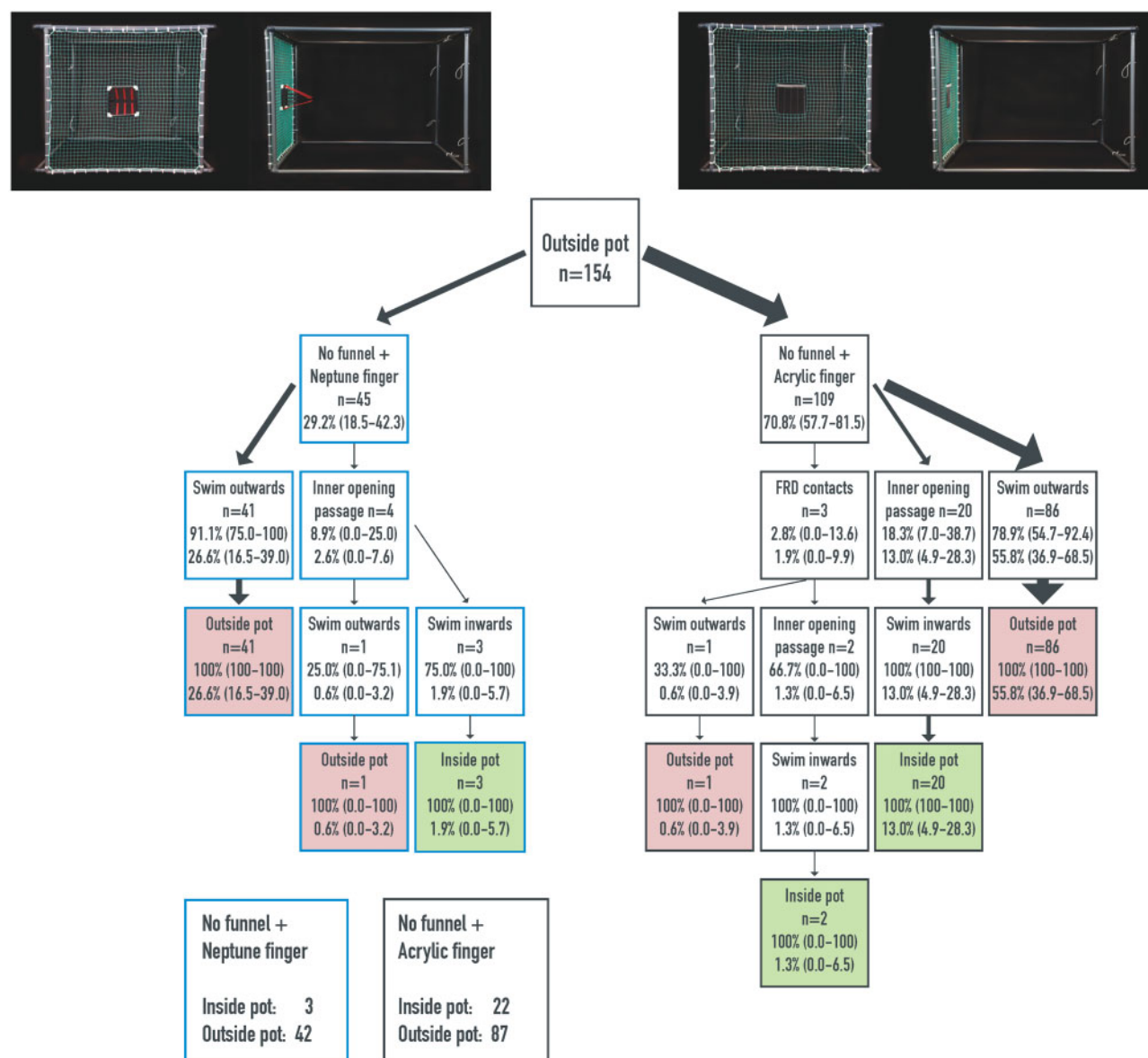
the pot bait, usually hung in front of the entrance (e.g. Furevik *et al.*, 2008; Meintzer *et al.*, 2017), which could be even more important when a bait light is used (Bryhn *et al.*, 2014; Humborstad *et al.*, 2018).

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

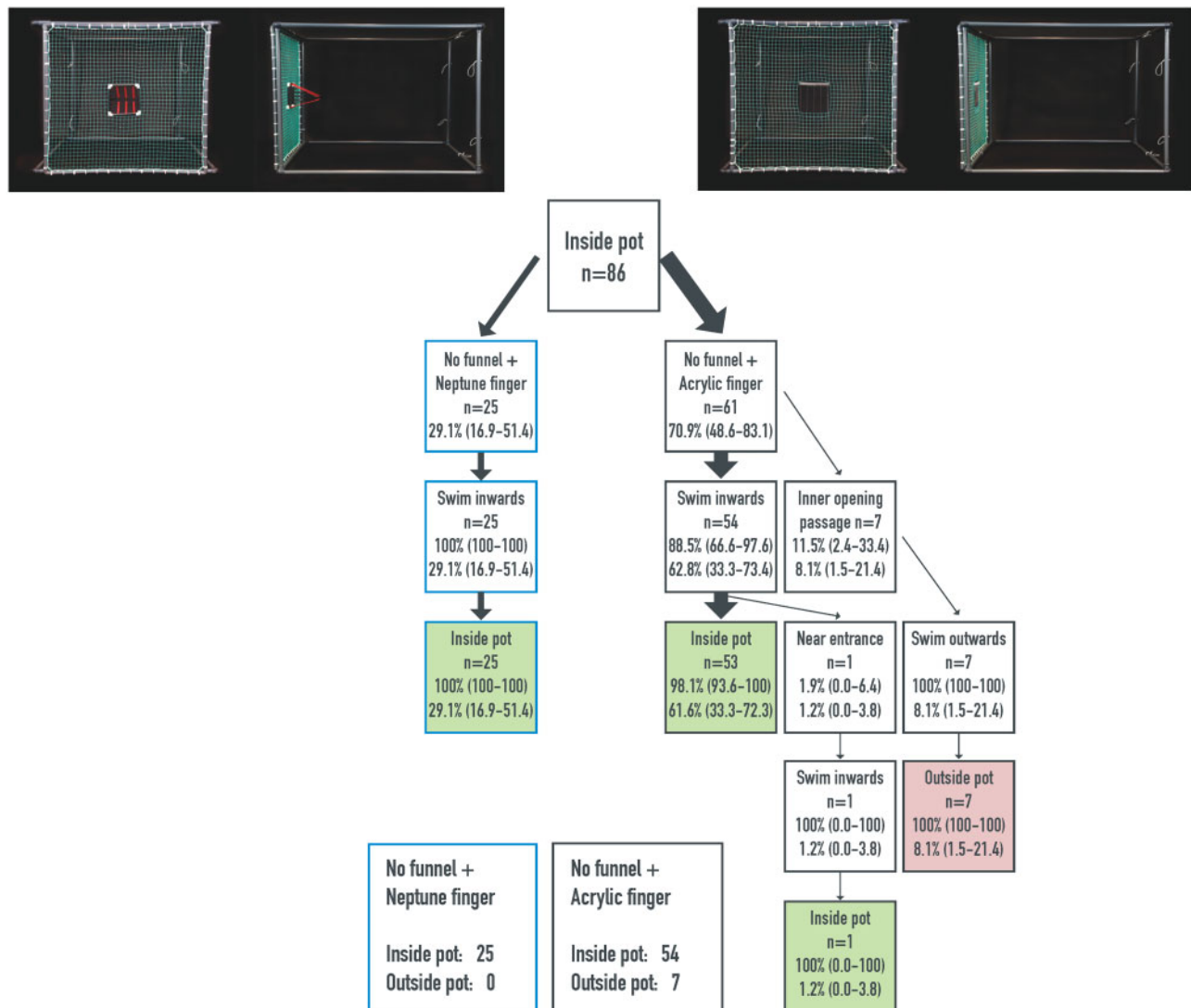
commercial fisheries, are thus warranted. Another study using the same experimental set-up found that cod movement through funnels increases when transparent funnel netting is used instead of white netting (Chladek *et al.*, 2020). Therefore, AF effectiveness could be increased further by using transparent 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 ICES/JMS 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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