The effect of pot design on behaviour and catch efficiency of gadoids

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Thesis in partial fulfilment of the degree

Master of Science in Fisheries Biology and Management

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2015

ACKNOWLEDGEMENTS

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ABSTRACT

The behavioural response of fish to pots is poorly understood but is a vital component of the fish capture process. Here, the behaviour of gadoids prior to and after capture in different baited fish pot designs was observed using *in situ* video footage. Bottom set and floated/lifted versions, respectively, of a collapsible and of a rigid pot were compared. A low entrance and high escape rate limited cod (*Gadus morhua*) catches, whilst a low encounter rate limited saithe (*Pollachius virens*) catches. Both species approached pots by swimming upstream. Cod tended to encounter and inspect pots more than saithe, which showed more cautious responses, characterised by a reluctance to inspect the pots at close range. Cod were thus more likely to enter the pots, and these differences in behaviour explain the observed differences in capture efficiency between the species. Once inside the pot, cod showed slow swimming (milling) and tended to search the pot walls in attempts to escape. Saithe tended to hang still and were less likely to escape than cod. With regards to the effect of pot design on behaviour, cod encountered pots less when they were floated/lifted above the seabed whilst saithe encountered floated and bottom set pots at the same rate. Entrance and escape rates for both species were not affected by floating collapsible pots above the seabed. The probability of capture for a fish was dependant on species and fish size, as well as social attraction and repulsion effects from other fish already caught. The findings of this study have important implications for future pot design and optimisation and contribute towards efforts to establish a pot fishery for gadoids in Norway.

1. INTRODUCTION

1.1 Fish behaviour and the fish capture process

The knowledge of fish behavioural processes is fundamental to the understanding of the interaction between fish and fishing gear. Such knowledge can be used to develop or adapt fishing gear in order to influence behaviour in a catch situation in the desired direction (Løkkeborg *et al.*, 1993, Fernö, 1993). This is particularly relevant in baited fishing gears, in which the effectiveness of the gear depends largely upon the behaviour of the target species (Stoner *et al.*, 2006). In Norway, quantitative research over the past few decades into the response of fish to longline gear has proved fruitful, describing species specific responses to baited hooks and leading to improved gear design (Huse & Fernö, 1990; Løkkeborg *et al.*, 1993). There has, however, been relatively little research attention given to fish pots.

1.2 Fish pots

Fish pots are small portable entrapment devices (Hubert, 1996). They generally consist of cages or baskets constructed from various materials with one or more entrances, designed to facilitate entrance and thereafter, prevent or hinder escape. Set at a fixed location and retrieved after a given soak time, most fish pots are baited in order to attract the target species (Nédélec & Prado, 1990).

Fish pots offer advantages over many other gear types in that they can have high selectivity for both size and species (Ovegård *et al.*, 2011), have generally low bycatch mortality (Thomsen *et al.*, 2010) and tend to have minimal habitat impact (Kaiser *et al.*, 2000). Pots are also generally cheap to construct and maintain, have the ability to target fish in areas often inaccessible to towed gear and have low energy use (Suuronen *et al.*, 2012). Catches are usually retained alive in pots, resulting in a higher market price for fresh or live catch delivery (Safer, 2010).

1.3 Fish pots in Norway

In Norway, collapsible fish pots have been identified as a possible alternative gear to gillnets for small inshore commercial coastal vessels targeting cod (*Gadus morhua*) (Furevik & Hågensen, 1997). Fishing trials have also revealed the potential of a rigid framed pot design to target wild saithe (*Pollachius virens*) and cod aggregations under aquaculture installations (Bagdonas *et al.*, 2012). There is, however, currently no established gadoid fishery using fish pots in Norway, likely due to their relatively low capture efficiency when compared to other gear types (Thomsen *et al.*, 2010).

1.4 Fish pot capture efficiency

In order for fish pots to be successfully adopted as an alternative capture method, they must be able to consistently compete in catching efficiency with more established gear types. Capture efficiency can be defined as "the proportion of fish encountering the gear which are retained in the catch" (MacLennan, 1992), and provides a useful framework for comparison between different gear designs. Reviews of the behavioural aspects of pot fishing tend to divide the capture process into several phases; approach, near-field behaviour, entry/exit behaviour and behaviour once inside the pot (Furevik, 1994; Thomsen *et al.*, 2010). By examining the ratios between the number of pot approaches, entries and exits, the particular phase of the capture process which may be limiting overall catching efficiency can be found and improved (Bravener & McLaughlin, 2013). This is of particular importance to pot fishing, as it is often difficult to distinguish between a lack of entries from a situation of many entries and subsequent exits (Cole *et al.*, 2004). To my knowledge, no studies to date have evaluated capture efficiency factors in Norwegian pot designs. If the chief determining factor of the capture process can be found, this could help to direct future design improvements in order to maximise catch efficiency.

1.5 Factors effecting entrance rates in pots

Behavioural observations have shown that although baited pots attract sufficient numbers of fish, too few proceed to enter to make them an economically viable alternative to other gear types (Furevik, 1994; Rose *et al.*, 2005; Thomsen *et al.*, 2010). Entrance behaviour is therefore the critical component of the capture process in pots. Examination of the factors which influence this entrance behaviour are of interest as they have the potential to explain the variability in pot entrance rates, and thereby the capture efficiency of the gear. The entrance rate of fish into pots can be thought of as the manifestation of three factors; the *ability* of the fish to enter, the *motivation* to enter and the *willingness* to enter.

The *ability* to enter a pot should be determined not only by the physical dimensions of the pot entrance and the size of the fish attempting to enter, but also that fish's ability to locate the entrance in the first place. In the near-field of the pot, this is likely to be chiefly determined by the visual acuity of the fish, which can be expected to vary between species and size as well as with light levels and turbidity (Stoner, 2004).

As fish respond and are attracted to pots chiefly because of bait (Furevik *et al.*, 2008), the *motivation* to enter a pot should be determined to a large degree by the feeding motivation of the fish. Feeding motivation is influenced by environmental factors such as temperature, but also by the hunger level of

the fish. Hunger level of a fish is likely to be mainly a product of the availability of natural prey (Stoner, 2004).

The *willingness* of a fish to enter a pot could be influenced the presence of other fish either responding to the gear or by those already caught by it. This is particularly relevant in pot fishing, as mode of capture results in fish being retained alive. Aggregation effects have been revealed to be an important aspect in approach and entry behaviour in Antillean reef fish pot fisheries (High & Beardsley, 1970; Munro *et al.*, 1971; Luckhurst & Ward, 1985; Renchen *et al.*, 2012). The converse can also be true, and the presence of predators inside the pot (High & Beardsley, 1970) or competitive interactions between species and fish sizes may serve to retard entry rates (Fogerty *et al.*, 1997). Bagdonas *et al.* (2012) observed avoidance behaviour in saithe when other conspecifics were observed to be caught in the pot mesh. Furthermore, as baited gear may selectively catch fish based on behavioural type (Diaz Pauli *et al.*, 2015), bolder species, sizes or individuals may be more susceptible to capture in gear types that require exploratory behaviour such as pots.

1.5 Fish behaviour in relation to pots

The biological basis for the behavioural response of fish to fishing gear comes from the primary sensory modalities of fish, those being the chemosensory (gustation and olfaction), vision and mechanosensory (hearing and detection of water movement) systems (Magnhagen, 2008). Different sensory modalities can be expected to be used to different extents at different stages of the capture process, depending upon the stimulus the fish is receiving from the gear at the time. Fish attraction to baited pots is thought to be based largely upon olfaction and the subsequent food-search process (Furevik, 1994). Providing the produced bait plume is above the detectable threshold of the fish (Løkkeborg *et al.*, 2010), any approach to the pot is likely to be similar to that described by Løkkeborg (1998) and Løkkeborg *et al.* (2000) for baited longlines. Fish tend to approach pots against the current direction (from where the bait plume has dispersed), using rheotaxis (Løkkeborg & Fernö, 1999; Furevik *et al.*, 2008).

Nearfield behavioural patterns are influenced by the additional sensory stimuli only available at closer range to the pot; not only are the fish exposed to the olfactory stimuli of the bait but now also the visual aspect, lateral line stimulation and possible physical contact of the pot. At this phase of the capture process, fish tend to mill around outside the pot in order to search for an entrance to gain access to the bait (Thomsen *et al.*, 2010). Territorial chasing behaviour against conspecifics has been recorded in the proximity of fish pots (Thomsen *et al.*, 2010). Having found an entrance and entered the pot, fish generally show limited further interest in the bait (Luckhurst & Ward, 1985). They tend to

mill around and undertake searching behaviour by pushing against the pot mesh (Thomsen *et al.* 2010; Bagdonas *et al.*, 2012). Fish also exhibit burst swimming behaviour in an attempt to escape through the pot mesh. Over time, captured fish tend to become less active and may rest (Furevik, 1994). It is important to note that any response of fish to pots is likely to be mediated to some extent by external variables, internal state, cognition and prior experience (Bendesky & Bargmann, 2011) and well as the particular behavioural phenotype (personality) of the fish (Sih *et al.*, 2004).

1.6 Species specific responses to pots

As fishing gear prompts naturally occurring behaviour patterns in fish (Fernö, 1993), individuals of different species typically show different behavioural repertoires in their response to fishing gear (Misund 1994; Løkkeborg *et al.*, 2010; Winger *et al.*, 2010). Interpretation of the adaptive value of such differences in behaviour may help explain why a species behaves in a particular way (Fernö, 1993). Furthermore, such differences could form the basis of progressive improvements in fish pot efficiency and selectivity, as has demonstrated in trawl fisheries for cod and haddock (*Melanogrammus aeglefinus*) (Krag *et al.*, 2010).

Both Furevik (1994) and Thomsen *et al.* (2010) noted differences in behaviour between species commonly targeted by Norwegian fish pots. Cod actively search for an entrance when outside of pots and tend to frequently push again the pot mesh while haddock and saithe are slower and more cautious. Before entering, cod are thought to repeatedly retire and return to the pot entrance where as other species may enter more readily. Once inside the pot, cod again tend to show more active search behaviour than either haddock or saithe.

Although there is a general understanding of the response of fish to pots in the literature, there has been little quantification of these observed patterns and differences. The quantification of defined units of behaviour is essential in fish capture studies, as it allows for detailed analysis and comparison (Ferno, 1993). Furthermore, as fish show a somewhat limited repertoire of behavioural responses (Løkkeborg *et al.*, 1993), quantitative studies could prove useful in identifying predictable behaviour patterns which could be exploited by the capture process and thereby improve capture efficiency. Recent advances in underwater video technology give the opportunity of extended behavioural observation time at a cheap cost, as well as creating a permanent record for thorough and repeatable analysis (Jury *et al.*, 2001).

1.7 The effect of pot design on fish behaviour

In Norwegian inshore waters north of latitude 68°, static fishing gear is susceptible to red king crab (*Paralithodes camtschaticus*) bycatch. In fish pots, crab bycatch generally survives the hauling process but their carapace and spines can damage the quality of any fish catch and increase handling times (Furevik *et al.*, 2008). One solution to avoid this unwanted bycatch is to take advantage of the different food search behaviours of fish and crustaceans, and to float the gear off the bottom (Godøy, 2005). Floated designs eliminate crab bycatch and can be more efficient than bottom set pots (Furevik *et al.*, 2008). However, pots designed to fish on the bottom may function sub-optimally in mid-water and no studies to date have examined how such modifications influence the behavioural response of fish.

Fish are unlikely to behave in the same way around different pot designs (Furevik, 1994), as different stimuli can be expected to elicit different responses. It is therefore important to have an understanding of how such design modifications influence fish behaviour, as any influences have the potential to effect capture efficiency. Comparison of behaviour between pot design may also prove useful in highlighting the function of certain aspects of pot design.

1.9 Aims and objectives

It can therefore be seen that the behavioural processes and responses involved in the pot capture process are complex and are not yet fully understood. Using *in situ* video footage, the aim of this study was to examine the behaviour of fish and capture efficiency in a number of fish pot designs. This was done in order to provide a quantitative description of behaviour of fish in and around fish pots. A fuller understanding of how fish and fish pots interact will help to inform future pot design decisions, in order to increase catch efficiency and selectivity. A substantial improvement in efficiency and selectivity could help to make pot fishing a viable alternative for commercial fishing in Norway.

The specific objectives of this study were as follows:

(1) Describe the catching efficiency of a number of different fish pot designs in order to determine the chief factor limiting overall capture success.

Based on previous finding that fish pots attract large numbers of fish but few enter (Furevik, 1994; Rose *et al.*, 2005; Thomsen *et al.*, 2010), I predicted the chief factor limiting catches in pots would be a low entrance rate.

(2) Determine factors which may influence the entrance rate in fish pots.

I hypothesized that entrance rates of the pots would be affected by the presence of other fish already captured. As cod show increased interest in situations in which they observe trapped (Løkkeborg *et al.*, 1989) or feeding fish (Brawn, 1969), I predicted that entrance rates would increase with numbers of fish retained in the pot. Furthermore, due to differences in ability, motivation and willingness to enter, I predicted that fish of different species and size would enter pots at different rates. I additionally hypothesized that pot design would influence entry rates, as different gear stimuli can be expected to elicit different responses in fish.

(3) Assess whether fish show species specific behavioural responses to fish pots.

Species-specific responses to baited fishing gear are well documented (e.g Løkkeborg *et al.*, 1989; Furevik, 1994; Thomsen *et al.*, 2010). I therefore hypothesised that different species would display consistent species-specific behavioural responses to fish pots.

(4) To test if pot design modifications affect fish behaviour and capture efficiency.

As design modifications are likely to alter the available behavioural stimuli, I predicted that different pot designs aimed at reducing crab bycatch would illicit different behavioural responses from fish. Additionally, due to the importance of behaviour to capture efficiency in baited gear (Stoner *et al.*, 2006), I predicted that designs modifications would also effect capture efficiency.

(5) To describe how fish approach and search pots, in order to inform future pot design.

Based on observations made in the literature (as reviewed by Furvik, 1994 and Thomsen, 2010), I selected a number of additional behavioural metrics to describe how fish approach and search pots. I predicted that fish would approach pots from downstream and that approach height will depend upon the setting position of the pot above the seabed.

2. MATERIALS AND METHODS

2.1 Pot Design

Behavioural observations were conducted on five different pot designs (Table 1 for salient features, Appendix 1 - 4 for detailed schematics). The first design type was the traditional bottom-set variant of the collapsible two-chamber pot used by Furevik *et al.* (2008) (referred to in this study as the "CB pot") (Figure 1a). This pot had two open entrances on opposite sides of the pot wall leading to a lower chamber. An additional inner entrance in this chamber led to an upper chamber above.

Floating pot designs have been shown to be beneficial for avoiding unwanted king crab bycatch (Furevik *et al.*, 2008). In order to assess what effect floating a pot above the seabed has on general fish behaviour, approach behaviour and catch efficiency, two other variants of the collapsible pot type were produced. These were similarly constructed, but with the addition of an adjustable bridle and added buoyancy in order to float the pot either 35 or 95 cm (Figures 1b & 1c) above the seabed (referred to hereafter as the C35 pot and C95 pot, respectively). Consequently, and in contrast to the bottom-set pots, these floated pots were able to continually orient into the prevailing current
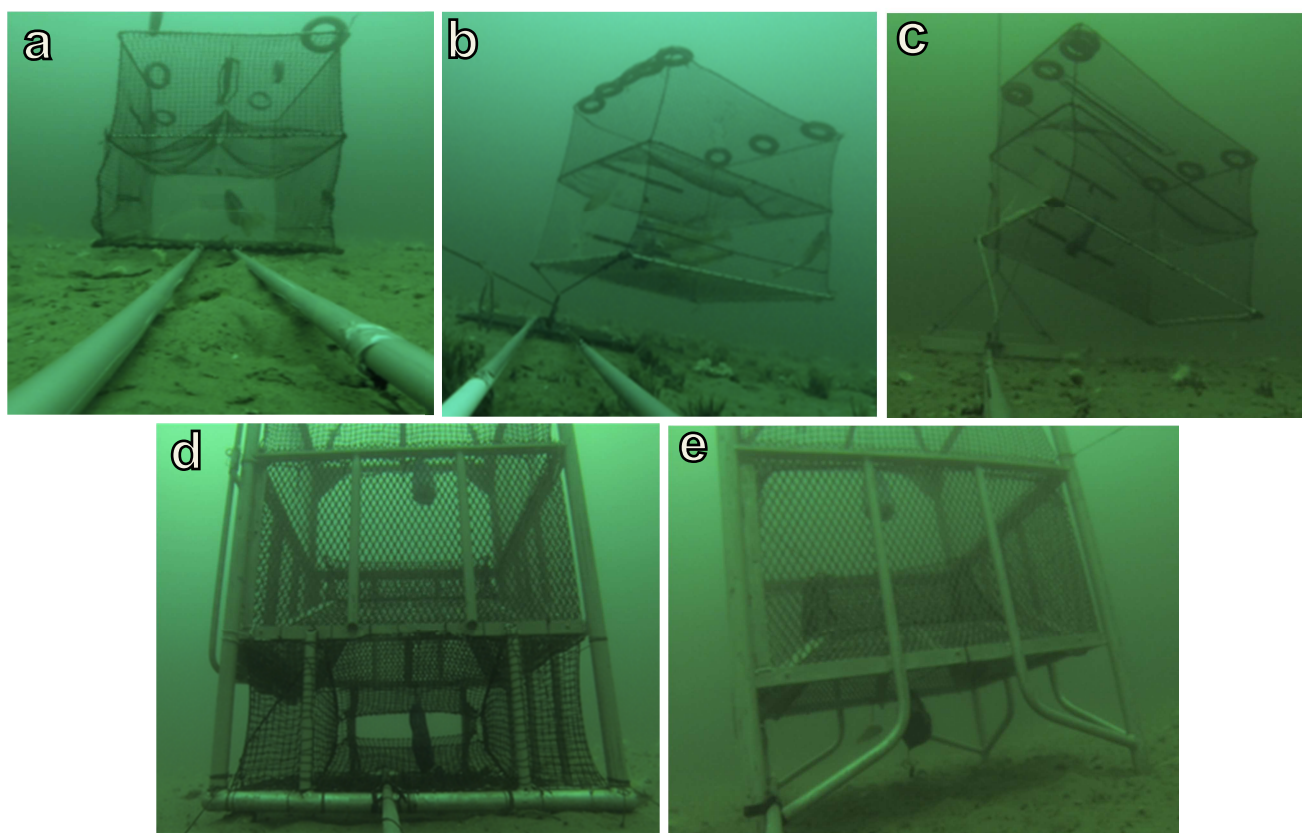
Figure 1. Pot designs used in the behavioural studies. Collapsible pots designs; a: bottom-set two chambered pot (CB pot); b: 35cm floated two chambered pot (C35 pot); c: 95cm floated two chambered pot (C95 pot). Rigid pot designs; d: rigid framed pot with bottom chamber (RC pot); e: rigid framed pot without bottom chamber (RNC pot).

Table 1. Salient features of the five pot designs used in the behavioural studies.

Pot code	Pot type	Positioning	Pot shape	Pot volume (m^3)	Entrance position	Entrance shape	Entrance construction	No. of entrances	No. of chambers	No. of bait bags	Bait position	Approx. lower bait height above seabed (cm)
CB	Collapsible	Bottom	Rectangular	1.8	Pot wall	Tapered funnel	Taut monofilament	2	2	1	Lower chamber	10
C35	Collapsible	35cm above seabed	Rectangular	1.8	Pot wall	Tapered funnel	Taut monofilament	1	2	1	Lower chamber	45
C95	Collapsible	95cm above seabed	Rectangular	1.8	Pot wall	Tapered funnel	Taut monofilament	1	2	1	Lower chamber	105
RC	Rigid	Bottom	Rectangular	4.18	Pot wall	Tapered funnel	Taut polyamide	2	2	2	Lower & upper chamber	20
RNC	Rigid	50cm above seabed	Rectangular	3.23	Pot floor	Tapered funnel	Taut polyamide	1	1	2	Inside pot & below entrance	20

conditions throughout their deployment. Floated collapsible pots had therefore only one entrance, situated downstream (opposite to the attachment point of the bridle).

The remaining two pot designs were smaller variants of the "rigid pot" used by Bagdonas *et al.* (2012). These pots were considerably larger than the others examined in this study, being originally designed to operate under aquaculture installations. The first was a bottom-set variant (referred to as the "RC pot", Figure 1d), with two opposite wall entrances leading to the lower chamber. An inner entrance in this lower chamber led to an upper chamber above.

In order to further assess what effect floating a pot above the seabed has on general fish behaviour, approach behaviour and catch efficiency, a second variant of this rigid pot was produced. This variant had a similar design to RC pot, apart from the removal of the net mesh surrounding the lower chamber. This effectively resulted in a one-chambered "floating" pot but lifted 50 cm above the seabed standing on struts (the "RNC pot", Figure 1e). Consequently, this variant had only one entrance, situated on the pot floor.

All pot designs were baited with bait bags containing three cut and defrosted squid (*Illex sp.*). In the collapsible pot designs, one bait bag was centrally hung in the bottom chamber, in line with the entrance/s. This was to ensure as much as possible that the odor plume dispersed through the entrances. In rigid pot designs, two bait bags were used; one in the approximate centre of the upper chamber and one in lower chamber in line with the entrances. The bait in the upper chamber was placed to encourage further search behaviour in caught fish and to lead them into the upper chamber. As the second variant of the rigid framed design effectively had no lower chamber, the lower bait bag hung outside of the pot and directly below the entrance. Although it may seem counter-intuitive to place bait *outside* of the pot, the justification for this design feature was to use the outside bait to aggregate fish under the pot in the hope that they would explore upwards and enter the pot.

2.2 Video camera system

The majority of video footage had already been collected prior to the commencement of this thesis. A Go-Pro Hero 3+[®] video camera with underwater housing was used to record *in situ* footage of fish behaviour in and around the fish pots. The camera recorded in high definition colour (1080 p) onto a SD card, making it suitable for detailed behaviour studies. Battery life limited video recording to a maximum of *c.* 2.25 h. In bottom-set pots, a pole was attached to the underside of the pot and the camera mounted on the pole to film in an inwards direction looking towards the pot. In the floated pots, the same camera pole set up was used but fixed to a weighted platform designed to lay on the seabed underneath the floating pot. The distance from the camera to pot was *c.* 1.5m, giving a

horizontal field of view of *c.* 4 m. On occasion, the distance from camera to pot was adjusted *c.* 10 – 20 cm between pot sets in order to optimise the quality of the recordings and to account for the dimensions of the different pots.

2.3 Study Site & Field Sampling

The study was made in Ramsfjord (69°33'29" N; 19°10'03"E), an inshore side branch of Balsfjord in the Troms Country of northern Norway during two periods; September 2013 and August – September 2014. Deployment sites were chosen from prior knowledge of areas likely to contain substantial numbers of fish, situated over sandy bottom areas and in average depths of 40 m in order to allow sufficient lighting for detailed video observations. The enclosed camera system required that video recording be started prior to pot deployment and the footage retrieved and analyzed only after hauling. Up to four pot deployments (referred to in this thesis as a "set") were video recorded per day at different times, but always during daylight hours to provide sufficient lighting. Pots were soaked for *c.* 2.5h, to approximately correspond to the maximum life of the camera battery. Video of the two rigid pot variants and the 95cm floated collapsible two-chamber variant was collected only in September 2013. Video footage of bottom-set and 35cm floated two chamber pot variants was recorded in both periods.

2.4 Video analysis

2.4.1 Preliminary video observations

Preliminary video observations of footage from all pot types were used to identify distinct behavioural units and to construct an ethogram of fish behaviour in and around the fish pots (Table 2). The behavioural units selected represent either *states* (prolonged activities with a quantifiable duration) or *events* (discrete behavioural units with relatively short duration, Martin & Bateson, 1993). States were considered to be mutually exclusive of one another. Video footage from sets with insufficient lighting, no fish entering the field of view or in which the pot was incorrectly set were rejected from further analysis.

Table 2. Ethogram of fish behaviour prior to and after capture in pots.

Behavioural unit	Code	Description	Behaviour type
Approach	APP	Fish outside pot. Orients towards and approaches the pot at a regular swimming speed	State
Bait (inside)	BAI	Fish inside pot. Feeding attempt on bait, including touching with the snout, mouthing, jerking etc.	State
Bait (outside)	BAO	Fish outside pot. Feeding attempt on bait, including touching with the snout, mouthing, jerking etc.	State
Capture	CAP	Whole body enters the lower chamber of the pot	Event
Escape	ESC	Whole body exits the pot, having previously been considered as captured	Event
Hang (inside)	HAN	Fish inside pot. Low frequency or zero tail beats, remaining mostly motionless and stationary	State
Hang (outside)	HAO	Fish outside pot. Low frequency or no tail beats, remaining mostly motionless and stationary	State
Inspect (inside)	INS	Fish inside pot. Slow swimming close to the pot walls, floor or roof (within approximately 1 body length distance)	State
Inspect (outside)	INO	Fish outside pot. Slow swimming close to the pot walls, floor or roof (within approximately 1 body length distance)	State
Leave	LEA	Fish outside pot. Having previously approached the pot, orients and moves away from the pot at a regular swimming speed	State
Mill (inside)	MIL	Fish inside pot. Slow, undirectional swimming	State
Mill (outside)	MIO	Fish outside pot. Slow, undirectional swimming	State
No Approach	NAP	Fish outside pot. Inside the field of view but showing no orientation or response towards the pot	State
Out of sight (inside)	OUT	Fish inside pot. No longer in the field of view or obscured from sight	State
Out of sight (outside)	OUO	Fish outside pot. No longer in the field of view or obscured from sight	State
Panic (inside)	PAN	Fish inside pot. Momentary sudden and rapid change in speed and swimming direction	State
Panic (outside)	PAO	Fish outside pot. Momentary sudden and rapid change in speed and swimming direction	State
Search (inside)	SEA	Fish inside pot. Snout touches or pushes against the pot structure or mesh	Event
Search (outside)	SEO	Fish outside pot. Snout touches or pushes against the pot structure or mesh	Event
Territorial (inside)	TER	Fish inside pot. Aggressive actions towards another, including chasing, nipping etc.	State
Territorial (outside)	TEO	Fish outside pot. Aggressive actions towards another, including chasing, nipping etc.	State
Upper chamber entrance	UPP	Fish inside pot. Whole body enters the upper chamber	Event
Other	OTH	None of the above	State

2.4.2 Capture efficiency sampling

A total of 76 hours 29 minutes of video footage (Table 3) was available to assess the capture efficiency of the pots. The numbers of individual fish entering the field of view of the camera and the numbers encountering the pot (defined as when a fish came within one body lengths distance from the pot, corresponding to "inspect outside" behaviour, Table 2) were recorded. The numbers of fish captured, escaping and entering the upper chamber (as defined in Table 2) were also recorded.

Table 3: Duration of video footage reviewed for each pot type. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm); C95: collapsible (floated 95cm); RC: rigid with bottom chamber; RNC: rigid without bottom chamber. Further details of pot design can be found in Table 1.

		Pot Type					
		CB	C35	C95	RC	RNC	Totals
Catch efficiency sampling	Total video footage (hh:mm)	23:41	17:20	06:53	13:23	06:52	76:29
	No. of sets	11	9	3	6	5	34
Behavioural sampling	Total video footage (hh:mm)	05:49	06:10	06:53	06:30	04:06	33:57
	No. of sets	3	3	3	3	3	15

Upon the first appearance of a fish, its species and size class (large: total length > 45cm; small: < 45cm) were noted. The number of other fish already captured in the pot was also recorded at this point. Size class was estimated by comparison to the known dimensions of the pot walls and entrances and recorded only if the fish passed close enough to the pot for it to be estimated accurately. Fish in which size class could not be estimated were recorded as "unmeasured". Fish in which the species could not be identified were recorded as "unidentified".

Fish often left and re-entered the field of view of the camera. Fish that were classed as "out of sight" (see Table 2 for definition) for more than 20 s and could not be positively identified upon re-entering the field of view were recorded as new individuals. If several fish of the same species and size left the field of view simultaneously, all subsequent re-entries were considered as new individuals (Løkkeborg *et al.*, 1989).

2.4.3 Behavioural sampling

2.4.3.1 Behavioural time budget and sequence sampling

From the same footage used for catch efficiency sampling, three sets per pot type were selected for detailed behavioural sampling. Sets which contained substantial numbers of fish were chosen (*non-random* selection), in order to maximize the number of fish available for observation. Although a *random* selection of video may have been more optimal, some pot sets contained very few observations of fish interacting with the pots. The consequences of this choice on the interpretation of the results is covered in the discussion. In total, 33 hours 57 minutes of video footage was used in behavioural sampling (Table 3).

A focal continuous sampling method was used in which an individual fish was followed throughout its time on camera and all instances and duration of its different behaviours recorded, according to pre-defined behavioural units (Table 2). This sampling method allows true behavioural durations to be measured, which is not possible using periodic time sampling (Martin & Bateson, 1993). The process was then repeated for all fish appearing throughout the video footage of the particular set. Species and size were recorded as for catch efficiency sampling. A total of 5 randomly selected individuals from each pot type were selected for re-sampling using the same methodology, to provide a measure of intra-observer reliability.

For example, a typical behaviour sequence prior to capture may involve a fish entering the field of view of the camera, swimming towards the pot, swimming around the pot and then proceeding to enter. This corresponds, respectively, to the behavioural units of no approach, approach, inspect (outside) and capture (Table 2). A typical behaviour sequence following capture could involve an attempt to feed on bait, then resting on pot floor, then a push against the mesh of the pot with the snout and finally escaping. This would correspond to the behavioural units of bait (inside), hang (inside), search (inside) and escape respectively (Table 2).

2.4.3.2 Additional behavioural metrics

In order to establish a fuller picture of fish behaviour and identify identifiable behaviour patterns which could be exploited in future pot design, a number of additional behavioural measures were collected. These measures were selected to address particular questions related to how fish locate and search pots in order inform future design improvements and were based on previous literature and preliminary video observations. At the onset of any "approach" behaviour (Table 2), the swimming direction relative to the current was recorded as either down-current, up-current, or across-current (Løkkeborg *et al.*, 1989). "Search outside" (when fish touched the outside of the pot, Table 2) direction relative to the current was recorded in the same way. Current direction was determined by

plankton drift or pot positioning in floated pot designs. The height of fish within the water column was also recorded during approach behaviour, as either along bottom (fish within one body lengths distance of the seabed for the majority of the duration of the approach) or in water column (fish more than one body lengths distance from the seabed for the majority of duration of the approach). For instances of "search inside" behaviour, the area of the pot in which search behaviour occurred was recorded as either on one of the four pot walls, on the floor or on the roof, irrespective of which chamber the fish was in. Video analysis was conducted using the event recording software Observer XT 12.0 (Noldus Information Technology, www.noldus.com).

2.5 Statistical methodology

All statistical analysis was undertaken using R version 3.0.2 (R Development Core Team, 2012).

2.5.1 Catch efficiency analysis

Counts of fish entering the field of view, encountering pots, being captured, escaping and entering the upper chamber were used to quantify the rates of encounter, entrance and escape for each pot type. Rates were calculated as:

$$(1) \; Encounter \; rate = \frac{n_{enc}}{n_{fov}}$$

$$(2) \; Entrance \; rate = \frac{n_{cap}}{n_{enc}}$$

$$(3) \; Escape \; rate = \frac{n_{esc}}{n_{cap}}$$

$$(4) \; Upper \; chamber \; entrance \; rate = \frac{n_{upp}}{n_{cap}}$$

where: n_{enc} = number of fish coming with 1 body lengths distance from the pot; n_{fov} = number of fish entering the field of view of the camera; n_{cap} = number of fish entering the pot; n_{esc} = number of fish escaping the pot; n_{upp} = number of fish entering upper chamber of the pot.

Generalized Linear Models (GLM) with binomial error structures were used to examine differences in rates between pot types and species. Refer to Appendices 5 – 11 for a detailed description of models.

2.5.2 Modeling capture success

Only fish which encountered pots were considered to have been available to capture. To be considered to have encountered a pot, a fish must come within one body lengths distance from the pot at some point whilst in the field of view of the camera (corresponding to inspect (outside) behaviour, Table 1). Due to limited numbers of observations of other species and of rigid pot types, the model was constructed using a dataset containing only cod, saithe and haddock interacting with collapsible pots.

To examine the effect of pot type, set number (a pot deployment was a set, see Section 2.3), species, fish size and number of captured fish (plus the interaction between species and size [species:size] and between fish and species [fish:species]) on the probability of fish capture, a GLMM (Generalized Linear Mixed Model) was first considered due to the clustered nature of the data. However, preliminary GLMM model exploration with set number nested within pot type as random effects found that very little (~ 4%) of the variance could be explained by these random effects (Appendix 36). Therefore, a binomial GLM was used to model the probability of fish capture, without further considering set number. A binomial error structure was chosen as the response variable (probability of capture) was binary (either captured or not captured).

The variable fish size contained three levels; large, small and unmeasured. This complicates the modeling process, as unmeasured individuals are likely to represent examples of both large and small fish. One option would be to remove these records from the dataset, although this wouldn't be optimal as unmeasured fish represented a large proportion of the dataset (26%). Therefore, the effect of the fish size variable on the model fit was tested first in preliminary model exploration using the full dataset containing all three levels of "fish size" (large, small and unmeasured). The comparison of a global model containing all candidate variables to one without the size variable found a significant effect of size (chi-squared test: $p < 0.001$, Appendix 37 - 39). Two separate models of capture success were therefore produced; one for large fish (> 45 cm) and one for small fish (< 45 cm).

For both large and small fish, ten candidate models containing all combinations of the variables of pot, captured fish, species and the interaction between captured fish and species (as well as an intercept only null model) were developed to explain the probability of capture. AIC (Akaike Information Criterion) was used to determine which models best explained the variation in capture success. In situations were there was considerable weight of evidence for more than one best approximating nested model (ie. a Δ AIC < 1), the significance of the omitted variable was tested using a chi-squared test to determine if it should be included in the model. Tukey post hoc testing was used to compare levels of significant predictor variables.

2.5.3 Behavioural time budget analysis

Multivariate analysis was used to examine differences in behavioural allocation times. Multivariate techniques are well suited to behavioural datasets as behavioural states are likely to be somewhat dependent on one another (Martin & Bateson, 1993). The amount of time an individual allocated to each state was converted to a proportion, square root transformed (to reduce the influence of the most common behaviours) and Bray-Curtis similarity matrices constructed (Clarke, 1993). Fish which showed no response to the pot (ie. the proportion of "no approach" behaviour = 1) were removed from the dataset.

Visualization and interpretation of behaviour was undertaken using non-metric multidimensional scaling (nMDS). nMDS is a multivariate non-analytical ordination technique that finds an iterative solution to the problem of placing samples in dimensional space whilst still preserving their between sample distance. Between sample distance is obtained from a distance matrix, in this case square root transformed Bray-Curtis similarity matrices (Jackson, 2014). As such, in nMDS, fish exhibiting similar behavioural time budgets are closer together in ordination space (Clarke, 1993). All nMDS plots produced showed low stress values (stress < 0.2 in all cases), suggesting a good representation of the multivariate data. Multivariate analysis was undertaken using the vegan package in R version 3.0.2 (R Development Core Team, 2012).

Apparent differences in fish behaviour between the different pot types and between species were tested using non-parametric analysis of similarity (ANOSIM), with a null hypothesis of no difference in the time allocated to different behavioural states between groups. The significance level (*p*) for ANOSIM was set at $p < 0.05$, although the interpretation of any significant differences were taken in light of the more informative *R*-statistic (R < 0.25 = not separated, R $= 0.25 – 0.5$ = barely separated R $= 0.5 – 0.75$ = overlapping but clearly different and R > 0.75 = well separated, Clarke & Warwick,

2001; Renchen *et al.*, 2012). Behavioural states which contributed the most to any observed similarity between groups were identified using similarity percentage analysis (SIMPER) on the transformed dataset. Applied to Bray-Curtis similarity matrices, the SIMPER method calculates the overall dissimilarity between groups as well as the average contribution of different behavioural states to this dissimilarity (Clarke & Warwick, 2001).

Intra-observer reliability of time budget sampling was calculated using the reliability analysis function in the Observer XT software. This function runs an algorithm to find agreements and disagreements in the duration and sequence of behavioural. The measure of reliability is reported as Cohen's kappa coefficient, based on a confusion matrix (Jansen *et al.*, 2003). Kappa coefficient values range from 0 (total disagreement) to 1 (total agreement).

2.5.4 Behavioural sequence analysis

Behavioural sequences were used to construct behavioural transition matrices of the probability of one behaviour following another (Brockmann, 1994). Observed transitions were then compared to a random matrix (in which all possible combinations of behaviour patterns had the same chance of occurring), in order to establish which behaviour patterns happened more or less than expected (Huse & Fernö, 1990). Behaviour patters which occurred more than expected were said to be over-represented. As not all transitions available in the matrix were possible (for example, fish could not transition directly from outside pot behaviours to inside behaviours), statistical analysis was problematic. Therefore, the matrices were inspected visually for large differences (Slater, 1973, Huse & Fernö, 1990). Common and over-represented transitions were then used to construct kinematic diagrams of the sequence of behaviour in and around pots.

2.5.5 Additional behavioural metrics analysis

A non-parametric Friedman test was used to test for differences in approach direction and search location for each pot type. A paired Wilcoxon signed rank test with Bonferroni correction (to allow for multiple comparisons) was used as a post hoc test to find which groups differed from the others. Friedman and Wilcoxon tests were appropriate due to the lack of independence in the data. For example, in approach direction, an individual fish could make approaches from multiple directions and therefore contribute to more than one level of the variable.

A paired Wilcoxon signed rank test was used to test for differences in approach height for each pot type. A quasibinomial GLM (to account for overdispersion in the data) was used to examine the

relationship between the probability of a water column approach and bait height. Differences in approach height between species were examined using a binomial GLM.

3. RESULTS

The majority of fish recorded around the pots were either cod (*Gadus morhua*) (55 % by number) or saithe (*Pollachius virens)* (28 %), with some haddock (*Melanogrammus aeglefinus)* (12%) and other species (3%) (Table 4). Only cod, saithe and haddock were captured in the pots. Of fish in which size could be estimated (64%), the percentage of large fish (> 45 cm) was 28%, 6% and 20% for cod, saithe and haddock respectively. Subsequent analysis focuses primarily on cod with comparison to saithe only, due to the relatively small haddock dataset.

Table 4: Number of observed fish for each pot type. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm); C95: collapsible (floated 95cm); RC: rigid with bottom chamber; RNC: rigid without bottom chamber. Further details of pot design can be found in Table 1.

Species	Pot Type					Totals
	CB	C35	C95	RC	RNC	
Cod (*Gadus morhua*)	1000	341	230	193	74	1838
Saithe (*Pollachius virens*)	519	130	222	77	2	950
Haddock (*Melanogrammus aeglefinus*)	185	70	77	23	54	409
Unidentified fish	65	31	8	3	3	110
Halibut (*Hippoglossus hippoglossus*)	1	0	0	3	0	4
Wolffish (*Anarhichas lupus*)	0	5	0	0	0	5
Skate (*Raja clavata*)	0	0	0	0	1	1
Totals	1770	577	537	299	134	3317

3.1 Capture efficiency

3.1.1 Cod and saithe capture efficiency

Cod tended to arrive at pots before saithe (mean time to first appearance after pot deployment of cod and saithe respectively: 9 mins 8 secs and 28 mins 12 secs). Across all pot types, the majority of cod in the field of view of the camera approached the pots (cod mean encounter rate: 0.66; Table 5). Saithe encounter rate was significantly lower (saithe mean encounter rate: 0.14, binomial GLM with logit link function: $p = <0.001$, Appendix 5). Having encountered the pots, fewer cod than saithe proceeded to enter (cod mean entrance rate: 0.16; saithe mean entrance rate: 0.57; Table 5), but the difference was not significant (binomial GLM: $p = 0.5$, Appendix 6). The average number of cod inside any pot type at any time was 1.54 (range: 0 to 9), for saithe it was 0.22 (range: 0 to 2). There were no captures of saithe in rigid pot types, preventing statistical comparison of rates for these pot types.

Table 5: Mean rates of encounter, entrance, escape and upper chamber entrance for cod and saithe for each pot type. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm); C95: collapsible (floated 95cm); RC: rigid with bottom chamber; RNC: rigid without bottom chamber. Further details of pot design can be found in Table 1.

		Pot Type				
		CB	C35	C95	RC	RNC
Cod	Encounter rate	0.66 (±0.04)	0.50 (±0.05)	0.81 (±0.08)	0.83 (±0.05)	0.52 (±0.14)
	Entrance rate	0.16 (±0.05)	0.22 (±0.06)	0.21 (±0.05)	0.22 (±0.09)	0.00 (±0.00)
	Escape rate	0.44 (±0.10)	0.37 (±0.13)	0.53 (±0.12)	0.89 (±0.03)	*no data*
	Upper chamber entrance rate	0.22 (±0.05)	0.18 (±0.07)	0.00 (±0.00)	0.13 (±0.07)	*n/a*
Saithe	Encounter rate	0.27 (±0.11)	0.27 (±0.10)	0.15 (±0.06)	0.00 (±0.00)	0.00 (±0.00)
	Entrance rate	0.44 (±0.19)	0.27 (±0.13)	1.00 (±0.00)	*no data*	*no data*
	Escape rate	0.25 (±0.25)	0.2 (±0.20)	0.11 (±0.11)	*no data*	*no data*
	Upper chamber entrance rate	0.75 (±0.25)	0.4 (±0.24)	0.44 (±0.29)	*no data*	*n/a*

Note: rates calculated as; encounter rate: number exhibiting inspection behaviour / number entering field of view of camera; entrance rate: number captured / number exhibiting inspection behaviour; escape rate: number escaping / number of cod captured; secondary chamber: number entering secondary chamber / number captured.

Following capture in collapsible pots, escape rates tended to be high for cod (mean: 0.55) and low for saithe (mean: 0.18, Table 5), but the difference was not significant (binomial GLM: $p = 0.17$, Appendix 7). Average residency time in a pot prior to escape was 5 mins 42 secs for cod and 1 min 10 secs for saithe. A significantly higher proportion of captured saithe than cod ultimately entered the upper chamber (mean secondary chamber entrance rate for saithe and cod respectively: 0.3 and 0.13; binomial GLM: $p = 0.01$, Appendix 8; Table 5). Cod entered the upper chambers on average 19 mins 30 secs after initial pot entry; saithe entered on average 27 mins 30 secs after initial entry. No escapes were recorded from the upper chamber in all pot types for both cod and saithe.

3.1.2 The effect of pot type on capture efficiency

Cod were significantly more likely to encounter the bottom set pot (CB) than the pot floated 35cm above the seabed (C35) (binomial GLM with logit link function: $p = 0.01$, Appendix 9, Table 5). There was no difference in encounter rate for saithe between the CB and C35 pots (quasi-binomial GLM: $p = 0.24$, Appendix 10, Table 5). Cod were also significantly more likely to encounter the bottom set rigid pot (RC) than the rigid pot suspended above the seabed (RNC) (binomial GLM: $p = 0.01$, Appendix 11, Table 5). There were insufficient observations to compare saithe encounter rates for rigid pot types. Furthermore, there were insufficient pot set replicates to compare C95 pot rates.

Cod and saithe entrance and escape rates were not significantly different between the CB and C35 pot types (cod entrance rate; quasi-binomial GLM: $p = 0.65$; cod escape rate; binomial GLM: $p = $

0.22; saithe entrance rate; binomial GLM: $p = 0.52$; saithe escape rate; binomial GLM; $p = 0.61$ Appendix 12 – 15, Table 5). Cod and saithe also entered the upper chamber at similar rates in both the CB and C35 pot types (cod binomial GLM: $p = 0.65$; saithe binomial GLM: $p = 0.71$, Appendix 16 & 17, Table 5). There were no captures of cod or saithe recorded in the RNC pot, preventing statistical comparisons of entrance, escape and upper chamber entrance rates for rigid pot types.

3.2 Modelling collapsible pot capture success

3.2.1 Model selection

Two separate models were produced; one of capture success for large fish (> 45 cm) and one for small fish (< 45 cm) (see to Section 2.5.2 for full details of preliminary model exploration). For large fish, there was a similar weight of evidence (Δ AIC < 1) for the two best approximating models (Table 6). These candidate models were nested in that they differed only by the addition of the "species : fish" interaction variable. The effect of the interaction term on model fit was therefore tested to determine the best approximating model. The addition of the interaction term did not improve the fit of the data (Chi-squared test: $p = 0.12$, Appendix 38). Consequently, the best approximating model for large fish therefore contained species and number of fish in the pot as covariates (Appendix 43).

For small fish, the two best models also had a similar weight of evidence (Δ AIC $= 1$, Table 6). These candidate models were nested in that they differed only by the addition of the "species : fish" interaction variable. However, the addition of the interaction term did not improve the fit of the data (Chi-squared test: $p = 0.08$, Appendix 39). The best approximating model for small fish therefore contained species and number of fish in pot as covariates (Appendix 44).

Both selected models were a significantly better fit to the data than a null model (Appendix 40).

Table 6: Ranking of candidate models using AIC (Akaike Information Criterion), for large and small fish datasets.

Covariates	AIC	Δ AIC	Weight
Large fish models			
Fish, species, fish:species	260.9	0.00	0.320
Fish, species	261.1	0.12	0.302
Fish	262.6	1.62	0.143
Fish, pot, species, fish:species	263.5	2.59	0.088
Fish, pot, species	263.9	2.98	0.072
Fish, pot	265.6	4.61	0.032
Species	265.7	4.76	0.030
(null model)	268.6	7.65	0.007
Pot, species	269.0	8.03	0.006
Pot	272.0	11.06	0.001
Small fish models			
Fish, species, fish:species	582.9	0.00	0.308
Fish, species	583.9	1.00	0.185
Fish, pot, species, fish:species	584.0	1.05	0.182
Fish, pot, species	584.4	1.46	0.148
Species	584.9	2.00	0.113
Pot, species	586.1	3.15	0.064
(null model)	608.8	25.84	0.000
Fish	610.1	27.14	0.000
Pot	612.2	29.26	0.000
Fish, pot	613.3	30.38	0.000

3.2.2 Model outcomes

Model predicted values found that small cod were significantly more likely to be caught in collapsible pots than either small saithe or small haddock (Tukey HSD test, $p < 0.01$ in both cases; Appendix 42) (Figure 2). There was no significant difference in the probability of capture between small saithe and small haddock (Tukey HSD test, $p = 0.89$; Appendix 42). Pairwise comparisons of large fish found no statistical difference in the probability of capture between species (Tukey HSD test, $p > 0.05$ in all cases, Appendix 42). However, mean values from the model suggested that large cod were five times more likely to be caught than large saithe and four times more likely to be caught than large haddock (Figure 2).

For large fish, the highest chance of capture occurred while one other fish was in the pot; for small fish it was with four other fish in the pot (Figure 3). Following these peaks, probability of capture tended to decrease with increasing numbers of fish into the pot. For both large and small fish, the probability of capture was lower when the maximum number of fish were in the pot than when there were no fish in the pot (Figure 3).
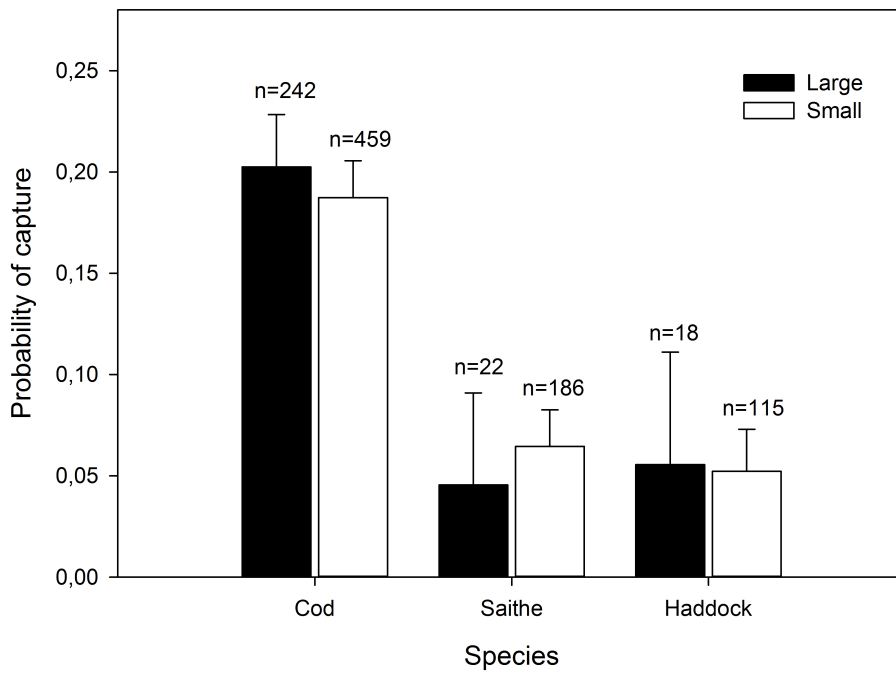
Figure 2: Model predicted mean probability of capture by species for collapsible pots. Bars indicate the mean value with standard error added as vertical lines. Black bars represent large fish (> 45 cm); white bars represent small fish (< 45 cm). Large and small fish are not directly relatable due to the lack of an interaction term of "species:size" in the model. n = number of observed fish.
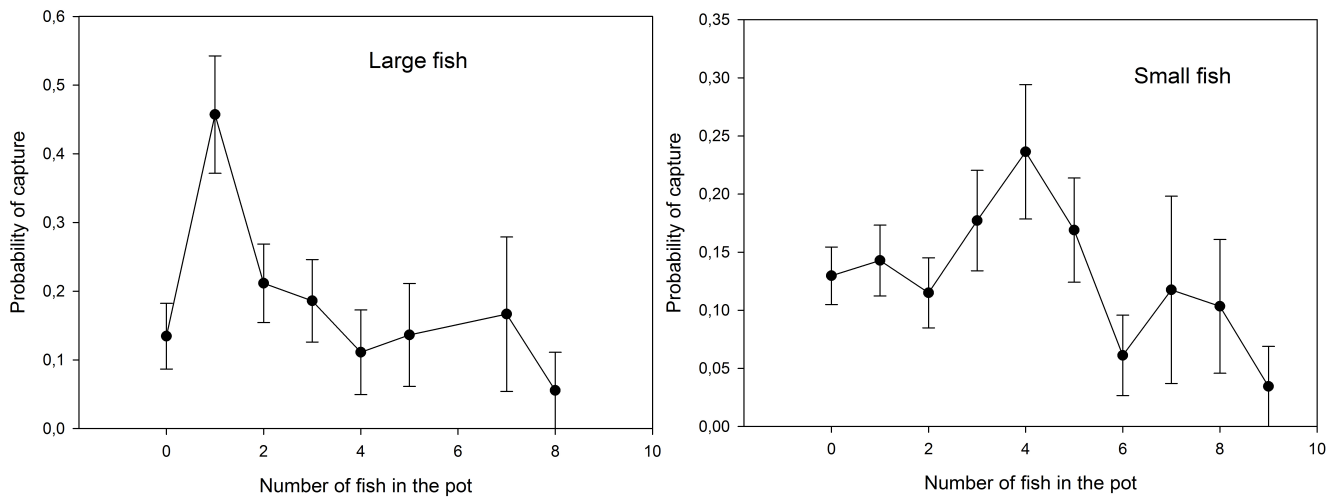
Figure 3: Model predicted mean probability of capture as a function of number of fish already captured for collapsible pots. Vertical lines indicate standard error. There were no captures recorded for large fish when six other fish were in the pot. The model therefore predicted a probability of capture of zero. This data point was therefore removed from the plot.

3.3 General behaviour of cod and saithe

Behavioural transition matrices (see Table 7 - 8 for cod and saithe for the CB pot, Appendix 22 for other pot types) and kinematic figures (see Figure 4 for the CB pot, Appendix 18 – 21 for other pot types) were examined visually to identify consistent behavioural patterns. Around all pot types, both cod and saithe showed a generally similar sequence of behaviour. All fish were classified as "no approach" upon their first appearance in the field of view of the camera; consequently all sequences began with "no approach" behaviour (Figure 4, Appendix 18 - 21). Swimming at a slow speed, the majority of cod and saithe would then approach the pots; the transition from no approach (NAP) to approach (APP) was over-represented by an average of 1200 and 320% for cod and saithe respectively (Appendix 22). The transition from no approach to out of sight (NAP-OUO) was also highly over-represented from both cod and saithe, corresponding to fish which did not approach the pot but immediately left the field of view of the camera.
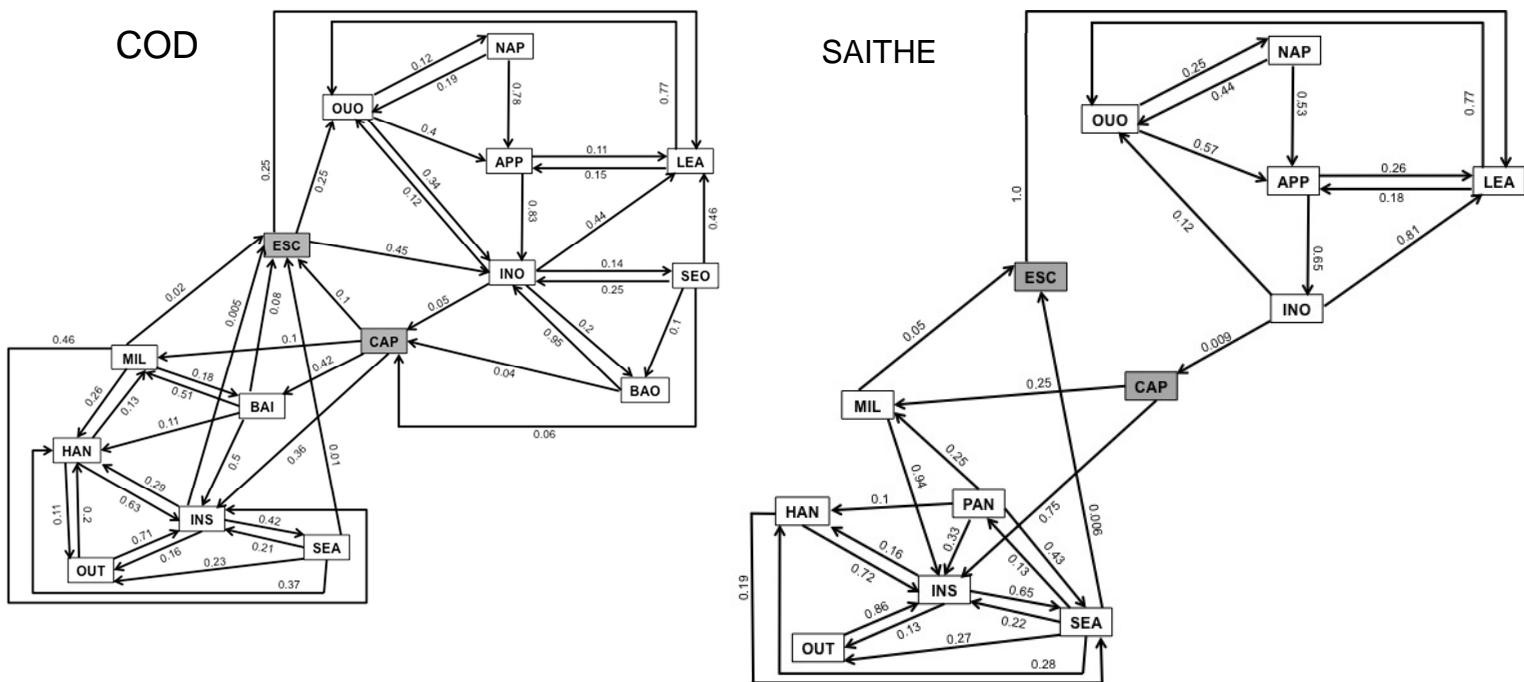
Figure 4: Kinematic diagrams of behavioural sequences of cod and saithe for the collapsible bottom set pot (CB pot). As fish had a generally similar sequence of behaviour around all pot type, further kinematic diagrams for other pot types can be found in Appendix 18 – 21. Arrows indicate the direction of behaviour and the associated transitional probability. Boxes represent behavioural units. Behavioural unit abbreviations; NAP: no approach; APP: approach; OUO: out of sight (outside); LEA: leave; INO: inspect (outside); SEO: search (outside); BAO: bait (outside); CAP: capture; ESC: escape; MIL: mill (inside); BAI: bait (inside); HAN: hang (inside); INS: inspect (inside); SEA: search (inside); OUT: out of sight (inside); PAN: panic (inside) (see Table 2 for behavioural unit definitions). All sequences start with NAP and end with the fish being classified as OUT or OUO. Infrequent transitions (p < 0.1) are not included, except for those leading to captures (CAP) or escapes (ESC) (highlighted in grey). Transitions to UPP are not included. Sequences are based on transition matrices (Appendix 22) and include only those transitions that were over-represented (see Section 2.5.4).

In the majority of designs, the most probable behaviour for both cod and saithe following an approach was to inspect the outside of the pots (INO) (Figure 4, Appendix 18 – 21). A considerable proportion of fish also transitioned directly from approach to leave (LEA); saithe were consistently more likely (apart from around the C35 pot) to transition from approach to leave than cod (Appendix 22). Leave behaviour was typically followed by the fish being out of sight (OUO) (over-represented by an average of 1015% and 550% for cod and saithe respectively), indicating that leaving fish tended to retire from the near-field of the pot and exit the field of view of the camera. Following inspection behaviour, fish tended to move between a suite of outside behaviours, with high probabilities of transitioning to leave, milling about (MIO) and searching on the pot structure (SEO) behaviours (Appendix 22). Saithe were consistently more likely than cod to transition from inspecting (INO) directly to leaving (LEA), and consistently less likely to follow any inspection with search behaviour (SEO). The most common behaviours leading to a capture were inspection (INO) and search (SEO).

Fish entered the pots individually and slowly. Following capture, the majority of cod transitioned directly to either milling behaviour (MIL) or feeding on the bait (BAI) (Figure 4, Appendix 18 - 21). Inside the pot, cod tended to transition between a suite of behaviours including hanging (HAN), searching the pot structure (SEA), feeding on the bait (BAI) and milling about (MIL), usually linked by inspection behaviour (INO) (Appendix 22). For entering the upper chamber, the transitions of searching the pot structure to entering the upper chamber (SEA-UPP) and inspecting to entering the upper chamber (INS-UPP) were particularly over-represented (Appendix 22). Comparison of cod and saithe behaviour patterns inside the pots was limited by the small number of observations of captured saithe. However, saithe were never observed to transition directly from capture (CAP) to feeding on the bait (BAI), whereas this transition was highly over-represented in cod (504%) (Appendix 22). Capture could lead directly to escape and visa versa, indicating that in some cases fish immediately entered and exited without taking up residence in the pot. The most common behaviour prior to escape for both cod and saithe across all pot type was mill swimming (MIL) (Figure 4, Appendix 18 - 21). Following escape, cod tended to transition to leave (LEA) (459% over-represented on average) or to inspection (INO) (570% over represented). This corresponds to two broad modes of behaviour following escape; fish which left the nearfield of the pot after escape and fish which started to re-inspect the pot from outside. Leave (LEA) was the only recorded behaviour following saithe escape (Appendix 22).

Table 7: Cod behavioural transition matrix for the CB (collapsible bottom set) pot type. The preceding behaviour is given to the left of the square and the subsequent. behaviour above. Transitional probabilities are displayed in the upper half of the squares; observed and expected values (in parenthesis) of transitions are shown in the lower half. Transitions which were over-represented (see Section 2.5.3) are highlighted in grey. Further cod transition matrices for other pot types can be found in Appendix 22. Abbreviations of different behaviours states are explained in Table 2.

	CODE	BAI	HAN	INS	MIL	OUT	PAN	TER	CAP	ESC	UPP	SEA	SEO	APP	LEA	NAP	BAO	HAO	INO	MIO	OTO	OUO	PAO	TEO	Total
Inside pot states	BAI	-	0.111 9 (7.8)	0.222 18 (12)	0.519 42 (3.7)	0.025 2 (4.6)	0.012 1 (0.2)	0 (0)	-	0.086 7 (0.7)	0 (0.3)	0.025 2 (6)	-	-	-	-	-	-	-	-	-	-	-	-	81
	HAN	0.035 13 (7.7)	-	0.635 235 (54.5)	0.132 49 (17)	0.119 44 (20.7)	0.005 2 (0.9)	0 (0)	-	0.003 1 (2.9)	0.003 1 (1)	0.068 25 (27)	-	-	-	-	-	-	-	-	-	-	-	-	370
	INS	0.016 9 (11.9)	0.296 169 (54.8)	-	0.072 41 (26.1)	0.168 96 (31.8)	0.002 1 (1.4)	0 (0)	-	0.014 8 (4.4)	0.005 3 (1.5)	0.427 244 (41.7)	-	-	-	-	-	-	-	-	-	-	-	-	571
	MIL	0.182 32 (3.7)	0.261 46 (16.9)	0.466 82 (26)	-	0.04 7 (9.9)	0.006 1 (0.5)	0 (0)	-	0.023 4 (1.4)	0 (0.5)	0.023 4 (12.9)	-	-	-	-	-	-	-	-	-	-	-	-	176
	OUT	0.024 5 (4.3)	0.204 42 (19.8)	0.718 148 (30.4)	0.024 5 (9.5)	-	0 (0.5)	0 (0)	-	0 (1.6)	0 (0.6)	0.029 6 (15.1)	-	-	-	-	-	-	-	-	-	-	-	-	206
	PAN	0 (0.2)	0.111 1 (0.9)	0.222 2 (1.4)	0.333 3 (0.5)	0 (0.6)	-	0 (0)	-	0 (0.1)	0 (0.1)	0.333 3 (0.7)	-	-	-	-	-	-	-	-	-	-	-	-	9
	TER	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
Events	CAP	0.426 20 (1)	0 (4.6)	0.362 17 (7)	0.106 5 (2.2)	0 (2.7)	0 (0.2)	0 (0)	-	0.106 5 (0.4)	0 (0.2)	0 (3.5)	-	-	-	-	-	-	-	-	-	-	-	-	47
	ESC	-	-	-	-	-	-	-	0 (0.4)	-	-	-	0 (0.7)	-	0.258 8 (3)	-	0 (1.1)	0 (0.3)	0.453 14 (4.6)	0 (0)	0 (0.2)	0.258 8 (3.7)	0 (0.1)	0.032 1 (0.1)	31
	UPP	-	0.3 3 (1)	0.5 5 (1.5)	0 (0.5)	0.2 2 (0.6)	0 (0.1)	0 (0)	-	-	-	0 (0.8)	-	-	-	-	-	-	-	-	-	-	-	-	10
	SEA	0.007 2 (5.8)	0.373 104 (26.8)	0.219 61 (41.1)	0.118 33 (12.8)	0.237 66 (15.6)	0.014 4 (0.7)	0 (0)	-	0.011 3 (2.2)	0.022 6 (0.8)	-	-	-	-	-	-	-	-	-	-	-	-	-	279
	SEO	-	-	-	-	-	-	-	0.06 5 (1.1)	-	-	-	-	-	0.446 37 (8)	-	0.108 9 (2.7)	0 (0.7)	0.253 21 (12.2)	0 (0)	0 (0.3)	0.108 9 (9.8)	0.024 2 (0.1)	0 (0.2)	83
Outside pot states	APP	-	-	-	-	-	-	-	0.002 1 (5)	-	-	-	0 (8.7)	-	0.111 45 (38.9)	0.002 1 (3.1)	0 (13.2)	0.022 9 (3.2)	0.833 339 (59.6)	0 (0)	0.005 2 (1.4)	0.022 9 (47.9)	0 (0.3)	0.003 1 (0.6)	407
	LEA	-	-	-	-	-	-	-	-	-	-	-	-	0.154 57 (38.6)	-	0.016 6 (2.8)	-	0.038 14 (2.9)	0.011 4 (54.3)	0 (0)	0.008 3 (1.3)	0.774 287 (43.7)	0 (0.2)	0 (0.5)	371
	NAP	-	-	-	-	-	-	-	-	-	-	-	-	0.785 263 (34.9)	0.003 1 (32)	-	-	0 (2.6)	0.015 5 (49)	0 (0)	0 (1.2)	0.191 64 (39.4)	0 (0.2)	0 (0.5)	333
	BAO	-	-	-	-	-	-	-	0.048 6 (1.6)	-	-	-	0 (2.7)	-	0 (12.1)	-	-	0 (1)	0.952 120 (18.5)	0 (0)	0 (0.5)	0 (14.9)	0 (0.1)	0 (0.2)	126
	HAO	-	-	-	-	-	-	-	0 (0.4)	-	-	-	0 (0.7)	0.467 14 (3.2)	0.2 6 (2.9)	0 (0.3)	0 (1)	-	0 (4.4)	0.2 6 (4.5)	0 (0.2)	0.133 4 (3.6)	0 (0.1)	0 (0.1)	30
	INO	-	-	-	-	-	-	-	0.059 34 (7)	-	-	-	0.145 83 (12.3)	-	0.448 257 (54.8)	-	0.202 116 (18.6)	0.003 2 (4.5)	-	0 (0)	0.01 6 (2)	0.129 74 (67.5)	0 (0.3)	0.003 2 (0.8)	574
	MIO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0
	OTO	-	-	-	-	-	-	-	0 (0.2)	-	-	-	0 (0.3)	0.077 1 (1.4)	0.308 4 (1.3)	0 (0.1)	0 (0.5)	0.154 2 (0.2)	0.385 5 (2)	0 (0)	-	0.077 1 (1.6)	0 (0.1)	0 (0.1)	13
	OUO	-	-	-	-	-	-	-	0.006 1 (2.1)	-	-	-	0 (3.7)	0.409 70 (17.8)	0.076 13 (16.4)	0.129 22 (1.3)	0.006 1 (5.6)	0.018 3 (1.4)	0.345 59 (25.1)	0 (0)	0.006 1 (0.6)	-	0 (0.1)	0.006 1 (0.3)	171
	PAO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	-	0 (0.2)	0 (0.1)	0 (0.1)	0 (0.1)	0 (0.3)	0 (0)	0.5 1 (0.1)	0.5 1 (0.3)	-	0 (0.1)	2
	TEO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.2)	-	0.2 1 (0.5)	0 (0.1)	0 (0.2)	0 (0.1)	0.6 3 (0.8)	0 (0)	0 (0.1)	0.2 1 (0.6)	0 (0.1)	-	5
	Total	81	374	568	178	217	9	0	47	28	10	284	83	405	372	29	126	30	570	6	13	458	2	5	3895

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Table 8: Saithe behavioural transition matrix for the CB (collapsible bottom set) pot type. The preceding behaviour is given to the left of the square and the subsequent behaviour above. Transitional probabilities are displayed in the upper half of the squares; observed and expected values (in parenthesis) of transitions are shown in the lower half. Transitions which were over-represented (see Section 2.5.3) are highlighted in grey. Further saithe transition matrices for other pot types can be found in Appendix 22. Abbreviations of different behaviours states are explained in Table 2.

		Inside pot states							Events					Outside pot states											
	CODE	BAI	HAN	INS	MIL	OUT	PAN	TER	CAP	ESC	UPP	SEA	SEO	APP	LEA	NAP	BAO	HAO	INO	MIO	OTO	OUO	PAO	TEO	Total
Inside pot states	BAI	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	HAN	0 (0)	-	0.723 60 (6.8)	0 (0.6)	0.072 6 (2.7)	0.012 1 (1.1)	0 (0)	-	0 (0.1)	0 (0.1)	0.193 16 (5.4)	-	-	-	-	-	-	-	-	-	-	-	-	83
	INS	0 (0)	0.162 31 (6.6)	-	0.01 2 (1.4)	0.136 26 (6.1)	0.037 7 (2.4)	0 (0)	-	0 (0.2)	0 (0.2)	0.654 125 (12.5)	-	-	-	-	-	-	-	-	-	-	-	-	191
	MIL	0 (0)	0 (0.6)	0.941 16 (1.4)	-	0 (0.6)	0 (0.3)	0 (0)	-	0.059 1 (0.1)	0 (0.1)	0 (1.2)	-	-	-	-	-	-	-	-	-	-	-	-	17
	OUT	0 (0)	0.066 5 (2.7)	0.868 66 (6.2)	0 (0.6)	-	0 (1)	0 (0)	-	0 (0.1)	0 (0.1)	0.066 5 (5)	-	-	-	-	-	-	-	-	-	-	-	-	76
	PAN	0 (0)	0.1 3 (1.1)	0.333 10 (2.5)	0.25 3 (0.3)	0.03 1 (1)	-	0 (0)	-	0 (0.1)	0 (0.1)	0.433 13 (2)	-	-	-	-	-	-	-	-	-	-	-	-	30
	TER	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
Events	CAP	0 (0)	0 (0.2)	0.75 3 (0.4)	0.25 1 (0.1)	0 (0.2)	0 (0.1)	0 (0)	-	0 (0.1)	0 (0.1)	0 (0.3)	-	-	-	-	-	-	-	-	-	-	-	-	4
	ESC	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	-	1.0 2 (0.4)	-	0 (0)	0 (0.1)	0 (0.3)	0 (0)	0 (0.1)	0 (0.5)	0 (0.1)	0 (0)	2
	UPP	-	0 (0.1)	0.5 1 (0.2)	0.5 1 (0.1)	0 (0.1)	0 (0.1)	0 (0)	-	-	-	0 (0.2)	-	-	-	-	-	-	-	-	-	-	-	-	2
	SEA	0 (0)	0.283 45 (5.5)	0.22 35 (12.9)	0.063 10 (1.2)	0.277 44 (5.1)	0.138 22 (2)	0 (0)	-	0.006 1 (0.2)	0.013 2 (0.2)	-	-	-	-	-	-	-	-	-	-	-	-	-	159
	SEO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	-	-	0.467 7 (2.6)	-	0 (0)	0 (0.2)	0.267 4 (2)	0 (0)	0 (0.2)	0.2 3 (3.6)	0.067 1 (0.1)	0 (0)	15
Outside pot states	APP	-	-	-	-	-	-	-	0 (0.8)	-	-	-	0 (2.7)	0 (0)	0.268 117 (74.4)	0.005 2 (9.2)	0 (0)	0.025 11 (3.4)	0.657 287 (56.7)	0 (0)	0.014 6 (4.2)	0.03 13 (103.7)	0.002 1 (2.2)	0 (0)	437
	LEA	-	-	-	-	-	-	-	-	-	-	-	-	0.180 75 (74.7)	-	0.01 4 (8.7)	-	0.005 2 (3.3)	0.007 3 (54)	0 (0)	0.017 7 (4)	0.779 324 (98.7)	0.002 1 (2.1)	0 (0)	416
	NAP	-	-	-	-	-	-	-	-	-	-	-	-	0.535 252 (84.6)	0 (80.2)	-	-	0.004 2 (3.7)	0.002 1 (61.1)	0 (0)	0.004 2 (4.5)	0.448 211 (111.8)	0.006 3 (2.4)	0 (0)	471
	BAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
	HAO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.2)	0.421 8 (3.5)	0.368 7 (3.3)	0 (0.4)	0 (0)	-	0.211 4 (1.6)	0 (0)	0 (0.2)	0 (4.6)	0 (0.1)	0 (0)	19
	INO	-	-	-	-	-	-	-	0.009 3 (0.6)	-	-	-	0.047 15 (2)	-	0.817 263 (54.8)	-	0 (0)	0.009 3 (2.6)	-	0 (0)	0.022 7 (3.1)	0.081 26 (76.4)	0.016 5 (1.6)	0 (0)	322
	MIO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0
	OTO	-	-	-	-	-	-	-	0.045 1 (0.1)	-	-	-	0 (0.2)	0.318 7 (4)	0.045 1 (3.8)	0.045 1 (0.5)	0 (0)	0.045 1 (0.2)	0.318 7 (2.9)	0 (0)	-	0.136 3 (5.3)	0.045 1 (0.2)	0 (0)	22
	OUO	-	-	-	-	-	-	-	0 (0.3)	-	-	-	0 (1.1)	0.574 97 (30.4)	0.083 14 (28.8)	0.254 43 (3.6)	0 (0)	0 (1.4)	0.089 15 (22)	0 (0)	0 (1.6)	-	0 (0.9)	0 (0)	169
	PAO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	-	0.5 5 (1.8)	0.1 1 (0.3)	0 (0)	0 (0.1)	0.3 3 (0.9)	0 (0)	0.1 1 (0.1)	0 (2.4)	-	0 (0)	10
	TEO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0
	Total	0	84	198	17	77	30	0	4	2	2	159	15	439	416	51	0	19	317	0	23	580	12	0	2445

3.4 The effect of pot type on behaviour

3.4.1 Cod behaviour prior to capture

The proportion of time cod allocated to different behavioural states prior to capture was not uniform across the pot types (Figure 5). In general, cod allocated the majority of their time to approach (APP), inspection (INO), leave (LEA) and milling (MIO) behaviours. Across all pots, cod allocated the largest proportion of time to inspection behaviour, with the exception of the RNC pot, in which mill swimming was the most dominant behaviour. Panic (PAO) and territorial (TEO) behaviours were rarely recorded (Figure 5).
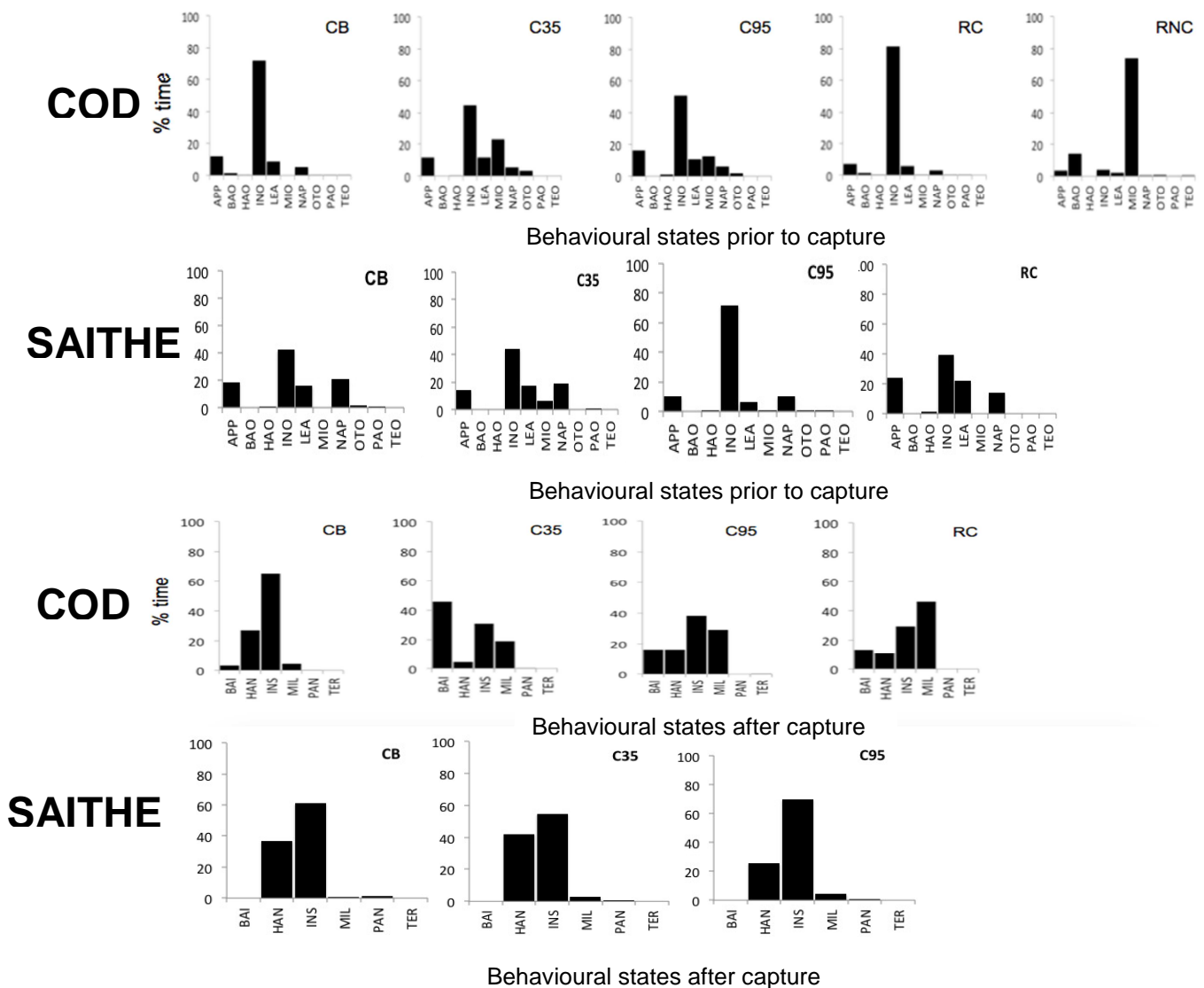
Figure 5: The proportion of time spent by cod and saithe in different behavioural states prior to and after capture. Abbreviations of different behaviours states are explained in Table 2. Pot type is indicated in the top right of each plot. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm); C95: collapsible (floated 95cm); RC: rigid with bottom chamber; RNC: rigid without bottom chamber. Further details of pot design can be found in Table 1.

For collapsible pot types (CB, C35 and C95), an nMDS ordination plot of behaviour prior to capture showed a high degree of overlap, suggesting cod allocated broadly similar amounts of time to different behavioural states around the different pots (Figure 6). However, behaviour associated with the CB pot appeared to show grouping in the lower portion of the plot, while C35 behaviour appeared to group in the upper portion. Subsequent pairwise comparisons found the behaviour outside the CB pot type to be significantly different to that of the C35 pot type (ANOSIM $R = 0.33$, $p < 0.01$, Table 9). SIMPER analysis revealed the average dissimilarity between these pot types to be 38%. The principal behaviours which contributed to this difference were inspection (INO, 11% contribution to overall dissimilarity), milling (MIO, 7%) and leaving (LEA, 7%) (Appendix 23). Cod spent more time in milling and leaving behaviours around the C35 pot, and less time in INO behaviour (Figure 5). There were no significant differences in behaviour between the CB and C95 pot types or between the C35 and C95 pot types (Table 9).
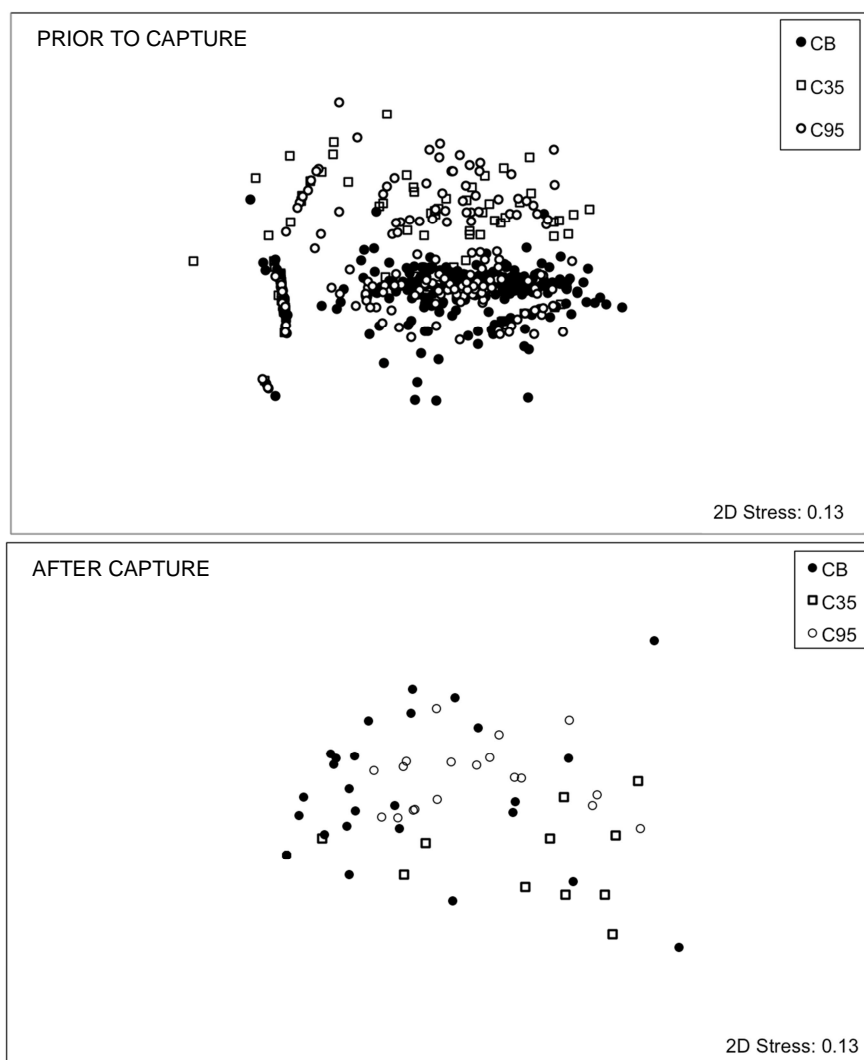
Figure 6: Non-metric multidimensional scaling ordination (nMDS) of the proportion of time cod allocated to different behavioural states for collapsible pots prior to and after capture. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm) and C95: collapsible (floated 95cm). Further details of pot design can be found in Table 1.

Table 9: Results of pairwise comparisons between collapsible pot types for the proportion of time cod allocated to different behavioural states using ANOSIM and SIMPER analysis. ANOSIM R < 0.25 = not separated, R = 0.25 – 0.5 = barely separated R = 0.5 – 0.75 = overlapping but clearly different and R > 0.75 = well separated. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm); C95: collapsible (floated 95cm). Further details of pot design can be found in Table 1.

		Outside behaviours		Inside behaviours	
		CB	C35	CB	C35
C35	R	0.336		0.292	
	p	0.001		0.003	
	AvDiss %	38		52	
C95	R	0.12	0.104	0.166	-0.026
	p	0.001	0.001	0.002	0.582
	AvDiss %	32	37	43	25

Note: *R:* ANOSIM statistic; *p*: significance level of *R* statistic; AvDiss: average dissimilarity (SIMPER).

For rigid pot types (RC and RNC), an nMDS ordination plot (Figure 7) displayed a high degree of separation, suggesting two modes of behaviour associated with the two different pots. The allocation of time given to different behavioural states was found to significantly different between the pot types (ANOSIM Global R = 0.80, *p* < 0.01). The overall average dissimilarity between the RC and RNC pots was 64% (SIMPER analysis). The behaviours which contributed the most to this observed difference were milling (MIO, 19% contribution to overall dissimilarity), inspection (INO, 19%) and leaving (LEA, 7%) (Appendix 25). Cod spent less time in inspection and leave behaviours and more time in milling behaviour around the RNC pot (Figure 5). Differences in behavioural time budgets after capture were not examined for rigid pot types, due to a lack of captures in the RNC pot.

Figure 7: Non-metric multidimensional scaling (nMDS) ordination of the proportion of time cod allocated to different behavioural states around rigid pots for behaviour prior to capture. Pot type codes; RC: rigid with bottom chamber; RNC: rigid without bottom chamber. Further details of pot design can be found in Table 1.

Cod approach height differed according to pot type. In CB, RC and RNC pot types, cod made significantly more approaches along the seabed (paired Wilcoxon signed rank test: $p < 0.01$ in all cases). For the CB, RC and RNC pots, 75 %, 78 % and 84% of approaches respectively were made along the seabed. In C35 and C95 pot types, there was no significant difference in the number of seabed and water column approaches ($p = 0.21$ and $p = 0.17$ respectively). For the C35 and C95 pots, 56 % and 53 % of approaches respectively were made along the seabed.

3.4.2 Cod behaviour after capture

Across the pot types examined (there were no captures recorded in the RNC pot type), cod allocated different amounts of time to different behavioural states after capture (Figure 5). The majority of time was spent feeding on bait (BAI), hanging (HAN), inspecting (INS) and mill swimming (MIL) behaviours. The most common behaviour differed between the pot types. Inspection (INS) was the most prevalent in the CB and C95 pots, with bait (BAI) and milling (MIL) behaviours dominating in the C35 and RC pots respectively. Panic (PAN) and territorial (TER) behaviours were rarely recorded (Figure 5).

Poor separation of points in the nMDS plot (Figure 6) suggested cod behaved similarly inside the different collapsible pot types. There was however, grouping of the CB pot type to the upper left of the plot and of the C35 pot type to the lower left. The allocation of time given to different behaviours was subsequently found to be significantly different between the CB and C35 pot types (ANOSIM R = 0.29, $p < 0.01$, Table 9), but not between the CB and C95 pot types or between the C35 and C95 pots. Average dissimilarity between the CB and C35 pot types was 52% (SIMPER analysis, Table 9). The principal behaviours which contributed to this difference were bait feeding (BAI, 19% contribution to overall dissimilarity), inspection (INS, 14%) and milling (MIL, 9%) (Appendix 24). Cod spent more time in bait and milling behaviours and less time in inspection behaviour in the C35 pot (Figure 5).

3.4.3 Saithe behaviour prior to capture

The proportion of time saithe allocated to different behavioural states prior to capture was not uniform across the pot types (Figure 5). Generally, saithe allocated the majority of their time to approach (APP), pot inspection (INO), leaving (LEA) and no approach (NAP) behaviours. Across all pot design examined, saithe allocated the largest proportion of time to inspection behaviour (Figure 5). For collapsible pot types (CB, C35 and C95), no significant differences in the proportion of time saithe allocated to different behaviours were evident between pots (ANOSIM R < 0.25 in all cases,

Table 10). This was supported by an nMDS ordination displaying a high degree of overlap of points, although there was a suggestion of grouping of the C95 behaviours to the right of the plot (Figure 8).

A lack of saithe captures prevented statistical comparison between rigid pot designs.

Table 10: Results of pairwise comparisons between collapsible pot types for the proportion of time saithe allocated to different behavioural states using ANOSIM and SIMPER analysis. ANOSIM R < 0.25 = not separated, R = 0.25 – 0.5 = barely separated R = 0.5 – 0.75 = overlapping but clearly different and R > 0.75 = well separated. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm); C95: collapsible (floated 95cm). Further details of pot design can be found in Table 1.

		Outside behaviours	
		CB	C35
C35	R	0.100	
	p	0.028	
	AvDiss %	39	
C95	R	0.234	0.017
	p	0.001	0.267
	AvDiss %	31	38

Note: R: ANOSIM statistic; p: significance level of R statistic; AvDiss: average dissimilarity (SIMPER).
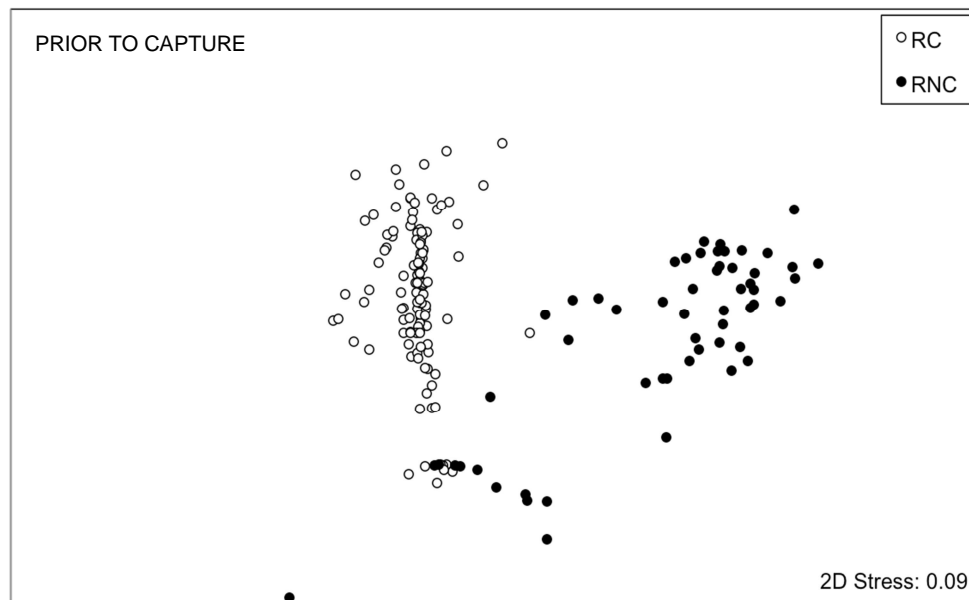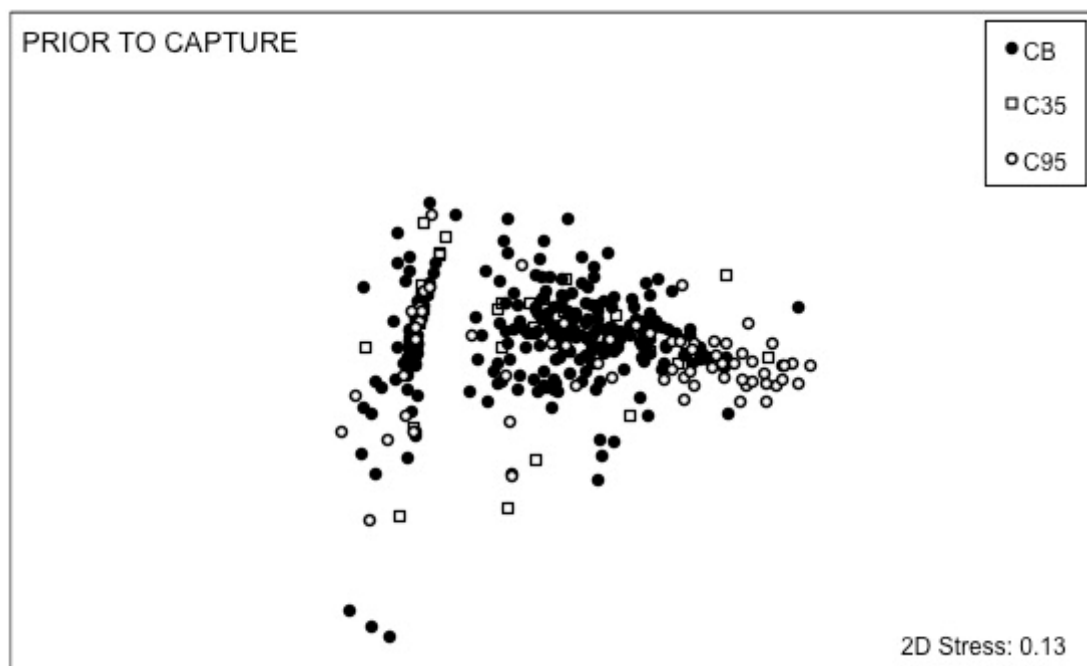

Figure 8: Non-metric multidimensional scaling (nMDS) ordination of the proportion of time saithe allocated to different behavioural states around collapsible pots for prior to capture. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm) and C95: collapsible (floated 95cm). Further details of pot design can be found in Table 1.

Saithe made significantly more approaches in the water column around all tested pot types (paired Wilcoxon signed rank test: $p < 0.05$ in all cases). The percentages of saithe approaching within the water column were 52 %, 85 %, 91 % and 67 % for pot types CB, C35, C95 and RC respectively.

3.4.4 Saithe behaviour after capture

There were insufficient observations to examine the effect of pot type on saithe behaviour after capture.

3.5 Species specific differences in behaviour

3.5.1 Behaviour prior to capture

For both cod and saithe, the most prevalent behaviour exhibited prior to capture was inspection (INO). Although both species allocated the majority of their time to approaching (APP), inspection (INO) and leaving (LEA) behaviours, the proportion of time allocated was not the same (Figure 5). No significant differences in the proportion of time allocated to different behaviours were evident between cod and saithe for all pot types (ANOSIM R < 0.25 in all cases, Table 11). This was supported by nMDS ordination plots of behaviour prior to capture, which showed a high degree of overlap of points and minimal grouping (Figure 9).

Saithe were significantly more likely to make a water column approach than cod (pooled data for all pot types, binomial GLM: $p < 0.009$, Appendix 32).

Table 11: Results of comparisons between cod and saithe for the proportion of time each species allocated to different behavioural states using ANOSIM and SIMPER analysis. ANOSIM R < 0.25 = not separated, R = 0.25 – 0.5 = barely separated R = 0.5 – 0.75 = overlapping but clearly different and R > 0.75 = well separated. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm); C95: collapsible (floated 95cm); RC: rigid with bottom chamber; RNC: rigid without bottom chamber. Further details of pot design can be found in Table 1.

		Pot type				
		CB	C35	C95	RC	RNC
Outside behaviours	*R*	0.116	0.03	0.094	0.137	*no data*
	p	0.001	0.125	0.001	0.001	
	Av. Diss.	37	39	37	30	
Inside behaviours	*R*	-0.036	0.547	0.262	*no data*	*no data*
	p	0.525	0.043	0.021		
	Av. Diss.	39	58	36		

Note: *R:* ANOSIM statistic; *p*: significance level of *R* statistic
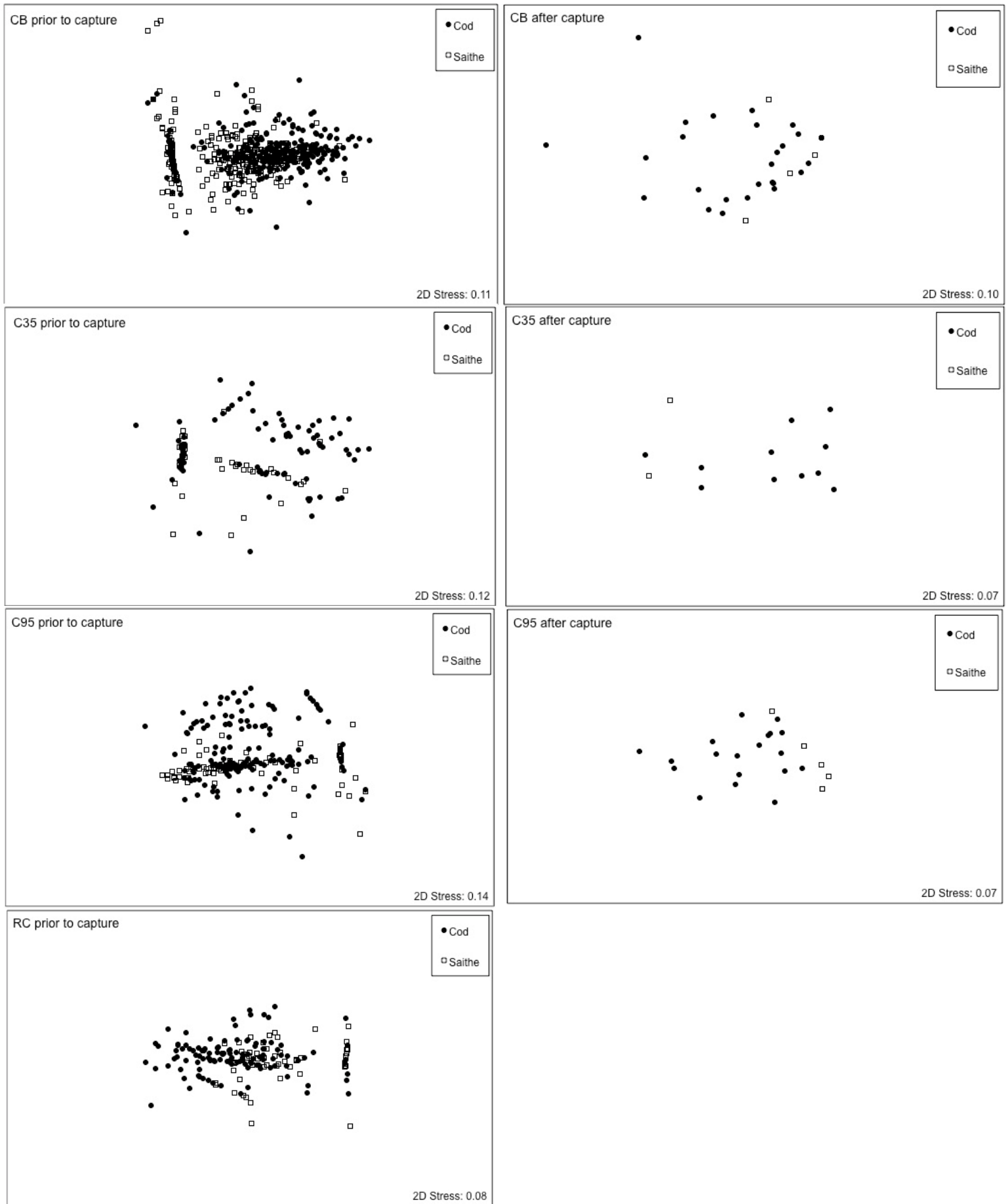
Figure 9: Non-metric multidimensional scaling (nMDS) ordination of the proportion of time cod and saithe allocated to different behavioural states prior to and after capture. Pot type is indicated in the top left of the plots. Pot type codes; CB: collapsible (bottom set); C35: collapsible (floated 35cm) and C95: collapsible (floated 95cm); RC: rigid with bottom chamber; RNC: rigid without bottom chamber. Further details of pot design can be found in Table 1.

3.5.2 Behaviour after capture

Comparisons of species behaviour after capture was limited to collapsible pot types, owing to a lack of observations of saithe inside rigid pots. Across the pot types examined, the most common behaviours exhibited by cod were hanging (HAN), inspecting (INS), feeding on bait (BAI) and mill swimming (MIL) (Figure 5). Hanging and inspection dominated saithe behaviour. Feeding on bait (BAI) behaviour was absent in saithe.

nMDS plots for behaviour after capture displayed some overlap but with possible groupings according to species (Figure 9), suggestive of two particular modes of behaviour. The allocation of time given to different behaviours was subsequently found to be significantly different between the cod and saithe in the C35 and C95 pots (ANOSIM R > 0.25 in both cases), but not inside the CB pot (Table 11).

In the C35 pot, the average dissimilarity between cod and saithe was 58% (SIMPER analysis, Table 11). The principal behaviours which contributed to this difference were feeding on bait (BAI, 22% contribution to overall dissimilarity), hanging (HAN, 16%) and inspection (INS, 12%) (Appendix 26). Saithe spent less time in bait behaviour and more time in hanging and inspection behaviours than cod (Figure 5). For the C95 pot, the average dissimilarity between species was 36% (SIMPER analysis, Table 11). The behaviours which contributed the most to this observed difference were mill swimming (MIL, 22% contribution to overall dissimilarity), hanging (HAN, 9%) and bait feeding (BAI, 9%) (Appendix 27); saithe spent less time engaged in milling and bait behaviour and more time hanging compared to cod (Figure 5).

Intra-observer reliability for time budget sampling was good (average Cohen's kappa = 0.68), suggesting accurate recording of the duration and sequence of the behavioural states.

3.6 Other behavioural metrics

3.6.1 Approach Direction

In all pot types, the number of cod swimming in downstream, upstream and across-stream directions was significantly different (Friedman test: $p < 0.001$ in all pot types, Appendix 28). Pairwise comparisons found the majority cod swam upstream while approaching pots (paired Wilcoxon

signed-rank test with Bonferroni correction: $p < 0.01$ in all pots). Overall, 78% of cod approaches were in an upstream direction.

For the CB and C35 pots, there were significant differences in saithe approach direction (Friedman test: $p < 0.001$ in both cases, Appendix 29). Saithe made significantly more approaches upstream (paired Wilcoxon signed-rank test with Bonferroni correction: $p < 0.01$ both cases). In the C95 and RC pots, no saithe approached in a downstream direction. Saithe also approached these pots upstream rather than across-stream (paired Wilcoxon signed-rank test: $p < 0.01$ in both cases). Overall, 74% of saithe approaches were in an upstream direction.

3.6.2 Approach Height

There was a significant positive relationship between bait height and the probability of a water column approach for both cod and saithe (quasi-binomial GLM: $p < 0.01$ in both cases, Figure 10, Appendix 30 & 31).
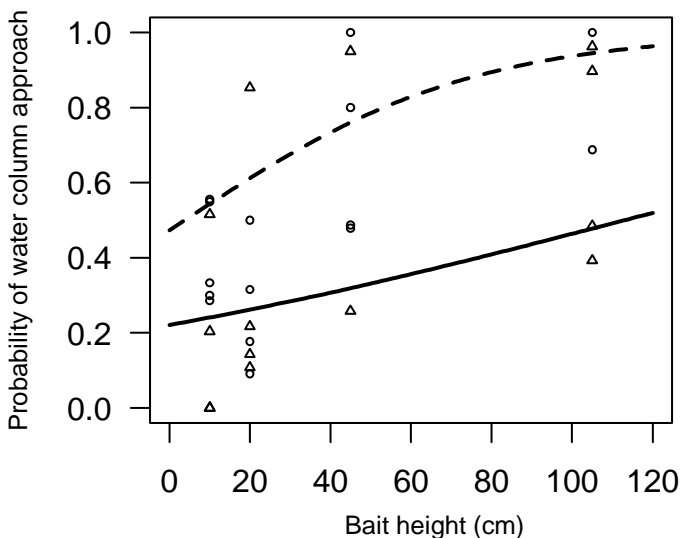
Figure 10: The relationship between lower bait height above the seabed and the probability of a water column approach for cod and saithe. Triangle and circles represent cod and saithe respectively. The solid line represents the model derived probability of a water column approach for cod; the dashed line represents model derived saithe probability. A water column approach was defined as a fish with more than one body lengths distance from the seabed for the majority of duration of its approach.

3.6.3 Search location and direction prior to capture

In the near-field, cod often made touches on the outside of the pot ("search (outside)" behaviour). Outside all pot types (except RNC, in which insufficient samples prevented statistical testing), there

were significant differences between the number of searches made on the pot walls, roof and floor (Friedman test: $p < 0.01$ in all cases, Appendix 33). Pairwise comparisons found that cod made significantly more searches on the pot walls rather than on the roof or floor (paired Wilcoxon signed-rank test with Bonferroni correction: $p < 0.05$ for all tested pot types).

There were also significant differences in the number of searches cod made in the upstream, downstream and across stream location in all tested pot types (Friedman test: $p < 0.01$ in all cases, Appendix 34). Cod made significantly more searches in an upstream rather than in the downstream or across-stream location (pairwise comparison using paired Wilcoxon signed-rank test with Bonferroni correction: $p < 0.05$ in all cases).

There were insufficient observations of saithe search location and direction to allow statistical testing. However, across all pot types, 85% of saithe searches were made in the upstream area of the pot. 100% of saithe searches were made on the pot walls.

3.6.4 Search location after capture

Having entered the pot, cod often made touches on the inside of the pot ("search (inside)" behaviour). For pot types (except RNC, for which no captures occurred), there were significant differences between the number of searches made on the inside walls, roof and floor (Friedman test: $p < 0.01$ in all cases, Appendix 35). Pairwise comparisons found that cod made significantly more searches on the walls than on the roof or floor, in all tested pot types (paired Wilcoxon signed-rank test with Bonferroni correction: $p < 0.05$ in all cases). For saithe, 80% of all searches following capture were directed towards the pot walls.

4. DISCUSSION

Fish pots are an environmentally benign fish capture method, but their successful adoption into a commercial fishery relies on them being able to compete in capture efficiency with other established gear types. As capture efficiency in baited gear relies largely upon the behaviour of the target species, an understanding of the behavioural response of fish to pots is essential. This study quantitatively described capture efficiency and fish behaviour in a number of pot designs, detailed factors influencing the entrance rate into pots, examined what effect pot design modifications have on behaviour, studied species specific responses to pots and described how fish approach and search pots.

4.1 Limitations and potential sources of error

This study has some potential sources of error which require further consideration. First, as fish continually left and re-entered the field of view of the camera, I was unable to determine if pot approaches, inspection and captures were made by the same individual or not. Fish were considered to be new individuals if they were out of sight of the camera for more than 20 seconds and could not be positively identified on re-entry. Therefore, rates of encounter and entrance to the pot were likely over-estimated as it is possible that the same individual was recorded more than once. Escape rate can be considered more accurate, as fish were nearly always observable once inside the pot. More accurate estimation of capture efficiency rates may be achieved by the use of PIT tags following the movement of tagged fish outside of the field of view of the camera (Bravener & McLaughlin, 2012).

Due to differences in fishing method, it is uncertain how far the behaviour recorded in this study is an accurate representation of what would occur in a commercial situation. Commercial pot fishing in Norway can take place in depths of up to 150 m (S. Løkkeborg *pers. comm.*), while the sets in this study were at a depth of around 40 m. Light levels in deeper water can be expected to be lower and as vision is likely to be the primary sensory modality in use in the near-field of pots, there is a possibility that fish behave differently when pots are set at depth. In particular, the reaction threshold of the fish to the visual stimulus of the gear can be expected to be lower. However, any change in behaviour is likely to be minor as cod have high sensitivity to low light conditions (Meager *et al.*, 2010). Commercial pot fishing also has typically longer soak times (around 48 hrs, S. Løkkeborg *pers. comm.*) than what was employed in this study (*c.* 2.25 hrs). Modification of behaviour in caught fish over time was noted by Furevik (1994), where fish were seen to become less active and rest more. This has important implications for the escape behaviour of fish, but the relatively short duration of the video footage did not permit a test of this effect. Further to this, the short duration of

the footage means that it is likely that all the behaviour recorded in this study occurred whilst the bait was still producing an odour plume. Video footage with longer duration may help to investigate how fish behave in response to pots in which the bait odour has been exhausted.

Video footage was collected over two different years, on different days and at different times due to practical constraints. Ideally, footage should have all been collected in as small a time period as possible, in order to minimise differences in fish behaviour caused by environmental variables. Temperature, light level, current and ambient prey density can all be expected to vary with time and season and have the potential to affect fish behaviour (Stoner, 2004). I attempted to control for this as much as possible by collecting video footage at the same time of year (August/September) for both years (2013 and 2014). This said, future research should attempt to detail to what extend the behaviour towards fish pots is modified between different seasons as this has potentially important consequences for the establishment of a commercial fishery. This is of particular importance to Norwegian pot fisheries, as the high latitude of many potential pot fishing grounds means that fishing must be conducted at some times of the year in either the polar night (*mørketid*) or the midnight sun (*midnattssol*).

There was an unexpected overlap in behaviour exhibited by cod between the C95 pot and the other collapsible designs. It would be expected that a pot floated 95cm above the seabed would, if anything, produce behaviour similar to the C35 pot and different behaviour from the CB pot. Although the ANOSIM results were not significant, SIMPER analysis of the average dissimilarity between the pots suggested that the behaviour in the C95 was more similar to the CB pot than the C35 pot. This surprising result may be related to technical problems in the setting of the pots. During video analysis it became apparent that some of the floats designed to keep the C95 pot open in the water had cracked and flooded. This resulted in the entrance end of the pot being pulled down towards the seabed, and in some cases, the pot made contact with the seabed. Although sets in which this effect was very pronounced was rejected from analysis, the video from the remaining sets showed this effect of the entrance being pulled towards the seabed to a small degree. This may have caused the fish to behave in a similar way to the other pot types, in particular the CB pot type.

In order to maximise the number of sampled individuals, I non-randomly selected video sets which contained substantial numbers of fish for behavioural sampling. Therefore, the behaviour recorded in this study describes situations in which fish density in the area was relatively high. It is important to note that behaviour may be modified in the presence of other fish due to factors such as territoriality and competitive interactions between species and size (Furevik, 1994). One could also imagine a

situation in which a fish passing through the entrance of the pot could "lead" others to follow in the same way. However, territorial actions were rarely recorded during the video observations (Figure 5) and fish tended to approach, interact and enter pots singly, and not as part of shoals or schools. Therefore, the selection of videos with substantial numbers of fish is unlikely to have biased the results to a large degree.

In the GLM of capture success, the number of other fish in the pot was recorded upon the first appearance of another fish into the field of view in the camera. Having exited the field of view or being caught, the fate of the fish (captured or not captured) was recorded. It is therefore possible that the numbers of fish in the pot changed (due to other fish entering or exiting) during the time the fish under observation was in the field of view of the camera. This could have the potential to influence the model outcome predicting the probability of capture as a function of the number of fish in the pot (Figure 3). However, entries and exits from the pots were rare events (Table 7 & 8, Appendix 22) and consequently the number of fish in the pot was relatively stable and did not change rapidly. Therefore, this limitation is unlikely to have affected the model outcome to a significant degree. Additionally, I was unable to include the variable of fish size directly into the GLM due to the prevalence of fish for which the size could not be estimated (see Section 2.5.2 for further details). I therefore produced two models of capture success; one for large fish and one for small fish (Table 6). This meant that although I was able to demonstrate an effect of fish size on capture probability, I was unable to test for which way fish size influences capture probability.

4.2 Capture efficiency

In situ video footage allowed observation of the number of approaches, entry and escapes of fish to the different fish pot designs. It was predicted that a low entrance rate would limit catches. My results show that, in general, the capture efficiency of cod in pots is low due to a low entrance rate coupled with a high escape rate, and not because cod failed to encounter the pots (Table 5). For saithe, a low encounter rate was the chief factor limiting overall capture efficiency (Table 5).

In previous research into gadoid pot fishing, measures of pot efficiency have generally been conducted through comparative fishing trails (eg. Furevik & Løkkeborg, 1994; Furevik *et al.*, 2008), in which one pot design is compared to another. My study extends this approach by employing video footage, which allowed me to directly estimate the efficiency of the various stages of the capture process. Although Valdemarsen *et al.* (1977) also used video footage to describe the catching efficiency of gadoids to pots, the authors were unable to identify fish to the species level due to the

low quality of their video recordings. By using high quality colour footage, I was able to describe the catch efficiency at the species level. Valdemarsen *et al.* (1977) also quantified the number of fish showing interest in the pot and the numbers entering. They found that although high numbers of gadoids were attracted to pots, few entered. My findings support this observation of a low entrance rate limiting catches, but also extend it to show that escape rates can also be an important aspect in gadoid pot catch efficiency. Although Valdemarsen *et al.* (1977) noted that fish did escape from pots, they were unable to quantify the rate of escape.

Outside of gadoid fishing, Cole *et al.* (2004) investigated blue cod (*Parapercis colias*) pot catches, and similarly demonstrated that a combination of a high escape rate coupled with a low entry rate was limiting catches. A situation of low entry and high escape was also described for lobster (*Homarus americanus*) pots (Jury *et al.*, 2001). However, the greatest inefficiency of capture in pot fisheries seems dependent on target species, as evidenced in this study by the difference in limiting factor between cod and saithe (Table 5). For sea lamprey (*Petromyzon marinus*) trapping, Bravener & McLaughlin (2013) reported a lack of pot encounters and subsequent entries as contributing to a lower than expected catching efficiency. Conversely, high rates of escape were found to be limiting catches in Antillean fish traps targeting mixed species assemblages (Munro, 1974). Rose *et al.*. (2005) described a situation in which sablefish (*Anoplopoma fimbria)* entered the vicinity of a pot over 5000 times but only 10 fish were caught.

In light of my results, improvements in catch efficiency for cod could be achieved by measures designed to increase the entrance rate and decrease the escape rate. Optimising entrance size and shape can be effective in increasing ingress rates, and has been demonstrated for cod (Furevik & Løkkeborg, 1994). Recent studies have also demonstrated the potential of green light to increase the ingress rate of cod into floated collapsible pots (Bryhn *et al.*, 2014). Escape rates could be reduced with technical measures such as non-return triggers on the pot entrances, although such devices have the potential to further retard entry rates (Munro, 1972). As saithe prefer mackerel bait to squid bait (Bjordal, 1983), the low encounter rate of saithe could be countered by optimising the bait type.

The capture process of longlining is similar to pots in that it involves an attraction phase and a phase in which the fish is in the near-field of the gear, prior to capture (either by entering the pot or by hooking, in the case of longlines). In a longlining field study using a similar camera setup, the proportion of cod responding to mackerel bait was 0.05 and the proportion caught was 0.37 (Løkkeborg *et al.*, 1989). The proportion responding was calculated as the ratio between the number of observed fish in the field of view of the camera to the number showing some response to the bait, and is analogous to the encounter rate in this study (range: 0.5 to 0.83). The proportion caught was

calculated as the ratio between hooked fish and the number of fish biting the bait, and is analogous to the entrance rate used in this study (range: 0.00 to 0.22). The differences between the capture efficiency of longlining and potting are likely to be due to difference in the capture process and the behavioural responses invoked between the two methods. Pots presumably offer a larger visual aspect to cod which is easier to locate than bait on a longline hook, which may explain the higher encounter rate observed in this study. Furthermore, entry into a pot is likely to represent a situation that requires a larger degree of exploratory behaviour than feeding on bait in open water, as is the situation in longlining. This may help explain the lower entrance rate observed in pots. It is important to note, however, that Løkkeborg *et al.* (1989) used mackerel bait while this study used squid bait. Squid is a more effective bait for cod than mackerel (Løkkeborg & Bjordal, 1992).

4.3 Factors influencing the entrance rate in fish pots

Due to the importance of entrance rates to overall capture efficiency, understanding the factors which may influence the probability of a pot entrance is of great interest. I predicted that the probability of capture would depend on the presence of retained fish already inside the pot. I further predicted that higher numbers of fish in the pot would result in a higher probability of entry. The findings of this study are in line with the first prediction but contrasts with the second prediction, as generalised linear modelling revealed the probability of entrance for large fish peaked with one fish in pot and thereafter decreased with increasing numbers of fish retained in the pot (Figure 3). For small fish, probability of entry peaked with four other fish in the pot, and declined afterwards (Figure 3).

Few studies have specifically addressed how the presence of caught fish influences capture efficiency in gadoid pot fishing. Valdemarsen *et al.* (1977) reported on an unbaited fish pot set with one live cod which contained eight cod two weeks later; the suggestion being that social attraction plays a role in capture. This observation is supported by Königson *et al.* (2015), who found pot catches peaked with a soak time of 6 – 7 days. Based on findings that the rate of release of attractants from bait rapidly declines and therefore a pot will only fish effectively for a few hours (Løkkeborg, 1990), the authors suggest that fish may have been attracted into pots after the bait has been depleted by aggregation effects.

To my knowledge, my results are the first to confirm the speculations made by previous authors that the social attraction influences capture efficiency in gadoid pot fishing. Further to confirming these suggestions, my results demonstrate that this effect is somewhat multifaceted in that the presence of other fish can both attract and repulse other fish. I suggest that this effect may be explained in the

context of social foraging behaviour of fish. To a fish approaching a pot due to bait localisation, other captured fish in the pot likely represent a feeding shoal. Providing the fish can locate the pot entrance and is motivated to enter, the decision then becomes whether to join this feeding shoal inside the pot or not. Feeding in a shoal can allow more effective feeding. In cod, shoaling allowed food pieces too large to be eaten to be pulled apart are shared between other fish (Brawn, 1969). The decision likely to represents a trade off between the benefits of social foraging and increased competition between other members of the shoal for any food that is located. Fish can evaluate the benefit of feeding decisions based on social information and cues from other fish. For example, when presented with two feeders with bait hidden inside, wild guppies (*Poecilia reticulata*) preferentially enter feeders which contain captured conspecifics over feeders which do not (Reader *et al.*, 2003). With no other fish in the pot, approaching fish receive no social information about the bait and must therefore base the decision to enter on private information alone. With low numbers of fish in the pot, social information is available and the benefits of joining outweigh the costs; more effective feeding but with low numbers of other fish with which to have to share. Consequently, probability of pot entry increases. However, with increasing numbers of other fish, social information informs the fish that any food resource (i.e the bait) must be shared between the others and probability of entry consequently decreases. Interestingly, the number of fish in the pot which maximised the probability of entry was higher for small fish than large fish (Figure 3). This could be explained by difference in predation pressure between the two sizes of fish. Smaller fish presumably have a higher predation pressure and would therefore be more willing to trade off the competition for food for enhanced predator protection. Increased predator protection has been shown to be a benefit of shoaling (Magnhagen, 2008).

It could be argued that the reduction in the probability of enter with increasing numbers of fish in the pot could be due to the saturation effect. As the capacity of a fish pot is not infinite and previous entries occupy space within the pot, saturation can be defined as "the tendency of the fishing power of a unit of gear to be reduced as the catch in it increases" (Beverton & Holt, 1957). However, this effect is unlikely to be of importance in this study, due to the generally small size and low number of fish observed inside the pot at any one time (maximum: 9). Therefore, there was always sufficient space within the pot for other fish to join. Another possible reason for this effect might be due to bait odour depletion. As the odor concentration from the bait declines due to washing out from the current, it would be expected that the motivation of a fish to enter the pot would decline also. However, the short set durations (2.25 hours) used in this study likely means that the bait odor concentration did not change considerably during the observation period. Løkkeborg (1990) reported on the release of attractants from mackerel bait and found a high rate of release for the first period,

and a decline in the rate thereafter up to 24 hrs. The same effect if likely for the squid bait used in this study. The fish in this study were observed directly after setting and were therefore interacting with the pot whilst the bait had its highest catching potential.

Another explanation of this effect might be that once significant numbers of fish are in the pot, their movements and pushes against the pot mesh deter other fish from entering. Bagdonas *et al.* (2012) described a situation were a saithe became entangled in a pot mesh, which subsequently evoked an avoidance reaction from fish schooling outside the pot.

Of particular interest would be to further explain the probability of entry as a function of hunger level. Ovegård *et al.* (2012) found the condition level of cod caught in pots to be lower than those caught by gillnet. A possible explanation to this is that low condition fish generally display a higher degree of boldness than high condition fish (Damsgård & Dill, 1998) and would therefore be more likely to enter the unfamiliar object which a pot likely represents to a fish. I therefore hypothesis that the probability of a fish entering a pot will depend on its hunger level, and that hungrier fish will enter more readily. Hunger levels could be determined through a proxy, such as the density of alternative prey items in the local area. As the density of alternative prey items can be expected to vary with season, knowledge of this factor may be useful in finding the times of the year in which pot entry probability is maximized, and thereby help to develop a commercial fishery.

I predicted that the probability of entry would depend on the species. I found that small cod were more likely to enter pots that either small saithe or haddock (Figure 2). Large cod were four more times likely to enter than large saithe or haddock (Figure 2), although the difference was not significant (likely due to a lack of statistical power). These differences likely reflect species specific behaviour responses to pots, and are discussed further in Section 4.5. I also predicted that the probability of entry would depend on the pot type. This is not supported by the results, as pot type was not a useful predictor for the probability of pot entrance (Table 6).

4.4 The effect of pot design on behaviour and catch efficiency

I predicted that alterations in pot design to avoid crab bycatch would produce changes in the behavioural response of fish and consequently changes in capture efficiency. My results indicate that cod were less likely to encounter floated pots (Table 5) and that, in general, floating pot designs (C35, C95 and RNC pots) tended to produce more milling ("slow, unidirectional swimming", Table 2) and less inspection behaviour prior to capture than bottom set designs (CB and RC pots) (Figure

5). Cod milling underneath floated pot types was a typical behaviour observed in video analysis (*personal observation*). A fish had to engage in inspection behaviour in order to considered to have encountered a pot (see Section 2.4.2). The prevalence of milling behaviour for cod in floated pot designs can be explained by observed differences in approach behaviour due to pot type. For pots in which the bait was close to the seabed (CB, RC and RNC pots), cod tended to approach along the seabed. Therefore, they encountered pots directly and took up inspection behaviour. For pots in which the bait was further from the seabed (C35 and C95), cod approached both along the seabed and in the water column. Cod which approached floated pots along the seabed would pass underneath, and thereby lose contact with the bait odour plume which is created by the current flowing parallel to the seabed. Cod could be then expected to take up behaviour milling behaviour ("slow, undirectional swimming", Table 2) in order to localize the source of the bait they are responding to.

Saithe tended to approach all pot types in the water column rather than along the seabed, which would explain why the saithe encounter rate for the CB and C35 pot was not different (Table 5). This tendency to approach in the water column could also explain why multivariate analysis found no significant differences in saithe behaviour due to pot type (Figure 8). A saithe approaching in the water column could still directly encounter and inspect a bottom set pot, as the pots reach a height of 120 cm (CB pot) and 220 cm (rigid pots) from the seabed. Therefore, it would be expected that saithe would behave in a similar way around both floated and non-floated pots as they encountered them both in the same manner.

Having located and entered the near-field of the pot, both cod and saithe entered the CB and C35 pots at the same rate (Table 5). This is supported by the result of the GLM of capture success, which found pot type was not a useful indicator of entrance probability (Table 6). It would seem that floating the collapsible pot 35cm above the seabed does not affect the mode of capture. This is to be expected, as the designs of the CB and C35 were identical expect for an extra entrance in the CB pot. Although an extra entrance might be expected to increase the rate of entrance, my results indicate that fish search for entrances into pots in the downstream area only. Therefore, they were more likely to find and use only the one entrance closest to downstream.

Escape rates were the same for both species from the CB and the C35 pot (Table 5). Multivariate analysis found cod behaviour after capture to be different in these two pot types (Figure 6). Cod spent relatively more time feeding on bait and milling in the floated pot (Figure 5). As milling was the most probable behaviour prior to escape (Figure 4), it might be expected that the escape rate would be higher in floated pot. However, the addition of an extra entrance (and therefore, an extra escape

route) in the CB pot increases the chance of escape, and may therefore have contributed to the lack of an overall difference in escape rates between the two pots.

nMDS ordination revealed the modification made to the rigid pot designs (removing the bottom chamber in order to "float" the pot above the seabed to create the RNC pot) produced a much more marked change in cod behaviour than the modifications to the collapsible designs did (Figure 7). This highlights the importance of the bottom chamber in the catch process in rigid pots. The RNC pot caught no fish, likely because of the prevalence of milling and lack of inspection behaviour associated with this pot type (Figure 5). Fish approaching this pot type would pass underneath the pot in the same way as in collapsible floated designs and take up milling behaviour, presumably in order to locate the bait. This effect was exasperated in this pot type, as this design had bait which hung outside of the pot itself. This meant there was no incentive for fish to inspect the pot itself as they already had access to bait prior to entering.

4.5 Species specific response to pots

As predicted, there were species specific responses to pots. Saithe were more likely than cod to approach in the water column (Figure 10). Following approach, saithe were consistently more likely than cod to leave before entering the near-field of the pot. Saithe that did enter the near-field of the pot tended to leave without engaging in further "pot-oriented" behaviour. Saithe also consistently engaged in less searching behaviour than cod (Table 7 & 8, Appendix 22). GLM found cod were more likely to be caught in pots than either saithe or haddock (Figure 2). Whereas some cod showed further interest in the pot following escape, saithe always left the area. There were also differences in the allocation of time the different species allocated to different behaviours after capture in the C35 and C95 pots (Figure 9). In general, cod were more active inside the pot and spent less time hanging than did saithe (Figure 5).

These results indicate that the response to saithe to pots is more cautious and displays a lesser degree of exploratory behaviour than cod. This mode of behaviour can help to explain some of the differences seen in capture efficiency between the species. Saithe encountered pots less than cod (Table 5), likely due to their lower tendency to enter the near-field of the pot. The GLM of capture success found that cod were more likely to enter pots than saithe (Figure 2). This can be explained by the result that saithe were more likely to leave the near-field of a pot without engaging in further exploratory behaviour such as inspect or search. Inspect and search were the most common behaviours leading to capture (Figure 4, Table 7 & 8, Appendix 22). Conversely, the capture

efficiency results suggested that saithe had a higher entrance rate than cod (Table 5), although the difference was not statistically significant. Saithe also escaped pots less often than cod (Table 5), although the difference was not significant. This could be explained by the stronger tendency of saithe to hang inside the pots after capture, whereas cod tended to engage in more mill behaviour. Mill was the most common behaviour prior to escape for both species (Figure 4, Table 7 & 8, Appendix 22). Alternatively, the lower escape rate could be explained by the higher tendency of saithe to enter the secondary chamber of the pots (Table 5). No escapes were recorded from the secondary chambers in all pot types. Taken together, my findings indicate that the behavioural characteristics of cod makes them more vulnerable to capture in pots than saithe, as well as giving them a higher capacity for escape.

My results corroborate the qualitative observations made by Furevik (1994) of the more "careful" nature of the response of saithe compared to cod prior to capture. The author noted that "pollack [saithe] have been observed swimming for hours in the downstream area, without touching the net", which reflects the findings in this study. After capture, Furevik (1994) also observed that cod where more active than other species. Bagdonas *et al.* (2012) observed saithe and cod behaviour inside pots. They found cod searched for exits more than saithe and that saithe tended to panic upon entering a pot before calming down and swimming slowly. My results take these observations further, by providing the first quantitative description of these differences.

Species dependant behavioural responses to baited fishing gear are widely recorded in the literature (eg. Løkkeborg *et al.*, 1989; Furevik, 1994; Løkkeborg *et al.*, 2010). As fishing gear prompts naturally occurring behaviour patterns in fish (Fernö, 1993), consistent differences between species probably reflect different naturally occurring behavioural strategies. Attraction to a pot involves a food-search response in fish. Saithe are known to feed primarily on pelagic prey and spend more time in the pelagic habitat than other gadoid species (Scott & Scott, 1998). Cod in Balsfjord tend to feed on benthic crustaceans (dos Santos & Falk-Petersen, 1989). This may explain the difference seen in approach height between the two species (Figure 10). The cautious nature of the response of saithe compared to cod likely reflects species-typical behaviour patterns. Predation risk has been shown to be instrumental in the evolution of species specific behaviours (Sih *et al.*, 2004). Evolutionary, if the predation risk for saithe is higher than for cod, then this would favour cautious behavioural types. Cautious behavioural types are heritable (Sih *et al.*, 2004).

4.6 Approach and search behaviour

As expected, both cod and saithe showed a general tendency to swim upstream when approaching pots. This observation is in line with previous observations of the response of fish to baited gear (eg. Valdemarsen *et al.*, 1977; Løkkeborg *et al.*, 1989), and indicates that attraction to pots is chiefly governed by the chemical stimuli of the bait, as dispersed by the current. In practical terms, this result suggests that entrances to pots should be situated on the downstream of the pot, in order to maximise the chance of an approaching fish to enter. This can be achieved in floated collapsible pots, as they are able to continually orient into the current (Furevik *et al.*, 2008). The small number of fish approaching from other directions probably represented fish re-entering the field of view of the camera having previously located the pot or fish transiting through the area attracted to the pot by visual means. The probability that a fish would approach pots in the water column was dependant on the height of the bait above the seabed (Figure 10). The higher the bait from the seabed, the higher the chance a fish would approach in the water column. This further indicates the importance of bait in approach behaviour and that fish are able to respond to changes in bait location.

The strong tendency for both cod and saithe to search only the downstream walls whilst inspecting pots suggests a specific and somewhat limited search pattern. This effect is likely due to fish following the dispersal path of the bait odor plume, as it passes through the pot walls due to the current. A similar effect was observed by Stiansen *et al.* (2010) in red king crab response to baited pots. The authors suggest that chemically mediated rheotaxis "locked" crab into searching only the bait plume area, as crab approaching outside of the bait plume employed a more flexible search strategy. Taken together, my results suggest that pot entrances should be situated on the downstream walls, in order to maximise the chance of ingress. This condition is met by floated collapsible designs.

After capture, fish showed a clear tendency to search the pot walls in attempts to escape, an observation which has important implications for future pot design. This behaviour pattern could explain the low rate of entry into the secondary chamber, which required fish to search upwards in order to enter. Retention levels in the pot may therefore be improved by situating the entrance to the secondary inner chamber as a vertical entrance on an inside pot wall, instead of on pot roof, as is the situation now. This would effectively create a "parlour pot", similar to those used in crustacean pot fisheries and could contribute towards making pots a more efficient fishing method. However, although this might increase ingress into the secondary chamber, there is a possibility that the rate of escape out of the secondary chamber would be also increase as a result. After capture in demersal trawl situations, cod and saithe tend to dive and stay low (Winger *et al.*, 2010), a response which may be a natural anti-predator response (Fernö, 1993). This effect was not seen in pots, as fish tended to

engage in milling behaviour upon entering the pots and searched the walls rather than the floor. Capture in a trawl could represent a higher stress situation to a fish and would therefore evoke an active anti-predator response (diving and staying low). Capture in a pot is likely to be a lower stress situation to a fish, and this could help to explain the behavioural differences seen between the two gear types.

4.7 Recommendations for further studies

This study confirmed the observations of previous studies that pots are relatively inefficient at catching fish. Therefore, further research efforts should focus on improving the efficiency. My results indicate that fish are attracted to pots by chemically situated rheotaxis due to bait. Although the results presented here suggest that cod pot catches are not limited by an inability to attract fish, further gains in efficiency may be achieved by employing long lasting baits (Thomsen *et al.*, 2010). As the ability of the bait to attract fish rapidly declines (Løkkeborg, 1990), a bait system which releases attractants slowly would be able to fish effectively for a longer period of time and potentially result in gains in capture efficiency. It is notable that the current understanding of the far-field and attraction behaviour to pots is based primarily on observations made for longline gear (Løkkeborg, 1998; Løkkeborg *et al.*, 2000). Future studies should therefore attempt to describe this process for pots specifically, as it is possible that the pot structure and bait bag cause the bait plume to develop in a different way than from longlines. Attention should also be given to the active space over which the pot attracts fish, as well as the chemosensory thresholds of the target species, in order to find at what levels of concentration of bait attractants fish are likely to respond too (Løkkeborg *et al.*. 2010).

However, the real challenge to improve pot catch efficiency is to increase entrance rates. Cod and saithe showed a limited search pattern whilst inspecting pots, tending to search the downstream walls. In floated collapsible designs (C35 and C95 pots, where the entrance orients to the current), this behaviour is optimal as this search pattern means that searches were directed towards the pot entrance. However, in pots which don't orient to the current (CB, RC and RNC pots), this search pattern may result in fish searching an area of the pot where an entrance isn't situated. This effect may be exacerbated by the rectangular shape of the pots used in this study, which may discourage fish from searching around the corners of the pot (*personal observation*). Circular shaped pots may encourage a less restricted search pattern and help to increase ingress. A circular pot design has been tested previously in Norway and was found to be, in the right conditions, comparable in catch efficiency to rectangular designs (Furevik & Løkkeborg, 1994). Controlled field experiments using *in situ* cameras are required in order to establish to what extent this gear parameter influences

behaviour. Similar efforts are needed in order to investigate how entrance design influences ingress behaviour, as although different entrance designs have been tested in fishing trials in Norway (Bjordal & Furevik, 1988), no behavioural observations have been undertaken. Technical measures such as green light (Bryhn *et al.*, 2014), moving bait (as cod prefer moving prey to stationary prey, Steingrund & Fernö, 1997) or other forms of fish stimulation may also help to increase fish ingress, and should be the subject of systematic investigation.

For cod, a high escape rate contributed to the low catch efficiency. My results suggest that a secondary chamber which is entered through the pot wall rather than the pot roof may help to retain more fish in the pot. Therefore, I suggest a prototype pot be produced conforming to these specifications and fishing trials conducted. It is important to collect video footage during these trials in order to detail how fish respond to the new design. At the time of writing, a prototype pot following these specifications is being produced by an industry partner (EscaNo).

Of further interest is to try to understand the factors which govern the entrance rate of fish into the pots, This said, there is a paucity of literature to explain such factors. My results indicated that fish size, species and the presence of captured fish in the pot are important factors, but the variance explained by the GLM was low, suggesting that there are other explanatory variables. Future studies should focus on highlighting these variables. Hunger levels may be one such factor (see Section 4.3). As fish are retained alive in pots, the particular behaviours of the fish in the pot (if they are feeding on the bait or searching for an exit, for example) also have the potential to further explain the choice of another fish to enter.

By using *in situ* video footage to monitor fish, I was able to offer a behavioural explanation for the observed differences in capture efficiency between the pots. It seems that this approach has been historically under-utilized in previous fish pot research, possibly due to the time consuming nature of video analysis and the costs associated with using cameras. However, in light of recent advances in video technology, it is now time to employ *in situ* observations on a more regular basis. In this way, researchers will be able to relate observations of catch efficiency to isolated gear parameters (as suggested by Furevik & Løkkeborg, 1994) or particular behaviour patterns, as has been shown in this study. The ethogram developed in this thesis can also be employed in future studies of fish behaviour in response to pots. Further comparative behaviour studies of different pot designs would also help to optimise pot design further and could help to contribute to the establishment of a commercial pot fishery in Norway. This is of importance because, as my findings show, behavioural mechanisms are key to the capture process of fish pots.

4.8 Concluding remarks

The results of this study support previous observations that fish pots are able to attract high numbers of fish but few enter (eg. Rose *et al.*, 2005; Thomsen *et al.*, 2010). Further to this, I demonstrated that a high rate of escape was also an important factor limiting cod catches. These observations have practical value in that they will help to direct research efforts attempting to improve catch efficiency, namely; efforts should be made to increase the entrance rate and decrease the escape rate. My findings indicate that the factors that influence the entrance rate are complex and confirmed for the first time the supposition of previous authors (Valdemarsen *et al.*, 1977; Königson *et al.*, 2015) that social attraction plays a role in gadoid pot fishing. My findings also supported the previous qualitative observations of species specific responses to pots (Furevik, 1994), but also added new knowledge by providing a quantitative description of these differences as well as the first detailed description of behavioural sequences and time budgets. An understanding of these differences helps to explain differences in capture efficiency between the species. With regards to the effect of pot design on capture efficiency, comparative fishing trails have been conducted previously with different pot designs and differences in capture efficiency have been demonstrated (Furevik & Løkkeborg, 1994). However, by using *in situ* video footage I was able to offer a behavioural explanation for the observed differences in catch efficiency between the pot designs used in this study. With regards to the approach and search behaviour towards pots, my findings indicate that pots which have entrances on the downstream walls are optimal in order to maximise the chance of capture. These conditions are met in floating pot designs The finding that fish tend to search the pot walls after capture rather than the roof or floor has an important practical implication. If a pot can be successfully designed to take advantage of this behaviour, real gains in capture efficiency may be made.

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6. APPENDICES

Schematic of bottom-set two chambered collapsible pot (pot type CB).
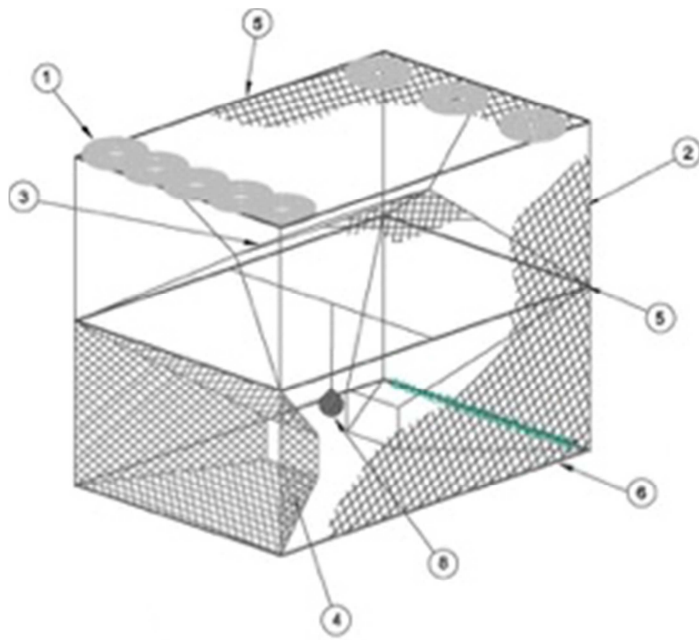
1. Floats: Rosendal 205/46 extra
2. Net: No. 14 EK 28.5mm 1/2 msk black
3. Inner Entrance
4. Net entrance: Monofile 25 mm 1/2 msk black
5. Aluminium frame 10 mm
6. Steel frame 14 mm
7. Zipper
8. Bait bag
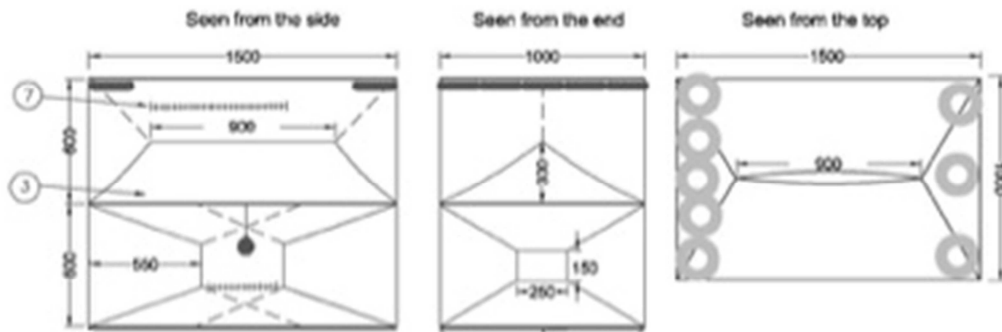
Schematic of the two floated two-chambered collapsible pots (pot types C35 and C95). Height above the seabed was adjusted to either 35cm or 95cm by altering the length of the adjustable bridle (9).
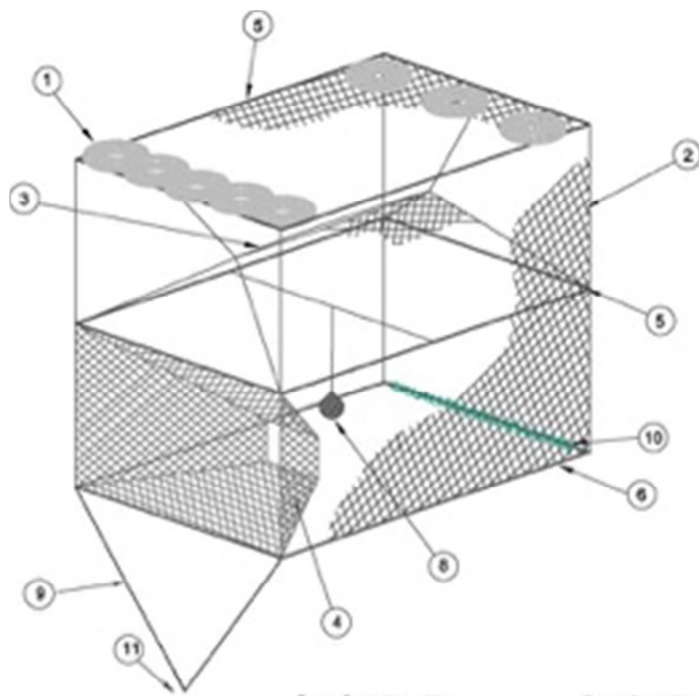
1. Floats: Rosendal 205/46 extra
2. Net: No. 14 EK 28.5mm 1/2 msk black
3. Inner Entrance
4. Net entrance: Monofile 25 mm 1/2 msk black
5. Aluminium frame 10 mm
6. Glass-fibre frame 14 mm
7. Zipper
8. Bait bag
9. Adjustable bridle (Length: 350 or 950mm)
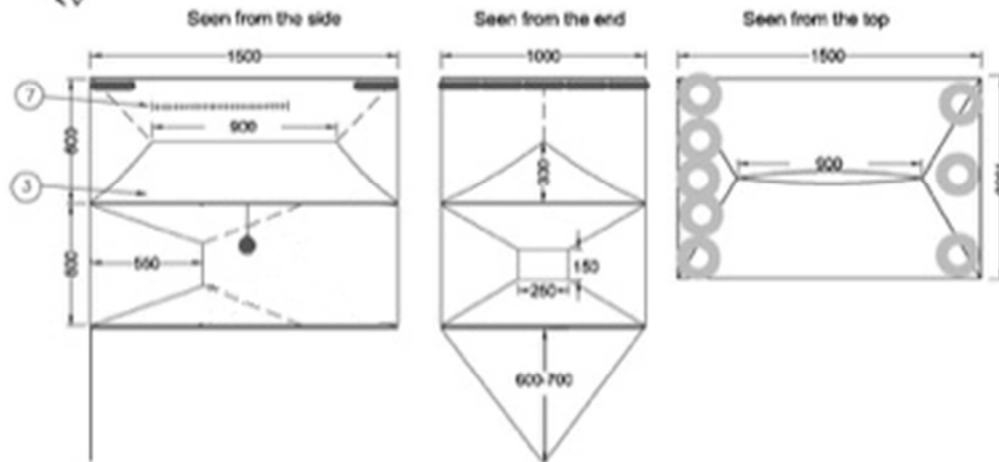
Appendix 3

Schematic of the rigid framed pot (pot type RC).
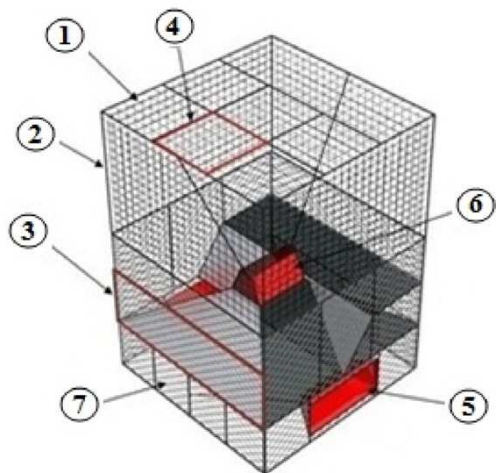
1. Net: No. 14 EK 28.5 mm black
2. Aluminium frame
3. Opening to remove fish
4. Upper opening
5. Entrance netting
6. Inner entrance
7. Net (see 1)
8. Aluminium frame

Side view   End view   Plan view
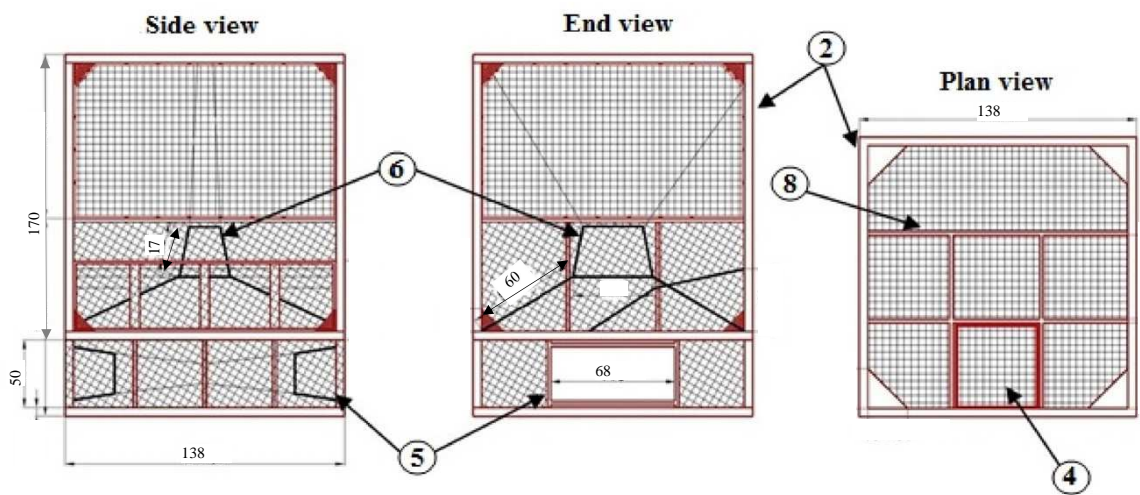
All dimensions in cm

Appendix 4

Schematic of the rigid framed pot without lower chamber (pot type RNC).
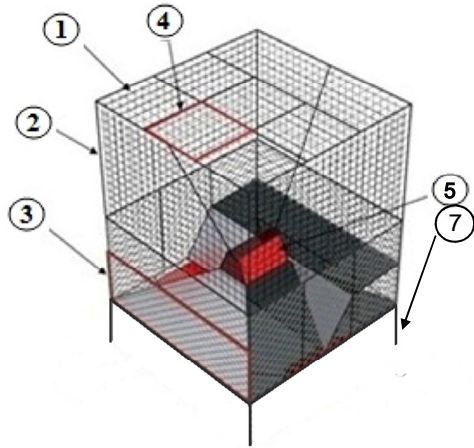
1. Net: No. 14 EK 28.5 mm black
2. Aluminium frame
3. Opening to remove fish
4. Upper opening
5. Inner entrance
6. Aluminium frame
7. Struts

Side view   End view   Plan view
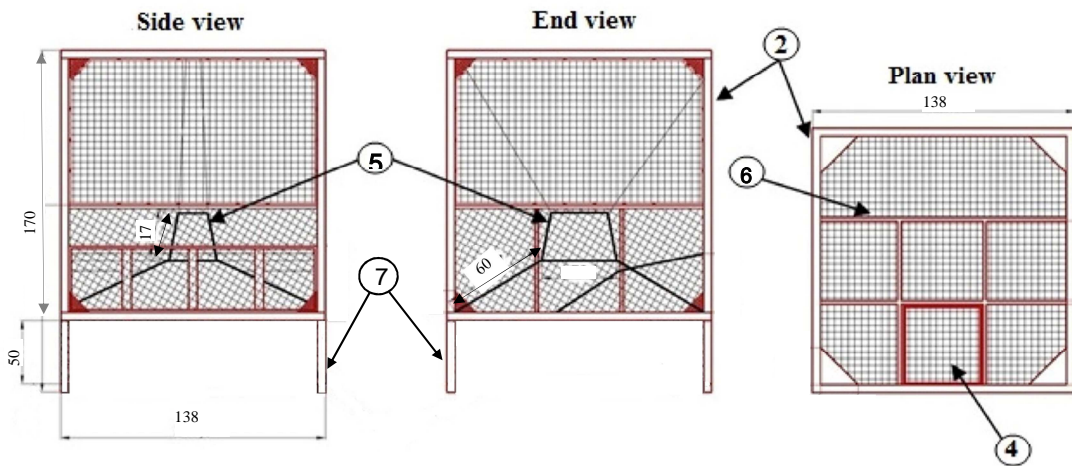
All dimensions in cm

Appendix 5

Comparing cod and saithe encounter rate

glm(cbind(Inspect,Present)~Species,quasibinomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-0.438	0.077	-5.674	<0.001
SpeciesSaithe	-1.907	0.254	-7.499	<0.001

Null deviance = 552.95 on 59 d.f; residual deviance = 216.94 on 58 d.f

Appendix 6

Comparing cod and saithe entrance rate

glm(cbind(Capture,Inspect)~Species,binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-1.819	0.079	-22.774	<0.001
SpeciesSaithe	0.197	0.293	0.671	0.502

AIC = 208.69; Null deviance = 107.58 on 50 d.f; residual deviance = 107.15 on 49 d.f

Appendix 7

Comparing cod and saithe escape rate

glm(cbind(Escape,Capture)~Species,binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-0.537	0.138	-3.886	<0.001
SpeciesSaithe	-0.784	0.579	-1.354	0.17

AIC = 72.285; Null deviance = 27.194 on 30 d.f; residual deviance = 25.125 on 29 d.f

Appendix 8

Comparing cod and saithe upper chamber entrance rate

glm(cbind(Capture,Secondary)~Species,binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-1.864	0.229	-8.139	<0.001
SpeciesSaithe	1.529	0.568	2.689	0.007

AIC = 72.285; Null deviance = 27.194 on 30 d.f; residual deviance = 25.125 on 29 d.f

Appendix 9

Cod encounter rate for CB and C35 pots

glm(cbind(Inspect,Present)~Pot_type,binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-0.721	0.097	-7.415	<0.001
Pot_typeCB	0.274	0.109	2.501	0.012

AIC = 104.11; Null deviance = 22.554 on 18 d.f; residual deviance = 16.190 on 17 d.f

Appendix 10

Saithe encounter rate for CB and C35 pots

glm(cbind(Inspect,Present)~Pot_type,quasibinomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-1.512	0.619	-2.441	0.025
Pot_typeCB	-0.972	0.778	-1.250	0.227

Null deviance = 150.35 on 19 d.f; residual deviance = 137.51 on 18 d.f

Appendix 11

Cod encounter rate for rigid pots

glm(cbind(Inspect,Present)~Pot_type,binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-0.200	0.107	-1.865	0.062
Pot_typeRNC	-0.548	0.231	-2.370	0.017

AIC = 50.256; Null deviance = 10.935 on 10 d.f; residual deviance = 5.127 on 9 d.f

Appendix 12

Cod entrance rate for CB and C35 pots

glm(cbind(Capture,Inspect)~Pot_type,quasibinomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-1.724	0.342	-5.034	<0.001
Pot_typeCB	-0.178	0.388	-0.460	0.651

AIC = 100.43; Null deviance = 44.740 on 18 d.f; residual deviance = 44.164 on 17 d.f

Appendix 13

Saithe entrance rate for CB and C35 pots

glm(cbind(Capture,Inspect)~Pot_type,quasibinomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-1.722	0.485	-3.548	<0.001
Pot_typeCB	-0.429	0.677	-0.633	0.526

AIC = 38.832; Null deviance = 20.431 on 14 d.f; residual deviance = 20.032 on 13 d.f

Appendix 14

Cod escape rate for CB and C35 pots

glm(cbind(Escape,Capture)~Pot_type,binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-0.934	0.355	-2.626	0.008
Pot_typeCB	0.474	0.392	1.211	0.226

AIC = 50.883; Null deviance = 17.771 on 15 d.f; residual deviance = 16.245 on 14 d.f

Appendix 15

Saithe escape rate for CB and C35 pots

glm(cbind(Escape,Capture)~Pot_type,binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-1.609	1.095	-1.469	0.142
Pot_typeCB	0.693	1.378	0.503	0.615

AIC = 12.813 Null deviance = 5.727 on 8 d.f; residual deviance = 5.464 on 7 d.f

Appendix 16

Cod upper chamber entrance rate for CB and C35 pots

glm(cbind(Secondary,Capture)~Pot_type,binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-1.540	0.449	-3.424	<0.001
Pot_typeCB	-0.240	0.524	-0.459	0.646

AIC = 45.864; Null deviance = 17.825 on 15 d.f; residual deviance = 17.620 on 14 d.f

Appendix 17

Saithe upper chamber entrance rate for CB and C35 pots

glm(cbind(Secondary,Capture)~Pot_type,binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-0.916	0.836	-1.095	0.273
Pot_typeCB	0.405	1.111	0.365	0.715

AIC = 16.029; Null deviance = 5.232 on 8 d.f; residual deviance = 5.097 on 7 d.f

COD C35
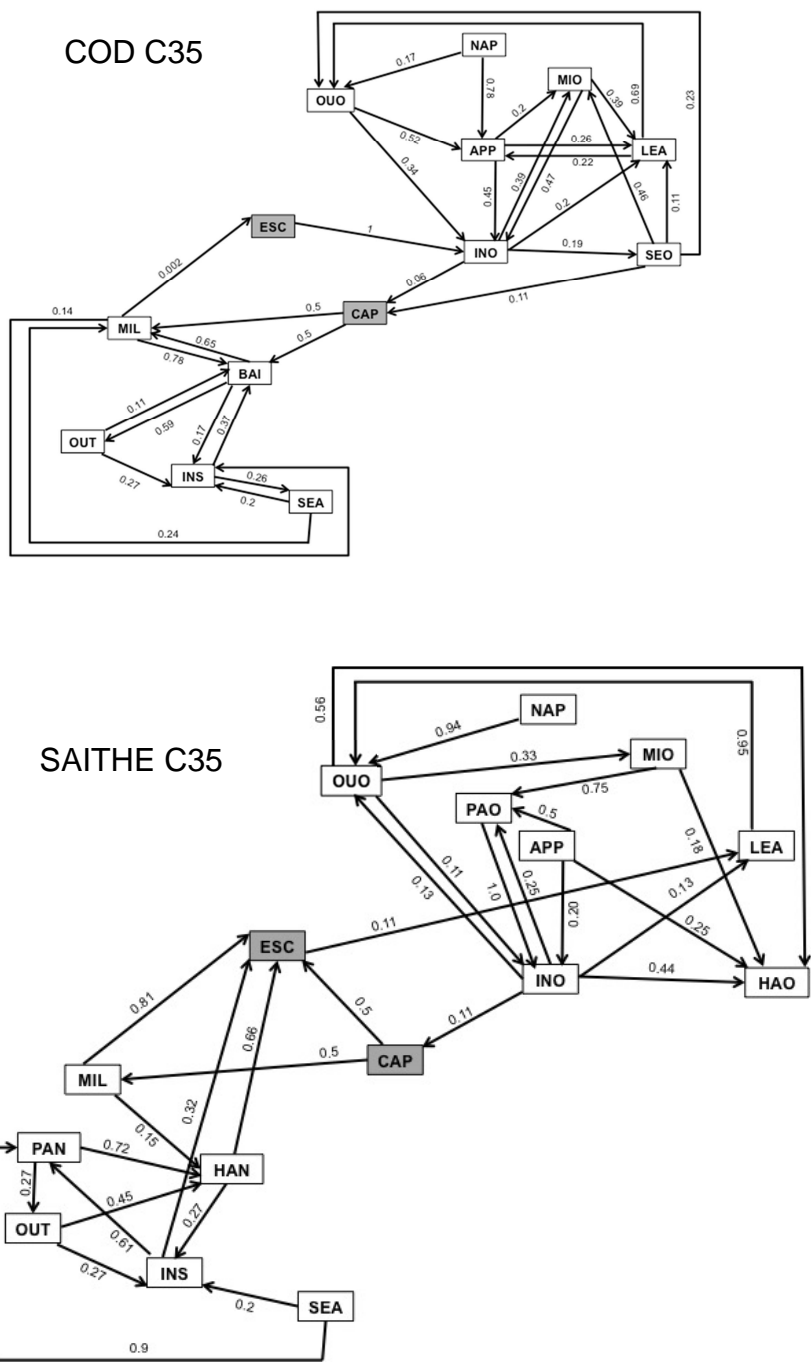
SAITHE C35

Appendix 18: Kinematic diagrams of behavioural sequences of cod and saithe for the collapsible floated 35cm pot (C35 pot). Boxes represent behavioural units. Behavioural unit abbreviations; NAP: no approach; APP: approach; OUO: out of sight (outside); LEA: leave; INO: inspect (outside); SEO: search (outside); BAO: bait (outside); HAO: hang (outside); PAO: panic (outside); CAP: capture; ESC: escape; MIL: mill (inside); BAI: bait (inside); HAN: hang (inside); INS: inspect (inside); SEA: search (inside); OUT: out of sight (inside); PAN: panic (inside) (see Table 2 for behavioural unit definitions). All sequences start with NAP and end with the fish being classified as OUT or OUO. Infrequent transitions (p < 0.1) are not included, except for those leading to captures (CAP) or escapes (ESC) (highlighted in grey). Transitions to UPP are not included. Sequences are based on transition matrices (Appendix 22) and include only those transitions that were over-represented (see Section 2.5.4).
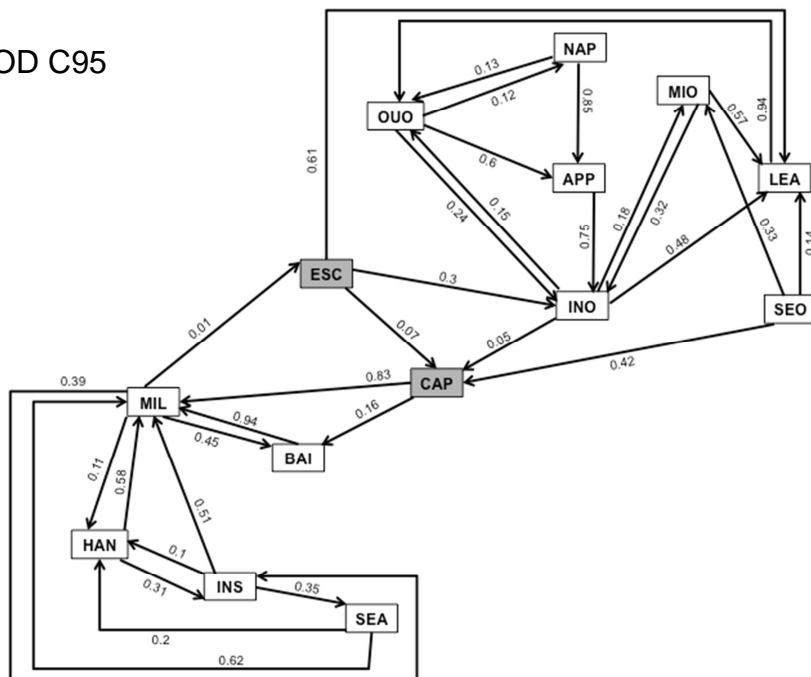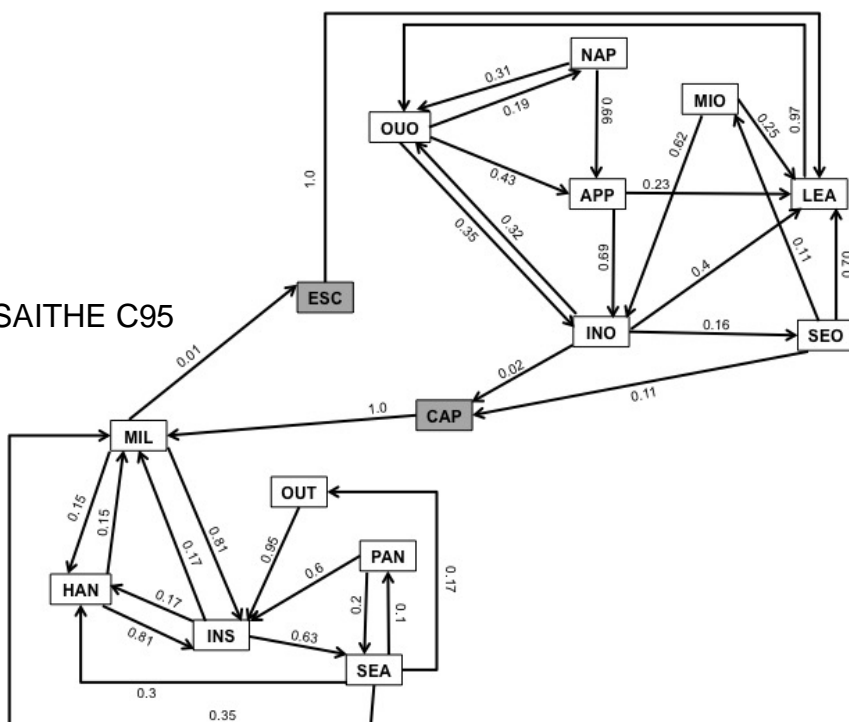
Appendix 19: Kinematic diagrams of behavioural sequences of cod and saithe for the collapsible floated 95cm pot (C95 pot). Boxes represent behavioural units. Behavioural unit abbreviations; NAP: no approach; APP: approach; OUO: out of sight (outside); LEA: leave; INO: inspect (outside); SEO: search (outside); BAO: bait (outside); CAP: capture; ESC: escape; MIL: mill (inside); BAI: bait (inside); HAN: hang (inside); INS: inspect (inside); SEA: search (inside); OUT: out of sight (inside); PAN: panic (inside) (see Table 2 for behavioural unit definitions). All sequences start with NAP and end with the fish being classified as OUT or OUO. Infrequent transitions ($p < 0.1$) are not included, except for those leading to captures (CAP) or escapes (ESC) (highlighted in grey). Transitions to UPP are not included. Sequences are based on transition matrices (Appendix 22) and include only those transitions that were over-represented (see Section 2.5.4).

Appendix 20: Kinematic diagrams of behavioural sequences of cod and saithe for the rigid pot with a bottom chamber (RC pot). Boxes represent behavioural units. Behavioural unit abbreviations; NAP: no approach; APP: approach; OUO: out of sight (outside); LEA: leave; INO: inspect (outside); SEO: search (outside); BAO: bait (outside); CAP: capture; ESC: escape; MIL: mill (inside); BAI: bait (inside); HAN: hang (inside); INS: inspect (inside); SEA: search (inside); OUT: out of sight (inside); PAN: panic (inside) (see Table 2 for behavioural unit definitions). All sequences start with NAP and end with the fish being classified as OUT or OUO. Infrequent transitions (p < 0.1) are not included, except for those leading to captures (CAP) or escapes (ESC) (highlighted in grey). Transitions to UPP are not included. Sequences are based on transition matrices (Appendix 22) and include only those transitions that were over-represented (see Section 2.5.4).

COD RNC
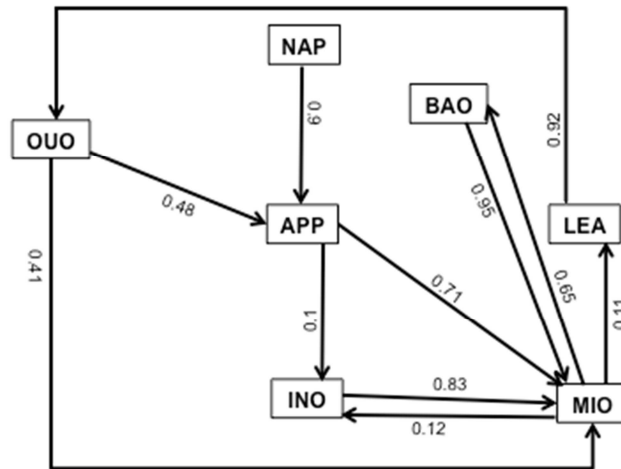
Appendix 21: Kinematic diagram of behavioural sequences of cod for the rigid pot with one chamber (RNC pot). Boxes represent behavioural units. Behavioural unit abbreviations; NAP: no approach; APP: approach; OUO: out of sight (outside); LEA: leave; MIO: mill (outside) INO: inspect (outside); SEO: search (outside) (see Table 2 for behavioural unit definitions). All sequences start with NAP and end with the fish being classified as OUT or OUO). Infrequent transitions ($p < 0.1$) are not included, except for those leading to captures (CAP) or escapes (ESC) (highlighted in grey). Transitions to UPP are not included. Sequences are based on transition matrices (Appendix 22) and include only those transitions that were over-represented (see Section 2.5.4).

		Inside pot states							Events					Outside pot states											
	CODE	BAI	HAN	INS	MIL	OUT	PAN	TER	CAP	ESC	UPP	SEA	SEO	APP	LEA	NAP	BAO	HAO	INO	MIO	OTO	OUO	PAO	TEO	**Total**
Inside pot states	BAI	-	0.05 27 (14.9)	0.177 95 (56.5)	0.654 352 (111.2)	0.117 63 (28.9)	0.002 1 (0.6)	0 (0)	-	0 (0.3)	0 (0.6)	0 (17.9)	-	-	-	-	-	-	-	-	-	-	-	-	538
	HAN	0.441 26 (14.9)	-	0.39 23 (6.2)	0.119 7 (12.2)	0.051 3 (3.2)	0 (0.1)	0 (0)	-	0 (0.1)	0 (0.1)	0 (2)	-	-	-	-	-	-	-	-	-	-	-	-	59
	INS	0.379 85 (56.5)	0.07 17 (6.2)	-	0.192 43 (46.3)	0.089 20 (12.1)	0 (0.3)	0 (0)	-	0 (0.2)	0 (0.3)	0.263 59 (7.5)	-	-	-	-	-	-	-	-	-	-	-	-	224
	MIL	0.789 345 (110.1)	0.016 7 (12.1)	0.142 62 (45.9)	-	0.027 12 (23.5)	0 (0.5)	0 (0)	-	0.002 1 (0.3)	0 (0.5)	0.023 10 (14.5)	-	-	-	-	-	-	-	-	-	-	-	-	437
	OUT	0.591 65 (27.8)	0.018 2 (3.1)	0.273 30 (11.6)	0.118 13 (22.8)	-	0 (0.2)	0 (0)	-	0 (0.1)	0 (0.2)	0 (3.7)	-	-	-	-	-	-	-	-	-	-	-	-	110
	PAN	0 (0.6)	0 (0.1)	0 (0.3)	0 (0.5)	0 (0.2)	-	0 (0)	-	0 (0.1)	0 (0.1)	1 2 (0.1)	-	-	-	-	-	-	-	-	-	-	-	-	2
	TER	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
Events	CAP	0.5 6 (3.1)	0 (0.4)	0 (1.3)	0.5 6 (2.5)	0 (0.7)	0 (0.1)	0 (0)	-	0 (0.1)	0 (0.1)	0 (0.4)	-	-	-	-	-	-	-	-	-	-	-	-	12
	ESC	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	-	0 (0.1)	-	0 (0)	0 (0.1)	1 1 (0.1)	0 (0.1)	0 (0.1)	0 (0.1)	0 (0)	0 (0)	1
	UPP	-	0 (0.1)	0.5 1 (0.3)	0.5 1 (0.5)	0 (0.2)	0 (0.1)	0 (0)	-	-	-	0 (0.1)	-	-	-	-	-	-	-	-	-	-	-	-	2
	SEA	0.186 13 (17.7)	0.086 6 (2)	0.2 14 (7.4)	0.243 17 (14.5)	0.054 4 (3.8)	0.014 1 (0.1)	0 (0)	-	0 (0.1)	0.029 2 (0.1)	-	-	-	-	-	-	-	-	-	-	-	-	-	70
	SEO	-	-	-	-	-	-	-	0.115 3 (0.2)	-	-	-	-	-	0.115 3 (1.5)	-	0 (0)	0 (0.1)	0.077 2 (1.7)	0.462 12 (1.3)	0 (0.2)	0.231 6 (1.7)	0 (0)	0 (0)	26
Outside pot states	APP	-	-	-	-	-	-	-	0 (0.8)	-	-	-	0 (1.7)	-	0.268 37 (7.6)	0 (0.6)	0 (0)	0 (0.2)	0.457 63 (8.8)	0.203 28 (6.6)	0.036 5 (0.6)	0.036 5 (8.7)	0 (0)	0 (0)	138
	LEA	-	-	-	-	-	-	-	-	-	-	-	-	0.224 26 (7.6)	-	0.026 3 (0.5)	-	0.009 1 (0.2)	0 (7.4)	0.043 5 (5.5)	0 (0.5)	0.698 81 (7.4)	0 (0)	0 (0)	116
	NAP	-	-	-	-	-	-	-	-	-	-	-	-	0.783 83 (6.9)	0.009 1 (5.8)	-	-	0 (0.2)	0 (6.8)	0 (5)	0 (0.5)	0.179 19 (6.7)	0 (0)	0 (0)	103
	BAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
	HAO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	0.333 1 (0.2)	0 (0.2)	0 (0.1)	0 (0)	-	0 (0.2)	0 (0.2)	0.333 1 (0.1)	0 (0.2)	0 (0)	0 (0)	2
	INO	-	-	-	-	-	-	-	0.066 9 (0.8)	-	-	-	0.191 26 (1.7)	-	0.206 28 (7.5)	-	0 (0)	0 (0.2)	-	0.397 54 (6.5)	0.022 3 (0.6)	0.118 16 (8.6)	0 (0)	0 (0)	136
	MIO	-	-	-	-	-	-	-	0 (0.6)	-	-	-	0 (1.3)	0.029 3 (6.9)	0.39 41 (5.8)	0.019 2 (0.4)	0 (0)	0.01 1 (0.2)	0.476 50 (6.7)	-	0 (0.5)	0.076 8 (6.7)	0 (0)	0 (0)	105
	OTO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.2)	0 (0.6)	0.556 5 (0.5)	0 (0.1)	0 (0)	0.111 1 (0.1)	0.333 3 (0.6)	0 (0.5)	-	0 (0.6)	0 (0)	0 (0)	9
	OUO	-	-	-	-	-	-	-	0 (0.3)	-	-	-	0 (0.7)	0.520 26 (3.3)	0.04 2 (2.8)	0.06 3 (0.2)	0 (0)	0 (0.1)	0.340 17 (3.2)	0.04 2 (2.4)	0 (0.3)	-	0 (0)	0 (0)	50
	PAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0
	TEO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0
	Total	540	59	225	439	115	2	0	12	1	2	71	26	139	117	8	0	3	136	101	9	130	0	0	2135

Cod behavioural transition matrix for the C35 pot type. The preceding behaviour is given to the left of the square and the subsequent behaviour above. Transitional probabilities are displayed in the upper half of the squares; observed and expected values (in parenthesis) of transitions are shown in the lower half. Transitions which were over-represented (see Section 2.5.3) are highlighted in grey.

	CODE	Inside pot states							Events					Outside pot states											Total
		BAI	HAN	INS	MIL	OUT	PAN	TER	CAP	ESC	UPP	SEA	SEO	APP	LEA	NAP	BAO	HAO	INO	MIO	OTO	OUO	PAO	TEO	Total
Inside pot states	BAI	-	0.029 17 (37.9)	0.013 8 (87.4)	0.941 561 (173.5)	0.017 10 (4.8)	0 (0)	0 (0.2)	-	0 (1.9)	0 (0)	0 (33.6)	-	-	-	-	-	-	-	-	-	-	-	-	596
	HAN	0.073 19 (38)	-	0.313 82 (38.5)	0.584 153 (76.3)	0.011 3 (2.1)	0 (0)	0 (0.1)	-	0 (0.9)	0 (0)	0.019 5 (14.8)	-	-	-	-	-	-	-	-	-	-	-	-	262
	INS	0.02 12 (87)	0.107 64 (38.1)	-	0.515 309 (174.7)	0.005 3 (4.8)	0 (0)	0 (0.2)	-	0 (1.9)	0 (0)	0.353 212 (33.8)		-	-	-	-	-	-	-	-	-	-	-	600
	MIL	0.458 548 (173.5)	0.112 134 (76)	0.396 474 (175.5)	-	0.011 13 (9.6)	0 (0)	0.001 1 (0.3)	-	0.011 13 (3.8)	0 (0)	0.012 14 (67.3)	-	-	-	-	-	-	-	-	-	-	-	-	1197
	OUT	0.303 10 (4.8)	0.03 1 (2.1)	0.242 8 (4.9)	0.394 13 (9.7)	-	0 (0)	0 (0.1)	-	0 (0.2)	0 (0)	0.03 1 (1.9)	-	-	-	-	-	-	-	-	-	-	-	-	33
	PAN	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	TER	0 (0.2)	0 (0.1)	0 (0.2)	1 1 (0.3)	0 (0.1)	0 (0)	-	-	0 (0.1)	0 (0)	0 (0.1)	-	-	-	-	-	-	-	-	-	-	-	-	1
Events	CAP	0.167 4 (3.5)	0 (1.6)	0 (3.6)	0.833 20 (7)	0 (0.2)	0 (0)	0 (0.1)	-	0 (0.1)	0 (0)	0 (1.4)	-	-	-	-	-	-	-	-	-	-	-	-	24
	ESC	-	-	-	-	-	-	-	0.077 1 (0.1)	-	-	-	0 (0.1)	-	0.615 8 (0.7)	-	0 (0)	0 (0.1)	0.308 4 (0.9)	0 (0.3)	0 (0.1)	0 (1)	0 (0)	0 (0)	13
	UPP	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	-	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	SEA	0.022 5 (33.2)	0.201 46 (14.6)	0.135 31 (33.6)	0.624 143 (66.7)	0.017 4 (1.9)	0 (0)	0 (0.1)	-	0 (0.8)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	229
	SEO	-	-	-	-	-	-	-	0.429 9 (0.2)	-	-	-	-	-	0.143 3 (1.2)	-	0 (0)	0 (0.1)	0 (1.4)	0.333 7 (0.5)	0 (0.1)	0.095 2 (1.5)	0 (0)	0 (0)	21
Outside pot states	APP	-	-	-	-	-	-	-	0 (1.5)	-	-	-	0 (1.3)	-	0.096 24 (13.3)	0 (1.3)	0 (0)	0.016 4 (0.5)	0.759 189 (15.6)	0.092 23 (5)	0.016 4 (0.8)	0.02 5 (17.4)	0 (0)	0 (0)	249
	LEA	-	-	-	-	-	-	-	-	-	-	-	-	0.032 7 (13.3)	-	0.014 3 (1.1)	-	0.005 1 (0.5)	0 (13.8)	0.005 1 (4.4)	0 (0.7)	0.945 208 (15.4)	0 (0)	0 (0)	220
	NAP	-	-	-	-	-	-	-	-	-	-	-	-	0.854 158 (11.2)	0.011 2 (9.9)	-	-	0 (0.4)	0 (11.6)	0 (3.7)	0 (0.6)	0.135 25 (13)	0 (0)	0 (0)	185
	BAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
	HAO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	0.125 1 (0.5)	0.25 2 (0.5)	0 (0.1)	0 (0)	-	0 (0.6)	0 (0.2)	0 (0.1)	0.25 2 (0.6)	0 (0)	0 (0)	5
	INO	-	-	-	-	-	-	-	0.054 14 (1.6)	-	-	-	0.081 21 (1.4)	-	0.481 125 (13.9)	-	0 (0)	0.004 1 (0.6)	-	0.188 49 (5.2)	0.035 9 (0.9)	0.158 41 (18.2)	0 (0)	0 (0)	260
	MIO	-	-	-	-	-	-	-	0 (0.5)	-	-	-	0 (0.5)	0.012 1 (5)	0.578 48 (4.5)	0 (0.5)	0 (0)	0.024 2 (0.2)	0.325 27 (5.2)	-	0 (0.3)	0.06 5 (5.8)	0 (0)	0 (0)	83
	OTO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	0 (0.8)	0.538 7 (0.7)	0 (0.1)	0 (0)	0 (0.1)	0.462 6 (0.9)	0 (0.3)	-	0 (1)	0 (0)	0 (0)	13
	OUO	-	-	-	-	-	-	-	0 (0.8)	-	-	-	0 (0.7)	0.609 81 (8)	0.008 1 (7.1)	0.128 17 (0.7)	0 (0)	0 (0.3)	0.241 32 (8.4)	0.015 2 (2.7)	0 (0.5)	-	0 (0)	0 (0)	133
	PAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0
	TEO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0
	Total	248	598	262	605	220	1201	20	33	0	1	24	13	0	232	21	0	8	258	82	13	288	0	0	4127

Cod behavioural transition matrix for the C95 pot type. The preceding behaviour is given to the left of the square and the subsequent behaviour above. Transitional probabilities are displayed in the upper half of the squares; observed and expected values (in parenthesis) of transitions are shown in the lower half. Transitions which were over-represented (see Section 2.5.3) are highlighted in grey.

Cod behavioural transition matrix table:

	CODE	BAI	HAN	INS	MIL	OUT	PAN	TER	CAP	ESC	UPP	SEA	SEO	APP	LEA	NAP	BAO	HAO	INO	MIO	OTO	OUO	PAO	TEO	Total
				Inside pot states							Events						Outside pot states								
Inside pot states	BAI	-	0.044 13 (6.2)	0.013 4 (44.1)	0.862 256 (68.4)	0.034 10 (42.7)	0.007 2 (0.3)	0 (0)	-	0.037 11 (8.5)	0 (0.6)	0.003 1 (11.8)	-	-	-	-	-	-	-	-	-	-	-	-	297
	HAN	0.197 14 (6.1)	-	0.155 11 (10.6)	0.563 40 (16.4)	0.085 6 (10.3)	0 (0.1)	0 (0)	-	0 (2.1)	0 (0.2)	0 (2.9)	-	-	-	-	-	-	-	-	-	-	-	-	71
	INS	0.027 14 (43.8)	0.016 8 (10.6)	-	0.324 166 (118.1)	0.392 201 (73.8)	0 (0.5)	0 (0)	-	0.012 6 (14.6)	0.004 2 (1.1)	0.226 116 (20.4)	-	-	-	-	-	-	-	-	-	-	-	-	513
	MIL	0.302 241 (68.1)	0.055 44 (16.6)	0.265 212 (118.5)	-	0.267 213 (114.9)	0.001 1 (0.7)	0 (0)	-	0.089 71 (22.7)	0.004 3 (1.7)	0.018 14 (31.7)	-	-	-	-	-	-	-	-	-	-	-	-	799
	OUT	0.028 14 (42.3)	0.012 6 (10.3)	0.53 263 (73.6)	0.413 205 (114.2)	-	0 (0.5)	0 (0)	-	0 (14.1)	0.002 1 (1)	0.014 7 (19.7)	-	-	-	-	-	-	-	-	-	-	-	-	496
	PAN	0 (0.3)	0 (0.1)	0 (0.5)	0.333 1 (0.7)	0.333 1 (0.5)	-	0 (0)	-	0.333 1 (0.1)	0 (0.1)	0 (0.2)	-	-	-	-	-	-	-	-	-	-	-	-	3
	TER	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
Events	CAP	0.093 10 (9.2)	0 (2.3)	0.028 3 (15.9)	0.832 89 (24.7)	0 (15.4)	0 (0.1)	0 (0)	-	0.047 5 (3.1)	0 (0.3)	0 (4.3)	-	-	-	-	-	-	-	-	-	-	-	-	107
	ESC	-	-	-	-	-	-	-	0.03 3 (3.1)				0 (2.1)	-	0.111 11 (4.1)	-	0 (1)	0 (0.2)	0.859 85 (9.1)	0 (0.2)	0 (0.1)	0 (5.7)	0 (0.1)	0 (0)	99
	UPP	-	0 (0.2)	0 (1.1)	1 7 (1.7)	0 (1.1)	0 (0.1)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
	SEA	0.029 4 (11.8)	0.007 1 (2.9)	0.145 20 (20.5)	0.268 37 (31.8)	0.507 70 (19.9)	0 (0.2)	0 (0)	-	0.036 5 (4)	0.007 1 (0.3)	-	-	-	-	-	-	-	-	-	-	-	-	-	138
	SEO	-	-	-	-	-	-	-	0.4 28 (2.2)	-	-	-	-	-	0.2 14 (2.9)	-	0.071 5 (0.7)	0.029 2 (0.2)	0.086 6 (6.4)	0.014 1 (0.1)	0 (0.1)	0.186 13 (4.1)	0.014 1 (0.1)	0 (0)	70
Outside pot states	APP	-	-	-	-	-	-	-	0 (4.9)	-	-	-	0 (3.3)	-	0.081 13 (6.6)	0 (0.4)	0 (1.6)	0.006 1 (0.3)	0.876 141 (14.7)	0.006 1 (0.2)	0.006 1 (0.1)	0.025 4 (9.3)	0 (0.1)	0 (0)	161
	LEA	-	-	-	-	-	-	-	-	-	-	-	-	0.099 14 (6.6)	-	0.014 2 (0.4)	-	0 (0.3)	0.007 1 (13)	0 (0.2)	0 (0.1)	0.88 125 (8.2)	0 (0.1)	0 (0)	142
	NAP	-	-	-	-	-	-	-	-	-	-	-	-	0.876 113 (6)	0 (5.3)	-	-	0 (0.2)	0.047 6 (11.8)	0 (0.2)	0 (0.1)	0.07 9 (7.5)	0 (0.1)	0 (0)	128
	BAO	-	-	-	-	-	-	-	0.03 1 (1.1)	-	-	-	0 (0.7)	-	0.03 1 (1.4)	-	-	0 (0.1)	0.909 30 (3.1)	0 (0.1)	0.03 1 (0.1)	0 (1.9)	0 (0.1)	0 (0)	33
	HAO	-	-	-	-	-	-	-	0 (0.2)	-	-	-	0 (0.2)	0 (0.3)	0 (0.3)	0 (0.1)	0 (0.1)	-	0.8 4 (0.8)	0 (0.1)	0 (0.1)	0.2 1 (0.3)	0 (0.1)	0 (0)	5
	INO	-	-	-	-	-	-	-	0.231 74 (9.8)	-	-	-	0.222 71 (6.6)	-	0.313 100 (13.1)	-	0.084 27 (3.1)	0.006 2 (0.5)	-	0 (0.4)	0 (0.2)	0.144 46 (18.4)	0 (0.1)	0 (0)	320
	MIO	-	-	-	-	-	-	-	0 (0.2)	-	-	-	0 (0.2)	0.6 3 (0.3)	0.2 1 (0.3)	0 (0.1)	0 (0.1)	0 (0.1)	0 (0.5)	-	0 (0.1)	0.2 1 (0.3)	0 (0.1)	0 (0)	5
	OTO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	0.5 1 (0.1)	0 (0.1)	0 (0.1)	0.5 1 (0.1)	0 (0.1)	0 (0.2)	0 (0.1)	-	0 (0.2)	0 (0.1)	0 (0)	2
	OUO	-	-	-	-	-	-	-	0 (2.7)	-	-	-	0 (1.8)	0.341 30 (4.1)	0.023 2 (3.6)	0.068 6 (0.3)	0 (0.9)	0 (0.2)	0.545 48 (8.1)	0.023 2 (0.2)	0 (0.1)	-	0 (0.1)	0 (0)	88
	PAO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	-	0 (0.1)	0 (0.1)	0 (0.1)	0 (0.1)	0 (0.1)	0 (0.1)	0 (0.1)	1 1 (0.1)	-	0 (0)	1
	TEO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0
	Total	297	72	513	801	501	3	8	106	99	7	138	71	161	142	8	33	5	321	4	2	200	1	0	3493

Cod behavioural transition matrix for the RC pot type. The preceding behaviour is given to the left of the square and the subsequent behaviour above. Transitional probabilities are displayed in the upper half of the squares; observed and expected values (in parenthesis) of transitions are shown in the lower half. Transitions which were over-represented (see Section 2.5.3) are highlighted in grey.

Row group labels (far left, top to bottom): **Inside pot states**, **Events**, **Outside pot states**.

CODE	BAI	HAN	INS	MIL	OUT	PAN	TER	CAP	ESC	UPP	SEA	SEO	APP	LEA	NAP	BAO	HAO	INO	MIO	OTO	OUO	PAO	TEO	Total
Inside pot states								**Events**					**Outside pot states**											
BAI	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
HAN	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
INS	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
MIL	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
OUT	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
PAN	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
TER	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
CAP	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
ESC	-	-	-	-	-	-	-	-	-	-	-	0 (0)	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
UPP	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	-	-	0 (0)	-	-	-	-	-	-	-	-	-	-	-	0
SEA	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	0
SEO	-	-	-	-	-	-	-	0 (0)	-	-	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
APP	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0.082, 8 (6.1)	0 (0)	0 (25.8)	0 (0)	0.103, 10 (7.1)	0.711, 69 (39.3)	0.093, 9 (0.9)	0.01, 1 (9.4)	0 (0.2)	0 (1.8)	97
LEA	-	-	-	-	-	-	-	-	-	-	-	-	0.071, 6 (6.1)	-	0 (0)	0 (0)	-	0 (6.1)	0 (34)	0 (0.8)	0.929, 78 (8.2)	0 (0.2)	0 (1.5)	84
NAP	-	-	-	-	-	-	-	-	-	-	-	-	0.902, 55 (4.4)	0 (3.8)	-	-	0 (0)	0 (4.5)	0 (24.7)	0 (0.6)	0.082, 5 (5.9)	0.016, 1 (0.1)	0 (1.1)	61
BAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0.003, 1 (22.3)	-	-	0 (0)	0.039, 14 (26)	0.95, 341 (145.1)	0 (3.2)	0 (34.7)	0 (0.6)	0.008, 3 (6.4)	359
HAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
INO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0.041, 4 (6.1)	-	0.051, 5 (26.1)	0 (0)	-	0.837, 82 (39.7)	0.01, 1 (0.9)	0.061, 6 (9.5)	0 (0.2)	0 (1.8)	98
MIO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (39)	0.11, 60 (33.8)	0 (0)	0.65, 354 (144.7)	0 (0)	0.128, 70 (39.4)	-	0.002, 1 (4.9)	0.07, 38 (52.7)	0.002, 1 (0.9)	0.039, 21 (9.7)	545
OTO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0.9)	0.75, 9 (0.8)	0 (0)	0 (3.2)	0 (0)	0 (0.9)	0.083, 1 (4.9)	-	0.167, 2 (1.2)	0 (0.1)	0 (0.3)	12
OUO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0.486, 36 (5.3)	0.014, 1 (4.6)	0 (0)	0.014, 1 (19.7)	0 (0)	0.054, 4 (5.4)	0.419, 31 (30)	0.014, 1 (0.7)	-	0 (0.2)	0 (1.4)	74
PAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0.5, 1 (0.2)	0 (0)	0 (0.6)	0 (0)	0 (0.2)	0 (0.9)	0 (0.1)	0.5, 1 (0.2)	-	0 (0.1)	2
TEO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (1.5)	0 (0)	0 (6.4)	0 (0)	0 (1.8)	1, 24 (9.7)	0 (0.3)	0 (2.4)	0 (0.1)	-	24
Total	0	0	0	0	0	0	0	0	0	0	0	0	97	84	0	360	0	98	548	12	131	2	24	1356

Cod behavioural transition matrix for the RNC pot type. The preceding behaviour is given to the left of the square and the subsequent behaviour above. Transitional probabilities are displayed in the upper half of the squares; observed and expected values (in parenthesis) of transitions are shown in the lower half. Transitions which were over-represented (see Section 2.5.3) are highlighted in grey.

	CODE	Inside pot states							Events					Outside pot states											Total
		BAI	HAN	INS	MIL	OUT	PAN	TER	CAP	ESC	UPP	SEA	SEO	APP	LEA	NAP	BAO	HAO	INO	MIO	OTO	OUO	TEO	PAO	Total
Inside pot states	BAI	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	HAN	0 (0)	-	0.276 27 (2.5)	0.031 3 (1)	0 (1.2)	0.031 3 (51)	0 (0)	-	0.663 65 (13.5)	0 (1.1)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	98
	INS	0 (0)	0.053 5 (2.8)	-	0.011 1 (1)	0 (1.2)	0.611 58 (49.4)	0 (0)	-	0.326 31 (13.1)	0 (1.1)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	95
	MIL	0 (0)	0.152 5 (1)	0.03 1 (0.9)	-	0 (0.4)	0 (17.2)	0 (0)	-	0.818 27 (4.6)	0 (0.4)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	33
	OUT	0 (0)	0.458 11 (0.7)	0 (0.6)	0 (0.3)	-	0 (12.5)	0 (0)	-	0 (3.3)	0.542 13 (0.3)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	24
	PAN	0 (0)	0.727 8 (0.4)	0 (0.3)	0 (0.2)	0.273 3 (0.2)	-	0 (0)	-	0 (1.6)	0 (0.2)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	11
	TER	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Events	CAP	0 (0)	0 (0.1)	0 (0.1)	0.5 1 (0.1)	0 (0.1)	0 (1.1)	0 (0)	-	0.5 1 (0.3)	0 (0.1)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	2
	ESC	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0.118 1 (0.1)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1
	UPP	-	1 1 (0.1)	0 (0.1)	0 (0.1)	0 (0.1)	0 (0.6)	0 (0)	-	-	-	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	1
	SEA	0 (0)	0.008 5 (18.3)	0.002 1 (15.7)	0.011 7 (6.3)	0.018 11 (7.4)	0.9 565 (326.6)	0 (0)	-	0.062 39 (86.1)	0 (6.8)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	628
	SEO	-	-	-	-	-	-	-	0 (0)	-	-	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
Outside pot states	APP	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0.025 3 (1.2)	0 (0)	0 (0.3)	0.254 31 (7.1)	0.205 25 (3)	0.008 1 (0.7)	0 (8.3)	0.008 1 (0.2)	0 (0)	0.5 61 (11.1)	122
	LEA	-	-	-	-	-	-	-	-	-	-	-	-	0 (0)	-	0 (0)	-	0 (2.4)	0 (1)	0.049 2 (0.3)	0 (0.1)	0.951 39 (2.8)	0 (0)	0 (3.8)	41
	NAP	-	-	-	-	-	-	-	-	-	-	-	-	0 (0)	0 (0.4)	-	-	0 (2.1)	0 (0.9)	0 (0.2)	0 (0.1)	0.944 34 (2.5)	0 (0)	0 (3.3)	36
	BAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
	HAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
	INO	-	-	-	-	-	-	-	0.118 2 (0.1)	-	-	-	0 (0)	-	0.136 8 (0.6)	-	0.034 2 (0.1)	0.441 26 (3.5)	-	0 (0.3)	0 (0.1)	0.136 8 (4)	0 (0)	0.254 15 (5.4)	59
	MIO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0)	0 (0.5)	0 (0)	0 (0.1)	0.182 8 (2.6)	0.068 3 (1.1)	-	0 (3)	0 (0.1)	0 (0)	0.750 33 (4)	44
	OTO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0
	OUO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0)	0 (0.1)	0 (0)	0 (0.1)	0.556 5 (0.6)	0.111 1 (0.3)	0.333 3 (0.1)	0 (0.7)	-	0 (0)	0 (0.9)	9
	PAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0.1)	0 (0)	0 (0.1)	0 (0.1)	1 1 (0.1)	0 (0.1)	0 (0.1)	0 (0.1)	-	0 (0.1)	1
	TEO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0
	Total	0	35	30	12	14	626	0	0	165	13	0	0	0	11	0	2	70	29	6	1	81	0	109	1204

Saithe behavioural transition matrix for the C35 pot type. The preceding behaviour is given to the left of the square and the subsequent behaviour above. Transitional probabilities are displayed in the upper half of the squares; observed and expected values (in parenthesis) of transitions are shown in the lower half. Transitions which were over-represented (see Section 2.5.3) are highlighted in grey.

		Inside pot states							Events					Outside pot states											
	CODE	BAI	HAN	INS	MIL	OUT	PAN	TER	CAP	ESC	UPP	SEA	SEO	APP	LEA	NAP	BAO	HAO	INO	MIO	OTO	OUO	PAO	TEO	**Total**
Inside pot states	BAI	-	0 (0.5)	0 (0.9)	1 5 (0.5)	0 (0.2)	0 (0.1)	0 (0)	-	0 (0.1)	0 (0.1)	0 (0.6)	-	-	-	-	-	-	-	-	-	-	-	-	5
	HAN	0 (0)	-	0.818 63 (13.6)	0.156 12 (7.2)	0 (1.8)	0 (1.2)	0 (0)	-	0 (0.1)	0 (0.2)	0.026 2 (9.1)	-	-	-	-	-	-	-	-	-	-	-	-	77
	INS	0 (0)	0.173 30 (13.9)	-	0.179 31 (16)	0.006 1 (3.9)	0.012 2 (2.7)	0 (0)	-	0 (0.2)	0 (0.4)	0.63 109 (20.4)	-	-	-	-	-	-	-	-	-	-	-	-	173
	MIL	0 (0)	0.152 14 (7.4)	0.815 75 (16.2)	-	0 (2.1)	0 (1.4)	0 (0)	-	0.011 1 (0.1)	0 (0.2)	0.022 2 (10.9)	-	-	-	-	-	-	-	-	-	-	-	-	92
	OUT	0 (0)	0 (1.8)	0.955 21 (3.9)	0 (2.1)	-	0.045 1 (0.4)	0 (0)	-	0 (0.1)	0 (0.1)	0 (2.6)	-	-	-	-	-	-	-	-	-	-	-	-	22
	PAN	0 (0)	0 (1.3)	0.6 9 (2.7)	0.067 1 (1.4)	0 (0.4)	-	0 (0)	-	0 (0.1)	0.133 2 (0.1)	0.2 3 (1.8)	-	-	-	-	-	-	-	-	-	-	-	-	15
	TER	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
Events	CAP	0 (0)	0 (0)	0 (0)	1 1 (0.1)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	1
	ESC	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	-	1 1 (0.1)	-	0 (0)	0 (0.1)	0 (0.2)	0 (0.1)	0 (0.1)	0 (0.2)	0 (0.1)	0 (0)	1
	UPP	-	0 (0.2)	0 (0.4)	0.5 1 (0.2)	0 (0.1)	0 (0.1)	0 (0)	-	-	-	0.5 1 (0.3)	-	-	-	-	-	-	-	-	-	-	-	-	2
	SEA	0 (0)	0.308 36 (9.4)	0.051 6 (20.6)	0.359 42 (10.9)	0.179 21 (2.6)	0.103 12 (1.8)	0 (0)	-	0 (0.2)	0 (0.3)	-	-	-	-	-	-	-	-	-	-	-	-	-	117
	SEO	-	-	-	-	-	-	-	0.118 2 (0.1)	-	-	-	-	-	0.706 12 (1.5)	-	0 (0)	0 (0.1)	0 (1.8)	0.118 2 (0.2)	0 (0.1)	0.059 1 (2.7)	0 (0.1)	0 (0)	17
Outside pot states	APP	-	-	-	-	-	-	-	0 (0.5)	-	-	-	0 (1.7)	-	0.232 23 (8.5)	0 (1.6)	0 (0)	0.01 1 (0.2)	0.697 69 (10.4)	0 (0.8)	0 (0.1)	0.061 6 (15.4)	0 (0.1)	0 (0)	99
	LEA	-	-	-	-	-	-	-	-	-	-	-	-	0.024 2 (8.5)	-	0 (1.4)	-	0 (0.2)	0 (8.9)	0 (0.7)	0 (0.1)	0.976 83 (13.2)	0 (0.1)	0 (0)	85
	NAP	-	-	-	-	-	-	-	-	-	-	-	-	0.667 62 (9.3)	0.022 2 (8)	-	-	0 (0.2)	0 (9.8)	0 (0.8)	0 (0.1)	0.312 29 (14.4)	0 (0.1)	0 (0)	93
	BAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
	HAO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	0 (0.2)	0.5 1 (0.2)	0 (0.1)	0 (0)	-	0 (0.3)	0 (0.1)	0 (0.1)	0 (0.4)	0 (0.1)	0 (0)	1
	INO	-	-	-	-	-	-	-	0.029 3 (0.6)	-	-	-	0.162 17 (1.8)	-	0.4 42 (9)	-	0 (0)	0.01 1 (0.3)	-	0.057 6 (0.9)	0.01 1 (0.2)	0.324 34 (16.3)	0.01 1 (0.2)	0 (0)	105
	MIO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.2)	0 (0.8)	0.25 2 (0.7)	0 (0.2)	0 (0)	0 (0.1)	0.625 5 (0.9)	-	0 (0.1)	0.125 1 (1.3)	0 (0.1)	0 (0)	8
	OTO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	0 (0.1)	0 (0.1)	0 (0.1)	0 (0)	0 (0.1)	1 1 (0.2)	0 (0.1)	-	0 (0.2)	0 (0.1)	0 (0)	1
	OUO	-	-	-	-	-	-	-	0 (0.5)	-	-	-	0 (1.4)	0.432 35 (8.1)	0.012 1 (7)	0.198 16 (1.4)	0 (0)	0 (0.2)	0.358 29 (8.5)	0 (0.7)	0 (0.1)	-	0 (0.1)	0 (0)	80
	PAO	-	-	-	-	-	-	-	0 (0.1)	-	-	-	0 (0.1)	-	1 1 (0.1)	0 (0.1)	0 (0)	0 (0.1)	0 (0.2)	0 (0.1)	0 (0.1)	0 (0.2)	-	0 (0)	1
	TEO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0
	Total	0	80	174	92	22	15	0	5	1	2	117	17	99	85	16	0	2	104	8	1	154	1	0	996

Saithe behavioural transition matrix for the C95 pot type. The preceding behaviour is given to the left of the square and the subsequent behaviour above. Transitional probabilities are displayed in the upper half of the squares; observed and expected values (in parenthesis) of transitions are shown in the lower half. Transitions which were over-represented (see Section 2.5.3) are highlighted in grey.

		Inside pot states							Events					Outside pot states											
	CODE	BAI	HAN	INS	MIL	OUT	PAN	TER	CAP	ESC	UPP	SEA	SEO	APP	LEA	NAP	BAO	HAO	INO	MIO	OTO	OUO	PAO	TEO	Total
Inside pot states	BAI	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	HAN	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	INS	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	MIL	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	OUT	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	PAN	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	TER	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
Events	CAP	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	0
	ESC	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
	UPP	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	-	-	-	0 (0)	-	-	-	-	-	-	-	-	-	-	-	0
	SEA	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	SEO	-	-	-	-	-	-	-	0 (0)	-	-	-	-	-	1 / 1 (0.3)	-	0 (0)	0 (0.1)	0 (0.3)	0 (0)	0 (0)	0 (0.4)	0 (0)	0 (0)	1
Outside pot states	APP	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0.3)	-	0.206 / 14 (14.2)	0 (0.3)	0 (0)	0 (1)	0.735 / 50 (14)	0 (0)	0 (0)	0.059 / 4 (22.5)	0 (0)	0 (0)	68
	LEA	-	-	-	-	-	-	-	-	-	-	-	-	0.1 / 6 (14.2)	-	0 (0.3)	-	0.067 / 4 (0.9)	0 (12.3)	0 (0)	0 (0)	0.833 / 50 (19.8)	0 (0)	0 (0)	60
	NAP	-	-	-	-	-	-	-	-	-	-	-	-	0.703 / 52 (17.5)	0 (15.5)	-	-	0 (1.1)	0 (15.2)	0 (0)	0 (0)	0.297 / 22 (24.5)	0 (0)	0 (0)	74
	BAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
	HAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0.1)	0.5 / 2 (1)	0.5 / 2 (0.9)	0 (0.1)	0 (0)	-	0 (0.9)	0 (0)	0 (0)	0 (1.4)	0 (0)	0 (0)	4
	INO	-	-	-	-	-	-	-	0 (0)	-	-	-	0.017 / 1 (0.3)	-	0.661 / 39 (12.3)	-	0 (0)	0 (0.9)	-	0 (0)	0 (0)	0.322 / 19 (19.5)	0 (0)	0 (0)	59
	MIO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0
	OTO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0
	OUO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0.1)	0.364 / 8 (5.2)	0.182 / 4 (4.6)	0.045 / 1 (0.1)	0 (0)	0 (0.4)	0.409 / 9 (4.6)	0 (0)	0 (0)	-	0 (0)	0 (0)	22
	PAO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0 (0)	0
	TEO	-	-	-	-	-	-	-	0 (0)	-	-	-	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-	0
	Total	0	0	0	0	0	0	0	0	0	0	0	1	68	60	1	0	4	59	0	0	95	0	0	288

Saithe behavioural transition matrix for the RC pot type. The preceding behaviour is given to the left of the square and the subsequent behaviour above. Transitional probabilities are displayed in the upper half of the squares; observed and expected values (in parenthesis) of transitions are shown in the lower half. Transitions which were over-represented (see Section 2.5.3) are highlighted in grey.

Appendix 23

SIMPER analysis: cod prior to capture, comparing CB & C35 pot types

Behaviour	Av. cont.	s.d	Ratio	Av. ab. CB	Av. ab. C35	Cum. cont.
INO	0.119265	0.09813	1.2154	0.43047	0.684364	0.307
MIO	0.069898	0.07839	0.8916	0.25526	0	0.488
LEA	0.069637	0.05534	1.2584	0.39712	0.335584	0.667
APP	0.056719	0.04512	1.2571	0.42884	0.420394	0.813
NAP	0.048458	0.04048	1.197	0.25901	0.243496	0.938
OTO	0.010652	0.04255	0.2503	0.03198	0.007519	0.966
HAO	0.006217	0.01829	0.34	0.00339	0.02027	0.982
BAO	0.005702	0.0184	0.3099	0	0.019997	0.996
TEO	0.001143	0.01183	0.0966	0	0.004237	0.999
PAO	0.000245	0.00286	0.0858	0	0.000833	1

Note: Av. cont: average contribution to overall dissimilarity; s.d: standard deviation of contribution; ratio: Average to s.d ratio; Av. ab CB: average abundance CB group; Av. ab. C35: average abundance C35 group; Cum. cont.: ordered cumulative contribution.

Appendix 24

SIMPER analysis: cod after capture, comparing CB & C35 pot types

Behaviour	Av. cont.	s.d	Ratio	Av. ab. CB	Av. ab. C35	Cum. cont.
BAI	0.19377	0.1161	1.669	0.6664	0.1785	0.371
INS	0.14677	0.1015	1.445	0.4797	0.7597	0.652
MIL	0.09209	0.0864	1.066	0.2529	0.1957	0.828
HAN	0.08255	0.0713	1.158	0.123	0.247	0.986
PAN	0.00742	0.0128	0.579	0.0143	0.0112	1
TER	0	0	NaN	0	0	1

Note: Av. cont: average contribution to overall dissimilarity; s.d: standard deviation of contribution; ratio: Average to s.d ratio; Av. ab CB: average abundance CB group; Av. ab. C35: average abundance C35 group; Cum. cont.: ordered cumulative contribution.

Appendix 25

SIMPER analysis: cod prior to capture, comparing RC & RNC pot types

Behaviour	Av. cont.	s.d	Ratio	Av. ab. RC	Av.ab. RNC	Cum. cont.
MIO	0.18794	0.10495	1.791	0.00974	0.65318	0.292
INO	0.18646	0.08525	2.187	0.74431	0.1341	0.582
LEA	0.0651	0.0464	1.403	0.31557	0.20758	0.683
APP	0.06335	0.04848	1.307	0.3521	0.31874	0.782
BAO	0.05768	0.05256	1.098	0.01249	0.20043	0.872
NAP	0.04885	0.04595	1.063	0.24821	0.15157	0.948
OTO	0.02708	0.06721	0.403	0.00422	0.09267	0.99
PAO	0.00368	0.02352	0.157	0.00173	0.00979	0.995
TEO	0.00153	0.00929	0.165	0	0.00541	0.998
HAO	0.00143	0.00799	0.179	0.00473	0	1

Note: Av. cont: average contribution to overall dissimilarity; s.d: standard deviation of contribution; ratio: Average to s.d ratio; Av. ab CB: average abundance RC group; Av. ab. RNC: average abundance C35 group; Cum. cont.: ordered cumulative contribution.

SIMPER analysis: C35 pot after capture, comparing cod and saithe

Behaviour	Av. cont.	s.d	Ratio	Av. ab. cod	Av.ab. sai	Cum. cont.
BAI	0.2158	0.10110	2.13	0.6664	0.000	0.371
HAN	0.1589	0.07392	2.15	0.1230	0.612	0.645
INS	0.1156	0.07724	1.50	0.4797	0.732	0.844
MIL	0.0672	0.06642	1.01	0.2529	0.134	0.959
PAN	0.0237	0.00605	3.91	0.0143	0.080	1.000

Note: Av. cont: average contribution to overall dissimilarity; s.d: standard deviation of contribution; ratio: Average to s.d ratio; Av. ab cod: average abundance cod group; Av. ab. sai: average abundance saithe group; Cum. cont.: ordered cumulative contribution.

SIMPER analysis: C95 pot after capture, comparing cod and saithe

Behaviour	Av. cont.	s.d	Ratio	Av. ab. cod	Av.ab. sai	Cum. cont.
MIL	0.095042	0.05572	1.706	0.546016	0.2728	0.259
HAN	0.086487	0.05943	1.455	0.248161	0.3697	0.496
BAI	0.085581	0.07157	1.196	0.280848	0.0000	0.729
INS	0.075549	0.07001	1.079	0.613344	0.8361	0.936
PAN	0.023363	0.01521	1.536	0.000000	0.0756	0.999
TER	0.000248	0.00106	0.234	0.000771	0.0000	1.000

Note: Av. cont: average contribution to overall dissimilarity; s.d: standard deviation of contribution; ratio: Average to s.d ratio; Av. ab cod: average abundance cod group; Av. ab. sai: average abundance saithe group; Cum. cont.: ordered cumulative contribution.

Cod approach direction, Friedman test results.

Pot Type	X^2	d.f	p
CB	307.5	2	<0.001
C35	52.9	2	<0.001
C95	153.7	2	<0.001
RC	77.6	2	<0.001
RNC	40.9	2	<0.001

Saithe approach direction, Friedman test results.

Pot Type	X^2	d.f	p
CB	765	1	<0.001
C35	108	1	<0.001

Appendix 30

Relationship between cod approach height and bait height

glm(cbind(Water,Bottom)~Bait_height,family=quasibinomial)

	Estimate	Standard error	*t*-value	*p*-value
intercept	-1.260	0.180	-6.992	<0.001
Bait_height	0.011	0.003	3.695	<0.001

Null deviance = 92.138 on 16 d.f; residual deviance = 49.199 on 15 d.f

Appendix 31

Relationship between saithe approach height and bait height

glm(cbind(Water,Bottom)~Bait_height,family=quasibinomial)

	Estimate	Standard error	*t*-value	*p*-value
intercept	-1.107	0.160	-0.669	0.518
Bait_height	0.028	0.006	4.589	<0.001

Null deviance = 96.790 on 11 d.f; residual deviance = 23.133 on 10 d.f

Appendix 32

Relationship between species & the probability of water column approach

glm(Prob_water~Species,family=binomial)

	Estimate	Standard error	*z*-value	*p*-value
intercept	-0.936	0.510	-1.836	0.066
SpeciesSaithe	1.967	0.454	2.427	0.015

AIC= 30.494; Null deviance = 15.600 on 31 d.f; residual deviance = 8.946 on 30 d.f

Appendix 33

Cod search location prior to capture, Friedman test results.

Pot Type	X^2	d.f	*p*
CB	120.7	2	<0.001
C35	15.4	2	<0.001
C95	24.4	2	<0.001
RC	84	2	<0.001

Appendix 34

Cod search direction prior to capture, Friedman test results.

Pot Type	X^2	d.f	p
CB	183	1	<0.001
C35	36	1	<0.001
C95	45	1	<0.001
RC	126	1	<0.001

Appendix 35

Cod search location after capture, Friedman test results.

Pot Type	X^2	d.f	p
CB	26.3	2	<0.001
C35	10.9	2	<0.001
C95	35.4	2	<0.001
RC	20.5	2	<0.001

Appendix 36

Preliminary model exploration using GLMM

glmer(Capture ~ Species + Size + Species*Size + Fish + (1|Pot/Set), family = binomial)

Random effects:

	Variance	Standard Deviance
Set – Pot (intercept)	0.437	0.661
Pot (intercept)	$7.56e^{-10}$	$2.75e^{-5}$

Fixed effects:

	Estimate	Standard error	z-value	p-value
intercept	-0.84879	0.25254	-3.361	0.000777
SpeciesH	-1.23555	1.07400	-1.150	0.249975
SpeciesS	-1.93816	1.07263	-1.807	0.070776
SizeS	-0.27842	0.22487	-1.238	0.215663
SizeU	-1.21992	0.32646	-3.737	0.000186
Fish	-0.16202	0.04505	-3.596	0.000323
SpeciesH:SizeS	-0.27436	1.16606	-0.235	0.813983
SpeciesS:SizeS	0.83337	1.12225	0.743	0.457732
SpeciesH:SizeU	-16.51367	3062.33205	-0.005	0.995697
SpeciesS:SizeU	-0.07343	1.50287	-0.049	0.961029

AIC= 939.7; Deviance = 915.7 d.f residual = 1409

Continued on next page.

Variance explained by the GLMM model:

r.squaredGLMM(GLMM)

	R^2
Marginal (fixed + random effects)	0.685
Conditional (fixed effects)	0.722
Random effects	0.037

Appendix 37

Comparison of nested models to test for significance of size variable

Model 1: Capture ~ Species + Fish + Size + Species : Fish + Pot
Model 2: Capture ~ Species + Fish + Species * Fish + Pot

	Residual d.f	Residual deviance	d.f	Deviance	*p*-value
Model 1	1411	940.85			
Model 2	1413	969.98	-2	-29.13	<0.001

Appendix 38

Comparison of large fish candidate models to test for significance of "fish:species" variable

Model 1: Capture ~ Species * Fish
Model 2: Capture ~ Fish + Species

	Residual d.f	Residual deviance	d.f	Deviance	*p*-value
Model 1	276	248.95			
Model 2	278	253.06	-2	-4.1184	0.127

Appendix 39

Comparison of small fish candidate models to test for significance of "fish:species" variable

Model 1: Capture ~ Species * Fish
Model 2: Capture ~ Fish + Species

	Residual d.f	Residual deviance	d.f	Deviance	*p*-value
Model 1	754	570.93			
Model 2	756	575.94	-2	-5.014	0.081

Appendix 40

Comparison of selected models to null model

	Residual d.f	Residual deviance	d.f	Deviance	*p*-value
Large fish					
Null	281	266.59			
Fish + Species	278	253.06	3	13.527	0.003
Small fish					
Null	759	606.77			
Fish + Species	756	575.94	3	30.823	<0.001

Appendix 41

Tukey HSD results comparing probability of capture of small fish by species

	Estimate	Std. Error	Z value	p-value
Haddock - Cod	-1.432	0.436	-3.285	0.002
Saithe - Cod	-1.206	0.321	-3.754	<0.001
Saithe - Haddock	0.225	0.514	0.438	0.896

Appendix 42

Tukey HSD results comparing probability of capture of large fish by species

	Estimate	Std. Error	Z value	p-value
Haddock - Cod	-1.462	1.041	-1.404	0.326
Saithe - Cod	-1.673	1.035	-1.616	0.228
Saithe - Haddock	-0.211	1.451	-0.146	0.988

Appendix 43

Best approximating model for large fish

glm(Capture ~ Species + Fish, family = binomial)

	Estimate	Standard error	z-value	p-value
(Intercept)	-0.89272	0.23850	-3.743	0.000182
SpeciesH	-1.29865	1.05061	-1.236	0.216426
SpeciesS	-1.58147	1.04215	-1.518	0.129137
Fish	-0.18535	0.07579	-2.446	0.014465

AIC= 261.07; Null deviance = 266.59 on 281 d.f; residual deviance = 253.07 on 278 d.f. McFadden's pseudo R^2 = 0.05

Appendix 44

Best approximating model for small fish

glm(Capture ~ Species + Fish, family = binomial)

	Estimate	Standard error	z-value	p-value
(Intercept)	-1.24992	0.17081	-7.317	2.53e-13
SpeciesH	-1.52420	0.43978	-3.466	0.000529
SpeciesS	-1.25774	0.32338	-3.889	0.000101
Fish	-0.07445	0.04403	-1.691	0.090886

AIC= 583.94; Null deviance = 606.77 on 759 d.f; residual deviance = 575.94 on 756 d.f. McFadden's pseudo R^2 = 0.05