Original Article

Correlation between catch method, condition, and diet patterns in Atlantic cod (*Gadus morhua*)

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With seal populations increasing significantly in the Baltic Sea, the conflict between seals and fisheries is growing. The most sustainable method for mitigating the seal–fishery conflict is to develop and use seal-safe fishing gear. Although pots have been shown to be a promising alternative to gillnets for catching cod (*Gadus morhua*), there are indications that cod caught in pots are in poorer condition than those caught in gillnets, potentially making the pots a less-economical alternative. This study investigates whether this difference in condition is consistent over larger spatial scales. Gear-specific cod condition was related to both short-term (determined from stomach contents) and long-term (determined by stable isotope analysis) diet composition. Results indicate that differences in fish condition between gear types are consistent over large areas, possibly due to temporal and spatial differences in feeding strategies. We argue that condition differences between pot- and gillnet-caught cod may be driven by differences in behavioural traits. Consequently, fishing with a certain gear type may have ecological consequences affecting population characteristics, with implications for fisheries management. From the perspective of the seal–fisheries conflict, pots may ultimately have consequences on the catch value of fish.

Keywords: cod, condition, diet, gillnet, pot, stable isotopes

Introduction

Seal populations in the Baltic Sea have increased significantly in recent decades, resulting in a growing conflict between seals and fisheries (Lunneryd *et al.*, 2005; Königson *et al.*, 2009; Varjopuro, 2011). A sustainable way of mitigating the seal–fishery conflict is to develop and use seal-safe fishing gear (Königson, 2011), and pots have shown themselves to be a promising alternative to gillnets when targeting cod (*Gadus morhua*), however, with strong seasonal catchability (Ovegård *et al.*, 2011; Königson *et al.*, 2015a; Marcella *et al.*, 2016). Previous studies have also revealed that pot-caught cod, compared with gillnet-caught cod, generally are in poorer condition and smaller at the same age (Huse *et al.*, 2000; Ovegård *et al.*, 2012).

Intrapopulation variation in e.g. diet, growth, and morphology is commonly found in fish (Bernatchez *et al.*, 1996; Sherwood and Grabowski, 2010). Changes in growth, reproductive rate, and maturity may be induced by selective fishing methods through the capture of certain phenotypes termed fisheries-induced evolution (FIE; Jørgensen *et al.*, 2007; Devine *et al.*, 2012), with cases described in both commercial (Kuparinen and Merilä, 2007; Devine *et al.*, 2012) and recreational fisheries (Cooke *et al.*, 2007). A plausible mechanism for FIE in fish populations is individual behavioural differences stable over time, termed "behavioural syndromes" or "personalities" (Bell *et al.*, 2009; Wolf and Weissing, 2012), making some fish (or part of a population) more susceptible to fishing activities (Biro and Post, 2008;

Uusi-Heikkilä *et al.*, 2008; Heino *et al.*, 2015; Diaz Pauli and Sih, 2017). Behavioural differences can be linked to both metabolism and fitness (Careau and Garland, 2012; Metcalfe *et al.*, 2016). Selecting fishing gear can thus be selective for behavioural syndromes correlated with e.g. diet, metabolism, growth patterns, and habitat use (Biro and Stamps, 2008; Mittelbach *et al.*, 2014; Pauli *et al.*, 2015).

Dietary data, such as stomach content data, are commonly used to identify short-term consumption (over days), whereas stable isotopes, predominantly nitrogen and carbon, have proven to be valuable tools for evaluating trophic, temporal, and spatial consumption patterns (Peterson and Fry, 1987; Vander Zanden and Rasmussen, 1999; Polunin and Pinnegar, 2002; Post, 2002; Layman *et al.*, 2012). The fractioning of the nitrogen isotope $\delta^{15}N$ generally elevates with size and trophic level and may be used to track ontogenetic divergence (Deniro and Epstein, 1981; Fry, 2006), whereas the carbon isotope $\delta^{13}C$ traces the source of primary production (Peterson and Fry, 1987; Hobson and Welch, 1992; Post, 2002).

Atlantic cod are opportunistic omnivores with a diet varying both seasonally and spatially (Hop *et al.*, 1992; Høines and Bergstad, 1999; Hanson and Chouinard, 2002; Link *et al.*, 2009). Recent studies have found intrapopulation differences in cod consumption patterns, grouping individuals into morphology- and diet-specific subgroups as some individuals had a diet depending more on fish than crustaceans along with a higher growth rate (Sherwood and Grabowski, 2010).

This study evaluates whether patterns shown by Ovegård *et al.* (2012), with differences in condition between pot- and gillnet-caught cod, are consistent for other areas in the Baltic Sea. Further, this study evaluates diet compositions in pot- and gillnet-caught cod to provide a basis for understanding how differences in condition may relate to diet and, through that, possible existence of subgroups within local populations. The aims were to examine (i) variations in cod condition by area and gear type; (ii) differences in niche width between fish caught in pots and gillnets by examining feeding strategy and ecological distance, based on stomach content data; and (iii) differences in niche width and diet overlap between pot- and gillnet-caught cod based on isotopic signals.

Material and methods
Study area and data collection
Two areas were chosen for the study: Öresund Strait and Simrishamn situated on either side of southern Sweden (Figure 1). Öresund is characterized by high water velocity, up to 4 knots, with permanent halo- and thermoclines at a depth of 10–15 m [Swedish Meteorological and Hydrological Institute (www.SMHI.se) database SHARK], because of the continuous exchange of water between the saline North Sea and the brackish Baltic. The maximum depth in Öresund is 50 m, with most commercial gillnet fishing conducted at depths of 5–30 m. The benthic environment mainly consists of sand and seagrass beds in the shallower areas and soft sediments in the deeper parts ("The Sound Water" Cooperation, www.oresundsvand.dk). Crustaceans dominate the faunal composition in Öresund and are a large component of the diet for all size classes of cod (Ljungberg, 2013). In Simrishamn, the southern part of Hanö Bay, the benthic environment generally lacks vegetation (Olsson, 2005). The halocline is deeper (50–70 m; www.SMHI.se, database SHARK), often with anoxic conditions below (Carstensen *et al.*, 2014) that force cod into primarily pelagic foraging (Schaber *et al.*, 2009). Cod are the target species of fisheries in this area, and most fishing is conducted at depths of 20–80 m, mainly using gillnets or trawls. Herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) are the main prey of Baltic cod (Casini *et al.*, 2011), in addition to benthic prey and smaller cod (Uzars, 1994; Eero *et al.*, 2012). The faunal composition in Simrishamn differs from that in Öresund having less biodiversity and a lower abundance of clupeid species (Eero *et al.*, 2012). Other spatial and temporal effects between sampling occasions are general differences in temperature regime, predominantly because of time of year. Fishing was carried out in collaboration with commercial fishers on three occasions: once in Öresund (in spring) and twice in Simrishamn (in summer and autumn). To compare gear types, gillnets and cod pots were deployed at the same depth range, with a maximum distance of 2000 m apart. Distance between gear types was chosen so that pot bait plumes would not attract cod into adjacent gillnets. Two different pot models were used within the study at all occasions. Both models were of the floating type, with an 8-mm stainless frame, 700-g buoys for buoyancy to keep the pot vertical, and
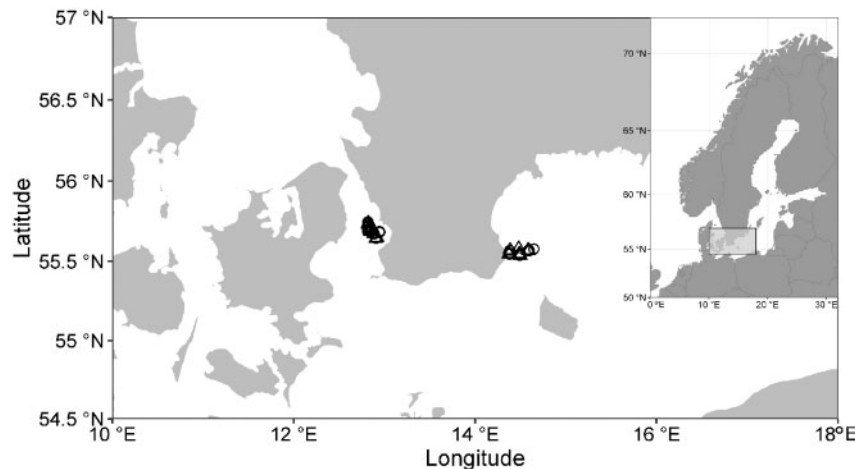

Figure 1. Map of the sampling areas, where symbols to the right indicate Öresund spring and to the left Simrishamn summer and autumn samplings. Circles specify gillnet locations and triangles pot locations (Kahle and Wickham, 2013).

25-mm green polyethylene mesh. The first model was a D-shaped construction (1100 × 700 mm, height 700 mm with a volume of 0.70 m^3 presented in Ljungberg *et al.* (2016). The second pot model was of a pentagonal type (bottom, 1100 × 850 mm; top, 900 × 700 mm; height, 750 mm; and volume, 0.63 m^3), referred to as "Pentagonal S" in Hedgärde *et al.* (2016). The second pot model came in two modifications: one collapsible, and one with a rigid holding chamber. In order to catch the same size range of cod, all pots were equipped with an elliptical metal entrance ring 15 cm wide and 56 cm in circumference (area 247 cm^2) to exclude seals without affecting the cod catch rate (Königson *et al.*, 2015b). All cod pots were also equipped with a panel of 45-mm^2 mesh to allow the escape of undersized cod smaller than 38 cm (Ovegård *et al.*, 2011). Pots were baited with ca. 250 g of fresh herring cut into 5-cm pieces and placed in fine-mesh bags within the pots. Soak-time was 1 day for gillnets and 1–3 days for pots. In Öresund, fishing was carried out between 14 April and 2 May 2013. Each pot string contained 4–6 pots, whereas gillnets were 3.5 m high, 1000 m long, and had a mesh size of 55–70 mm between knots. Fishing depth in Öresund was 10–20 m. In Simrishamn, summer fishing was carried out between 9 July and 7 August 2013. Each pot string contained 1–12 pots, whereas gillnets used were 3 m high, 200 m long, and had a mesh size of 55 mm between knots. Simrishamn summer sampling was conducted at depths of 20–60 m. In Simrishamn, autumn sampling was carried out 15–16 October. Each pot string contained 1–8 pots. Gillnet-caught cod for the Simrishamn autumn sampling were bought from a local fisher who deployed his gillnets adjacent to the pot strings. Gillnets were 3 m high, 1000 m long, and had a mesh size of 55 mm between knots. Sampling depth was 25–60 m. A 45-mm^2 selection panel in pots allowed for a minimum length of 38 cm (Ovegård *et al.*, 2011), as did a 55 mm between knots in the gillnet (Madsen, 2007). However, size selectivity works differently in the two gear types. Although catch size in gillnets exhibits a bell-shaped distribution in selectivity, regulated by mesh size, pots are ultimately regulated by a selection panel mesh size, giving catch sizes a more sigmoid shaped distribution, as entrance size rarely is regulating maximum fish size. Length, weight, capture depth, capture date, and gear type were recorded for each individual cod caught. Also, for each individual, ca. 1 cm^3 of dorsal muscle tissue, giving a turnover rate up to about 2 months (Boecklen *et al.*, 2011), was saved for stable isotope analysis along with the stomach, both which were frozen at −20°C for later laboratory analysis. Because of spatial and temporal variability in environmental conditions (i.e. water temperature, salinity, and prey distribution), each fishing period and area was evaluated as an individual occasion; this resulted in all three fishing occasions.

Condition and length

To find possible differences in cod conditions between sampling occasions and gear types, Fulton's *K* was calculated using Equation (1) for each cod (Table 1):

$$K = 100 \times WL^3. \tag{1}$$

This formula, in which *W* is gutted weight (g) and *L* is length (cm), gives a *K*-value around 1, with lower values indicating more meagre fish. To account for weight loss because of gut evacuation, gutted weight was calculated by subtracting stomach

Table 1. Number of cod individuals (*n*), mean length (cm ± 1 SD), and mean Fulton index (*K*), based on somatic weight, for the three sampling occasions and two gear types.

Occasion	Gear	*n*	Length, ±1 SD (cm)	Fulton index (*K*)
Öresund, spring	Pot	45	52.1 ± 11.9	0.76 ± 0.1
	Gillnet	84	55.8 ± 10.7	0.81 ± 0.1
Simrishamn, summer	Pot	107	44.5 ± 7.0	0.64 ± 0.1
	Gillnet	81	44.4 ± 8.2	0.69 ± 0.1
Simrishamn, autumn	Pot	88	42.8 ± 4.7	0.68 ± 0.2
	Gillnet	93	41.5 ± 7.1	0.72 ± 0.1

and intestine weight from total weight for both pot- and gillnet-caught cod, allowing the weight loss to be neglected. Note that the *K*-value will appear lower here than in other studies in which *W* includes gut (stomach and intestine) weight. To test whether the Fulton index values were normally distributed, a Kolmogorov–Smirnov test (henceforth, "K–S test") was performed for each sampling occasion and gear type. To allow for analysis of differences in fitness (Fulton's *K*) regarding not only gear type, but also fish length, linear regression analyses were included for each sampling occasion. By also including the interaction effect between gear type and fish length in the model, potential effects on fitness (*K*) over cod length between the two gear types could be identified.

Diet

Stomach contents

Stomach contents were identified to acquire information about recent diet patterns. Frozen stomachs were thawed and weighed. Stomach contents were filtered through a 1-mm sieve and sorted into the lowest taxonomic levels possible under a dissection microscope. Diets were compared based on the proportion of wet weight of each prey taxon.

The soak-time range of 1–3 days may introduce difficulties comparing stomach contents, as digestion can be expected to be influenced by time in the stomach. To test for differences because of digestion during the variable soak-time, stomach content weights were compared using the Scheirer–Ray–Hare test (Sokal and Rohlf, 1995) by gear type and soak-time. Soak-time analysis was limited to the Simrishamn summer sampling, for which multiple replicates of all soak-time combinations were available (Table 2). In theory, if soak-time matters for further analyses, there should be a decrease in stomach content weight over time.

Niche width: stomach data

Niche width, based on stomach content, was calculated using Levin's niche index (*B*; Levin, 1968) using Equation (2):

$$B = 1/\sum p_j^2, \tag{2}$$

where p_j is the proportion of individuals in the stomach contents in food category *j* or the fraction of diet items in *j* (estimated from N_j/Y; $\sum p_j = 1.0$), N_j is the number of individuals found in or using resource state *j*, and $Y = \sum N_j$ is the total number of individuals sampled. *B* ranges from 1 to *n*, where *n* is the total number of resource states. The index ranges from 1 to 28, based

on the number of prey groups in the study (Table 3). Test for gear-specific differences in niche width was done using the Wilcoxon test.

Diet overlap: stomach data

Schoener's index, Equation (3; Schoener, 1968), was used to calculate diet overlap between cod caught on the different sampling occasions and with the different gear types, respectively. Schoener's index (α) was calculated as follows:

$$\alpha = 1 - 0.5 \sum |P_{ij} - P_{ik}|, \tag{3}$$

where P_i is the proportion of prey in category i in the diet of cod from the two gear types (j and k), respectively. The α-value ranges from 0 to 1, where 0 indicates no overlap and 1 total overlap. The α-value indicates high (>0.6), intermediate (0.3–0.6), or low (<0.3) dietary overlap (Langton, 1982).

Ecological distance: stomach data

Differences in prey species composition between stomachs of cod caught with the two different gear types were examined visually using constrained canonical analysis of principal coordinate (CAP; Anderson and Willis, 2003) ordinations for each of the three occasions. Each CAP was based on the most important species groups per occasion (Figure 2a–c), and a predefined grouping by gear type (i.e. gillnet and pot) was used as an explanatory variable. The CAP ordinations are based on relative biomass data, using a Bray–Curtis dissimilarity index, and were carried out using the capscale function in the Vegan package (v. 2.4-6) in R. The Bray–Curtis index weights the diet composition of each individual cod based on the percentage of wet weight per prey species,

Table 2. Number (n) and stomach contents in mean wet weight ($g \pm 1 SD$) of cod caught in the Simrishamn summer sampling in pots and gillnets for three different soak-times.

Gear	Parameter	Soak-time (days)		
		1	2	3
Pot	n	10	56	34
	weight (g)	22.1 ± 45.4	5.3 ± 10.9	13.5 ± 25.8
Gillnet	n	10	39	60
	weight (g)	29.8 ± 51.5	30.2 ± 67.7	10.4 ± 26.5

Table 3. Mean contribution in percentage wet weight per diet group/species per cod stomach on the three occasions (i.e. Öresund spring, Simrishamn summer, and Simrishamn autumn) in cod caught in pots and gillnets.

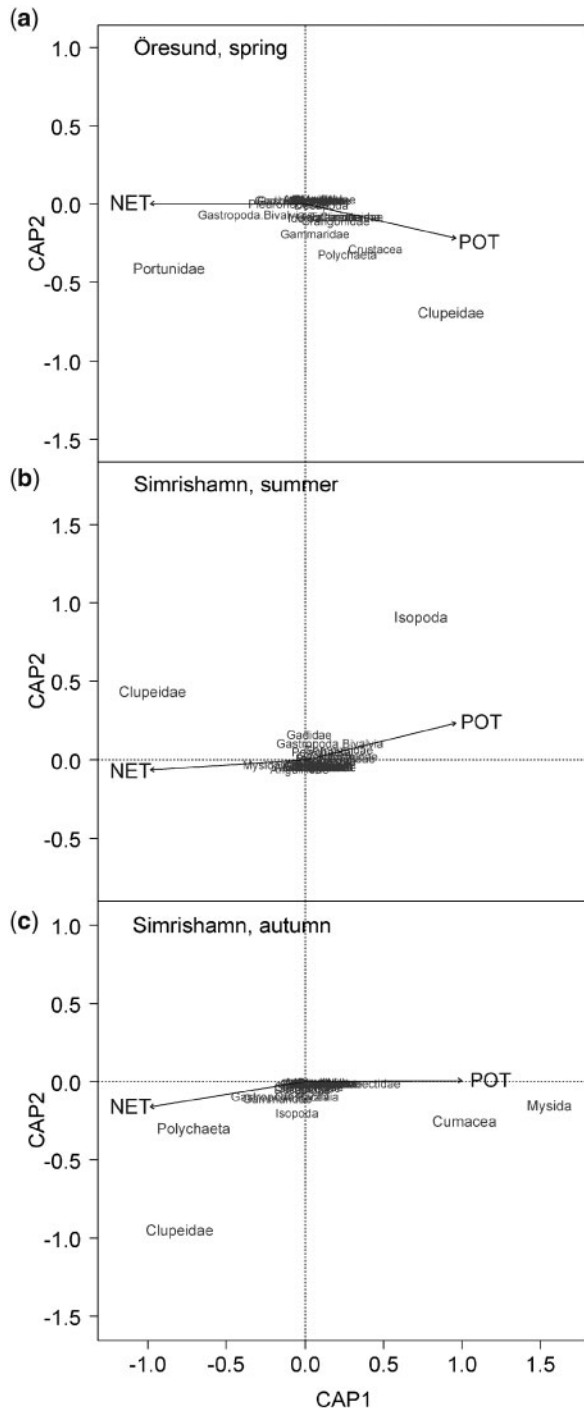|	Öresund		Simrishamn			
	Spring		Summer		Autumn	
Species	Pot (%)	Gillnet (%)	Pot (%)	Gillnet (%)	Pot (%)	Gillnet (%)
Invertebrates						
Caridea	0.4	0.0	0.0	0.0	0.0	0.0
Crangonidae	0.3	0.1	0.0	0.0	0.0	0.1
Crustacea	1.2	0.0	0.0	0.0	0.8	0.0
Cumacea	0.0	0.0	0.1	0.0	6.5	0.2
Decapoda	6.3	0.0	0.0	0.0	0.0	0.0
Echinoderma	0.9	0.0	0.0	0.0	0.0	0.0
Gammaridae	0.4	0.1	0.1	0.1	0.1	0.1
Gastropoda/Bivalvia	0.2	0.6	0.7	0.1	0.1	0.0
Idotea	0.3	0.1	1.6	0.0	0.0	0.0
Isopoda	0.0	0.0	19.7	6.1	3.0	0.4
Mysida	0.0	0.0	0.2	0.1	14.6	0.2
Nemertea	0.0	0.0	0.0	0.0	0.0	0.0
Palaemonidae	0.1	0.0	0.0	0.0	0.0	0.0
Polychaeta	7.3	0.3	0.4	0.3	0.1	0.4
Portunidae	49.6	75.2	0.3	0.0	0.0	0.0
Pterygota	0.0	0.0	0.2	0.0	0.2	0.0
Total invertebrates	67.0	76.3	23.2	6.7	25.4	1.3
Fish						
Ammodytidae	0.0	0.0	0.0	1.5	0.0	0.0
Anguillidae	0.0	0.0	0.0	1.0	0.0	0.0
Belonidae	0.0	0.0	3.0	0.0	0.0	0.0
Clupeidae	32.4	6.3	34.6	59.4	66.9	95.7
Cottidae	0.0	0.0	0.4	12.1	0.0	0.0
Gadidae	0.0	12.2	38.5	19.3	1.7	1.4
Gasterosteidae	0.0	0.3	0.1	0.0	0.0	0.0
Gobiidae	0.2	0.8	0.0	0.0	0.0	0.0
Pholidae	0.0	0.5	0.0	0.0	0.0	0.0
Pleuronectidae	0.4	3.1	0.1	0.0	6.0	0.0
Salmonidae	0.0	0.0	0.0	0.0	0.0	1.6
Zoarcidae	0.0	0.4	0.0	0.0	0.0	0.0
Total fish	33.0	23.7	76.8	93.3	74.6	98.7

Figure 2. Important species groups contributing to the differences in species composition (biomass) in cod stomachs between cod caught in (a) Öresund spring, (b) Simrishamn summer, and (c) Simrishamn autumn. The first two axes of the CAP analyses are visualized, and the axes are based on Bray–Curtis distances for relative biomass in cod stomachs, with type of gear as the explanatory factor.

with the contents of each stomach adding up to 100%. Parasites and other structures, such as vegetation and stones, were excluded and assumed to have ended up in the cod stomachs through secondary consumption, i.e. from cod prey stomachs.

Further, unidentified fish and crustaceans were removed to prevent influencing the ordination and were, therefore, excluded from the total percentage per stomach. To test statistically for differences in diet composition between pot- and gillnet-caught cod, a permutational multivariate analysis of variance (PerManova) was conducted on the Bray–Curtis dissimilarity index, blocking for occasion as strata to remove the influence of diet differences through occasion.

Stable isotopes

Between 19 and 30 cod were sampled for each sampling occasion and gear type for isotope analysis (Table 4). Only individuals with non-empty stomachs (Table 5) were considered. The entire size range of cod caught at each occasion was covered in order to reduce potential bias from size-dependent feeding, as individuals generally increase in trophic position as they increase in size. Size differences between net- and pot-caught cod, within location, were tested using an ANOVA.

Muscle tissue samples ($1 \, cm^3$) were dried for a minimum of 48 h at 60°C. Dried samples (0.8–1.0 mg) were sent to Lund University Stable Isotope Facility (Lund, Sweden) for analysis of $\delta^{15}N$ and $\delta^{13}C$ using an isotope ratio mass spectrophotometer (Thermo DELTA V with ConFlo IV; Thermo Fisher Scientific, Waltham, MA). Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 were used as standards for carbon and nitrogen, respectively. Duplicates of 10% of the samples revealed analytical error of $0.38 \pm 0.54‰$ for $\delta^{15}N$ and $0.30 \pm 0.32‰$ for $\delta^{13}C$ (mean $\pm$ 1 SD).

For stable isotope analysis, ratios were calculated using Equation (4):

$$\delta^{13}C \text{ or } \delta^{15}N = ([Rsample/Rstandard] - 1) \times 1000. \quad (4)$$

Typically, $\delta^{15}N$ is enriched by ca. 3–4‰ with each succeeding trophic level in the foodweb (Deniro and Epstein, 1981; Peterson and Fry, 1987; Post, 2002). The carbon isotope $\delta^{13}C$ can be used as a proxy for the carbon source origin as it varies with resource type because of differences in photosynthetic pathways, but stays relatively intact through trophic transfer (Peterson and Fry, 1987; McCutchan *et al.*, 2003; Fry, 2006). Trophic fractioning in $\delta^{13}C$ is 0.5–1‰ (Deniro and Epstein, 1981; Peterson and Fry, 1987; Post, 2002). Carbon originating in pelagic phytoplankton has a low (i.e. more negative) $\delta^{13}C$, whereas the benthic and littoral zones are more enriched in $\delta^{13}C$ (i.e. less negative $\delta^{13}C$). In this study, the deep habitat was expected to display a lower $\delta^{13}C$ signal as it was dominated by a carbon source originating in phytoplankton, and the shallow habitat a higher $\delta^{13}C$ signal because of its connection to the littoral zones.

Differences in isotopic signal between occasions and gear were tested using ANOVA for $\delta^{15}N$ and Scheirer–Ray–Hare for $\delta^{13}C$. To test for within-occasion, linear regression was used with gear type as factor and length covariate. To analyse isotopic niche width, a Bayesian approach introduced by Jackson *et al.* (2011) was applied. The method is based on an ellipse-based variance estimation metric, called standard ellipse area (SEA_B), in a bivariate isotopic space formed by values of $\delta^{15}N$ and $\delta^{13}C$, with the output SEA_B being two-dimensional analogues of standard deviation. SEA_B consider all individual niches within a population sample and can be used for groups of unequal sample size. The methodology is an expansion of the convex hull metrics (Layman *et al.*, 2007).

Table 4. Sample size and isotope metric ranges for pot- and gillnet-caught cod on the three sampling occasions.

Occasion	Gear	n	$\delta^{15}N$	$\delta^{13}C$	SEA_B
Öresund, spring	Pot	29	14.1–17.9	−21.3 to −18.7	1.39 ± 0.27
	Gillnet	22	13.5–16.3	−21.3 to −19.2	1.52 ± 0.33
Simrishamn, summer	Pot	30	12.1–14.8	−22.1 to −20.2	0.94 ± 0.18
	Gillnet	29	12.0–15.8	−22.3 to −19.7	1.55 ± 0.29
Simrishamn, autumn	Pot	30	14.1–17.9	−25.5 to −18.7	2.86 ± 0.53
	Gillnet	19	13.9–16.3	−21.3 to −19.2	1.45 ± 0.34

SEA_B = standard ellipse area representing isotope niche width for each subgroup.

Table 5. Number of cod individuals (n), Levin's niche width index ($\pm 1\,SD$), and Schoener's index of diet overlap (α), based on wet weight in stomachs per occasion and gear type.

Occasion	Gear	n	Levin's index, $\pm 1\,SD$	Schoener's index (α)
Öresund, spring	Pot	45	1.11 ± 0.28	0.66
	Gillnet	80	1.31 ± 0.53	
Simrishamn, summer	Pot	93	1.23 ± 0.37	0.75
	Gillnet	67	1.19 ± 0.36	
Simrishamn, autumn	Pot	85	1.41 ± 0.48	0.63
	Gillnet	90	1.33 ± 0.55	

The convex hull uses the total niche of all individuals and is thus more sensitive to differences in sample size than SEA_B. Therefore, SEA_B was used to visualize the trophic niche of the cod caught with each of the two gear types and on the three occasions. Calculations were performed using the SIAR package (v. 4.2) in R (Parnell *et al.*, 2010).

Statistical analysis

All statistics were performed using R (v. 3.4.3), (R Core Team, 2017).

Results

Condition and length variations

In all 498 cod were caught and used for Fulton index analysis (Table 1, Figure 3). Data showing on non-normality (K–S test; Fulton: $D = 0.6635$, $p < 0.001$; Length: $D = 1$, $p < 0.001$), There were no size differences between cod caught with the different gear types in the Öresund spring ($W = 1918$, $p = 0.17$) and Simrishamn autumn ($W = 2870$, $p = 0.24$) samplings, but a tendency for larger cod in pots in the Simrishamn summer sampling ($W = 5056.5$, $p = 0.051$). Regression analyses on differences in Fulton index regarding gear type and fish length for the three occasions (Öresund spring, Simrishamn summer, and Simrishamn autumn) revealed that gear type had a significant effect on the Fulton index for all three sampling occasions, with cod caught in gillnets being in better condition than pot-caught cod (Table 1; Öresund spring: $F_{1,110} = 8.73$, $p < 0.01$; Simrishamn summer: $F_{1,184} = 13.38$, $p < 0.001$); and Simrishamn autumn: $F_{1,154} = 10.53$, $p < 0.01$), (Figure 4). The Fulton index over the length interval of cod caught in the different occasions revealed a difference in Öresund spring ($F_{1,110} = 19.06$, $p < 0.001$) and Simrishamn autumn ($F_{1,154} = 16.71$, $p < 0.001$), whereas there was no difference in the Simrishamn summer sampling ($F_{1,184} = 0.98$, $p = 0.32$; Figure 4). For none of the sampling occasions was there any interaction effect between gear type and length of cod (Öresund spring: $F_{1,110} = 2.02$, $p = 0.16$; Simrishamn summer: $F_{1,184} = 0.14$, $p = 0.70$); and Simrishamn
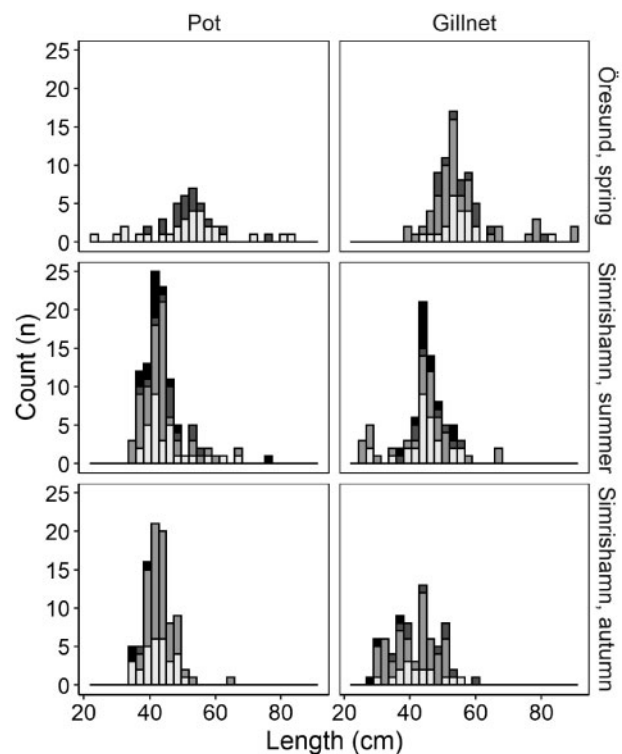

Figure 3. Number of cod (stacked) used in the different analyses (black, condition; dark grey, stomach content analyses; light grey, CAP analysis; and white, stable isotopes) for the two gear types, pots, and gillnet, and the three different occasions, Öresund spring, Simrishamn summer, and Simrishamn autumn. With the same individuals used throughout the study, the amount used within each analysis was narrowed down from the total amount used in the former analysis.

autumn: $F_{1,154} = 0.33$, $p = 0.57$; Figure 4), indicating that both gear types selected for the same fitness range over the whole length interval.
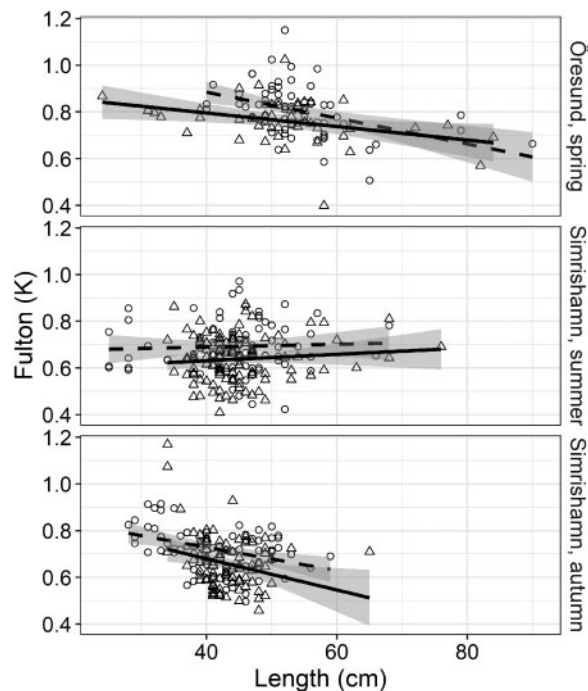
Figure 4. Fitness (Fulton *K*) for all cod individuals used in the condition analysis based on cod length (cm), gear type; pots (triangles) and gillnet (circles), faceted by occasion (Öresund spring, Simrishamn summer, and Simrishamn autumn). Solid trend lines for pots and dashed for gillnet.

Stomach contents

Of the initial 498 cod, 460 were used in the diet and niche analyses (Table 5, Figure 3), as remaining stomachs were either empty or their contents fully digested. Presence of prey resource groups in cod diet are presented in Table 3 and are sorted alphabetically, divided into invertebrates and fish. Stomach content weights were not normally distributed, which is why ANOVA results were ranked using the Scheirer–Ray–Hare test. Digestion rate analyses indicated a significant difference in the weights of stomach contents independently of soak days ($H = 6.93$, $p < 0.01$), with higher content weight in gillnet-caught cod (Table 2). However, neither soak days ($H = 1.58$, $p = 0.21$) nor the interaction between gear type and soak days ($H = 1.38$, $p = 0.24$) was significant. There was no tendency for faster digestion of smaller species groups like isopods and mysids in cod caught in pots with longer soak-time (Table 2), which is why it was assumed that soak-time as an independent factor did not substantially affect the outcome of stomach data analyses.

Niche width: stomach data

In Öresund, cod caught in gillnets had a larger diet niche than cod caught in pots ($W = 2264$, $p < 0.05$), (Table 5). No difference between gear types was detected for either of the sampling occasions at Simrishamn (summer: $W = 2902$, $p = 0.43$ and autumn: $W = 24556$, $p = 0.16$).

Diet overlap: stomach data

Schoener's index of dietary overlap (α), based on prey presented in Table 3, revealed an overlap of 0.66 for the Öresund spring

samples. In Simrishamn, the index was 0.75 and 0.63 for summer and autumn samples, respectively, indicating a high dietary overlap (Langton, 1982) for all three occasions (Table 5).

Ecological distance: stomach data

In total, the contents of 397 cod stomachs were used in the CAP ordinations (Figure 3), 96 from Öresund (67 for gillnet- and 29 for pot-caught cod), 139 from Simrishamn in summer (57 for gillnet- and 82 for pot-caught cod), and 162 from Simrishamn in autumn (78 for gillnet- and 84 for pot-caught cod; Figure 2a–c). The overall results of the CAP ordinations indicate differences in diet composition (in relative biomass) between cod caught in pots and gillnets as well as differences in diet between occasions. The first axis from the CAP analysis for the Öresund spring sample separated cod based largely on a diet of clupeids (mainly *C. harengus*) for pot-caught cod and of portunids: *Carcinus maenas* (shore crab) for gillnet-caught cod. The first two axes from both CAP analyses (the two axes in the graphs in Figure 2, i.e. CAP 1 and CAP 2) based on individuals from the Simrishamn samples separated cod based largely on a diet of clupeids (herring) for gillnet-caught cod and of isopods in summer and cumaceans and mysids in autumn for pot-caught cod. In other words, pot-caught cod in Öresund had larger proportions of herring and sprat than did gillnet-caught cod, whereas the reverse was the case in Simrishamn.

PerManova results, including all occasions, revealed a significant difference in relative prey species biomass contribution between stomach contents of pot- and gillnet-caught cod, i.e. PerManova: d.f. $= 1$, F model $= 5.34$, $r^2 = 0.014$, $p < 0.001$ (blocking for occasion as strata).

Stable isotopes

In all 159 cod were used in the stable isotope analyses (Table 4, Figure 3). The size range of those cod differed only between sampling occasions ($F_{2,150} = 28.2$, $p < 0.001$), whereas no difference was found between gear types ($F_{1,150} = 0.28$, $p = 0.54$) within occasions, with cod in Öresund being generally larger than cod caught in Simrishamn during both summer and autumn ($p < 0.001$). Cod length did not differ between the two Simrishamn sampling occasions ($p = 0.28$).

The $\delta^{15}N$ fraction level for cod ranged between 12.0 and 17.9‰, whereas the $\delta^{13}C$ level ranged between -25.5 and -18.7‰ (Table 4). The nitrogen signal, proxy for trophic level, differed between both gear types ($F_{1,155} = 10.66$, $p < 0.01$) and occasions ($F_{2,155} = 90.23$, $p < 0.001$). Analyses on within-occasion differences in nitrogen fraction by gear types and fish length revealed a difference between gear types in the Öresund spring sampling ($F_{1,47} = 4.81$, $p < 0.05$) and the Simrishamn autumn sampling ($F_{1,42} = 4.90$, $p < 0.05$), where pot-caught cod had a higher nitrogen signal than gillnet-caught cod. For the Simrishamn summer sampling, there was no difference in nitrogen signal between the two gear types ($F_{1,55} = 0.54$, $p = 0.47$). Differences in nitrogen fractioning over cod length interval revealed a higher nitrogen signal with increasing size in the Simrishamn summer sampling ($F_{1,55} = 9.37$, $p < 0.01$), whereas there was no difference over the length span in Öresund spring ($F_{1,47} = 0.07$, $p = 0.79$) and Simrishamn autumn ($F_{1,42} = 0.01$, $p = 0.091$). For the nitrogen fractioning, there was no interaction effect between the combination of gear type and length at any sampling occasion (Öresund spring: $F_{1,47} = 3.44$, $p = 0.07$;

Simrishamn summer: $F_{1,55} = 0.65$, $p = 0.42$; and Simrishamn autumn: $F_{1,42} = 0.36$, $p = 0.85$), indicating that both gear types selected for the same fitness range over the whole length interval. For carbon, no gear-type differences were detected (Scheirer–Ray–Hare test: $H = 0$, $p = 0.94$), but significant differences were detected between occasions (Scheirer–Ray–Hare test: $H = 80.4$, $p < 0.001$). For all sampling occasions, the SEA_B overlapped between the two gear types (Figure 5a, 43%; Figure 5b, 100%; and Figure 5c, 66%).There was no difference in Öresund ($p = 0.39$), whereas pot-caught cod had a smaller niche width than did gillnet-caught cod ($p < 0.05$) in the Simrishamn summer sampling ($p < 0.05$). For the Simrishamn autumn sampling, pot-caught cod had a greater niche width than did gillnet-caught cod ($p < 0.001$).

Discussion

This study showed that the lower condition observed for cod caught in pots in relation to gillnets, initially described by Ovegård et al. (2012), are not a local phenomenon as similar patterns also occur in other areas in the Baltic Sea. Further, this study indicated that there is a divergence in short-term foraging patterns between cod caught in the two gear types, although they primarily feed on similar prey species, with differences partly notable also in long-term diet patterns.

Mean length did not vary between cod caught in the different gear types, only between occasions; however, there was a difference in Fulton index (K) over the length interval in the Öresund spring and Simrishamn summer sampling, where larger cod had lower fitness. An assumption could be that gillnets would target smaller individuals with higher Fulton index and larger individuals with lower Fulton index, as catchability is tightly connected to girth width. Knowledge of condition-induced differences in selectivity is, however, generally lacking from the literature. None of the interactions for any of the occasions of gear type and length on Fulton K showed any differences (Figure 4). If an interaction effect would have been present, there would be a difference in the regression slopes between the two gear types, ultimately meaning that different gears would catch cod with different fitness over the length span. If so, difference in fitness (K) could be linked to differences in gear selectivity on size and condition between the two gear types. In this study, several cod caught in gillnets were below the minimum landing size (38 cm), down to 25 cm in the Simrishamn summer sampling (Figure 1). Mean length of gillnet-caught cod in Simrishamn summer was 44.4 cm with a K-value of 0.69 (Table 1). The smallest sized cod caught in gillnets had a K-value of 0.6 (Figure 4), indicating that gillnets may catch smaller cod also with lower fitness. With non-significant interaction effect along with catch of smaller cod with low fitness, we argue that both pots and gillnets fish on the same population of cod with similar size selectivity, within sampling occasions.

In a general perspective, active fish will have a higher encounter rate with passive fishing gear, such as pots and gillnets, than less active fish (Biro and Post, 2008; Uusi-Heikkilä et al., 2008). A possible explanation for the lower condition of cod caught in pots is that fish in poorer condition may respond more strongly to bait stimuli than fish in better condition. Previous studies have shown how fish that have experienced uncertainty in resource availability express more boldness in their foraging behaviour
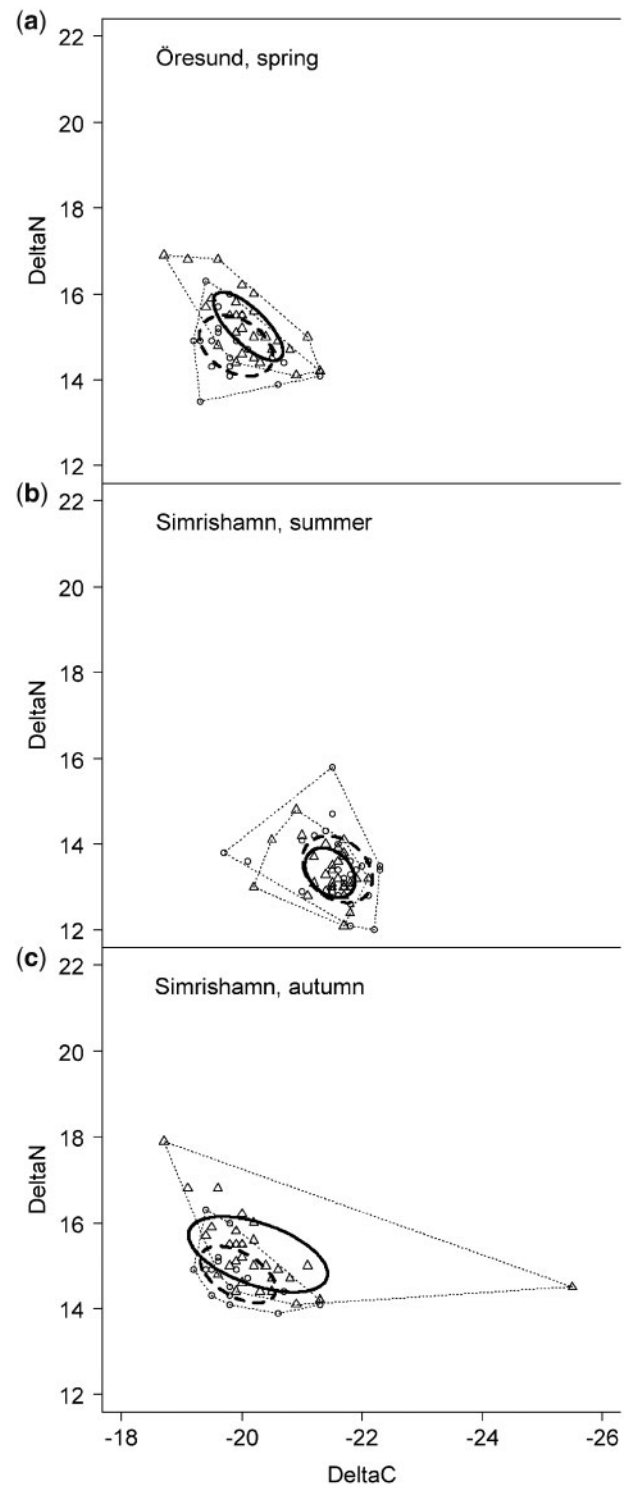

Figure 5. Bi-plots of $\delta^{15}N$ and $\delta^{13}C$ contents in cod caught in (a) Öresund spring, (b) Simrishamn summer, and (c) Simrishamn autumn, with triangles indicating pot-caught cod and circles gillnet-caught cod. Dashed lines are convex hulls representing total niche width, following Layman et al. (2007). Ellipses are standard ellipse areas (SEA_B) representing isotopic niches, following Jackson et al. (2011), for the three occasions and two gear types, where dashed lines are pot-caught and solid lines are gillnet-caught cod.

(Damsgard and Dill, 1998; Chapman *et al.*, 2010; Sébastien *et al.*, 2016). Also, bold and aggressive individuals are less likely to hide and generally take more risks when foraging (Brauhn and Kincaid, 1982; Cooke *et al.*, 2007; Biro and Post, 2008). Entering a pot is a novel experience for the individual, which may call for higher willingness, with entrance size and hunger-level function as limiting factors (Stoner *et al.*, 2006; He, 2010). Hence, hungrier fish, which are in poorer condition, may be more likely to enter baited pots, whereas gillnets may catch a wider variety of individuals.

As stable isotope signatures may differ both temporally and spatially, comparisons between areas and over time should not be done without resource baseline correction (Deniro and Epstein, 1981; Peterson and Fry, 1987), which is why this paper focuses on within-occasion effects. With no difference in carbon isotopic signature δ13C between fish caught in gillnets and pots, the results indicate that cod utilize food resources with the same carbon source pathway. Stomach content weight differed only between gear types, but was not dependant on the number of soak days, with smaller prey present in pot and gillnet cod stomachs, even for fish caught in pots soaked for 3 days (Table 2). This might be explained either by a low digestion rate or, more likely, that cod enter pots throughout their entire soak-time. The latter is supported by an earlier study on cod pots in the Baltic sea, where optimal soak-time for cod ranged up to 8 days (Königson *et al.*, 2015a).

In Simrishamn on both occasions (Table 3, Figure 2b and c), small crustaceans were more common prey of pot-caught cod, whereas fish were more common prey of gillnet-caught cod. The diet patterns in Simrishamn indicate that the pot- and gillnet-caught cod utilized somewhat different parts of the foodweb, with pot-caught cod eating more benthic prey and gillnet-caught cod eating more pelagic prey (Table 3). Optimal foraging theory predicts that a predator should use a strategy that maximizes its energy intake per unit time, regulated by the diversity of available prey (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). However, co-occurring individuals might consume different prey, leading to between-individual differences in diet. The reason for this can be found in different prey rank preferences induced by differences in ability to detect, capture, handle, and/or digest prey, but also because of some individuals choosing prey to minimize predation risk, whereas other individuals are less risk averse and act only to maximize energy intake.

Why nitrogen patterns differ between the two sampling occasions in Simrishamn is more difficult to explain. Nitrogen values varied by 2‰ between sampling occasions, corresponding to ca. half a trophic level (Post, 2002). One explanation is that cod in autumn consume prey with a higher trophic position not present during summer, a matter that is difficult to control for without baseline correction. Another explanation could be starvation, which several studies have demonstrated that it progressively enriches δ15N levels (Hobson and Welch, 1992; Hertz *et al.*, 2015; Varela *et al.*, 2015). As the Fulton index value was lower in pot-caught cod, while nitrogen was enriched, starvation, as proposed by Eero *et al.* (2012), may be a plausible cause of our observations in the Simrishamn autumn sampling. This may ultimately be driven by food limitations and oxygen depletion (Schaber *et al.*, 2009) in the benthic environment during the months before sampling, resulting in a reversal of the nitrogen signal between summer and autumn.

Also, cod from Simrishamn were generally in poorer condition than cod from Öresund (Table 1), indicating that cod in

Simrishamn are food-limited, which is consistent with recent studies in the area (Eero *et al.*, 2012). Additionally, the combination of absent benthic prey, such as shore crab, mainly because of lower salinity, along with widespread oxygen depletion may force cod to search for additional prey (Eero *et al.*, 2011). When preferred prey are scarce, individuals which for genetic or environmental reasons are in poorer condition and are, therefore, unable to exploit the most profitable prey, shift their selection to other prey categories (Costa *et al.*, 2015), resulting in a diet with a lower net energy gain (Milinski, 1982). The absence of larger benthic prey in Simrishamn makes clupeid species, because of their high energetic content (www.fishbase.org) a profitable diet choice. However, pot-caught cod had a diet consisting more of smaller prey; this indicates a possible lower net energetic return, negatively affecting cod condition and potentially resulting in more meagre fish.

In Öresund, where prey are plentiful, the differing nitrogen values between gear types may be because of separation in prey resource use, in accordance with short-term consumption patterns showing that gillnet-caught cod had more crustaceans in their stomachs (Table 3). Applying optimal foraging theory to Öresund cod, the difference could be explained by the abundance of shore crabs, large prey with a potentially high net energy gain in relation to handling time. Also, the benthic environment to which the shore crabs are bound also provides a refuge for cod from predation, potentially making it a preferred habitat choice. Pot-caught cod consumed more pelagic fish, which may be rewarding from an energetic perspective, but exposes the cod to a higher risk of predation. The condition of pot-caught cod may thereby be explained by differences in prey-search behaviour and boldness in relation to gillnet-caught cod.

Summary

This study illustrates how condition, diet composition, and, partially, isotopic patterns differed between pot- and gillnet-caught cod. Carbon isotopic signatures indicated that all cod utilize the same primary production sources, meaning that they use the same habitat, also over time, which may indicate that cod in the Baltic Sea are structured into phenotypes diverging in diet and potentially behavioural traits. Comparison of the nitrogen isotope δ15N and stomach contents indicated seasonal starvation patterns in which cod are forced to prey on unfavourable prey, generating lower energetic return. Recent studies have stressed that difference in foraging behaviour is associated with behavioural types also in fish (Mittelbach *et al.*, 2014), which may have implications for how cod are exposed to various fishing gear types (Berndt, 2006; Ovegård *et al.*, 2012). This effect may be a driver for the differences in cod diet between fishing gear types. Bolder individuals may be more likely to enter pots (He, 2010; Mittelbach *et al.*, 2014), which, along with a more opportunistic foraging approach, may lead to energetic depression and deterioration in condition through the consumption of energetically inferior prey when resources are scarce. By extension, recreational and commercial fishing is known to potentially affect population characteristics based on subpopulation differences in susceptibility to gear types, which has implications for fishery management and the use of different fishing gear (Biro and Post, 2008; Uusi-Heikkilä *et al.*, 2008; Diaz Pauli and Sih, 2017). Further research on diverging foraging behaviour also under food-deprived conditions and on other forms of intrapopulation niche variation in relation to gear-type selectivity would improve our understanding

of the complexity and evolution of such ecological interactions. We, therefore, stress the importance of considering the diet of targeted species, along with awareness of individual behavioural traits, but also potential genetic effects in the development and evaluation of fishing gear.

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