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1 **Title:** Disparate movement behaviour and feeding ecology in sympatric ecotypes of Atlantic cod

2 **Short title:** Behaviour and feeding ecology of Atlantic cod

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14

15 **Abstract:**

16 Co-existence of ecotypes, genetically divergent population units, is a widespread phenomenon,
17 potentially affecting ecosystem functioning and local food web stability. In coastal Skagerrak,
18 Atlantic cod (*Gadus morhua*) occur as two such co-existing ecotypes. We applied a combination of
19 acoustic telemetry, genotyping and stable isotope analysis to 72 individuals to investigate movement
20 ecology and food niche of putative local “Fjord” and putative oceanic “North Sea” ecotypes – thus
21 named based on previous molecular studies. Genotyping and individual origin assignment suggested
22 41 individuals were Fjord and 31 were North Sea ecotypes. Both ecotypes were found throughout the
23 fjord. Seven percent of Fjord ecotype individuals left the study system during the study while 42 %
24 of North Sea individuals left, potentially homing to natal spawning grounds. Home range sizes were

25 similar for the two ecotypes but highly variable among individuals. Fjord ecotype cod had
26 significantly higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values than North Sea ecotype cod, suggesting they
27 exploited different food niches. The results suggest coexisting ecotypes may possess innate
28 differences in feeding- and movement ecologies and may thus fill different functional roles in marine
29 ecosystems. This highlights the importance of conserving interconnected populations to ensure stable
30 ecosystem functioning and food web structures.

31

32 **Keywords:** Atlantic cod, behaviour, ecotypes, stable isotopes, telemetry, trophic ecology

33

34 **Introduction**

35 The evolutionary divergence of ecotypes is common in both terrestrial and aquatic ecosystems and
36 represents an important component of intraspecific diversity. A large body of empirical and
37 theoretical studies have examined the evolution of ecotypes, for instance in the context of ecological
38 speciation (Hendry, 2017). Ecotype variation may also have wide-ranging consequences for
39 ecosystems. For instance, anadromous salmon ecotypes support freshwater- and terrestrial
40 ecosystems by transporting large amounts of nutrients from oceanic ecosystems as part of their
41 feeding- and spawning migration (Carlson et al., 2011). Understanding potential eco-evolutionary
42 effects of ecotype variation is therefore highly relevant for conservation and management.

43

44 The Atlantic cod (*Gadus morhua*) is an iconic marine fish found across coastal and offshore shelf
45 areas in the North Atlantic Ocean. Traditionally, a variety of morphs and life history forms have been
46 recognised (Sherwood & Grabowski, 2010; Karlsen et al., 2013). Migratory forms in e.g. Northern
47 Norway, Iceland and Canada utilize shallow or coastal areas for spawning and open oceans for
48 feeding while sedentary forms in e.g. Iceland, Canada and Southern Norway are fjord residents during

49 most of their lifecycle (Pálsson & Thorsteinsson, 2003; Wroblewski et al., 2005). Parallel to this,
50 different colour morphs may represent variants with overlapping distribution areas but different
51 preferences in terms of food or habitat (Gosse & Wroblewski 2004). In Skagerrak, southern Norway,
52 two genetically differentiated ecotypes coexist within coastal habitats. Individuals assigned to the
53 “North Sea” ecotype are genetically similar to cod sampled from offshore spawning grounds in the
54 North Sea and most likely conform to this population, in contrast to assignments to local “Fjord”
55 ecotype more commonly sampled from inshore coastal populations (Knutsen et al., 2018). This
56 evolutionary divergence of the Fjord- and North Sea ecotypes could in fact represent intermediate
57 stages of an ecological speciation process (Roney et al., 2018). However, the genomic inversions that
58 separate the two ecotypes (Sodeland et al., 2016) which might be both old and stable, represent
59 potential for persistent local adaptations and limited scope for sub-population mixing (see Barth et
60 al., (2019)). Even within similar habitats such as eelgrass beds or kelp forests, the North Sea ecotype
61 typically grows faster and reaches a larger juvenile body size compared to the fjord ecotype (Knutsen
62 et al., 2018; Jørgensen et al., 2020), suggesting that they may have different ecological roles,
63 including feeding- and behavioural strategies. Also, there is empirical support for the North Sea
64 ecotype having lower fitness (survival) in the fjord environment compared to the local fjord ecotype
65 (Barth et al., 2019).

66 Cod is recognised as a cornerstone species and dominant top predator that may shape the trophic
67 structure and function of marine ecosystems. When cod populations collapsed in Atlantic Canada,
68 there was a correlated change in fish biodiversity affecting the stability of the entire ecosystem
69 (Ellingsen et al., 2015). In coastal Skagerrak, the decline of cod has been linked to a trophic cascade
70 leading to the degradation of nearshore seagrass and seaweed habitats (Östman et al., 2016). There
71 could be a negative feedback loop on cod recruitment linked to this trophic cascade, since seaweed,
72 and particularly the seagrass habitats, represent high-quality nursery areas where juvenile cod have

73 larger growth compared to more barren habitats (Knutsen et al., 2018). Cod fisheries in Skagerrak are
74 highly diverse and involves a significant recreational fishery as well as commercial fishing (Kleiven
75 et al., 2016; Fernández-Chacón et al., 2017). Both fisheries mainly catch the North Sea ecotype,
76 probably reflecting the Fjord ecotype being in a depleted state (Knutsen et al., 2018; Jorde, Kleiven
77 et al., 2018). Therefore, there is an urgent need to understand the ecological function of the fjord
78 ecotype compared to the oceanic North Sea ecotype.

79

80 Here, we explore the detailed movement ecology and trophic role of the Fjord and North Sea ecotypes
81 within a fjord system. To this end, we apply a novel combination of acoustic telemetry, population
82 genetics and stable isotope analyses. We hypothesise that the Fjord ecotype will display a more
83 resident behaviour in the inner parts of the fjord compared to the North Sea ecotype. Based on current
84 knowledge about juvenile growth rates (Jørgensen et al. 2020), we also anticipate that the two
85 ecotypes will have different trophic niches.

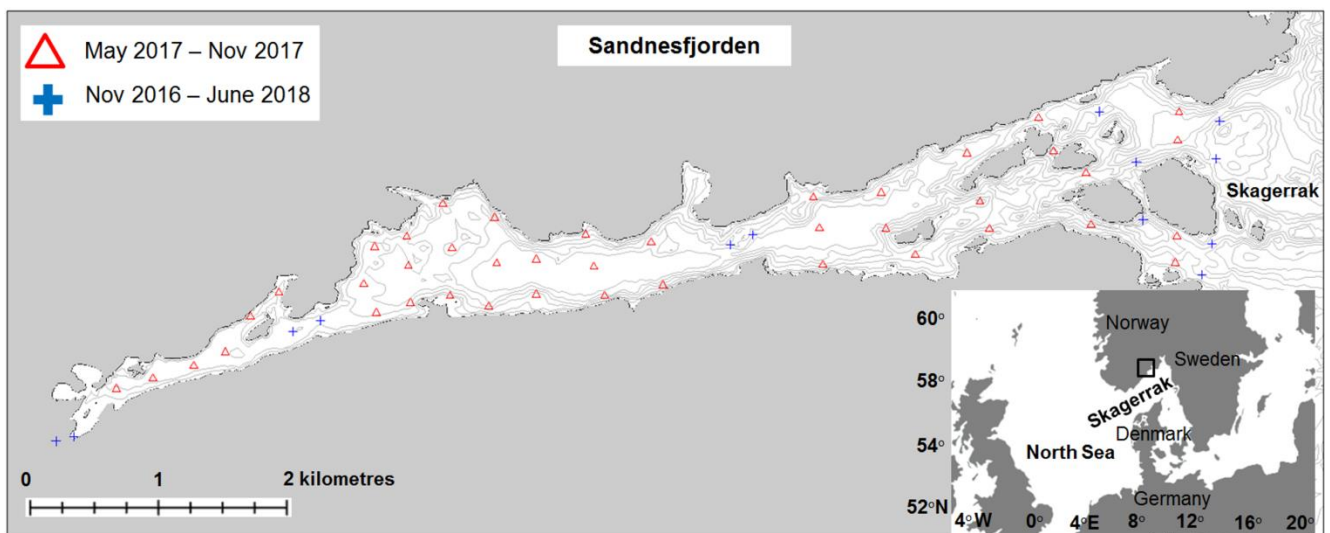
86

87 **Materials and Methods**

88 **Study area**

89 The study took place in the Sandnesfjord, a nine km long fjord system located on the southern coast
90 of Norway (Figure 1). The Sandnesfjord is 70 metres deep at the deepest point and has a mixture of
91 bottom substrate types including hard and soft sediments and areas with submerged macrophytes.
92 The system was chosen for its relative narrowness, easing instrumentation of the system, and because
93 the data reported by (Knutsen et al., 2018) suggested the fjord would contain a mixture of the North
94 Sea and Fjord ecotypes.

95 Tidal amplitude of the system is 0.5 metres on average. The surface current may be outgoing even
96 during rising tides in periods with high freshwater runoff from rivers and streams entering the fjord
97 and mixing poorly with more saline waters deeper down. The surface salinity is roughly 8-12 PSU in
98 the inner fjord and 15-18 PSU in the outer fjord, while waters below a depth of roughly 6 metres have
99 a relatively stable salinity around 30-32 PSU.



100
101 **Figure 1.** Map of the Sandnesfjord with red triangles representing positions of receivers in the array and blue crosses
102 representing positions of receivers deployed throughout the study period.

103

104

105 **Instrumenting the fjord**

106 During October 2016, 13 acoustic receivers (Vemco VR2W, www.innovasea.com) were deployed in
107 the fjord (Figure 1). Six receivers were deployed pairwise at three different transects of the fjord to
108 facilitate an overall survey of what part of the fjord the different fish preferred to reside in. Two
109 receiver gates with three and four receivers, respectively, were deployed in the outer part of the fjord
110 to track movements of tagged fish in and out of the fjord system. The maximum detection distance to
111 a receiver at the outermost transect was 130 metres. Data was downloaded from the receivers in May,
112 September and November 2017 and in June 2018.

113 From May to November 2017, the receiver setup was expanded to an array covering the entire fjord
114 when an additional 42 receivers (Thelma TBR 700, www.thelmabiotel.com) were deployed in the
115 fjord system for another study. This provided more detailed position estimates of the tagged fish that
116 were still residing in the fjord during this period. The array was not set up to perform precise 3D
117 position estimates, but the array-data could be used to provide position average estimates.

118 All receivers included in the study were deployed by anchoring the receiver to the bottom. The
119 receivers were kept afloat, c. three metres below the surface by an 8" float. Receivers and floats were
120 covered in anti-fouling paint to prevent sinking and reduced detection range due to biofouling.

121

122 **Sampling and tagging**

123 104 cod were caught in collaboration with a local fisher using fyke nets on various locations at depths
124 ranging between 1-8 metres throughout the fjord between October 25th and November 17th 2016.

125 Immediately after capture, the fork length of each fish was measured with a precision of 1 cm and a
126 small fin-clip was taken and stored in Eppendorf tubes containing ethanol to enable genetic origin
127 assignment. Only fish measuring above 33 cm in length were sampled and tagged in order to narrow
128 the size distribution of the fish included in the study. Apart from size, no selection was made on which

129 fish to include, except for one individual that was bleeding from a severe injury, probably incurred
130 by a seal, and therefore discarded. The fish included in the study were tagged with a T-bar tag
131 (Hallprint TBA2, 30 X 2 mm) printed with a serial number, return address, and a reward notice, and
132 transported to a holding facility while being kept in a livewell on the boat. The holding facility
133 consisted of fine-meshed nets attached to a pontoon, enabling the fish to reside at depths down to four
134 metres while waiting to be tagged.

135 After a mean holding period of 13.2 days (range: 3 – 34 days) the fish were tagged with acoustic
136 transmitters after being anesthetized with clove oil until the opercular rate became slow and irregular
137 (2-4 min). An experienced fish surgeon tagged the fish with 9 mm Thelma acoustic tags (ID-LP9L
138 tags, www.thelmabiotel.com, 24 mm length by 9 mm diameter, 4 g in air, 2.5 g in water, transmitting
139 with 142 dB re 1 uPa at 1m) through a small incision on the ventral surface of the peritoneal cavity.
140 The tags transmitted a unique ID at a random interval between 30 - 90 seconds (mean: 60 seconds)
141 and had an expected battery life of 18 months.

142 The incisions were closed with two absorbable sutures and a small (≈ 0.05 g) muscle biopsy was
143 obtained from the dorsal region of each individual and stored in ethanol for subsequent analysis of
144 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the fish. Fish were then left to recover in 200 L containers of fresh fjord
145 water. The operation lasted between one and two minutes and the recovery time was 2-5 minutes. All
146 tagged fish recovered from the procedure and were subsequently transported back and released at
147 each of their respective sites of capture. All procedures were carried out in accordance with
148 permission no. 6037 issued by the Norwegian Food Safety Authority.

149

150 **Muscle sample analysis**

151 Muscle tissue samples from biopsies of the 50 fish that generated data on the array deployed between
152 May and November 2017 were analysed with regard to stable carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$

153 and $\delta^{15}\text{N}$). Muscle samples were dried in aluminium foil trays at 45°C for 2-3 days. After drying, the
154 samples were crushed and duplicate samples of 0.38 ± 0.1 (SD) mg tissue were packed in tin (Sn) cups
155 for stable isotope analysis. All samples were analysed at Department of Bioscience, Center for
156 Geomicrobiology, University of Aarhus, Aarhus Denmark. The samples were measured by means of
157 Isotope Ratio Mass Spectrometry (IRMS) in combination with an Element Analyzer (EA) and an
158 operational interface (Thermo Electron Corporation Flash EA 1112 series and Thermo Scientific Delta
159 V Plus Isotope Ratio MS).

160 The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were standardised using a Gelatine A (Gel-A) standard with known isotopic
161 values of $\delta^{15}\text{N} = 5.4\text{‰}$ and $\delta^{13}\text{C} = -21.8\text{‰}$. For each nine or ten muscle tissue samples, three or two
162 internal 0.2-0.7 mg Gel-A standards were analysed. The standards were used to correct for daily
163 offsets and drift by regressing the measured isotope value of the internal standards on run number and
164 correcting all muscle samples using the slope and intercept of this relationship and the known isotopic values
165 of the internal standards. Low sample size bias was also assessed using the standards. The mean of the
166 duplicate samples was used in data analyses.

167

168 **Genetic analysis**

169 A total of 104 tissue samples from candidate cod sampled in Sandnesfjord were genotyped for the
170 present study. Tissue samples were extracted for DNA using the E.Z.N.A MicroElute Genomic DNA
171 Kit (Omega Bio-tek, Norcross, GA), following the manufacturer's instructions for tissue samples with
172 only one minor modification: the last elution buffer step being done twice through the same filter (50
173 μl was eluted). Genomic DNA from juvenile and spawning cod was extracted from a small piece of
174 the dorsal fin, using E.Z.N.A Tissue DNA kit (Omega biotek) following the protocol. DNA from
175 every individual was quality-verified and quantified with a NanoDrop instrument (NanoVue Plus,
176 GE healthcare). 27 SNPs were previously developed to segregate between "Fjord-" and "North Sea"

177 individuals and there were genotyped on a MassARRAY platform (Sequenom Inc.) at the IMR
178 laboratory in Bergen, Norway. Genetic assignment of individual cod to ecotype was computed using
179 the GeneClass2 software (Piry et al., 2004), using previously sampled reference populations of
180 “Fjord” and “North Sea” cod (see (Jorde, Synnes et al., 2018) for additional information). The
181 Bayesian method of (Rannala & Mountain, 1997) was used where a score > 80% is needed in order
182 to classify each individual either as a North Sea ecotype or Fjord ecotype. Omission of scores lower
183 than 80% (n=24) and individuals that were genotyped at <20 SNPs (n=3) from further analysis,
184 resulted in 77 individuals being assigned successfully enabling selection for acoustic tagging. Five
185 individuals had escaped or were potentially predated from the holding facility in the meanwhile,
186 ultimately leading to 72 individuals being tagged.

187

188 **Data analysis**

189 Tagged fish were considered to have left the fjord system if their last detection occurred on one of
190 the receivers in the outer transect (Villegas-Rios et al., 2020). The time of departure from the fjord
191 was defined as the time of the last detection in the outer transect and any subsequent returns to the
192 fjord system were defined as the time of the first detection back at the outer transect.

193 Position averages were calculated with the array data (deployment time May – November 2017) for
194 a total of 50 tagged fish still generating data in the fjord during this time. The position average (in
195 UTM coordinates) of a fish detected a number of times on e.g. receiver X1 and X2 during an i'th 30
196 minute period were acquired as follows (Simpfendorfer et al., 2002):

$$197 \quad Position_i = \frac{(No. detections_{X1} * Coordinates_{X1} + No. detections_{X2} * Coordinates_{X2} \dots)}{(No. detections_{X1} + No. detections_{X2} \dots)}$$

198 The distance to the fjord outlet was calculated for each position average and used in the further
199 analysis. Estimated 95 % home range of each fish was calculated based on the position averages using
200 the minimum convex polygon from the R-package adehabitat (Calenge, 2006). Mean distance to the

201 Skagerrak and the 95 % home range size were entered into general linear models as dependent
202 variables along with fish ecotype (North Sea or Fjord) and fish length. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the
203 tagged fish were entered as response variables to investigate whether behaviour (home range size and
204 mean distance to the Skagerrak), fish size or ecotype could explain any differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
205 values in the fish. Insignificant covariates were dropped from the model. Collinearity between the
206 entered variables were tested with the VIF-function from the car package in R (Fox & Weisberg,
207 2019). Isotopic niche widths were calculated based on residuals from a GLM with isotope value ($\delta^{13}\text{C}$
208 or $\delta^{15}\text{N}$) as response variable and distance to Skagerrak as predictor. Convex hull and standard ellipses
209 were calculated and plotted using the package SIBER v2.1.4 in R (Jackson et al., 2011).
210 Home range sizes were analysed with a general linear model with log transformed home range sizes
211 entered as response variable and ecotype and fish length entered as dependent variables.
212 A gamma distributed linear mixed effects model from the R package glmmTMB (Brooks et al., 2017)
213 with a log link was used to investigate whether fish of different ecotypes preferred residency closer
214 or farther from the Skagerrak than each other throughout the period when the array was deployed.
215 Distance to the fjord outlet was entered as response variable and fish origin (North Sea vs. Fjord),
216 fish size and time since May 1st 2017 were entered as dependent variables.

217

218 **Results**

219 **Tagged fish**

220 Seventy-two cod were sampled, tagged and subsequently released at their capture location in the
221 Sandnesfjord (Table 1 and A1). Thirty-one of these (43 %) were North Sea ecotypes and 41
222 individuals (57 %) were Fjord ecotypes. The fish were caught and released on locations with a mean
223 distance to the Skagerrak of 3.42 km (North Sea fish) and 3.68 km (Fjord fish).

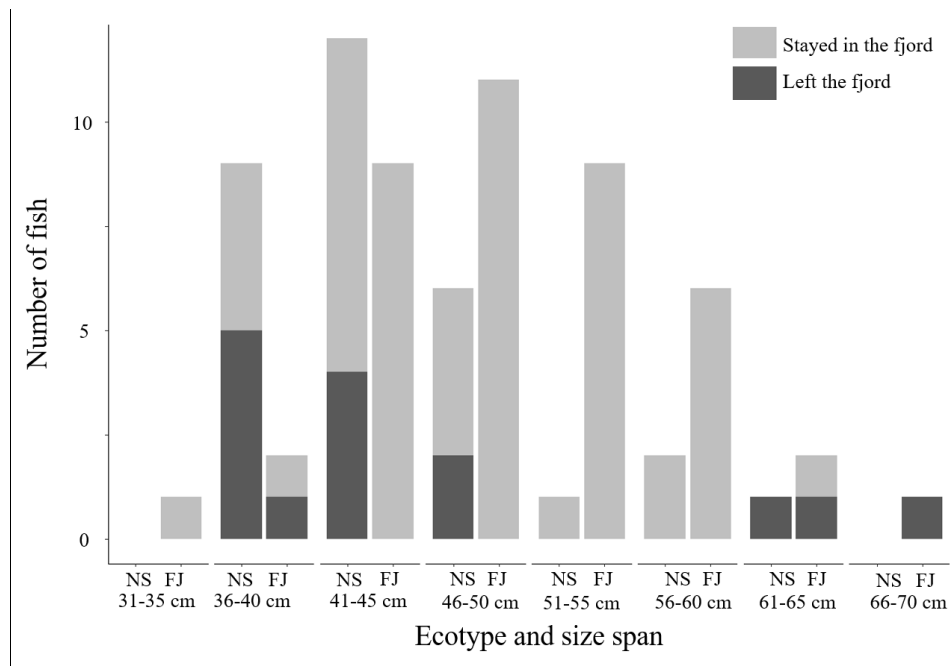
224

225 **Table 1.** Summary data on tagged Atlantic cod *Gadus morhua* of the two ecotypes. Fish lengths were obtained at the time
 226 of capture in autumn 2016. Columns to the left show the data for all tagged fish while columns to the right show the data
 227 for the subset of individuals still alive and present in May-November 2017 when the array was deployed. Detailed
 228 information is reported in Table A1.

All tagged individuals			Fish present in May-November 2017	
Ecotype	N	Mean length (cm)	N	Mean length (cm)
NS	31	44.4 (range: 36-63)	15	44.1 (range: 36-60)
FJ	41	50.0 (range: 33-70)	35	50.4 (range: 33-70)
All	72	47.6	50	48.5

229

230



231

232 **Figure 2.** Size distribution and ecotype (NS = North Sea, FJ = Fjord) of tagged Atlantic cod *Gadus morhua*. Dark grey
 233 shading denotes fish that were detected as having left the fjord during the study period.

234

235

236

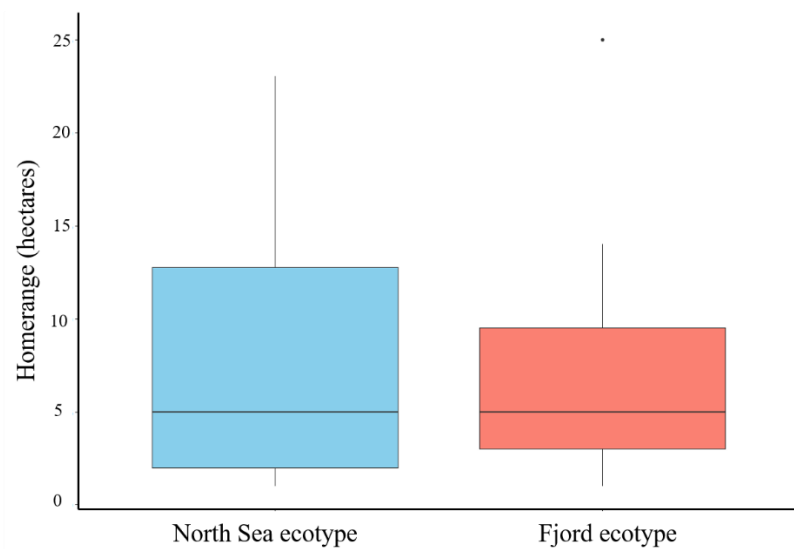
237 **Movement ecology**

238 During the entire study period, 12 North Sea ecotype (39 % of tagged individuals assigned to the
239 North Sea ecotype) and three Fjord ecotype (seven percent of tagged individuals assigned to the Fjord
240 ecotype) left the fjord without returning (Figure 2). In addition, one North Sea ecotype individual left
241 the fjord in December 2016 and returned again in April 2017, meaning that a total of 42 % of tagged
242 North Sea ecotype individuals left the fjord permanently or for a prolonged period of time (months)
243 during the study. Of the fish that left the fjord, nine North Sea individuals and two Fjord individuals
244 did so during the first winter (December 2016 – February 2017), one North Sea fish did so during
245 spring 2017 (March), two North Sea and one Fjord fish did so during summer 2017 (June – August)
246 and one North Sea fish did so in winter 2018 (February). In addition to the fish that left the fjord
247 permanently or for a long period of time, six individuals left the fjord for short periods of time (<2
248 days) during the study period. The fish that left the fjord for short periods of time were generally
249 residing in the outer parts of the fjord system. No fish were detected on the outermost receiver transect
250 without prior detection on the secondary transect located roughly 500 m further into the fjord, and no
251 returning fish were detected on the secondary transect without prior detection at the outermost
252 transect. The efficiency of the receiver gates at the fjord entrance was therefore considered high.
253 The two km long, inner section of the fjord was only rarely used by the tagged fish. Nine fish were
254 detected in this fjord section for short periods of time (<2 days) during the study period while one
255 North Sea individual resided there throughout the study period. The remaining fish that did not leave
256 the fjord system spent all of their time within the seven km of fjord stretching from the receivers at
257 the inner fjord section to the outer receiver line at the Skagerrak boundary.
258 Fifty of the 72 individuals that were tagged and assigned, were still present in the fjord during May -
259 November 2017 when the expanded array was operational. Twelve tagged fish had left before the

260 array was deployed, meaning a total of 10 tagged fish had either died or shed the tag into an
261 undetectable place, left the system undetected or been removed from the system by fisheries.

262

263 The majority of the 50 fish present during the array deployment were sedentary most of the time and
264 mostly detected on the same 2-3 receivers. Some individuals did perform excursions throughout
265 larger areas in the fjord. As a consequence, home range sizes varied from 1 to 25 hectares (mean: 7.1
266 ha, SD: 5.9 ha, median: 5.0 ha), with no clear difference between the two ecotypes (Figure 3).



267

268 **Figure 3.** Boxplot of 95 % home range area of tagged Atlantic cod *Gadus Morhua* with black horizontal lines representing
269 median values, boxes representing the interquartile range of values from the 25th to the 75th percentile, vertical lines
270 extending to 1.5 times the inter quartile range and points representing outliers.

271

272 The general linear model output had no significant effect of ecotype ($P = 0.660$) or fish length ($P =$
273 0.637) on home range sizes of the fish (Table 2). Also, the interaction between ecotype and length
274 was not significant ($P = 0.695$). Adjusted R^2 of the model was 0.05.

275

276

277 **Table 2.** Output from the general linear model of the effect of ecotype and fish length and the interaction between the
278 two on home range size.

279

	Value	SE	T-value	P
Intercept	2.449	1.581	1.546	0.129
Ecotype	-0.845	1.914	-0.443	0.660
Length	-0.016	0.034	-0.475	0.637
Type*length	0.016	0.041	0.394	0.695

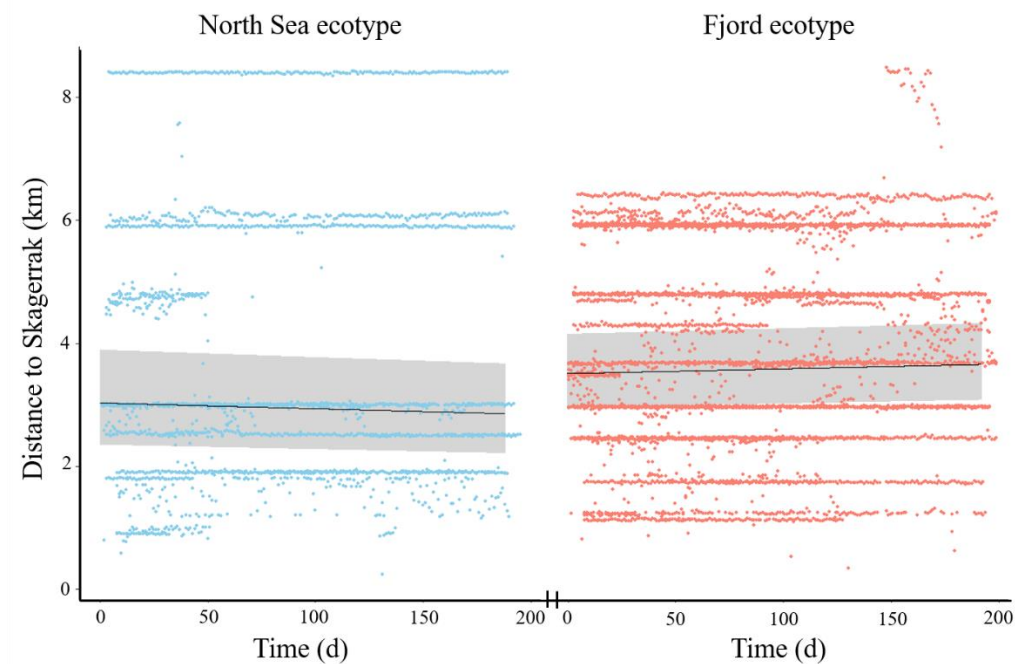
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281 The generalized linear mixed modelling of residence distance from the sea found no significant
282 difference between the ecotypes and detected no overall movement towards or away from the
283 Skagerrak over time (Table 3). The results suggested individuals of both the North Sea and Fjord
284 ecotypes were scattered across the fjord system with a small but insignificant skew of North Sea fish
285 closer to the Skagerrak than individuals of the Fjord ecotype (Figure 4).

286

287

288



289

290 **Figure 4.** Distance to the Skagerrak for daily position averages for the two ecotypes of Atlantic cod *Gadus morhua* from
 291 May – November 2017 (dots) and output from mixed effects model of distance to the Skagerrak for the two ecotypes
 292 during May-November 2017 (black lines). Shaded areas represent 95 % confidence intervals of the model.

293

294 **Table 3.** Output from the mixed effects model of distance to the Skagerrak with time for the two ecotypes during May-
 295 November 2017.

	Value	SE	z-value	P
Intercept	1.109	0.1276	8.695	<0.0001
Ecotype	0.1534	0.1525	1.006	0.315
Time	-0.0031	0.0004	-6.891	<0.0001
Type*time	0.0005	0.0001	9.403	<0.0001

296

297 **Isotopic niche**

298 General linear models were used to investigate if behaviour (95 % home range and distance to
 299 Skagerrak), ecotype (North Sea or Fjord) and fish length affected the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the fish
 300 and thus their trophic niche. There was no correlation between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from North Sea

301 (Pearson, $r=0.22$, $P = 0.23$) or Fjord cod (Pearson, $r=-0.003$, $P = 0.98$), hence the analysis was
302 performed on the actual untransformed isotope values.

303 The $\delta^{15}\text{N}$ value ($P = 0.010$) and distance to the Skagerrak ($P = 0.001$) were significantly different
304 between cod ecotypes (Figure 5, Table 4). VIF-score of the two variables (1.052) suggested no
305 problems with collinearity between them (24). The $\delta^{13}\text{C}$ value was significantly different between
306 cod ecotype ($P = 0.003$, Figure 5, Table 4). The interaction effect between ecotype and distance was
307 not significant for either $\delta^{15}\text{N}$ ($P = 0.647$) or $\delta^{13}\text{C}$ ($P = 0.121$) and were therefore dropped from the
308 final models. R^2 -values of the final models were 0.248 for $\delta^{15}\text{N}$ and 0.133 for $\delta^{13}\text{C}$.

309 Residuals from the linear model of isotope values versus distance were plotted as a biplot (Figure 6).
310 This showed a clear distinction between the two ecotypes, the Fjord ecotype having higher average
311 residual values for both nitrogen and carbon than the North Sea ecotype. There was an overlap in
312 isotope niche space among between the two ecotypes, but the isotopic niche width was considerably
313 larger in the combined data than in either of the two ecotypes. The isotopic niche widths as expressed
314 by sample size corrected standard ellipse areas (SEAc) were similar among ecotypes (North Sea =
315 1.00‰^2 and Fjord = 0.99‰^2) despite the indications of different feeding ecologies. The overlap in
316 sample size corrected standard ellipse area between the two ecotypes was 0.28‰^2 , which is less than
317 $1/3$ of the individual ecotype standard ellipse areas and the sample size corrected standard ellipse area
318 of the combined dataset consequently increased to 1.11‰^2 . The isotopic niche width expressed as the
319 convex hull areas were (TA) 2.35‰^2 for the North Sea ecotype and 3.49‰^2 for the Fjord ecotype.
320 Treating the cod as one group yields a convex hull areas of 5.33‰^2 or between 1.53-2.27 times the
321 sizes of the individual trophic niche widths.

322

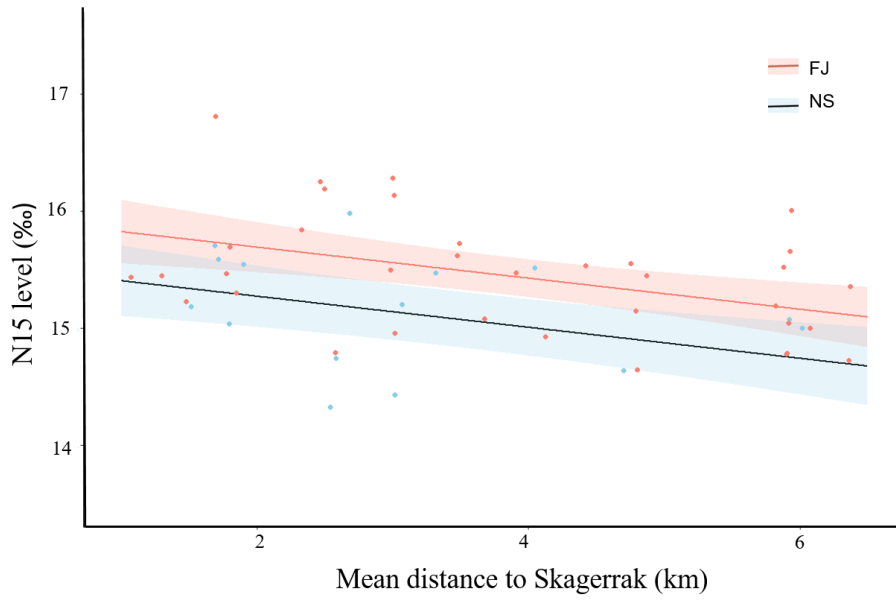
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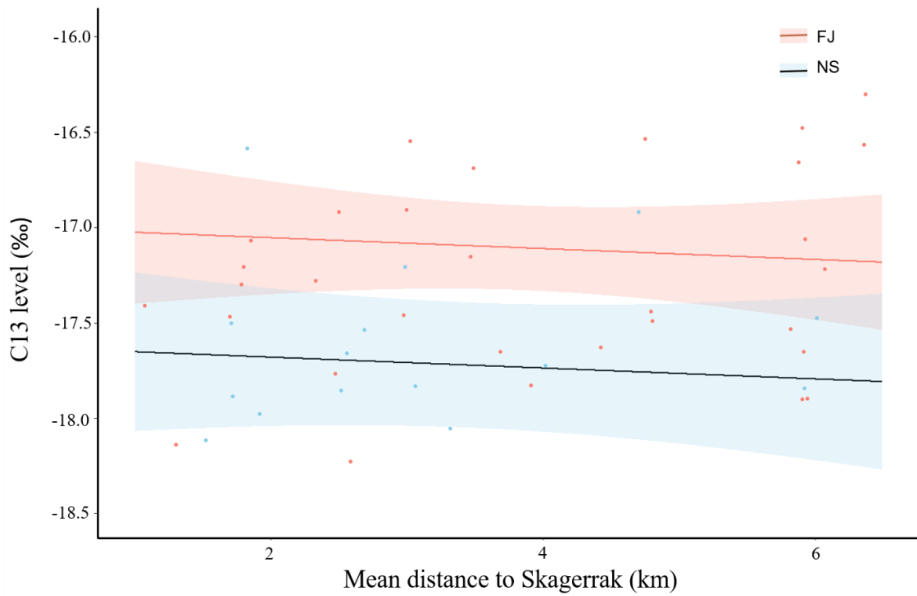
325 **Table 4.** Output from the general linear models of the effect of ecotype, distance to the Skagerrak, fish length, home range
 326 size and the interaction between ecotype and distance to the Skagerrak on stable isotope values.

327

	Nitrogen				Carbon			
	Value	SE	T-value	P	Value	SE	T-value	P
Ecotype	0.389	0.146	2.663	0.010	0.626	0.198	3.160	0.003
Distance	-0.135	0.038	-3.566	0.001	-0.038	0.055	-0.696	0.490
Eco*Dist.	0.032	0.080	0.408	0.647	0.173	0.110	1.579	0.121
Length	-0.009	0.010	-0.859	0.592	-0.013	0.014	-0.954	0.351
Homerange	0.011	0.013	0.911	0.505	0.004	0.017	0.245	0.539



328

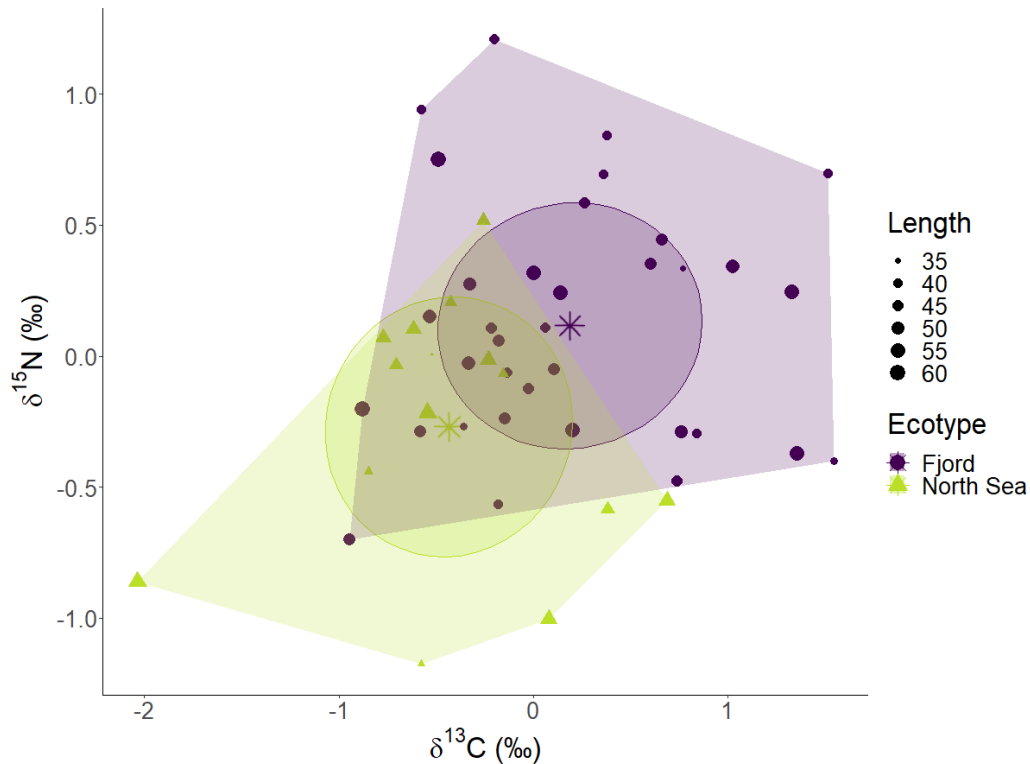


329

330 **Figure 5.** Linear model of $\delta^{15}\text{N}$ (top panel) and $\delta^{13}\text{C}$ (lower panel) in Atlantic cod *Gadus morhua* of the two ecotypes
 331 related to the mean residence distance from the Skagerrak in May – November 2017. Shaded areas represent 95 %
 332 confidence intervals of the model and points represent isotope levels and mean residence distances from Skagerrak for
 333 individual fish.

334

335



336
 337 **Figure 6.** Biplot of residuals from the linear model of isotope values versus distance to Skagerrak. The convex hulls
 338 (polygons) and standard ellipse area (SEA) (ellipses) are plotted. Bivariate means for each ecotype are shown with stars
 339 and fish standard length in cm is indicated by symbol size.

340

341 Discussion

342 Our results document that sympatric, co-existing Atlantic cod ecotypes exhibit divergent migratory
 343 behaviours and feeding ecology. The North Sea ecotype were more likely to leave the fjord system
 344 compared to local Fjord cod and had significantly lower values of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes.
 345 Given the potential importance of cod as a top predator, differences in fjord residence and trophic
 346 ecology may have an important effect on the overall structure and functioning of temperate coastal
 347 ecosystems.

348 In total, 43% of cod tagged with acoustic transmitters belonged to be North Sea ecotype, while the
 349 remaining 57% belonged to the Fjord ecotype. The genetic origin analysis has some uncertainty (5
 350 %) in assigning fjord individuals correctly (Jorde, Synnes et al., 2018) and a few individuals might

351 have been misclassified in our data. Despite any uncertainty, these results document that both
352 ecotypes coexist at the same time in Skagerrak fjords, possibly with more or less asynchronously
353 fluctuations in abundance among years (e.g. Knutsen et al., 2018). As a consequence, abundance of
354 cod in the fjords may fluctuate regardless of local management initiatives.

355 The two cod ecotypes displayed divergent migratory behaviour: 42 % (N = 13) of the North Sea cod
356 left the fjord permanently (N = 12) or for a prolonged period of time (4 months, N = 1) while only
357 7% (N = 3) of the Fjord cod left the fjord permanently. The size at maturity (50 % probability) for
358 broad samples of cod varied between 35 – 63 cm in different fjord systems along the Skagerrak coast
359 in Olsen et al. (2004) while mean length of spawners of the FJ ecotype was 40 cm in Olsen et al.
360 (2008). Estimates of the same for NS ecotype individuals inhabiting the coastal Skagerrak fjord
361 systems are not available to date. Recent estimates of age and size at maturity (50% probability) in
362 cod from the North Sea proper was 2.7 years and 44.6 cm, and 2.8 years and 46.1 cm for male and
363 female cod, respectively (Marty et al. 2014). If assuming that the NS ecotype found in coastal
364 Skagerrak is indeed similar to cod from North Sea proper in this regard, this would imply that fish in
365 the size-window of emigrating cod (36 – 70 cm at the time of tagging) observed in the present study
366 might have been mature individuals and that their departure from the fjord might have been related
367 to spawning. Natal homing has been extensively documented on Atlantic cod (Svedäng et al., 2010;
368 André et al., 2016), and we hypothesize that North Sea cod left the fjord in order to return to their
369 natal spawning grounds. This is supported by the time of departure from the fjord, as 10 of the North
370 Sea individuals and two of the Fjord individuals left during spawning season in winter, similar to the
371 migration timing observed in (Svedäng et al., 2007). Other population structuring mechanisms
372 besides natal homing persist in cod populations (Svedäng et al., 2010, André et al., 2016; Skjaeraasen
373 et al., 2011) where straying may be one of the most significant ones (Svedäng et al., 2010; Kovach et
374 al., 2010). The Fjord fish that left during the spawning season could have done so to spawn in

375 neighbouring fjords or potentially strayed elsewhere although the mechanisms behind straying in cod
376 are still poorly understood (Robichaud & Rose, 2001). The 58 % (N = 18) of North Sea cod that
377 stayed in the fjord or potentially died in it during the study period might be termed strayers if they
378 spawned in the fjord. Barth et al. (2019) observed a similar and stable degree of co-occurrence of
379 ecotypes in a neighbouring fjord system. Further exploration of fine-scale behaviour might uncover
380 whether long-term residents of the NS ecotype spawn separately from FJ individuals within fjord
381 systems along the Skagerrak coast.

382 Two North Sea individuals and one Fjord individual left the fjord during summer without returning
383 during the study period. These summer migrations were unlikely related to spawning, but could be a
384 consequence of home ranges extending outside the fjord, a movement to avoid high summer
385 temperatures within the fjord or a consequence of predation events. As observed in our study and
386 with greater detail on cod in an adjacent fjord system by (Villegas-Rios et al., 2017), cod individuals
387 may exhibit a wide variety in home range size from almost completely sedentary to highly migratory.
388 The fish that left during summer could have simply died while residing outside the fjord. It has
389 previously been documented that Atlantic cod avoid extreme temperature ranges either by vertical
390 positioning in the water column (Espeland et al., 2010; Righton et al., 2010) or by selecting habitat
391 based on bottom substrate (Freitas et al., 2016). This is important because sub-optimal temperature
392 may have various effect on physiological state of the fish and through that may have negative effect
393 on different fitness related components, for example growth (Righton et al., 2010). Therefore, it may
394 be that conditions outside the fjord, in deeper and colder waters, may be more suitable for some
395 individuals during the warmer months. Finally, the fish could have been predated inside the fjord by
396 seals that subsequently left the fjord towards the seal colony located outside the fjord and array with
397 tags still in their belly.

398

399 Individuals from both ecotypes were present throughout most of the fjord system and displayed
400 similar home range sizes. The Fjord cod resemble cod from the southern Kattegat and western Baltic
401 Sea (Barth et al., 2017) that are adapted to lower salinities (Larsen et al., 2012) and a relatively higher
402 distribution of Fjord cod could have been expected deeper in the fjord where salinities are lower. The
403 capture and release location of the 10 North Sea fish that left the fjord during the spawning season
404 was 3.58 km as opposed to 3.42 km in all the assigned North Sea individuals, suggesting that the
405 North Sea fish that left the system before the array was deployed had been similarly distributed
406 throughout the fjord compared to the individuals that stayed.

407 Overall home range patterns for the fish included in the present study resembled those observed with
408 greater detail by (Villegas-Rios et al., 2017) although generally smaller in the present study. This is
409 likely a methodologically driven difference, as position averages as used in the present study will
410 draw the fish positions towards the centre of detection likelihood and thus underestimate the home
411 range size. Position averaging delivers too coarse positions to enable unbiased determination of dead
412 fish in the system, and some of the sedentary individuals in the present study could be dead
413 individuals. The natural mortality for larger cod in neighbouring fjords is, however, very low as a
414 contrary to the annual fishery induced mortality of 50 % or more, accounting for up to nearly 100 %
415 of the total mortality in large cod in coastal areas (Féernandez-Chacón et al., 2017; Olsen & Moland,
416 2011). Tag shedding also acts as a potential error source, although considered to be a small one.
417 Twenty cod recaptured in a neighbouring fjord after being acoustically tagged by the same fish
418 surgeon as in the present study, all carried the tag when recaptured later on (E. Moland Olsen, pers.
419 comm.). In spite of these sources of uncertainty, home range sizes estimated from position averages
420 should still reveal differences between the ecotypes on a group level. Although highly variable
421 between individuals, results from the present study suggested no such differences in home range sizes
422 were present between the North Sea and Fjord ecotypes.

423

424 Differences in isotopic niche were observed between the two ecotypes. Cod from the North Sea
425 exhibited lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values compared to Fjord cod; and for both ecotypes, the $\delta^{15}\text{N}$ values
426 were related to the distance to the outlet of the fjord. These results suggest that the diet composition
427 of the North Sea ecotype differ from that of the Fjord ecotype.

428 Cod in the southern Norwegian fjords are omnivorous and in the present size range they primarily
429 feed on a mixture of fish, decapods, polychaetes and gastropods (Salvanes et al., 2004). The
430 proportions of these prey groups vary by season, similar to what is seen in other populations (Link et
431 al., 2009; GrønkJær et al., 2020). While the fish ingested may be both benthic and pelagic; the
432 decapods, polychaetes and gastropods are primarily benthic predators, deposit feeders or scavengers
433 forming part of a benthic food web. Pelagic and benthic food webs can be distinguished based on the
434 $\delta^{13}\text{C}$ values as benthic food webs are characterised by higher $\delta^{13}\text{C}$ values than their pelagic
435 counterparts (Telsnig et al., 2019). Unfortunately, there are no prey isotope data from the fjords
436 investigated in this study, but the pattern has been documented in a comparable fjord system in
437 Northern Norway, where the benthic community showed higher $\delta^{13}\text{C}$ (Shrimps $\delta^{13}\text{C} = -17.5\%$; Large
438 crustaceans $\delta^{13}\text{C} = -20.0\%$; Predatory benthos $\delta^{13}\text{C} = -17.9$) compared to pelagic prey (Herring $\delta^{13}\text{C}$
439 $= -21.3$; Krill $\delta^{13}\text{C} = -22.4$). An explanation for the ecotype specific isotopic values, which is consistent
440 with known diet composition (Link et al., 2009; GrønkJær et al., 2020; Mattson et al., 1990) and
441 isotopic values of prey (Telsnig et al., 2019; Giraldo et al., 2017), could therefore be an increased
442 proportion of benthic scavengers and deposit feeders compared to pelagic organisms in the diet of the
443 Fjord ecotype. The increased reliance on benthic food sources may be an adaptation to the shallow
444 coastal and fjord habitats, where the production of benthic prey is higher than in offshore habitats. In
445 more offshore populations and locations, there is a tendency towards increasing proportions of fish
446 in the diet compared to coastal locations (Dalpadado & Bogstad, 2004; Hedeholm et al., 2017; Pálsson

447 & Björnsson, 2011). This may be driven by increased availability of a wider range of pelagic fish
448 species (e.g. herring, sand lance) and the effect of occupancy is augmented by the general larger size
449 of offshore cod (Berg & Albert, 2003; Roff, 1988), which allow them to prey more efficiently on
450 larger fish prey. In contrast, for the coastal populations, higher biomasses of benthic prey in the
451 shallower waters provide these cod with improved benthic feeding conditions (Mattson, 1990). The
452 higher $\delta^{15}\text{N}$ in the fjord ecotype suggest that a large proportion of their diet consist of benthic
453 scavengers and predators which have high $\delta^{15}\text{N}$ values (Giraldo et al., 2017; Tamelander et al., 2006)
454 compared to benthic suspension feeders and grazers. The importance of brachyuran (true crabs) and
455 anomuran decapods in the diet of cod in the area supports this (Hop et al., 1992). The decrease of
456 $\delta^{15}\text{N}$ towards the mouth of the fjord is consistent with anthropogenic eutrophication within the fjord
457 and mixing with less eutrophied coastal water as seen in other systems (Cabana & Rasmussen, 1996;
458 Kristensen et al., 2019). This leading to a decreasing $\delta^{15}\text{N}$ baseline from the head to the mouth of the
459 fjord, which is reflected in the consumers.

460

461 This is the first study to document dietary differences among genetically divergent ecotypes of cod
462 inhabiting the same environment and subsequently study the behaviour of individual fish. The results
463 indicate adaptation to local prey types in the local Fjord ecotype and lack of adaptation within a month
464 to year timescale in the alien North Sea ecotype. Previous studies of reared cod have shown
465 differences in behaviour of individuals from genetically different populations and suggested that
466 higher growth of cod from the Northern coast of Norway was due to more active feeding strategy on
467 pelagic prey compared to the Southern origin cod (Salvanes et al., 2004). Our study takes this down
468 to the level of co-occurring ecotypes. Also, (Knutsen et al., 2018) and (Jørgensen et al., 2020) found
469 growth differences between the two ecotypes, where juveniles of the North Sea ecotype display faster
470 growth than the local Fjord type. The present study and the study by Salvanes et al., (2004) suggest

471 that observed growth differences may be driven by differences in feeding ecology and be maintained
472 throughout the life of the cod.

473

474 The clear differences in diets, behaviour and growth of the Fjord and North Sea ecotype cod suggest
475 that the two ecotypes will have distinct effects on the fjord ecosystem. Depending on the ratio between
476 ecotypes within the fjord, which is subject to change over time (Knutsen et al., 2018), different prey
477 items will be under dynamic predatory pressure, which may have an effect on the abundance and
478 composition of different elements in the food web. Similarly, the abundance of the two ecotypes may
479 be driven by availability of the relevant prey types (pelagic vs benthic) and hence the occurrence of
480 two ecotypes with distinct prey requirements may offer resilience in terms of cod survival. The
481 distinct prey requirements are seen in the low degree of overlap in isotopic niche, which allow cod
482 ecotypes to coexist and together utilize a broader dietary niche than if only one of the ecotypes had
483 been present. Therefore, the loss of one ecotype fish may have significant ecological effects on the
484 overall functioning of the ecosystem. Our results highlight the importance of ensuring sustainable
485 population developments in interconnected populations in order to maintain marine ecosystem
486 functioning and resilience to environmental change.

487

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495 **Conflict of Interest**

496 All authors declare to have no conflicts of interest.

497

498 **Authors' Contributions**

499 **Martin Lykke Kristensen:** Conceptualization (Supporting), Data curation (Lead), Formal analysis
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504 & editing (Supporting). **Even Moland:** Conceptualization (Supporting), Data curation (Equal),
505 Formal analysis (Supporting), Funding acquisition (Supporting), Investigation (Equal), Methodology
506 (Equal), Supervision (Equal), Writing-original draft (Equal), Writing-review & editing (Supporting).
507 **Halvor Knutsen:** Conceptualization (Equal), Data curation (Equal), Formal analysis (Equal),
508 Funding acquisition (Lead), Investigation (Equal), Methodology (Equal), Project administration
509 (Lead), Resources (Equal), Writing-original draft (Equal), Writing-review & editing (Supporting).
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513 (Supporting), Funding acquisition (Supporting), Methodology (Supporting), Project administration
514 (Supporting), Resources (Equal), Supervision (Supporting), Writing-original draft (Equal), Writing-
515 review & editing (Supporting). **Kristi Källo:** Formal analysis (Supporting), Methodology
516 (Supporting), Writing-original draft (Equal), Writing-review & editing (Supporting). **Kim**
517 **Aarestrup:** Conceptualization (Lead), Funding acquisition (Equal), Methodology (Equal), Project

518 administration (Equal), Supervision (Equal), Writing-original draft (Equal), Writing-review & editing
519 (Supporting).

520

521 **Data Accessibility Statement**

522 Fish and tagging information are provided in the appendices. All data can be downloaded from the
523 Dryad repository at <https://doi.org/10.5061/dryad.5hqbzkh63>

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749 **Appendices**

750 **A1.** Fish tagging, movement and stable isotope data.

Tag ID	Nitrogen	Carbon	Fishtype (1 = NS. 2 = FJ)	Length	Homerange	Distance to Skagerrak
1917	15.15	-17.44	2	42	8	4.8

1919	16.19	-16.92	2	41	3	2.5
1921	16.13	-15.77	2	40	1	3.0
1922	14.78	-16.48	2	40	13	5.9
1924	15.47	-17.30	2	45	11	1.8
1925	15.69	-17.21	2	42	2	1.8
1927	15.62	-17.15	2	56	3	3.5
1928	15.51	-17.72	1	43	15	4.0
1929	15.72	-16.69	2	48	2	3.5
1930	14.78	-17.90	2	48	3	5.9
1931	15.53	-17.63	2	50	7	4.4
1932	14.79	-18.23	2	48	4	2.6
1933	15.18	-18.11	1	38	4	1.5
1935	14.64	-16.92	1	45	5	4.7
1936	16.81	-17.47	2	42	10	1.7
1937	15.35	-16.30	2	54	10	6.4
1938	14.92	-15.94	2	55	10	4.1
1939	15.22	-15.72	2	37	2	1.5
1940	15.52	-16.66	2	48	6	5.9
1941	15.00	-17.22	2	48	3	6.1
1942	15.45	-18.14	2	60	1	1.3
1943	15.46	-18.06	1	50	23	3.3
1944	15.65	-17.06	2	44	8	5.9
1946	14.43	-17.21	1	52	2	3.0
1947	14.99	-17.48	1	40	21	6.0
1949	14.72	-16.56	2	51	25	6.4

1950	16.25	-17.77	2	59	5	2.5
1951	15.08	-17.84	1	34	8	5.9
1952	16.01	-17.90	2	41	11	5.9
1953	15.19	-17.53	2	44	5	5.8
1954	15.58	-17.50	1	51	12	1.7
1955	14.32	-17.85	1	36	5	2.5
1957	14.96	-16.55	2	44	3	3.0
1964	15.70	-17.88	1	50	2	1.7
1966	15.45	-15.98	2	58	5	4.9
1972	13.90	-19.38	1	55	1	8.4
1973	15.04	-17.65	2	52	9	5.9
1975	15.49	-17.46	2	48	5	3.0
1977	15.84	-17.28	2	57	1	2.3
1978	16.28	-16.91	2	40	2	3.0
1979	15.30	-17.07	2	56	14	1.9
1980	15.03	-16.58	1	52	4	1.8
1981	15.08	-17.65	2	38	5	3.7
1982	15.99	-17.54	1	46	5	2.7
1985	15.44	-17.41	2	47	12	1.1
1986	15.21	-17.83	1	58	22	3.1
1987	15.55	-16.54	2	35	7	4.8
1988	15.54	-17.98	1	45	1	1.9
1989	15.47	-17.83	2	52	7	3.9
1991	14.64	-17.49	2	41	5	4.8