



HAL
open science

Killer whales (*Orcinus orca*) feeding on lumpfish (*Cyclopterus lumpus*) in northern Norway

Eve Jourdain, Richard Karoliussen, Jacques Vos, Stanislav Zakharov,
Christelle Tougard

► To cite this version:

Eve Jourdain, Richard Karoliussen, Jacques Vos, Stanislav Zakharov, Christelle Tougard. Killer whales (*Orcinus orca*) feeding on lumpfish (*Cyclopterus lumpus*) in northern Norway. *Marine Mammal Science*, 2020, 36 (1), pp.89-102. 10.1111/mms.12618 . hal-02162319

HAL Id: hal-02162319

<https://hal.science/hal-02162319>

Submitted on 7 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Killer whales (*Orcinus orca*) feeding on lumpfish (*Cyclopterus lumpus*) in northern Norway

2 E. Jourdain^{1*}, R. Karoliussen¹, J. de Vos¹, S. E. Zakharov¹, C. Tougard²

3

4 ¹Norwegian Orca Survey, Haugesveien 30, 8480 Andenes, Norway

5 ²ISEM, Université de Montpellier, CNRS, EPHE, IRD, 34 090 Montpellier, France

6

7 *Corresponding author email: post@norwegianorcasurvey.no

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27 Abstract

28 Killer whales (*Orcinus orca*) in Norwegian waters have long been known to rely on
29 Atlantic herring (*Clupea harengus*) as a main prey resource. However, research almost
30 exclusively conducted at seasonal herring grounds may have biased studies away from
31 detecting other potentially significant prey species. Since 2013, dedicated research efforts
32 have focused on monitoring killer whale occurrence and foraging ecology throughout the year
33 in northern Norway. This study presents results on site-fidelity of photographically identified
34 individuals, predation records and behavioral patterns from five spring seasons (March-April)
35 in 2014-2018 in Andfjord, northern Norway. A minimum number of 75 adult and subadult
36 killer whales (out of a catalogue of 971 individuals) returned seasonally to the study area for
37 foraging and residency for up to six weeks. Lumpfish (or lumpsucker, *Cyclopterus lumpus*)
38 was the only type of prey identified (based on molecular or visual identification) on 22
39 predation events from 2016 ($n=4$), 2017 ($n=2$) and 2018 ($n=16$). Spatial group cohesion
40 observed when foraging was a potential adaptation for efficiently hunting this prey species.
41 These whales were also encountered at herring wintering grounds the same years, but with
42 different group sizes. Such behavioral adaptations suggested intra-annual switching between
43 prey resources and foraging strategies.

44

45

46 Keywords

47 Killer whale, *Orcinus orca*, Foraging, Feeding behavior, Foraging strategy, Seasonality, Site-
48 fidelity

49

50

51

52

53 Introduction

54 The killer whale (*Orcinus orca*) is found in all the world's oceans and as a species is
55 generalist, with a wide range of prey documented including fish, marine mammals,
56 cephalopods, reptiles and seabirds (Ford 2009). However, populations have been shown to be
57 prey specialists. For example, in the temperate coastal northeastern Pacific, killer whales feed
58 exclusively on either marine mammals or fish (e.g., Baird and Dill 1995, Ford *et al.* 1998,
59 Ford and Ellis 2006). Such prey specialization, including underlying foraging behavior and
60 knowledge about particular prolific feeding areas, are culturally transmitted in the form of
61 learned behavior within groups and persist over time (Ford *et al.* 1998, Riesch *et al.* 2012).
62 Resulting ecological and cultural divergences among social groups promote the formation of
63 sympatric socially and genetically isolated ecotypes (Ford and Ellis 2014, Foote *et al.* 2016).
64 Divergent foraging strategies, by creating differences in occurrence and movement patterns as
65 well as social organization, may further play a role in population structuring (Hoelzel *et al.*
66 2007, Morin *et al.* 2010, Parsons *et al.* 2013).

67

68 In the North Atlantic, two ecotypes of killer whales were proposed based on dietary
69 specialization, Type 1 and Type 2, with nitrogen stable isotope values and tooth wear used as
70 proxies to indicate key prey choice for each type (Foote *et al.* 2009, 2012). Type 1 refers to
71 killer whales from Iceland, Norway, and the North Sea, which rely on the Atlantic herring
72 (*Clupea harengus*) and/or the Atlantic mackerel (*Scomber scombrus*) as their main food
73 source(s). In contrast, Type 2 primarily feeds on other cetaceans. However, this simplistic
74 classification seems unlikely to encapsulate the broad-scale diversity of the diet of North
75 Atlantic killer whales. In fact, there is strong evidence for inter-individual variation in the

76 relative proportions of prey types consumed within Type 1 killer whales. For example, some
77 may also prey on pinnipeds, as evidenced by field observations (Foote *et al.* 2010, Vongraven
78 and Bisther 2014, Jourdain *et al.* 2017, Samarra *et al.* 2018). As such, different feeding
79 specializations may exist within populations. Recent studies using ecological tracers were
80 further supportive of inter-individual variation in dietary habits among regions (*e.g.*, Faroe
81 Islands/Denmark vs Greenland; Bourque *et al.* 2018), within regions (Samarra *et al.* 2017),
82 and within social groups (in Greenland, see Bourque *et al.* 2018). However, the lack of killer
83 whale identification data and predation records for most regions has impeded our
84 understanding of fine-scale seasonal and/or group-specific prey specializations so far. The
85 potential occurrence of variable foraging strategies and dependence on main and alternative
86 prey resources remains to be investigated further in the North Atlantic.

87

88 Between 1986 and 2005, Norwegian killer whale studies were mainly focused on
89 wintering grounds of the Norwegian Spring Spawning (NSS) stock of the Atlantic herring. At
90 that time these grounds were located in a fjord system (Vestfjord-Ofotfjord-Tysfjord) in the
91 Lofoten region, northern Norway (68°13'N, 15°37'E). Research efforts were focused on
92 photographic identification and investigation of feeding behavior, occurrence patterns, social
93 ecology, and acoustics (Similä and Ugarte 1993, Similä *et al.* 1996, Similä 1997, Domenici *et al.*
94 *al.* 2000, Van Parijs *et al.* 2004, Van Opzeeland *et al.* 2005). These studies highlighted killer
95 whales as efficient herring predators using specialized feeding strategies (*e.g.*, Similä and
96 Ugarte 1993). Photo-identification surveys conducted on both wintering and spawning
97 grounds of the NSS herring, combined with satellite tracking of six individual whales tagged
98 in 2000 and 2001, further suggested that some groups may follow the herring's movements for
99 most of the year (Bisther and Vongraven 1995, Similä *et al.* 1996, Stenersen and Similä
100 2004), though effective herring-foraging offshore remained largely inconclusive. As a result,

101 and due to lack of evidence for additional prey items, herring has been regarded as the main
102 prey for killer whales in Norwegian waters. This conclusion was further supported by a lack
103 of intra-population variation in stable isotope values from skin samples collected from whales
104 in the NSS wintering grounds (Foote *et al.* 2012).

105

106 However, focusing research efforts on seasonal herring grounds may have biased studies
107 away from detecting other potentially significant prey species. In fact, recent studies
108 conducted outside seasonal herring grounds documented predation on Atlantic salmon (*Salmo*
109 *salar*, Vester and Hammerschmidt 2013), Atlantic mackerel (Nøttestad *et al.* 2014), harbor
110 porpoise (*Phocoena phocoena*, Cosentino 2015), and on pinnipeds (Vongraven and Bisther
111 2014, Jourdain *et al.* 2017), suggesting intra-population ecological variation. Combining
112 sighting and predation records of individuals over time would help in assessing prey
113 specializations of killer whales in this region.

114

115 Longitudinal photo-identification studies, as initiated by colleagues three decades ago,
116 have been re-established in 2013 at current herring wintering (November-February) grounds
117 (see Huse *et al.* 2010, Jourdain and Vongraven 2017). From mid-January to mid-February, the
118 herring migrate to the main spawning area located 800-1,000 km south, off the central coast
119 of Norway (Dragesund 1997), leading to the departure of the winter aggregating killer whales.
120 Research efforts yet maintained throughout the rest of the year in the study area aimed at
121 collecting photo-identification data and predation records.

122

123 Here, we report on a subset of known herring-feeding killer whales showing site-fidelity
124 in a northern Norwegian fjord in spring (March-April), after the herring has departed, for the
125 period 2014-2018. Behavior and predation records were collected over multiple years in order

126 to assess foraging as a predominant function for seasonal use of the area in spring, and to
127 identify the target prey. Group cohesion was investigated with reference to the focal prey and
128 group sizes were compared to winter observations for insights into behavioral adaptations and
129 therefore, indication of seasonal prey switching and specialization for these whales.

130

131

132 Materials & Methods

133 *Data collection*

134 Data were collected in March - April of 2015 – 2018 east of Andøya (Andfjord, 69°19'N,
135 16°08'E; Fig. 1), in Vesterålen region, northern Norway. Because killer whale presence was
136 not known to be regular in the study area at this specific time of year, surveys were largely
137 opportunistic, and effort varied considerably across years. In 2015, surveys were always
138 conducted in response to sightings being reported by locals. In the following years, and based
139 on the 2015 sighting records, land-based watches searched for killer whales on good weather
140 days, as did opportunistic boat surveys, in addition to relying on sighting reports.

141 Supplementary photographs of individual killer whales within the study area with associated
142 date and time data were provided by local wildlife photographers for April-March of 2014-
143 2017, and those of high enough quality were accepted for use in the analyses.

144

145 Surveys were conducted on a 20-foot-long aluminum research vessel in sea conditions of
146 Beaufort scale 4 or less. We defined an encounter as a sighting of a group of killer whales. A
147 group was defined as all individuals observed in apparent association, acting in a coordinated
148 manner during the observation period and which were within the visual range of the observers
149 (as per Baird and Dill 1995). For each encounter, the geographic position (GPS Garmin) was
150 recorded and the whales were systematically photographed using a digital reflex camera and a

151 mounted lens of 70-200 mm in focal length. Predominant behavioral pattern, group size
152 estimate and cohesion index (see below) were also recorded at five-minute intervals for the
153 majority of surveys. Surveys terminated when the group was lost from sight, travelled away
154 from the study site, or if light and/or sea conditions deteriorated.

155

156 Behavior was divided into five categories (adapted from Ford 1989): (1) *Foraging* –
157 erratic swimming in varying directions, sudden lunges and high-speed swimming, presence of
158 prey fragments and seabirds; (2) *Travelling* – consistent movement with all group members,
159 in a tight group formation, following the same course at the same speed, while displaying
160 synchronous dives and surfacings; (3) *Milling* – low speed movement with individuals
161 engaged in frequent changes in direction leading to no directional movement by the group; (4)
162 *Resting* – low level activity with individuals being stationary lined-up and floating motionless
163 at the surface while displaying coordinated breathings; (5) *Socializing* – high energy activity
164 in which individuals may physically interact with one another and/or perform aerial displays
165 such as leaps, tail slaps, and spy-hops (defined as vertical half-rise of the body out of the
166 water). Activities displayed by the majority of the whales was considered as the main
167 behavioral pattern for the group.

168

169 Spatial cohesion of the group, often variable throughout encounters, was characterized
170 using a cohesion index (CI) (adapted from Daura-Jorge *et al.* 2005). Within a group,
171 individuals scattered over distances (visually assessed) greater than 200 m were classified as
172 low cohesion (CI=1), individuals occupying a 60 to 200 m area were classified as
173 intermediate cohesion (CI=2) and individuals aggregated within 50 m were classified as high
174 cohesion (CI=3). Smaller sub-groups, often composed of adult female(s) with offspring, were

175 considered as part of the main group. Classifications were made by the same observer
176 throughout the study, reducing potential observer-related bias.

177

178 From 2016 onwards, collection of tissue fragments from prey killed and consumed by
179 killer whales was also attempted. Based on the methods developed by Ford *et al.* (1998), we
180 used speed bursts, directional chases, fast and sharp turns, and head nodding-movements of
181 surfacing whales along with scavenging seabirds as clues to feeding events. Upon detection of
182 such events, the research vessel slowly approached the focal whale, stopped in the fluke print
183 (glassy area visible at the surface as the whale dives and its tail creates an upwelling, as
184 defined by Ford and Ellis 2006) and observers assessed potential presence of prey remains in
185 the water column. Using a long-handled (3 m) fine-mesh net, one observer onboard collected
186 any accessible prey fragments. Because collection was challenged by fast-sinking prey parts
187 and common rough sea state, a professional free-diver assisted in collection of prey remains
188 in April 2018. Upon collection, fragments were placed in a plastic bag and stored in a cooling
189 box while in the field. Ashore, fragments were stored in 1.5 mL vials containing 95% ethanol
190 at -20°C until analysis.

191

192 Whenever a focal whale was observed feeding at close range to the vessel, photographs
193 were also taken in an attempt to visually-identify target prey species. An unmanned aircraft
194 DJI Phantom IV carrying a DJI 1/2.3" CMOS camera was used on three days in 2018 to
195 capture still images and video footage of prey capture events.

196

197 *Data processing*

198 Killer whales were individually identified based on location and number of notches in the
199 leading and/or trailing edge of the dorsal fin, along with pigmentation pattern of and natural

200 markings occurring on the saddle patch (Bigg 1982). Only individuals displaying one or
201 several unique features were considered as distinctive and effectively catalogued. Calves and
202 other individuals lacking persistent identifying markings were excluded. Individuals with
203 distinctly taller dorsal fins were classified as ‘Male’ (Olesiuk *et al.* 1990), adult female-sized
204 individuals repeatedly seen with one calf or older offspring(s) swimming in echelon position
205 throughout the study period were qualified as ‘Female’ and individuals for which sex was
206 uncertain were qualified as ‘Unknown’. Photographs were scored for quality ($0 < Q < 2$)
207 based upon sharpness, contrast and angle. To minimize misidentification, only excellent
208 quality (Q2) photographic records of distinctive catalogued killer whales were considered in
209 this study. Both left and right-side identification photos were used for ID, but only whales
210 catalogued from the left side were retained for analysis.

211

212 *Data analysis*

213 *Sighting and behavioral patterns*

214 To assess site-fidelity patterns, individual sighting records were compared across days
215 and years. Despite sampling biases due to uneven effort throughout seasons and across years,
216 we considered minimum residency to be informative of individuals’ site-fidelity periods
217 within seasons. Therefore, the number of days elapsed from the first to the last sighting within
218 each season was calculated for each individual, as compared to the total length of survey
219 period for each given season (as per Weinrich *et al.* 1997). Mean residency values were
220 calculated across individuals per season, excluding individuals not seen, and averaged for the
221 entire study period.

222

223 To investigate seasonal usage of the study area, relative predominance of observed
224 behavioral states was calculated. Further seasonal behavioral characteristics, assumed to be

225 adaptive to the target prey, were tested as follows. A Chi-Squared test was used to test the
226 relationship between behavior and cohesion index (CI). Due to low occurrence, records of
227 resting and socializing behaviors were not included in the test. Records of group size
228 collected for this study were compared to group sizes recorded at herring wintering grounds
229 for these same whales in 2015-2018 (S1) using a Mann-Whitney-Wilcoxon test. Statistical
230 tests were performed in R software (R Core Team 2016).

231

232 *Molecular and visual prey identification*

233 Molecular analyses were conducted on prey tissue samples for identification of target
234 species. Total DNA from 11 samples was extracted from ethanol-preserved samples following
235 standard procedures (Sambrook *et al.* 1989). A fragment of the cytochrome *c* oxidase I gene
236 (COI) was PCR-amplified using the GoTaq® G2 Hot Start Colorless Master Mix (Promega)
237 and the primers Pros1Fwd and Pros2Rev (Sparks and Smith 2004) with an annealing step at
238 46°C. Direct sequencing was carried out in both directions at the technical facilities of the
239 Genotyping and Sequencing Platform of the ‘Institut des Sciences de l’Evolution de
240 Montpellier’ (ISEM). Sequences were then aligned in MEGA v7 (Kumar *et al.* 2016) and
241 blasted (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) against sequences from the GenBank
242 database (<https://www.ncbi.nlm.nih.gov/genbank/>). Photographs and video footages of
243 predation events were scanned for visual identification of prey species.

244

245

246 Results

247 *Effort*

248 From 2015 to 2018, 42 d at sea in March-April resulted in 123.2 h spent with killer
249 whales and 14,170 photographs taken over 51 encounters from a dedicated research vessel.

250 Photographic contributions from wildlife photographers led to 11 additional encounter days
251 for the period 2014-2017. Behavior and CI were recorded for 62 h from 48 encounters.
252 Molecular ($n=11$) and photographic ($n=11$) evidence enabled positive identification of prey
253 species for 22 predation events from 11 encounter days in 2016-2018. For the period 2014-
254 2018, photographs resulted in 276 identifications of 75 distinctively marked individuals (Fig.
255 2). The number of identified individuals per season varied from a minimum of six (in 2014) to
256 a maximum of 42 (in 2018), with a mean of 27 (standard deviation $SD=13.3$). Poor weather
257 conditions in 2015 and 2017 resulted in lower numbers of encounter days and identifications
258 for these years. Sampling effort is summarized in Table 1.

259

260 *Characterization of individual killer whales*

261 The 75 identified individuals represent 7.7% of the 971 killer whales identified in the
262 study area (Jourdain and Karoliussen 2018). Of these, 34 (45.3%) were adult males, 21 (28%)
263 were adult females and 20 (26.7%) were of unknown sex; 61 (81.3%) were encountered at
264 herring wintering grounds on one or multiple years between 2013 and 2018 (unpublished
265 data). Social associations appeared highly variable across encounters, and thus we considered
266 individuals independently. Plotting the cumulative number of newly identified individuals in
267 the period March-April from 2014 to 2018 revealed a steadily decreasing identification rate,
268 suggesting that most distinctive whales using Andfjord in spring had been identified during
269 the study (Fig. 2).

270

271 *Sighting frequencies*

272 Of 75 individuals, 20 (26.7%) were sighted only once, while 55 (73.3%) were sighted
273 during two or more encounters in March-April from 2014 to 2018. Of these, 40 were seen in
274 multiple years (range=2-4; Fig. 3). Averaging all five spring seasons, individuals were sighted

275 during a mean of 1.8 seasons (SD=0.9; range=1-4) and on 3.7 d (SD=2.7; range=1-12). For
276 individuals sighted on a minimum of two encounter days within each spring season (Fig. 3),
277 mean (minimum) residency varied from 8.3 d (in 2015) to 16 d (in 2018) leading to a mean of
278 11.3 d (SD=6.2; range=2-39; Table 2) throughout the study period.

279

280 *Behavioral patterns*

281 Foraging (70.3%) and traveling (23.9%) represented the most frequently observed
282 behavioral states, while milling, resting, and socializing accounted for less than 6% of the
283 observations. Group cohesion varied with behavior ($X^2=3,940$; $df=4$; $P<0.001$). Individuals
284 adopted a tighter group formation when travelling as opposed to scattered over several
285 hundred meters and up to 1 km when foraging. Groups encountered were significantly smaller
286 (Mann-Whitney-Wilcoxon: $W=297$, $P=0.001$) in spring (median=8, range=1–30, $n=49$) than
287 in winter (median=14, range=1-40, $n=23$; Fig. 4).

288

289 *Prey identification*

290 Prey fragments from all 11 predation events sampled were identified to be from lumpfish
291 (*Cyclopterus lumpus*; Table 3). The alignment of the COI fragment was 587 nucleotides long.
292 From the 11 sequences obtained for molecular identification, all BLAST queries resulted in
293 the identification of the lumpfish with 99% to 100% of similarity with the sequence
294 JN311799 (Knebelsberger *et al.* 2014). The new sequences were deposited in GenBank under
295 the accession numbers MF688049 and MH922998-MH923009.

296 Photo and aerial video material enabled unambiguous identification of the lumpfish as the
297 consumed prey for seven and four additional predation events, respectively (Fig. 5, Table 3).

298 Thirteen individual killer whales were confirmed feeding on lumpfish from these 22 predation
299 events, of which five were adult males, three were adult females and five were of unknown

300 sex including three sub-adults (Table 3). Five individuals (NKW-0004, NKW-0572, NKW-
301 0712, NKW-0715 and Y093) fed on lumpfish on multiple occasions (range=2-4) during the
302 same encounter. Adult male NKW-0004 was further confirmed to be feeding on lumpfish
303 over two different days, five days apart, in April 2018.

304

305

306 Discussion

307 We have shown that a subset of killer whales seasonally visited Andfjord in March-April
308 of 2014-2018 and remained in the area for several days and up to several weeks. Most of
309 these whales were also encountered at herring wintering grounds in the same years. This
310 further supports the idea that killer whales make adaptive seasonal movements in response to
311 spatial and temporal changes in prey availability in this region (Similä *et al.* 1996). Marked
312 seasonality and predominance of foraging in spring suggests the use of a seasonally reliable
313 food source. All 22 predation events where the prey was identified revealed lumpfish to be the
314 target prey species in March and April.

315

316 The lumpfish is widely distributed throughout the Norwegian Sea (Holst 1993). It
317 remains offshore often at abyssal depths most of the year and migrates to coastal breeding
318 areas from April to July (Davenport 1985). Due to dorsal muscles allowing only limited
319 locomotory abilities (Davenport and Kjørsvik 1986), the lumpfish travels at low swimming
320 speeds (*i.e.*, 0.72 km/h in Mitamura *et al.* 2012). Spawning male and female lumpfish are
321 about 28-30 and 40-45 cm in length, respectively (Albert *et al.* 2002). Spent females may
322 complete spawning over a period of a few weeks and then return to the open ocean, or
323 alternatively may visit adjacent fjords to lay eggs at multiple locations (Goulet *et al.* 1986,
324 Mitamura *et al.* 2012). Males then guard the nest until the eggs hatch six to 10 weeks later

325 (Davenport 1985). These movement patterns suggest seasonal increased availability of the
326 lumpfish nearshore in spring, as supported by exclusive seasonal fishery from April through
327 mid-June for this species (Bertelsen 1994).

328

329 To the best of our knowledge, the lumpfish has not hitherto been reported as a prey
330 species of Norwegian killer whales, despite previous analysis of 95 stomach contents
331 (Christensen 1982) and observational studies (*e.g.*, Similä and Ugarte 1993, Similä *et al.*
332 1996). However, the lumpfish was listed as prey of killer whales off West Greenland where
333 stomachs of 30 harvested killer whales contained only lumpfish (Laidre *et al.* 2006), and off
334 Iceland from sporadic predation records (Samarra *et al.* 2018). Our results list the lumpfish as
335 prey for killer whales in an additional region of the North Atlantic. Lumpfish repeatedly
336 recorded as prey within single season ($n=16$ records in 2018) and across years (2016-2018;
337 Fig. 5, Table 3) in this study suggests consistency of this seasonal dietary pattern, likely in
338 response to the increased availability of lumpfish when migrating horizontally towards
339 spawning areas.

340

341 In spring, not only were encountered killer whales and predation records consistent
342 across seasons, but observed foraging behavior was in striking contrast to cooperative herring
343 feeding strategies observed from November to February in the same region (Jourdain and
344 Vongraven 2017). When feeding on herring, killer whales aggregate in a tight group
345 formation for coordinated school-herding, prior to slapping the fish with the underside of their
346 flukes and then individually consuming stunned fish (Similä and Ugarte 1993, Similä 1997).
347 Similar hunting behavior of killer whales feeding on schooling mackerel in the Norwegian
348 Sea in July-August has also been observed (Nøttestad *et al.* 2014). In contrast, killer whales
349 foraging on solitary lumpfish (Davenport 1985) were spread over several hundred meters and

350 aerial footage supported individual rather than group-based foraging. This behavior appears
351 more similar to that of killer whales feeding on loose patches of Atlantic salmon in the
352 Lofoten region, Norway (Vester and Hammerschmidt 2013). This is in further support of
353 killer whales adapting feeding strategies to behavioral traits of target prey (*e.g.*, Similä and
354 Ugarte 1993, Baird and Dill 1995, Samarra and Miller 2015). Lumpfish-feeding killer whales
355 also adopted smaller group sizes in spring than when observed at herring wintering grounds
356 (Fig. 4). By maximizing energetic gain, smaller groups could be adaptive to foraging on a
357 scattered prey resource as opposed to highly concentrated wintering herring where a more
358 cooperative foraging strategy is required (Nøttestad and Axelsen 1999, Nøttestad *et al.* 2002).
359 Our results bring the first robust evidence, featuring individual records of site-fidelity,
360 behavior and predation over several years, for seasonal adaptation and switching between
361 alternative prey resources in Norwegian waters.

362

363 The NSS herring is found in most dense aggregations on its wintering grounds, compared
364 to lower densities due to looser schools on spawning and feeding grounds (Nøttestad *et al.*
365 1996). The NSS herring is also subject to important changes in fat content throughout its life
366 cycle with the highest rate of energy depletion occurring during the spawning migration. As
367 such, herring fat content is about 22% when entering the wintering area in September and is
368 reduced to eight to 10% after spawning in February-April (Slotte 1999). As herring both loses
369 fat content and becomes more dispersed in spring, lumpfish with fat content ranging from
370 >8% for gravid females to 20% for males (Davenport and Kjørsvik 1986) enters the coastal
371 waters to spawn. Some killer whale groups may have diversified their diet and be able to
372 switch to foraging on this alternative, seasonally abundant and apparently relatively
373 nutritious, prey.

374

375 Our results showed that at least 75 different killer whales have adapted to the seasonality
376 of spawning lumpfish in Andfjord, returning year after year for temporary residence and
377 foraging (Fig. 2 and 3, Table 2). This represents 7.7 % of the total number of marked
378 individuals identified in the study area between 2007 and 2018 (Jourdain and Karoliussen
379 2018). This number should be considered as a baseline minimum since it does not include
380 unmarked individuals and calves also observed feeding on lumpfish during this study.
381 Additionally, because this study was entirely based on opportunistic efforts and covered a
382 relatively small area, and because killer whales may temporarily travel away from feeding
383 sites or display group-specific preferences in habitat use, individuals or entire groups may
384 have been undetected (Kuningas *et al.* 2014). While the lumpfish is a common species along
385 the Norwegian coast with spawning grounds found in multiple regions (Davenport 1985,
386 Holst 1993) it could very well be part of the diet of killer whales elsewhere and this feeding
387 behavior could be important at the population level.

388

389 Although the NSS herring has long been assumed to be the main prey of killer whales in
390 Norway, recent year-round data collection efforts uncovered persistent dietary specializations
391 on pinnipeds (Jourdain *et al.* 2017) and on lumpfish (present study) in northern Norway. This
392 highlights the likelihood that killer whale research conducted on a seasonal basis can miss
393 seasonal specialized feeding behaviors and underestimating important prey resources. Our
394 results further emphasize the importance of individual-focused studies, allowing for the
395 detection of inter-individual variations in dietary habits and prey specializations.

396

397

398 Acknowledgements

399 This research was supported by grants from the Sea World and Busch Gardens
400 Conservation fund and from Sea World and Parks Entertainment. CT thanks the team of the
401 Genotyping and Sequencing platform shared with the LabEx CeMEB (Centre Méditerranéen
402 de l'Environnement et de la Biodiversité, Montpellier, France) for their technical help.
403 Photographs contributed by Northern Explorers, Marten Bril (Sea Safari Andenes AS),
404 Camilla Ilmoni, Helge Hellesund and Daniele Zanoni (Whale Safari AS) enabled
405 identifications of individuals that were included in this study. We thank Dag Vongraven for
406 mapping the study area. Comments and suggestions from three anonymous reviewers
407 substantially improved the manuscript.

408

409

410 Literature cited

411 Albert, O. T., E. Torstensen, B. Bertelsen, S. T. Jonsson, I. H. Pettersen and J. C. Holst. 2002.

412 Age-reading of lumpsucker (*Cyclopterus lumpus*) otoliths: dissection, interpretation
413 and comparison with length frequencies. Fisheries Research 55:239-252.

414 Baird, R. W. and L. M. Dill. 1995. Occurrence and behaviour of transient killer whales:

415 seasonal and pod-specific variability, foraging behaviour, and prey handling. Canadian
416 Journal of Zoology 73:1300-1311.

417 Bertelsen, B. 1994. Bestandsutvikling og bestandsstruktur hos rognkjeks og rognkall

418 (*Cyclopterus lumpus* L.) i Sifjorden i Troms, og maskeseleksjon og fangsteffektivitet

419 ved garn- og rusefiske etter arten. Fiskerikandidatoppgave, The Norwegian College of

420 Fishery Science, University of Tromsø, 89 pp.

421 Bigg, M. 1982. An assessment of killer whale *Orcinus orca* stocks off Vancouver Island,

422 British Columbia. Report of the International Whaling Commission 32:655-666.

423 Bisther, A. and D. Vongraven. 1995. Studies of social ecology of Norwegian killer whales
424 (*Orcinus orca*). Pages 169-176 in A. S. Blix, L. Walløe and Ø. Ulltang eds. Whales,
425 seals, fish and man. Elsevier Science.

426 Bourque, J., R. Dietz, C. Sonne, *et al.* 2018. Feeding habits of a new Arctic predator: insight
427 from full-depth blubber fatty acid signatures of Greenland, Faroe Islands, Denmark,
428 and managed-care killer whales *Orcinus orca*. Marine Ecology Progress Series 603:1-
429 12.

430 Christensen, I. 1982. Killer whales in Norwegian coastal waters. Report of the International
431 Whaling Commission 32:633-641.

432 Cosentino, A. M. 2015. First record of Norwegian killer whales attacking and feeding on a
433 harbour porpoise. Marine Biodiversity Records 8.

434 Daura-Jorge, F. G., L. L. Wedekin, V. D. Q. Piacentini and P. C. Simões-Lopes. 2005.
435 Seasonal and daily patterns of group size, cohesion and activity of the estuarine
436 dolphin, *Sotalia guianensis* (P.J. van Bénédén) (*Cetacea, Delphinidae*), in southern
437 Brazil. Revista Brasileira de Zoologia 22:1014-1021.

438 Davenport, J. 1985. Synopsis of biological data on the lumpsucker, *Cyclopterus lumpus*
439 (Linnaeus, 1758). Food & Agriculture Org.

440 Davenport, J. and E. Kjørsvik. 1986. Buoyancy in the lumpsucker *Cyclopterus lumpus*.
441 Journal of the Marine Biological Association of the UK 66:159-174.

442 Domenici, P., R. S. Batty, T. Similä and E. Ogam. 2000. Killer whales (*Orcinus orca*) feeding
443 on schooling herring (*Clupea Harengus*) using underwater tail-slaps: kinematic
444 analyses of field observations. Journal of Experimental Biology 203:283-294.

445 Dragesund, O., Johannessen, A., & Ulltang, Ø. 1997. Variation in migration and abundance of
446 Norwegian Spring Spawning herring (*Clupea harengus* L.). Sarsia, 82:97-105.

447 Foote, A. D., J. Newton, S. B. Piertney, E. Willerslev and M. T. P. Gilbert. 2009. Ecological,
448 morphological and genetic divergence of sympatric North Atlantic killer whale
449 populations. *Molecular Ecology* 18:5207-5217.

450 Foote, A. D., T. Similä, G. Vikingsson and P. T. Stevick. 2010. Movement, site fidelity and
451 connectivity in a top marine predator, the killer whale. *Evolutionary Ecology* 24:803-
452 814.

453 Foote, A. D., H. Vester, G. A. Vikingsson and J. Newton. 2012. Dietary variation within and
454 between populations of Northeast Atlantic killer whales, *Orcinus orca*, inferred from
455 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses. *Marine Mammal Science* 28:E472-E485.

456 Foote, A. D., N. Vijay, M. C. Avila-Arcos, *et al.* 2016. Genome-culture coevolution promotes
457 rapid divergence of killer whale ecotypes. *Nature Communications* 7.

458 Ford, J. K. B. 1989. Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver
459 Island, British Columbia. *Canadian Journal of Zoology* 67:727-745.

460 Ford, J. K. B. 2009. Killer whales *Orcinus orca*. Pages 650-657 in W. F. Perrin, B. Würsig
461 and J. G. M. Thewissen eds. *The encyclopedia of marine mammals*. Academic Press,
462 San Diego, USA.

463 Ford, J. K. B. and G. M. Ellis. 2006. Selective foraging by fish-eating killer whales *Orcinus*
464 *orca* in British Columbia. *Marine Ecology Progress Series* 316:185-199.

465 Ford, J. K. B. and G. M. Ellis. 2014. You are what you eat: foraging specializations and their
466 influence on the social organization and behavior of killer whales. Pages 75-98 in J.
467 Yamagiwa and L. Karczmarski eds. *Primates and cetaceans: field research and*
468 *conservation of complex mammalian societies*. Springer.

469 Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm and K. C.
470 Balcomb. 1998. Dietary specialization in two sympatric populations of killer whales

471 (*Orcinus orca*) in Coastal British Columbia and adjacent waters. Canadian Journal of
472 Zoology 76:1456-1471.

473 Goulet, D., J. M. Green and T. H. Shears. 1986. Courtship, spawning, and parental care
474 behavior of the lumpfish, *Cyclopterus lumpus* L., in Newfoundland. Canadian Journal
475 of Zoology 64:1320-1325.

476 Hoelzel, A. R., J. Hey, M. E. Dahlheim, C. Nicholson, V. Burkanov and N. Black. 2007.
477 Evolution of population structure in a highly social top predator, the killer whale.
478 Molecular Biology and Evolution 24:1407-1415.

479 Holst, J. C. 1993. Observations on the distribution of lumpsucker (*Cyclopterus Lumpus*, L.) in
480 the Norwegian Sea. Fisheries Research 17:369-372.

481 Huse, G., A. Fernö and J. C. Holst. 2010. Establishment of new wintering areas in herring co-
482 occurs with peaks in the 'first time/repeat spawner' ratio. Marine Ecology Progress
483 Series 409:189-198.

484 Jourdain, E. and R. Karoliussen. 2018. Identification catalogue of Norwegian killer whales:
485 2007-2018. doi: 10.6084/m9.figshare.4205226.

486 Jourdain, E. and D. Vongraven. 2017. Humpback whale (*Megaptera Novaeangliae*) and killer
487 whale (*Orcinus orca*) feeding aggregations for foraging on herring (*Clupea harengus*)
488 in Northern Norway. Mammalian Biology - Zeitschrift fur Saugetierkunde 86:27-32.

489 Jourdain, E., D. Vongraven, A. Bisther and R. Karoliussen. 2017. First longitudinal study of
490 seal-feeding killer whales (*Orcinus orca*) in Norwegian coastal waters. Plos One
491 12:e0180099.

492 Knebelsberger, T., M. Landi, H. Neumann, *et al.* 2014. A reliable DNA barcode reference
493 library for the identification of the North European shelf fish fauna. Molecular
494 Ecology Resources 14:1060-1071.

495 Kumar, S., G. Stecher and K. Tamura. 2016. MEGA7: Molecular evolutionary genetics
496 analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33:1870-
497 1874.

498 Kuningas, S., T. Similä and P. S. Hammond. 2014. Population size, survival and reproductive
499 rates of Northern Norwegian killer whales (*Orcinus orca*) in 1986-2003. *Journal of the*
500 *Marine Biological Association of the United Kingdom* 94:1277-1291.

501 Laidre, K. L., M. P. Heide-Jorgensen and J. R. Orr. 2006. Reactions of narwhals, *Monodon*
502 *monoceros*, to killer whale, *Orcinus orca*, attacks in the Eastern Canadian Arctic.
503 *Canadian Field-Naturalist* 120:457-465.

504 Mitamura, H., E. B. Thorstad, I. Uglem, *et al.* 2012. Movements of lump sucker females in a
505 Northern Norwegian fjord during the spawning season. *Environmental Biology of*
506 *Fishes* 93:475-481.

507 Morin, P. A., F. I. Archer, A. D. Foote, *et al.* 2010. Complete mitochondrial genome
508 phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species.
509 *Genome Research* 20:908-916.

510 Nøttestad, L., M. Aksland, A. Beltestad, A. Fernö, A. Johannessen and O. Arve Misund.
511 1996. Schooling dynamics of Norwegian Spring Spawning herring (*Clupea harengus*
512 L.) in a coastal spawning area. *Sarsia* 80:277-284.

513 Nøttestad, L. and B. E. Axelsen. 1999. Herring schooling manoeuvres in response to killer
514 whale attacks. *Canadian Journal of Zoology* 77:1540-1546.

515 Nøttestad, L., A. Ferno and B. E. Axelsen. 2002. Digging in the deep: killer whales' advanced
516 hunting tactic. *Polar Biology* 25:939-941.

517 Nøttestad, L., L. D. Sivle, B. A. Krafft, *et al.* 2014. Prey selection of offshore killer whales
518 *Orcinus orca* in the Northeast Atlantic in late summer: spatial associations with
519 mackerel. *Marine Ecology Progress Series* 499:275-283.

520 Olesiuk, P. F., M. A. Bigg and G. M. Ellis. 1990. Life history and population dynamics of
521 resident killer whales *Orcinus orca* in the coastal waters of British Columbia and
522 Washington State. Report of the International Whaling Commission 12:209-243.

523 Parsons, K. M., J. W. Durban, A. M. Burdin, *et al.* 2013. Geographic patterns of genetic
524 differentiation among killer whales in the Northern North Pacific. Journal of Heredity
525 104:737-754.

526 R Core Team. 2016. R: A Language and Environment for Statistical Computing. R
527 Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.

528 Riesch, R., L. G. Barrett-Lennard, G. M. Ellis, J. K. B. Ford and V. B. Deecke. 2012. Cultural
529 traditions and the evolution of reproductive isolation: ecological speciation in killer
530 whales? Biological Journal of the Linnean Society 106:1-17.

531 Samarra, F. I. P., M. Bassoi, J. Beesau, *et al.* 2018. Prey of killer whales (*Orcinus orca*) in
532 Iceland. Plos One 13:e0207287.

533 Samarra, F. I. P. and P. J. O. Miller. 2015. Prey-induced behavioural plasticity of herring-
534 eating killer whales. Marine Biology 162:809-821.

535 Samarra, F. I. P., M. Vighi, A. Aguilar and G. A. Vikingsson. 2017. Intra-population variation
536 in isotopic niche in herring-eating killer whales off Iceland. Marine Ecology Progress
537 Series 564:199-210.

538 Sambrook, J., E. F. Fritsch and T. Maniatis. 1989. Molecular cloning: a laboratory manual.
539 Cold Spring Harbor Laboratory Press, New York.

540 Similä, T. 1997. Sonar observations of killer whales (*Orcinus orca*) feeding on herring
541 schools. Aquatic Mammals 23:119-126.

542 Similä, T., J. C. Holst and I. Christensen. 1996. Occurrence and diet of killer whales in
543 Northern Norway: seasonal patterns relative to the distribution and abundance of

544 Norwegian Spring-Spawning Herring. Canadian Journal of Fisheries and Aquatic
545 Sciences 53:769-779.

546 Similä, T. and F. Ugarte. 1993. Surface and underwater observations of cooperatively feeding
547 killer whales in Northern Norway. Canadian Journal of Zoology 71:1494-1499.

548 Slotte, A. 1999. Differential utilisation of energy during wintering and spawning migration in
549 Norwegian Spring-Spawning Herring. Journal of Fish Biology 54:338-355.

550 Sparks, J. S. and W. L. Smith. 2004. Phylogeny and biogeography of cichlid fishes (Teleostei:
551 Perciformes: Cichlidae). Cladistics 20:501-517.

552 Stenersen, J. and T. Similä. 2004. Norwegian Killer Whales. Tringa forlag.

553 Van Opzeeland, I. C., P. J. Corkeron, T. Leyssen, T. Similä and S. M. Van Parijs. 2005.
554 Acoustic behaviour of Norwegian killer whales, *Orcinus orca*, during carousel and
555 seiner foraging on Spring-Spawning Herring. Aquatic Mammals 31:110-119.

556 Van Parijs, S. M., T. Leyssen and T. Similä. 2004. Sounds produced by Norwegian killer
557 whales, *Orcinus orca*, during capture. Journal of the Acoustical Society of America
558 116:557-560.

559 Vester, H. and K. Hammerschmidt. 2013. First record of killer whales (*Orcinus orca*) feeding
560 on Atlantic salmon (*Salmo salar*) in Northern Norway suggest a multi-prey feeding
561 type. Marine Biodiversity Records 6:1-5.

562 Vongraven, D. and A. Bisther. 2014. Prey switching by killer whales in the North-East
563 Atlantic: observational evidence and experimental insights. Journal of the Marine
564 Biological Association of the United Kingdom 94:1357-1365.

565 Weinrich, M., M. Martin, R. Griffiths, J. Bove and M. Schilling. 1997. A shift in distribution
566 of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern
567 Gulf of Maine. Fishery Bulletin 95:826-836.

568

569

570 Figure 1. Location of the study area in northern Norway. Box A corresponds to Andfjord
571 where the data presented in this study were collected. Box B locates the wintering herring
572 grounds where the whales identified in this study were encountered in November-February in
573 2015-2018 while feeding on herring. Spatial distribution of killer whale encounters during
574 March-April in 2014-2018, with corresponding behavioral patterns are plotted. Depth
575 contours (m), as well as GPS tracks (blue plots) of the opportunistic surveys conducted in
576 2018 are also shown.

577

578 Figure 2. Cumulative number of identified individual killer whales in Andfjord in March-
579 April plotted against cumulative identifications. Each data point represents a survey. The 1:1
580 plot is shown for reference. Dashed lines separate the five calendar years (2014-2018).

581

582 Figure 3. (A) Distribution of individual sighting frequencies within season (March-April),
583 averaged over the entire study period 2014-2018; (B) Distribution of individual sighting
584 frequencies across years, *i.e.* number of seasons (March-April) in which individuals were
585 photographed from 2014 to 2018.

586

587 Figure 4. Distribution of group size adopted by the lumpfish-feeding killer whales when
588 encountered at the lumpfish spawning grounds ($n=49$) vs herring wintering grounds ($n=23$) in
589 2015-2018. Data distribution is displayed as second and third quartiles (box plot), median
590 (vertical crossing line) and mean (star symbol) values for spring and winter seasons.

591

592 Figure 5. Sample of photographs used as evidence supportive of killer whale predation on
593 lumpfish in Andfjord. All photos were taken in April 2016-2018; (A) Lumpfish observed

594 below the surface prior to capture and consumption by adult male killer whale NKW-0572;
595 (B) Adult male killer whale NKW-0712 catching a lumpfish; (C) Adult female-sized killer
596 whale feeding on the carcass of a lumpfish; (D) A subadult killer whale consumed the inner
597 part of a lumpfish before discarding the carcass.

598

599

600

601

602

603

604

605

606

607

608

609

610

611

612

613

614

615

616

617 Table 1. Sampling effort for the period March-April in 2014-2018 in Andfjord.

	2014	2015	2016	2017	2018	Total
<i>Dedicated effort by researchers</i>						
Effort days	0	7	11	6	20	44
Encounter days	0	7	11	4	20	42
Killer whale encounters	0	7	15	4	25	51
Hours spent with whales	0	11.7	22.8	8.1	80.6	123.2
Hours of behavioral sampling	0	6.0	13.7	4.3	38.0	62.0
Photographs taken	0	2,480	5,080	990	5,620	14,170
Predation events for which prey remains were collected	0	0	2	0	9	11
Predation events for which prey were visually identified	0	0	2	2	7	11
<i>Additional photographic contributions</i>						
Encounter days	1	0	3	7	0	11
Photographs provided	300	0	127	1280	0	1707
<i>Total</i>						
Encounter days	1	7	14	11	20	53

Identifications	6	41	70	40	119	276
Distinct individuals	6	29	33	25	42	-

618

619

620

621

622 Table 2. Summary of the parameters used to assess minimum residency of killer whales in Andfjord during March-April in 2014–2018.

623 Calculated residency should be considered as minimum values due to opportunistic data collection.

	2014	2015	2016	2017	2018
Number of encounter days	1	7	14	11	20
First-to-last encounter period (d)	-	19	32	42	44
Individuals resighted	-	9	21	8	26
Residency mean \pm SD (min–max)	-	8.3 \pm 3.7 (2-14)	10.6 \pm 4.8 (3-20)	10.3 \pm 6.2 (4-16)	16 \pm 10.3 (4-39)

624

625

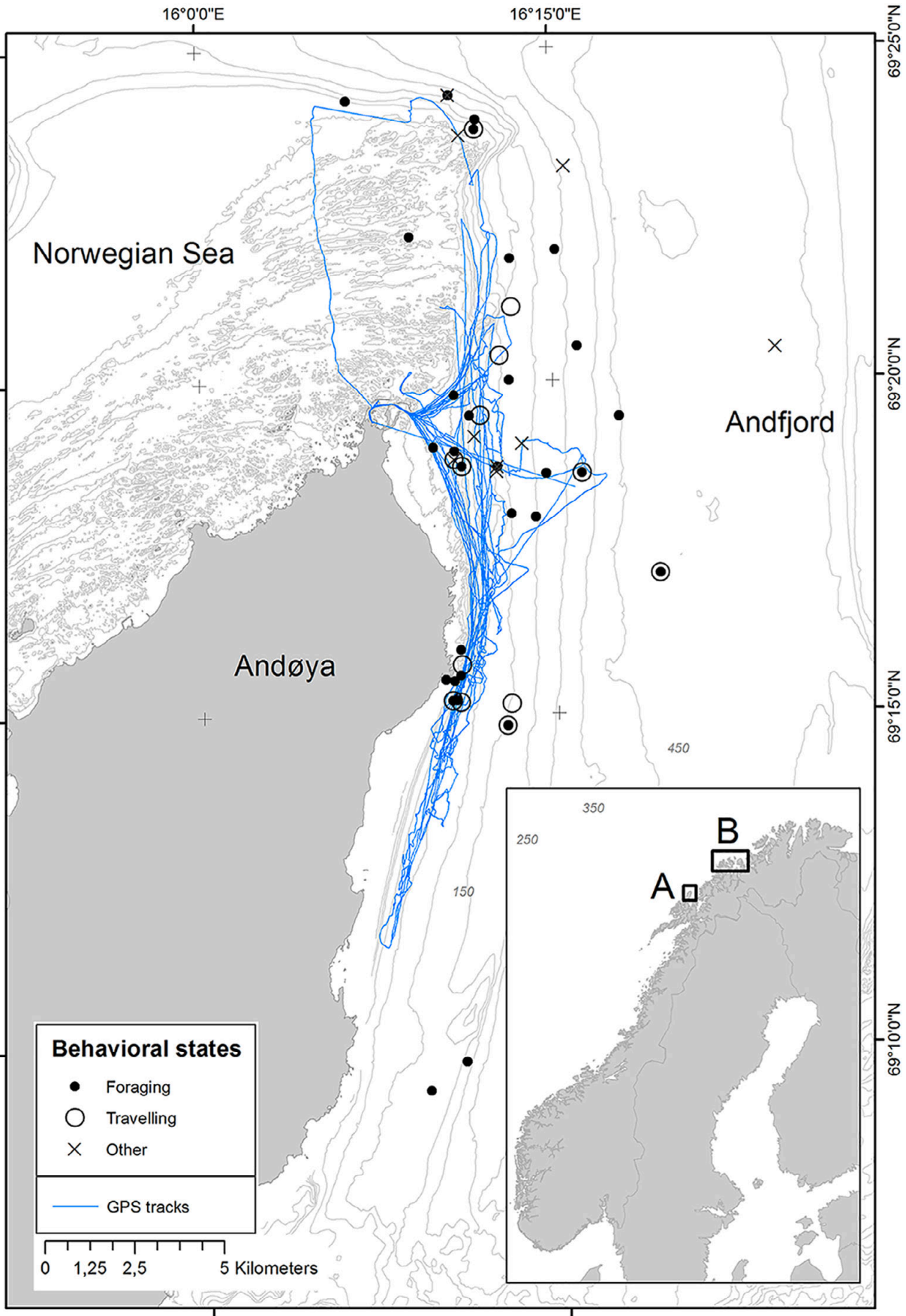
626

627 Table 3. Summary of predation events for which evidence was collected for identification of the target prey. All resulted in identification of the
628 lumpfish as prey species.

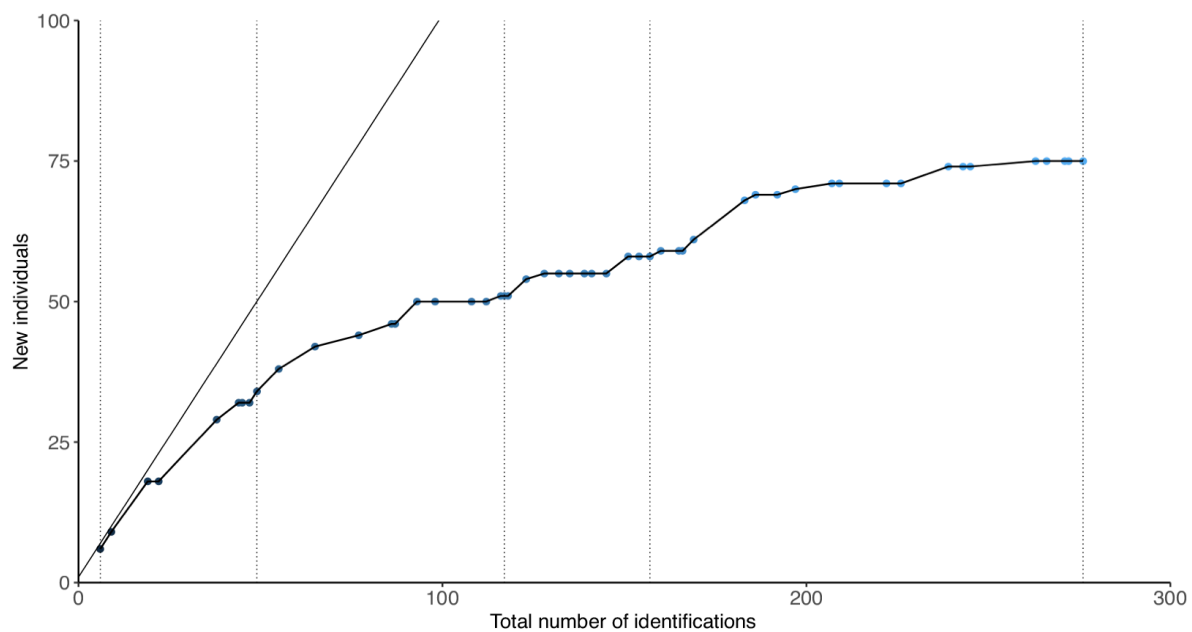
629

Events	Season (day/month)	Evidence	ID
1, 2	2016 (30/4)	Prey fragments	NKW-0712
3, 4	2016 (30/4)	Photographs	NKW-0712
5, 6	2017 (12/4)	Photograph	NKW-0572
7	2018 (5/4)	Prey fragments	NKW-0004
8-10	2018 (9/4)	Prey fragments	NKW-0004
11	2018 (9/4)	Photographs	NKW-0912
12	2018 (11/4)	Photographs	NKW-0079
13	2018 (12/4)	Prey fragments	NKW-0910
14	2018 (13/4)	Aerial footage	Unidentified sub-adult
15	2018 (13/4)	Aerial footage	NKW-0998
16	2018 (14/4)	Aerial footage	NKW-0908
17	2018 (15/4)	Aerial footage	Unidentified sub-adult

18, 19	2018 (22/4)	Prey fragments	NKW-0715
20	2018 (22/4)	Prey fragments	NKW-0716
21	2018 (24/4)	Prey fragments	Y093
22	2018 (24/4)	Photographs	Y093



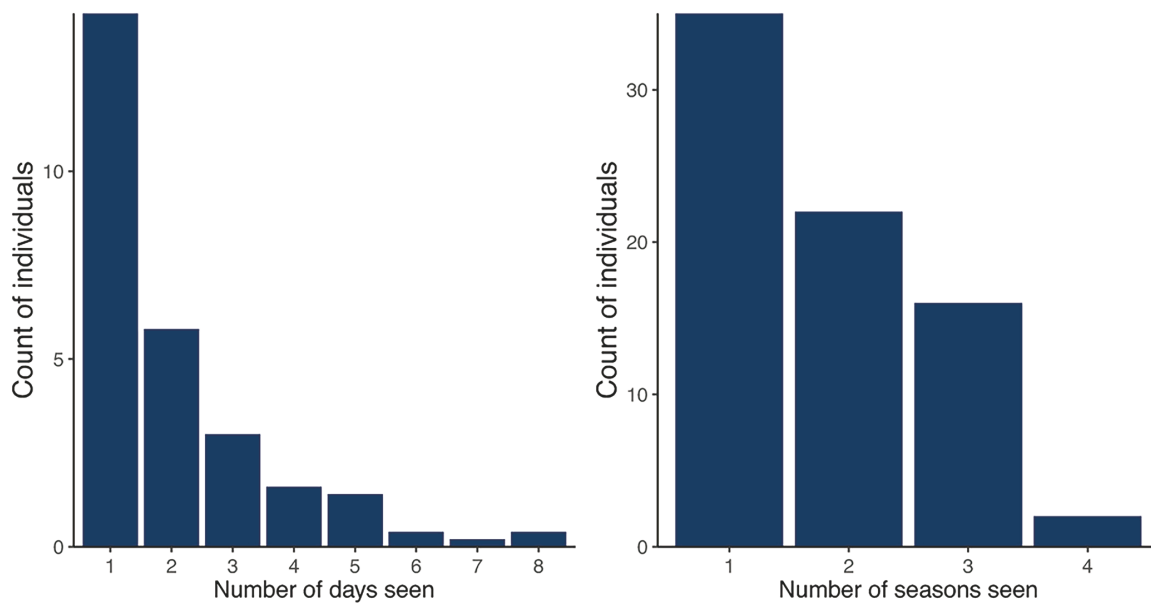
630
631 Figure 1



632

633 Figure 2

634



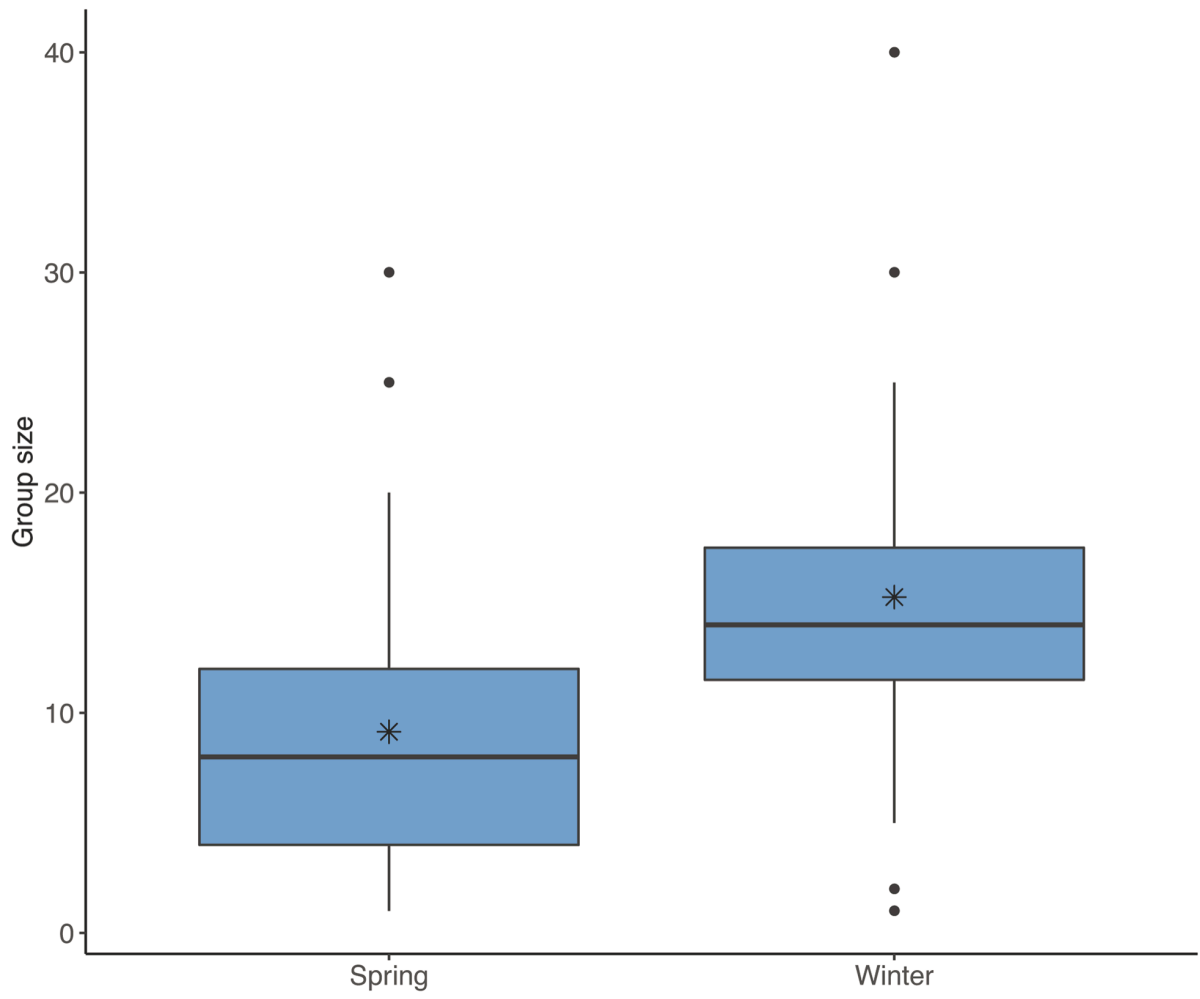
635

636 Figure 3

637

638

639



640

641 Figure 4

642

