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Long-distance migrations, population mixing, and growth rate of lumpfish (Cyclopterus lumpus) revealed from tag-recaptures

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Abstract

We reveal that lumpfish (Cyclopterus lumpus) frequently migrate over long distances between their summer feeding area in the open ocean and their spring spawning sites in coastal areas, through applying tag-recapture methodology. A total of 2750 C. lumpus were tagged in the Irminger Sea around Iceland and in the Norwegian Sea over 6 years, of which 17 C. lumpus were recaptured. Interestingly, four individuals were recaptured more than 1000 km distant from where they were tagged. C. lumpus tagged in the Irminger Sea and north of Iceland were recaptured around Iceland, whereas none of the fish tagged in other areas of the Norwegian Sea were recaptured in Iceland. This difference in recapture rate from different areas suggests that a higher proportion of C. lumpus from the Irminger Sea and north of Iceland spawns around Iceland in comparison with C. lumpus in other areas. Two fish tagged east of Iceland were recaptured on the coast of Denmark, with one fish having a displacement distance of 1612 km. The recapture of these two fish in Denmark demonstrates that part of the C. lumpus population spawning in Denmark utilizes the Norwegian Sea as a major feeding area and that the Norwegian Sea is a common feeding area for several distinct populations of C. lumpus. The growth rate of tagged fish varied from 1.2 to 11.1 cm year⁻¹, indicating that males that are >20 cm and females that are >25 cm during the summer are capable of sufficient growth to achieve a suitable size for spawning (\geq 25 and \geq 35 cm for males and females, respectively) the following spring.

KEYWORDS Atlantic Ocean, lumpsucker, Nordic seas, pelagic

INTRODUCTION 1

The assessment and management of fish populations requires a thorough understanding of the population structure and origin of the fish being assessed (Begg et al., 1999). It is common for different populations of the same fish species, which display differences in population dynamics, to mix during part of their life cycle (Cadrin et al., 2010; Jónsdóttir et al., 2007; Ruzzante et al., 2006). If a population survey takes place during the period of mixing, then methods need to be developed to understand the proportion of fish belonging to the different natal populations to avoid biased estimates of population abundance, which can affect biomass/biological reference points and maximum sustainable yield targets (Hintzen et al., 2015).

Lumpfish Cyclopterus lumpus (Linnaeus 1758) is a pelagic fish species inhabiting the North Atlantic Ocean which spawns in coastal areas but spends much of its life in the open sea (Davenport, 1985). Important spawning areas, deduced from the distribution of catches from the female commercial roe fishery, consist of shallow coastal areas of Iceland, Norway, and West Greenland (Kennedy et al., 2019). C. lumpus also spawn, to a lesser degree, around other coastal areas of the North Atlantic, including the Faroe Islands, Denmark, and the British Isles (Davenport, 1985). While individual fish spawn two batches

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of eggs with the time between batches being approximately 1-2 weeks, at the population level, spawning occurs from early spring through to autumn (Kennedy, 2018). Post-spawning mortality is thought to be high (Hedeholm et al., 2014; Kasper et al., 2014), but some fish do survive after spawning and will return to spawn, often in the same area, the following year (Kennedy & Ólafsson, 2019).

During the summer, *C. lumpus* are frequently found throughout the eastern Atlantic, from the Irminger Sea in the west to the Baltic Sea in the east and as far north as Svalbard and the Barents Sea, and as far south as the North Sea and the English Channel (Ellis, 2015; Eriksen et al., 2014). The population structure of *C. lumpus* is poorly understood, but there is known to be a separation between populations in the eastern and western Atlantic (Pampoulie et al., 2014). There is also known to be structuring within the eastern Atlantic, with several genetically distinct populations in the Baltic Sea and the English Channel as well as local structuring within Iceland, Norway, and Greenland (Garcia-Mayoral et al., 2016; Jansson et al., 2023; Pampoulie et al., 2014; Whittaker et al., 2018).

The International Ecosystem Summer Survey of the Nordic Seas (IESSNS) is an annual pelagic survey that primarily targets Atlantic mackerel (Scomber scombrus), using standardized pelagic swept area trawling in the upper 30-35 m of the water column, for abundance estimation and stock assessment purposes (Nøttestad et al., 2016). C. lumpus are often caught during the IESSNS over vast oceanic and coastal areas at \sim 70–80% of the stations (Nøttestad et al., 2023). This survey has the potential to provide useful information for stock assessment of C. lumpus due to the large geographical coverage and standardized pelagic trawl sampling. However, the natal origin of C. lumpus found in the open ocean of different areas within the eastern Atlantic, along with their growth patterns, is unknown. This uncertainty hinders catch observations from being used meaningfully for assessment purposes. There is an almost continuous distribution of fish ≥18 cm between Iceland and Norway, indicating there is some mixing between the different natal populations outside of the breeding season. C. lumpus, despite its non-streamlined appearance, is a competent swimmer and has a metabolic capacity similar to Atlantic cod Gadus morhua (Linnaeus 1758) (Eisenberg et al., 2024). They have been documented travelling up to 587 km between tagging and recapture locations, and can swim up to 49 km per day (Kennedy et al., 2015), suggesting potential for population mixing in feeding areas.

Information on size-at-age and growth of *C. lumpus* is limited, with current evidence pointing to a lifespan of 3–5 years (Hedeholm et al., 2014), although some fish have been estimated to be as old as 12 years (Thorsteinsson, 1981). Males appear to mature earlier than females, with mature individuals in west Greenland being 2–5 years for males and 3–4 years for females. Most of the growth takes place prior to maturity, with estimates following maturation at 2–4 cm year⁻¹ for females and a single male was found to have grown 2 cm after 1 year following a tag-recapture event (Bagge, 1967; Kasper et al., 2014).

The aim of the current study was to determine the possible migration routes and spawning areas of *C. lumpus* caught in different areas of the Nordic Seas using tag-recapture methodology. Additionally, we also aim to gather information on the time between tagging and recapture at the spawning location and relate this to the size at tagging and examine the growth of individuals between tagging and recapture.

2 | MATERIALS AND METHODS

The care and use of experimental animals complied with Icelandic and Greenlandic animal welfare laws but no specific permits were required. The study complied with Norwegian animal welfare laws, guidelines, and policies as approved by the Norwegian Food Safety Authority with two applications approved (application IDs 20276 and 29610, available at https://www.mattilsynet.no/dyr/forsoksdyr/ soknader).

C. lumpus captured during the annual IESSNS were tagged and released from 2018 to 2023. Three countries participated in the C. lumpus tagging: Iceland, Greenland, and Norway (Table 1). The C. lumpus were captured using a standardized pelagic trawl (Multpelt832) deployed for 30 min. On capture, C. lumpus were placed in a tank with flow-through sea water until tagged. The total length of each fish was measured, and a Peterson tag (FLOY TAG Inc.) containing a unique identification number and contact details was inserted through the dorsal hump (Figure 1). As C. lumpus are sexually dimorphic, the sex of mature C. lumpus can often be discerned from size and coloration, but the size range of the tagged fish likely consisted of a mix of immature and mature individuals so the sex of tagged individuals was not identified during tagging. After tagging, the tagged individuals were released back into the ocean. A reward of 5000 Icelandic kroner was provided for the return of each tag and the tagging program was communicated to fishers through the Icelandic National Association of Small Boat Owners and Icelandic fishing news websites as well as the websites of the Marine and Freshwater Research Institute (Iceland) and the Greenland Institute of Natural Resources (Greenland). If a fish was reported as recaptured, information was requested on capture location, length, and sex. If possible, it was requested for the fish to be returned to the Marine and Freshwater Research Institute in Iceland.

TABLE 1 The number of *Cyclopterus lumpus* tagged by each country in each year during the International Ecosystem Summer Survey in the Nordic Seas 2018–2023.

Year	Greenland	Iceland	Norway	Total
2018	36	253	0	289
2019	256	216	0	472
2020	159	370	186	715
2021	0	451	155	606
2022	48	67	179	294
2023	0	126	248	374

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Displacement distance was calculated for each fish using Google Earth (Google LLC) and set as the shortest distance between release and recapture location without crossing land. Average daily growth rate was calculated as (length at recapture – length at tagging)/days



FIGURE 1 Tagged *Cyclopterus lumpus* released during the International Ecosystem Summer Survey in the Nordic Seas. Photograph taken by James Kennedy.

at liberty, which was then multiplied by 365 days to give the average annual growth rate (cm year⁻¹). To estimate the growth rate for the four female fish which were not measured on recapture, the final length was inferred to be at least 35 cm and the growth rate was calculated based on a length of 35 cm. All four of these fish were captured in the Icelandic *C. lumpus* fishery where >99% of the *C. lumpus* caught were \geq 35 cm (Kennedy, 2021).

To examine the growth rate, data were taken from previous tagging studies which give length at tagging and at recapture for fish which were at liberty for approximately 1 year or longer (Bagge, 1967; Kasper et al., 2014; Kennedy et al., 2015). Data from Kasper et al. (2014) provides precise information on days at liberty, while information from Bagge (1967) does not, so days at liberty was considered as 365. Annual growth rate was calculated for the fish taken from previous studies in a similar manner to that described above.

3 | RESULTS

A total of 2750 C. *lumpus* were tagged in the Irminger Sea, around Iceland, and in the Norwegian Sea over 6 years (Figure 2 and

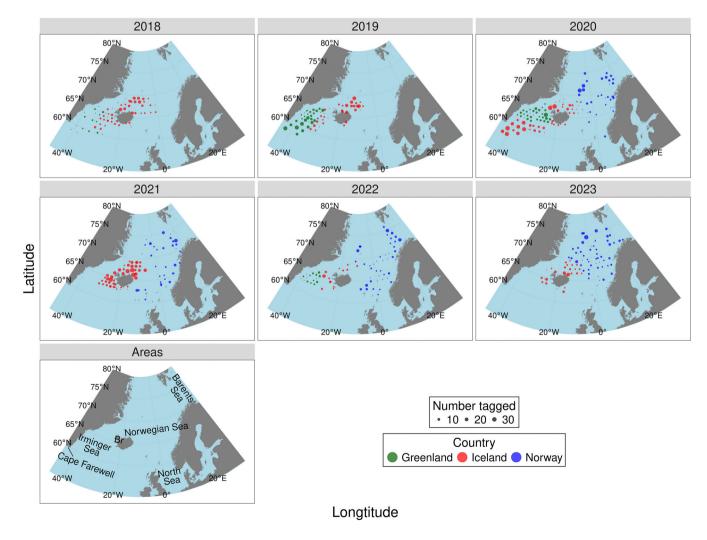


FIGURE 2 The location and number of *Cyclopterus lumpus* tagged by each country during the International Ecosystem Summer Survey in the Nordic Seas 2018–2023. The final panel shows the geographical locations mentioned in the text. Br, Breiðafjörður.

Table S1). The fish ranged in length from 5 to 56 cm (Figure 3). A total of 17 *C. lumpus* were recaptured, with days at liberty ranging from 16 to 627 days. These consisted of six males and 11 females (Figure 3 and Table S1). Displacement distances ranged from 138 to 1612 km. All the recaptures were reported by fishers targeting *C. lumpus* except for one which was recaptured by a pelagic trawler targeting Atlantic mackerel. The male fish which were recaptured were between 22 and 26 cm in length when tagged, while females were between 28 and 42 cm (Figure 3).

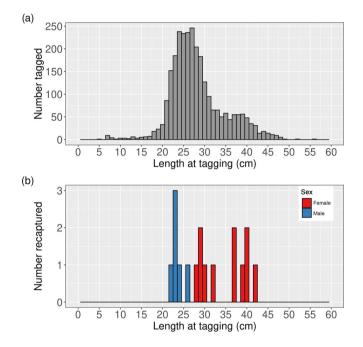


FIGURE 3 (a) Length distribution of all *Cyclopterus lumpus* tagged during the International Ecosystem Summer Survey in the Nordic Seas 2018–2023 and (b) length at tagging of the fish which were recaptured.

Of the 17 fish recaptured, 14 individuals were recaptured close to the coast of Iceland, while two were recaptured close to the coast of Denmark. One fish which was tagged south of the Faroe Islands was recaptured by a pelagic trawler in the Norwegian Sea (Figure 4). The length at recapture was available for five fish, with growth rate varying from 1.2 to 11.1 cm year⁻¹ (Figure 5). When the growth data of females from various sources were combined (excluding fish with inferred growth), there was a significant negative correlation between length at tagging and subsequent average annual growth rate (linear regression, n = 55, $F_{1,53} = 13.4$, p < 0.0001, $r^2 = 0.19$). The relationship between length at tagging and growth rate was still significant even if the fish measuring <30 cm at tagging was removed from the dataset (linear regression, n = 54, $F_{1,52} = 6.7$, p < 0.05, $r^2 = 0.10$).

4 | DISCUSSION

With only 17 recaptures from 2750 tagged fish (0.62%), this total is considered low and likely due to several contributing factors. The tagging method, where fish were captured using a pelagic trawl, could have led to internal injuries that were not externally visible, for example from the codend, resulting in mortality following tagging and release. However, since the fish were kept in water tanks after capture and only healthy fish (assessed by their swimming behavior) were tagged, we believe the mortality caused by tagging was minimal. Additionally, the low recapture rate may be due to low fishing mortality in general or to the fish originating from populations where fishing mortality is virtually zero. In Iceland and Norway, catches are managed based on relative fishing mortality (F_{proxy}) but the actual mortality is unknown (Durif et al., 2023; Kennedy et al., 2021). It may be that the proportion of the population(s) that was tagged was low, resulting in few recaptures. Between 2018 and 2023, the Icelandic fishery, which accounted for >95% of C. lumpus landings in the past decade in the

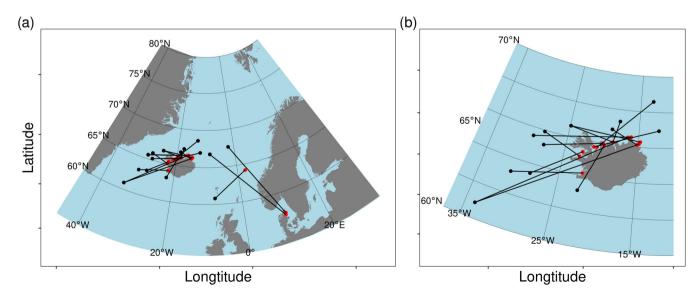


FIGURE 4 Map of the tagging (black dots) and recapture (red dots) locations of *Cyclopterus lumpus* tagged during the International Ecosystem Summer Survey in the Nordic Seas for the whole northeast Atlantic area (a) and for the area around Iceland only (b).

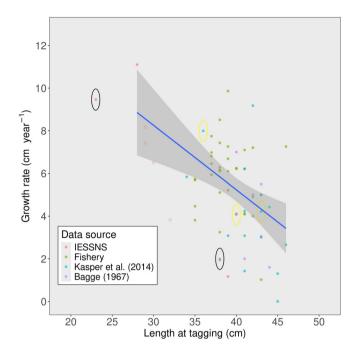


FIGURE 5 Annual average growth rate versus length at tagging for *Cyclopterus lumpus* tagged during the International Ecosystem Summer Survey in the Nordic Seas (IESSNS), the *C. lumpus* fishery in Iceland, and from previously published studies. The linear regression line for female *C. lumpus* is shown (p < 0.0001, $r^2 = 0.19$). Squares represent fish whose length at recapture was inferred. Black circles highlight male fish. Yellow circles highlight fish which were at liberty for >600 days. All other fish were at liberty ≤ 420 days.

eastern Atlantic Ocean (i.e., east of Cape Farewell so excluding landings from west Greenland) (Kennedy et al., 2019), landed an average of 5279 tonnes annually, which equates to approximately 1.76 million individuals (assuming an average weight of 3 kg at capture). With an average of 458 fish tagged per year in the current study, this equates to less than 0.05% of the fish landed, meaning that the actual tagging rate would be considerably lower than this. The fishing effort in Norway is considerably lower than in Iceland and primarily takes place from Vestfjorden to Varanger in northern Norway (Durif et al., 2023) so if any tagged fish migrated to spawn in Norway, there would be a very low probability of it being recaptured. Lastly, another reason for a low return rate could be that fishers do not return all caught tags, as observed in some tagging programs (Meyer et al., 2012). This rate is affected by factors such as public awareness and reward systems (Pollock et al., 2001; Thorsteinsson, 2002), which were implemented in our study, although their effects were not systematically evaluated.

Our study demonstrates that long-distance movement of *C. lumpus* is a common feature of the population found in open waters, with displacement/migration distances of four fish exceeding 1000 km and the highest displacement/migration distance being 1612 km, which is almost three times the previously documented maximum displacement distance (Kennedy et al., 2015). With an ability to migrate such an extensive distance, it is unsurprising that the capture location of *C. lumpus* in summer is not a good indicator of where they would migrate to spawn; fish in the Irminger Sea migrating to Iceland, even

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though the coast of Greenland was closer, and fish tagged east of Iceland being recaptured on the coast of Denmark. The recapture of three *C. lumpus* in Iceland which were tagged in the Irminger Sea indicates the fish in the Irminger Sea originate, at least in part, from the Icelandic population. This agrees with genetic evidence that indicates fish from the Irminger Sea are likely of Icelandic origin (Garcia-Mayoral et al., 2016). The fish tagged in the Norwegian Sea were recaptured in Iceland and Denmark, indicating the existence of a common feeding area within the Norwegian Sea for fish of different origins, which is supported by the results of a genetic study (Jansson et al., 2023).

Due to biases in the level of fishing effort in different areas, it is difficult to quantify the proportion of fish in each summer feeding area that are spawning in different countries. Nevertheless, the results do offer useful indications, including that all recaptured fish that were tagged north of Iceland were recaptured in Icelandic coastal areas during the spawning season. Those results suggest that at least a substantial portion of the fish found north of Iceland are of Icelandic origin. In contrast, none of the fish tagged towards the central and eastern parts of the Norwegian Sea were recaptured in Iceland (or Norway), indicating that a much lower proportion of the fish in that area migrated to Iceland. It should also be noted that no fish were recaptured in west Greenland, where there is a fishery for *C*. *lumpus* that in terms of landings is similar to that of Iceland. The whereabouts of C. lumpus that spawn in west Greenland outside of the spawning season is currently unknown, but the lack of tagged fish being recaptured in the west Greenland fishery indicates that they do not utilize the Irminger Sea. This is in line with the results from genetic studies which indicate that populations in the eastern and western Atlantic Ocean are genetically distinct (Garcia-Mayoral et al., 2016; Pampoulie et al., 2014).

The two fish recaptured in Danish coastal waters are of particular interest regarding the C. lumpus population in Denmark. C. lumpus in Denmark are fished commercially during the spring, albeit on a much smaller scale than in Iceland. The fish have been known to be only present in coastal areas of Denmark as juveniles <10 cm and as mature adults when spawning, but their location in the intervening time has been unknown (Bagge, 1964; Møller et al., 2019). The current study demonstrates that at least part of the population migrates out to the Norwegian Sea for feeding. The fish recaptured by the pelagic trawler in the Norwegian Sea is also of interest as this individual was tagged south of the Faroe Islands and recaptured 653 km away in the Norwegian Sea. This fish was recaptured in September, several months before the spawning season, and hence it is unclear whether this movement is linked to migration towards the spawning area or where this fish would eventually spawn. As most of the tagged fish displayed long displacement distances, it appears that C. lumpus commonly make extensive movements in open water between the feeding and spawning seasons.

C. lumpus are known to spawn from April until August in Iceland, but spawning is likely taking place in other months as well (Kennedy, 2018). The Icelandic annual groundfish survey, which takes place in March, captures *C. lumpus* during their migration to the coast (Kennedy et al., 2015; Kennedy & Jónsson, 2017). The *C. lumpus*

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caught during the groundfish survey consist of fish which will spawn throughout the whole spawning season (Kennedy, 2018). This indicates that fish migrate from offshore areas and stay in the coastal areas until they are ready to spawn. However, one fish recaptured in Breiðafjörður in Iceland on July 19, 2018 was tagged 16 days previously, northwest of Iceland, outside of the area of the Icelandic groundfish area. This recapture indicates that fish continue to migrate from offshore areas to the spawning area during the spawning season. However, this was only a single fish and the extent to which fish migrate from offshore to coastal areas during the spawning season is still an open question.

Current data for stock assessment of C. lumpus are limited, resulting in considerable uncertainties. The annual IESSNS survey, which captures C. lumpus in 70%-80% of stations throughout the northeast Atlantic, offers a substantial source of quantitative and standardized data that could potentially enhance the assessment for different populations. However, integrating IESSNS survey data into stock assessment and forecasting of C. lumpus abundance during the spawning season is, at present, hindered by uncertainties in the population structure, mortality, spawning time, and growth rate of the captured fish. Knowledge on C. lumpus growth and age at maturity is still limited, although current evidence suggests that male C. lumpus spawn at 2-5 years of age while females spawn at 3-5 years of age (Albert et al., 2002; Hedeholm et al., 2014), corresponding to lengths of >20 cm and >34 cm for males and females, respectively. Length distributions from the IESSNS (Nøttestad et al., 2023) and age readings from other sources (Albert et al., 2002) indicate that fish with a length of 20-30 cm are typically 2-3 years old. The growth rates of the fish tagged when <30 cm suggests that males and females larger than 20 and 25 cm, respectively, could reach spawning size the following year. This is partly corroborated with the examination of maturity during the IESSNS, which showed that all female fish \geq 28 cm (smaller fish were not examined) had begun ovary development in preparation for spawning the following year (Kennedy, 2018). Hence it appears, pending further investigations on maturity-at-size, it may be possible to use the catch of C. lumpus north of Iceland and in the Irminger Sea as an indication of the spawning population around Iceland.

Given that we inferred a minimum size of female fish whose length at recapture was unavailable, we are likely underestimating the growth of fish <33 cm. We can only be sure they reached the minimum size for capture in the fishery, with C. lumpus <35 cm being rare in the fishery (Kennedy, 2021), but their actual size when recaptured was unknown. As with any growth data from tag-recapture studies, interpretation of the results should be done with caution (Francis, 1988). The growth rate from mark-recapture data is an average rate over the time at which the fish is at liberty. However, daily and seasonal growth rates can vary through the year and between years, respectively (Coggan, 1997; Tattam et al., 2017), thus estimated annual growth can be influenced by the timing of tagging and recapture. C. lumpus inhabits temporal and Arctic regions which experience high seasonal changes in productivity and food abundance, thus daily and seasonal growth rate would be expected to vary between seasons. The estimated growth rate will be affected by the timing of the tagging and if the fish are at liberty

for multiple years. Fish tagged during the spawning season (in the fishery) and during the feeding season (during the IESSNS) will spend a different amount of their time at liberty in the summer feeding grounds. An effect is expected but given the current limited knowledge on the feeding and growth of *C. lumpus*, we can only speculate on the extent of this effect. For fish at liberty for multiple years, their growth will be underestimated as it will be an average growth rate over the entire period. Smaller fish have higher growth rates, so growth in the first year will be higher than in the second, but the estimated growth rate will be an average from these 2 years.

To conclude, *C. lumpus* are clearly capable swimmers, with many individuals partaking in long-distance migrations between feeding and spawning grounds. We found that a higher proportion of *C. lumpus* occurring north of Iceland and in the Irminger Sea during summer spawn in Iceland in comparison with other areas of the Norwegian Sea. The Norwegian Sea is a common feeding area for different natal populations of *C. lumpus*, including those that spawn along the coast of Denmark. None of the tagged fish were caught in the west Greenland *C. lumpus* fishery, suggesting that fish in this region do not use the northeast Atlantic as summer feeding area. Male and female *C. lumpus* that are larger than 20 and 25 cm, respectively, during the summer are likely to grow sufficiently by the following spawning season to reach a size similar to those found at the spawning grounds.

AUTHOR CONTRIBUTIONS

J.K. conceived and initiated the study, coordinated the tagging of the fish aboard the Icelandic vessel, analyzed the data, and prepared the first draft of the manuscript. S.P. and L.N. coordinated the tagging aboard the Greenlandic and Norwegian vessels, respectively, and participated in the writing of the manuscript.

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ETHICS STATEMENT

The care and use of experimental animals complied with Icelandic and Greenlandic animal welfare laws, but no specific permits were required. The study complied with Norwegian animal welfare laws, guidelines, and policies as approved by the Norwegian Food Safety Authority with two applications approved (application IDs 20276 and 29610, available at https://www.mattilsynet.no/dyr/forsoksdyr/ soknader).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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