Received: 16 January 2023 | Revised: 14 September 2023 | Accepted: 6 November 2023

DOI: 10.1111/jfb.15611

REGULAR ARTICLE

JOURNAL OF FISH BIOLOGY fsbi

Biological information on a rare pelagic fish, black ruff *Centrolophus niger*, caught in Icelandic waters: Distribution, feeding, and otoliths

James Kennedy[1] | Anna Heiða Ólafsdóttir[2] | Svandís Eva Aradóttir[2] | Svanhildur Egilsdóttir[2] | Christophe Pampoulie[2]

[1]Marine and Freshwater Research Institute, Ísafjörður, Iceland

[2]Marine and Freshwater Research Institute, Hafnarfjörður, Iceland

Correspondence
James Kennedy, Marine and Freshwater Research Institute, 400 Ísafjörður, Iceland.
Email: james.kennedy@hafogvatn.is

Funding information
H2020 Societal Challenges, Grant/Award Number: 817806

Abstract

Black ruff (*Centrolophus niger*) is a rare and poorly studied species found in both the Atlantic and Pacific Oceans and also in the Mediterranean Sea. It is sporadically caught south of Iceland during the annual International Ecosystem Summer Survey of the Nordic Seas. In total, 43 specimens were caught from 2009 to 2021, of which 41 specimens were caught during 2017–2021. All specimens, except one, were caught using a pelagic trawl (cod-end mesh-size: 50 mm) close to the surface (trawl depth: 0–35 m) with in situ temperature ranging from 9 to 13°C. The area south of Iceland is characterized by having warmer temperatures than other areas around the island, which might be indicative of a northern limit for the distribution of black ruff. The fish were primarily in the range of 29–46 cm with a few larger individuals up to 71 cm. Fourteen fish, caught in 2017 and 2021, were dissected to gather biological information on this species. These fish were all juveniles with no obvious sign of gonad development. Correlations between total length, fork length, and standard length are presented. Otoliths were thin and delicate with a length of ~13–16 mm, and otolith size (length, width, and area) was correlated with fish size. Much of the stomach content was at an advanced stage of digestion, but some contents could be identified and consisted of invertebrates, primarily of the orders Amphipoda and Calanoida with some unidentified fish also present.

KEYWORDS

Centrolophus niger, mesopelagic, prey, rarity, stomach contents

1 | INTRODUCTION

The black ruff *Centrolophus niger* (Gmelin, 1789) (Figure 1), also known as rudderfish or blackfish, is a rare and poorly studied species that is found in the northern and southern Atlantic Ocean as well as the Pacific Ocean and the Mediterranean Sea (Macpherson & Roel, 1987; Reyes et al., 2007; Templeman & Haedrich, 1966). It is described in Fishbase as "an oceanic, epipelagic or mesopelagic species. Juveniles occurring in surface waters and associated with pelagic medusas and salps, adults found deeper. May form small schools. Appears to feed on whatever is available, small fish, squid, large pelagic crustaceans, and other plankton" (Froese & Pauly, 2022 [accessed May 20, 2022]).

FIGURE 1 Three specimens of black fish (*Centrolophus niger*) caught during the International Ecosystem Summer Survey of the Nordic Seas in 2021. Specimens were photographed prior to freezing. Photograph by James Kennedy.

The source of this information consists of three fish identification guides/books all from the same author (Haedrich, 1986a, 1986b, 1990), who probably based this information from his study published in 1966 that currently forms the primary source of information for *C. niger* (Templeman & Haedrich, 1966).

Most records of *C. niger* are generally the result of by-catch from commercial or recreational fishing or dead fish discovered on the shore (Battaglia et al., 2014; Quigley, 1986; Templeman & Haedrich, 1966). Very few published records are from scientific surveys (Templeman & Haedrich, 1966), which may be due to *C. niger* being an oceanic fish; regular scientific surveys are primarily limited to coastal areas, and generally extend only as far as the edge of the continental shelf. This makes it difficult to get a precise picture of its distribution and depth range as specimens will only be caught where their distribution overlaps with ongoing fisheries that are primarily in coastal continental shelf areas. Therefore, their oceanic distribution is not well known, but two specimens were caught during the Dana expeditions in open water close to the mid-Atlantic ridge (Templeman & Haedrich, 1966). It appears to be present across the Mediterranean Sea and its marginal seas based on multiple records (Ayas et al., 2018; Ben Amor et al., 2018; Capapé et al., 2017; Cengiz et al., 2019; Ceyhan & Akyol, 2011; Čolić et al., 2020; Farrag, 2016). In addition, there are reports of it being caught in Madeira, Spain, and there are multiple records from along the coast of Ireland and other countries in Europe (Fernández & Fariña, 1985; Fowler, 1936; Templeman & Haedrich, 1966; Went, 1963, 1966, 1968, 1969, 1971). It has also been caught in the southern areas of Icelandic waters and in southern Norway, which appears to be the northern limit of this species (Pálsson, 2005; Templeman & Haedrich, 1966).

Information on the prey of *C. niger* is limited as there appear to be only two previous studies (Battaglia et al., 2014; Macpherson & Roel, 1987), while it has not been investigated in the Northern Atlantic Ocean. Prey items include Medusae, ctenophores, Chaetognatha, Copepoda, and Amphipoda. The diet of other members of Centrolophidae has been examined, including bluenose warehou *Hyperoglyphe antarctica* (Carmichael, 1819), which is a generalist with prey items dominated by mesopelagic cephalopods, Thaliacea and fish (Laptikhovsky et al., 2020), whereas *Schedophilus medusophagus* (Cocco, 1839) showed specialized predation of Scyphozoa, and *Seriolelfa porosa* (Guichenot, 1848) feed almost exclusively on ctenophores (Mianzan et al., 1996).

In 2009, Iceland began to participate in the International Ecosystem Summer Survey of the Nordic Seas (IESSNS). This annual survey collects information on the various pelagic species present in Icelandic waters, through trawl sampling, both at the surface at predetermined locations and deeper in the water column, maximum depth 500 m, to ground truth species composition of acoustic scatter. Information on environmental variables is collected using a conductivity, temperature, depth (CTD) probe, and measurements of plankton biomass are taken at every surface trawl station. This survey overlaps with the presumed northerly distribution of *C. niger*, and it is sporadically caught since the beginning of the survey time series and more frequently since 2017. *C. niger* seems to be an elusive species, and very little biological information exists. During the IESSNS in 2017, three individuals were frozen to confirm species identification, and in 2021, 11 individuals were purposefully frozen for the present study. Using these 14 sampled individuals, along with other data collected throughout the time series of this survey, this study aims at documenting the distribution of *C. niger* in Icelandic waters and how its presence in the survey has evolved over time; presenting a detailed examination of basic biological information; examining the relationship between alternative measures of length to aid comparison with previous studies (e.g. Ben Amor et al., 2018; Quigley, 1986; Templeman & Haedrich, 1966); presenting a relationship between otolith and fish sizes that can be used in future studies when only otoliths are available, for example, in studies of stomach content analysis (Granquist & Hauksson, 2016; Sørlie et al., 2020) of predators of *C. niger*; and finally presenting further information on *C. niger* feeding behavior through stomach contents analysis.

2 | MATERIALS AND METHODS

2.1 | IESSNS survey

Data from the Icelandic part of the IESSNS were utilized during this study. *C. niger* are known to be caught by other participating countries during the IESSNS, but specimens were only available from the Icelandic part, and hence the study was limited to Icelandic waters. The Icelandic part of the IESSNS commenced in 2009 and is carried out annually, during the month of July or August (Table 1), with the survey area varying between years, depending on the predicted distribution of Atlantic mackerel (*Scomber scombrus* [Linnaeus, 1758]) and coverage of the survey vessels from partner institutes. The survey

TABLE 1 The start date, end date, and the number of stations (*n*) in the Icelandic component of the International Ecosystem Summer Survey of the Nordic Seas (IESSNS) for each year.

Year	Start	End	*n*
2009	August 04	August 18	80
2010	July 20	August 12	86
2011	August 04	August 30	110
2012	July 13	August 09	106
2013	July 11	August 08	111
2014	July 11	August 11	117
2015	July 07	August 10	111
2016	July 02	July 31	139
2017	July 04	August 02	110
2018	July 03	August 01	91
2019	July 04	July 28	78
2020	July 02	July 30	77
2021	July 06	July 26	76

employs a random stratified design with even sampling effort within each survey stratum. The first transect is randomly placed within the maximum distance between transects (sampling effort) from the edge of a stratum, and all other transects are placed at regular intervals from that one. In a similar way, the first trawl station is randomly placed along the transect with subsequent stations being placed at regular intervals along the transect.

At each predetermined surface trawl station (Figure 2), a multpelt 832 pelagic trawl was towed at the surface for 30 min at a speed of ~5 knots (ICES, 2015). The trawl had a height of ~35 m and a width of ~65 m during towing, thus sampling fish present at ~0–35 m of the water column, depending on the shape of the trawl. Trawling on acoustic registrations was carried out in a similar manner to the surface trawls except the trawl was lowered to a depth that coincided with the acoustic registrations and towed for 60 min. After towing, the catch was sorted by species and weighed. The total length of all *C. niger* captured was measured. At each predetermined surface trawl station, a CTD probe (Sea-Bird Electronics or SAIV A/S) was taken down to ~20 m above the seabed or to 500 m depth when depth exceeded 500 m. A plankton sample was also taken by performing a vertical haul with a WP2 net (diameter 56 cm) from 50 m to the surface. Mesh-size of the WP2 net was 200 μm following IESSNS standards, and sampling speed was 0.5 ms^{-1} (ICES, 2015). The mesozooplankton samples were frozen and, later on, were dried for 24 h at 70°C, and dry weight was measured to the nearest milligram (ICES, 2015).

To examine how environmental conditions have changed through the years of the survey in the area where most of the *C. niger* were caught, mean temperature at 10, 20, and 30 m and the mean dry weight of plankton in the upper 50 m of the water column were calculated utilizing all stations south of Iceland between −22 and −15° longitude.

2.2 | Individual samples

In 2017 and 2021, 3 and 11 *C. niger*, respectively, were frozen within an hour of being caught for later dissection in the laboratory. All of the individuals were caught during predetermined surface trawl stations, whereas one individual was caught during a trawl of acoustic registrations at ~250 m depth. In the laboratory, the specimens were given a unique identification number. They were subsequently weighed to the nearest gram (g) while frozen and left to thaw overnight at room temperature. After they had been thawed, they were reweighed, and total length, standard length, and fork length were measured to the nearest millimeter (mm) below for each fish. The fish were dissected with the gonads and stomach collected for further investigation. Sex and macroscopic maturity were assessed from the gonad that was preserved in 3.6% formalin. The stomach content was taken and preserved in ethanol for later analysis. The otoliths were also removed for further structural analyses and potential age-reading.

At a later date, the digestive state of the stomach contents was assessed as presented in Table 2. Any organisms found in the stomach were identified to the lowest taxonomic group possible.

The *C. niger* otoliths were photographed under a dissecting microscope with a black background. Using Image-J (Schneider et al., 2012), the length and width of each otolith were measured to the nearest 0.01 mm (Figure 3). The area, to the nearest square millimeter, was also measured in Image-J using threshold to detect the edges and the measurement tool that can calculate the area. These measurements were not made for one of the otoliths because it was broken into two pieces during removal. An attempt was made to measure the size of any vitellogenic oocytes present in the ovaries of female fish, but no vitellogenic oocytes were present.

To assess how measurements compare with previous studies, data from previously published studies were collected or extracted using a data extraction tool (WebPlotDigitizer; Rohatgi, 2022) if the measurements were not printed within the report. Data from the following studies were used: Ayas et al. (2018), Ben Amor et al. (2018), Čolić et al. (2020), Coull et al. (1989), Ergüden et al. (2012), Fernández and Fariña (1985), Mackay (1972), Quigley (1986), and Templeman and Haedrich (1966). When examining the data on the relationship between standard and fork lengths, we decided to combine the data from the three following studies, Ayas et al. (2018), Quigley (1986), and Templeman and Haedrich (1966) for comparison purposes as there was no significant difference between the two former datasets (see results), and that the single fish from Ayas et al. (2018) was included based on visual inspection of the data.

3 | RESULTS

3.1 | Distribution

From 2009 to 2021, a total of 43 *C. niger* were caught during the IESSNS surveys. Although catches were relatively low in numbers in the early years of the survey (1 in 2009 and 2010), the number of fish caught in recent years (2017, 2019, and 2021) was considerably

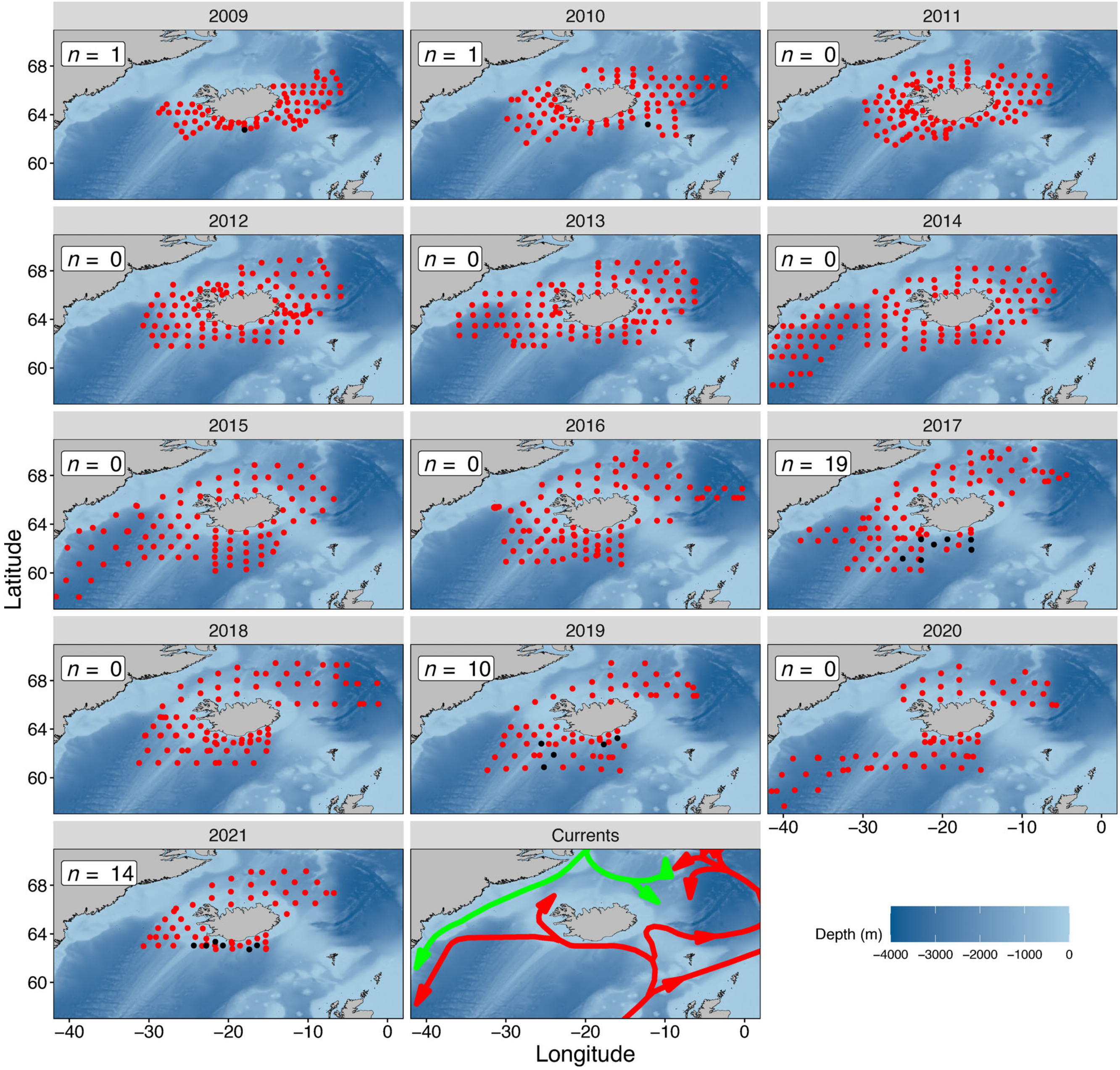

FIGURE 2 Location of sampling stations of the Icelandic component of the International Ecosystem Summer Survey of the Nordic Seas 2009–2021. Stations where black ruff *Centrolophus niger* (Gmelin, 1789) were caught are shown in Black. The main surface currents in the Northeast Atlantic are shown in the final panel; the cold East Greenland current (green) and the warm Atlantic current (red) (Blindheim & Østerhus, 2005).

higher (18, 9, and 14, respectively). All these fish were caught along the continental shelf, south, and south-west of Iceland (Figure 2) between 0 and 35 m depth with the exception of one fish that was caught during a deep tow at 250 m depth. A CTD probe was deployed in 18 of the 20 stations where *C. niger* were caught with the water temperature varying from 9 to 13°C (Figure 4). The total length of *C. niger* varied from 29 to 71 cm (measured to the nearest centimeter below; Figure 5), and there was no significant difference in length between years 2017, 2019, and 2021 (ANOVA, $p > 0.05$).

Temperature within the water column at 10, 20, and 30 m was significantly different between years for all depths (ANOVA, $p < 0.001$) with a decreasing trend from 2009 to 2015 (Figure 6). Temperatures were generally lower in 2016–2021 than in 2009–2015. Dry weight of plankton in the upper 50 m showed no distinct trend with the highest value in 2013 and the lowest value in 2014 (Figure 6).

3.2 | Biological traits

Of the 14 fish examined for biological information, 12 were male and 2 were female, measuring between 32.7 and 42.1 cm total length. None of the fish showed signs of gonad development and were all likely to be immature. Fish weight decreased between 2.0% and 8.5% (mean = 5.2%) during the thawing process (Figure 7). There was no significant relationship between frozen weight and subsequent weight loss (linear regression, $p > 0.05$) even though a negative trend was apparent (data not shown). Fork length, standard length, and body weight were significantly and positively correlated with total length (Table 3; Figure 7).

Weight-at-length was significantly higher in the current study than in the two previously published studies (Figure 8); Quigley (1986) (ANCOVA, $df = 1, 29$, $p < 0.001$, data were log-transformed) and Coull et al. (1989) (ANCOVA, $df = 1, 43$, $p < 0.001$, data were log-transformed).

There was no significant difference in the relationship between standard length and fork length, calculated using the data from Templeman and Haedrich (1966) and Quigley (1986) (ANCOVA, $df = 1, 14$, $p > 0.05$). The difference in standard length and fork length for the single fish from Ayas et al. (2018) appeared to be consistent (based on visual inspection) with the relationships from Quigley (1986) and Templeman and Haedrich (1966) (Figure 8). The data from the current study were significantly different from the combined data from previous studies (Ayas et al., 2018; Quigley, 1986; Templeman & Haedrich, 1966) (ANCOVA, $df = 1, 29$, $p < 0.05$). However, in practical terms, the difference was small. Given the small difference, and the limited length range of the current study, all the data were combined to provide a common relationship between these two measurements of length (Table 3).

For the data on total length and standard length, the data from all previous studies were combined based on visual inspection of the data (Figure 8). There was a significant difference in the relationship between total length and standard length between the current and previous data (Ancova, $p < 0.001$). This would result in a difference of ~1.0–1.4 cm when converting between these two measurements of length.

TABLE 2 Criteria used to assess the state of digestion of stomach contents.

Digestive state	Description
1	Undigested
2	Digestion started, species easy to identify
3	Advanced digestion, species or groups may be identified
4	Digestion almost complete, only remnants of main groups of prey can be identified
5	Complete decomposition (soup), cannot be identified or counted

3.3 | Otoliths

The otoliths from *C. niger* were thin and delicate. Their size varied in length from 13.1 to 16.11 mm and width from 6.06 to 7.89 mm. All the otoliths had a single translucent zone close to the center, whereas some individuals had an additional translucent zones further from the center (Figure 3; Kennedy et al., 2023). There was no significant difference in the length, width, or area between the right and left otoliths (ANOVA, $p > 0.05$). The length, width, and area of the otoliths were significantly and positively correlated with the total length of the fish for both the left and right otoliths (Table 4; Figure 9).

3.4 | Stomach analysis

For all individuals except for one, which was at Stage 3, the stomachs were either at digestion state 4 or 5 so we could not identify much of

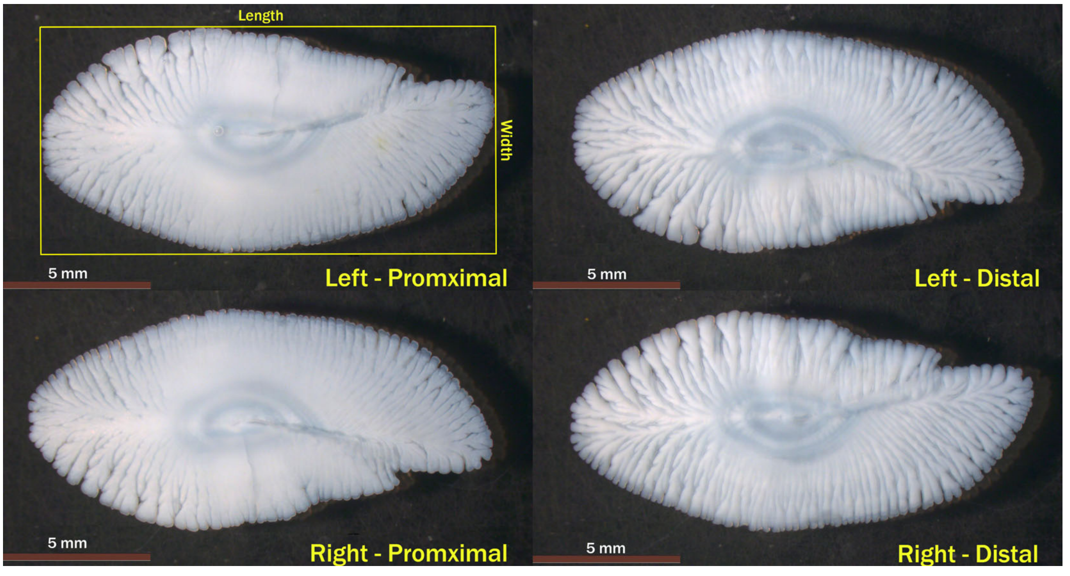

FIGURE 3 Images of the proximal and distal sides of the right and left otoliths from black ruff *Centrolophus niger* (Gmelin, 1789). Scale bar and the plane at which the length and width of the otolith were measured are shown.

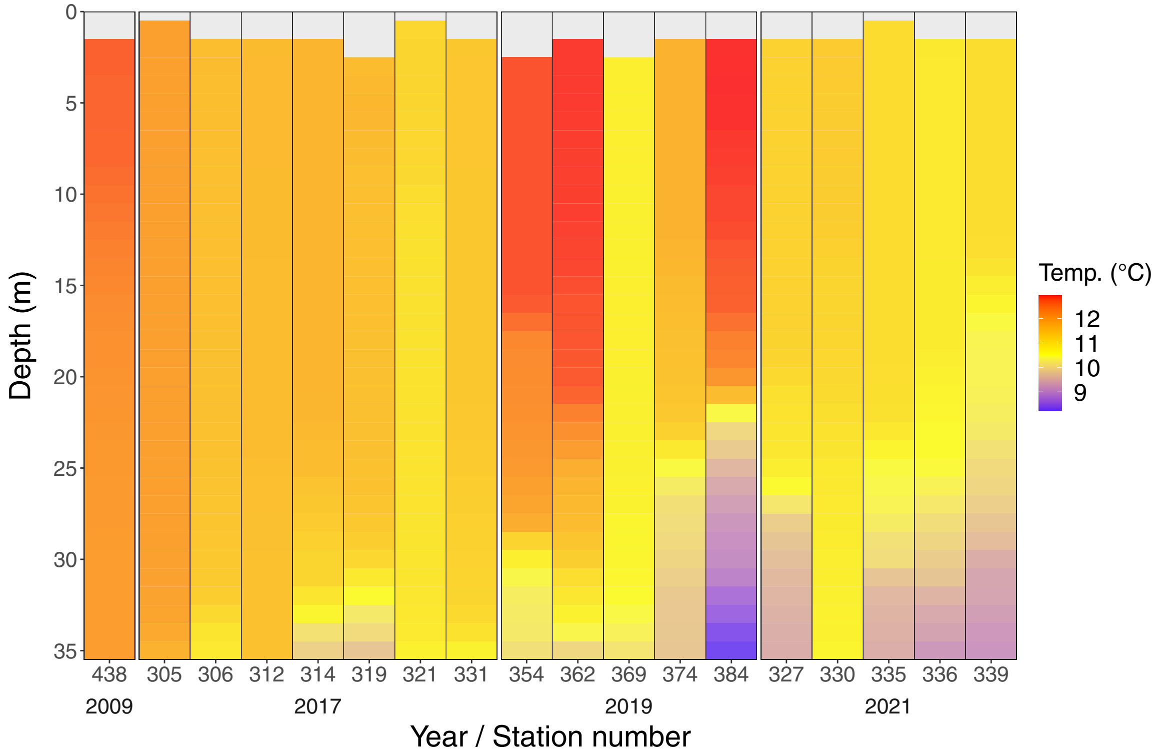

FIGURE 4 Temperature profiles from the CTD probe at each station of the Icelandic part of the International Ecosystem Summer Survey of the Nordic Seas (IESSNS) where black ruff *Centrolophus niger* (Gmelin, 1789) were caught.

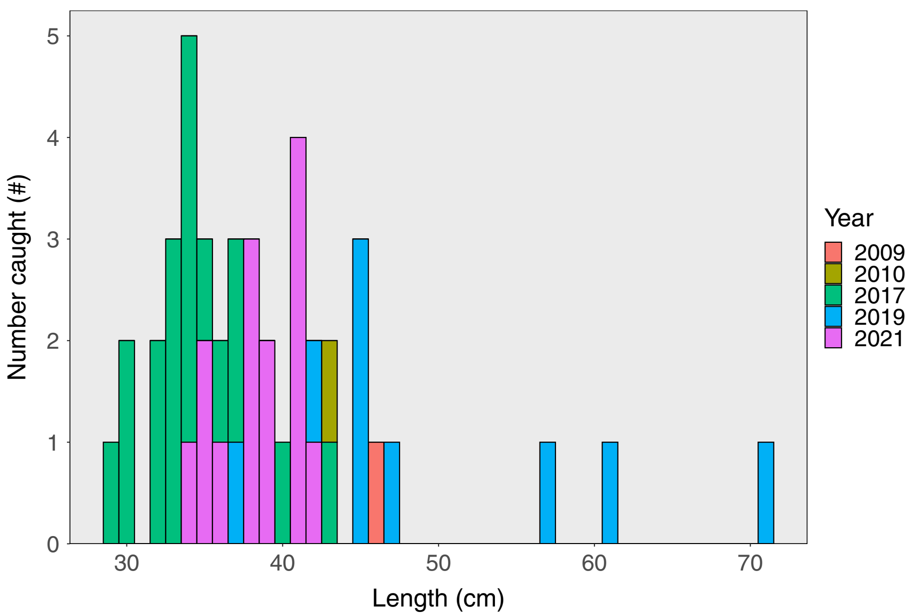

FIGURE 5 Length distribution of all black ruff *Centrolophus niger* (Gmelin, 1789) caught during the Icelandic part of the International Ecosystem Summer Survey of the Nordic Seas (IESSNS) from 2009 to 2021 with colors depicting the year caught.

the contents. In terms of weight, unidentified digested organisms made up the bulk of the weight for the majority of the stomachs (Figure 10). In five of the stomachs, unidentified fish made up a high proportion of the stomach contents by weight. The majority of the identified organisms were invertebrates, primarily of the orders Amphipoda and Calanoida. In fish number 5, the stomach contained 27 *Calanus finmarchicus* and 1 fish, but the fish made up 99% of the weight.

4 | DISCUSSION

C. niger has been sporadically observed in the southern region of Icelandic waters, which might constitute the northern limit of the distribution range of this species. The stations in which *C. niger* were caught are in the area of the survey with the warmest water. The presence of this area of warm water is the result of the warm north

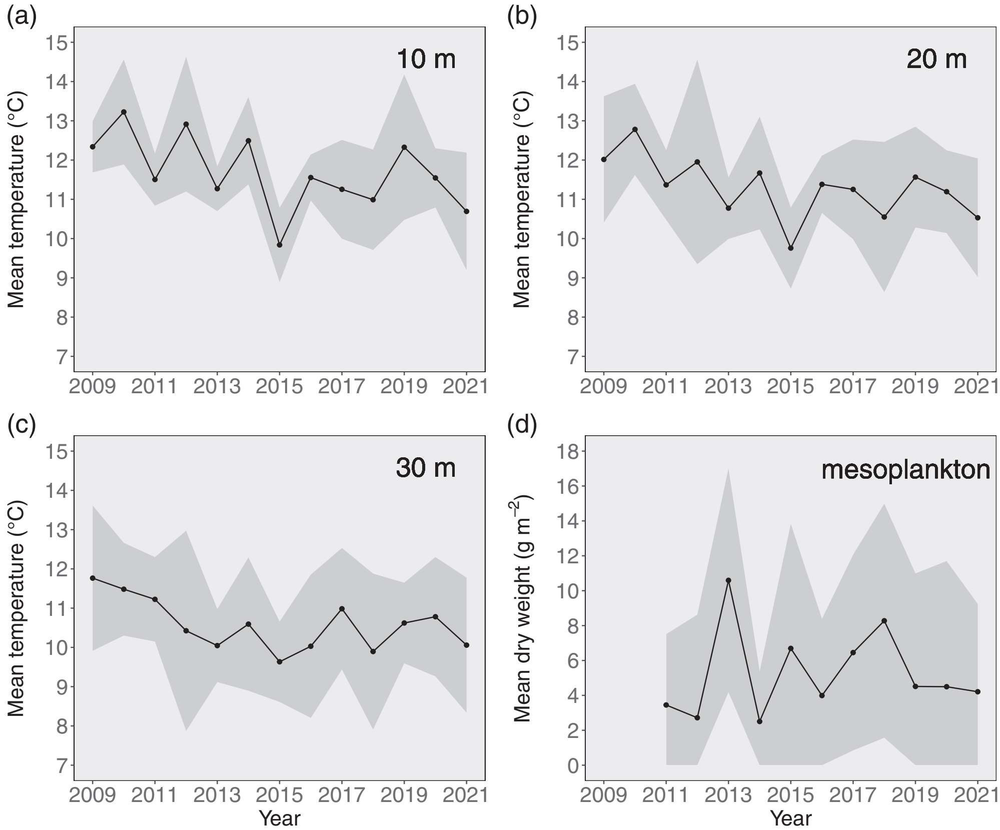

FIGURE 6 Environmental conditions between −22 and −15° longitude south of Iceland between 2009 and 2021 with an average annual temperature at 10, 20, and 30 m depth (a–c), and mean dry weight of mesoplankton in the upper 50 m (d). ±1.96 standard deviation is shown by shaded area.

Atlantic and Irminger currents flowing north from the Gulf Stream (Blindheim & Østerhus, 2005). This warm water diverts around Iceland and meets the colder polar water flowing south. Assuming *C. niger* continue to be caught in this area in the future, further observations may allow a prediction of suitable habitat of the north Atlantic Ocean.

From 2009 to 2016, *C. niger* were essentially absent from the survey with an abrupt increase in numbers in 2017, and then again in 2019 and 2021. The reasons for this increase are not entirely clear as 2017, 2019, and 2021 do not stand out as unusual in terms of temperature or zooplankton dry weight. The distribution of species is complex and dependent on multiple factors. Increased presence of *C. niger* in Icelandic waters could have been the result of increased population size as larger populations lead to an increase in competition for resources, leading to expansion of the occupied area (Nye et al., 2009; Olafsdottir et al., 2018; Staby et al., 2018). It could also be that variations in hydrographic conditions could have led to an increase in the transport of early life stages of *C. niger* into Icelandic waters, as is the case of for blue whiting where oceanic conditions affect the distribution of juveniles between years (Kloppmann et al., 2001). It may also be that the depth they inhabit varies between years, the survey only samples the upper 35 m of the water column, and in some years they may inhabit ocean layers below the sampling depth. It should be noted that one individual was caught while trawling at around 250 m depth, but it is certainly possible it entered the net when it was being brought to the surface. Given the low number of individuals caught in the survey, and lack of population data on black ruff, gaining information on the reasons behind variations in the abundance of black ruff in Icelandic waters will be difficult.

Although there is no statistical difference in the length distribution between years, there is a noticeable difference between 2017 and 2019 with much larger fish in 2019. The reason is unclear, but perhaps it is a cohort effect. Individuals from the population migrate into Icelandic waters during the summer, and the fish caught are simply the most dominant size/year class in the population. Perhaps the catches in 2017 and 2019 are from the same year class, and the difference in size is the result of growth, and the absence in 2018 may be due to differences in migration between years. The fish caught in 2021 may represent a new strong year class.

The use of the CTD probe at each trawl station gave an insight into the temperatures experienced by *C. niger* in the area they were caught, with temperatures ranging from ∼9 to 13°C from 0 to 35 m depth. However, the temperature experienced by *C. niger* will be affected by the actual depth they inhabit and with the methodology used in the present study, it was not possible to get more precise information on depth inhabited than 0–35 m depth. Such information could be obtained using data storage tags, but to date, no such investigation has been carried out. Although the temperature range between 0 and 35 m, where black ruff were caught, was generally low (<2°C at 15 of the 18 stations), the data presented give a reasonably precise temperature range experienced by *C. niger* when present in surface waters.

Of the fish that were sampled for maturity, none showed any obvious signs of gonad development and thus were classified as

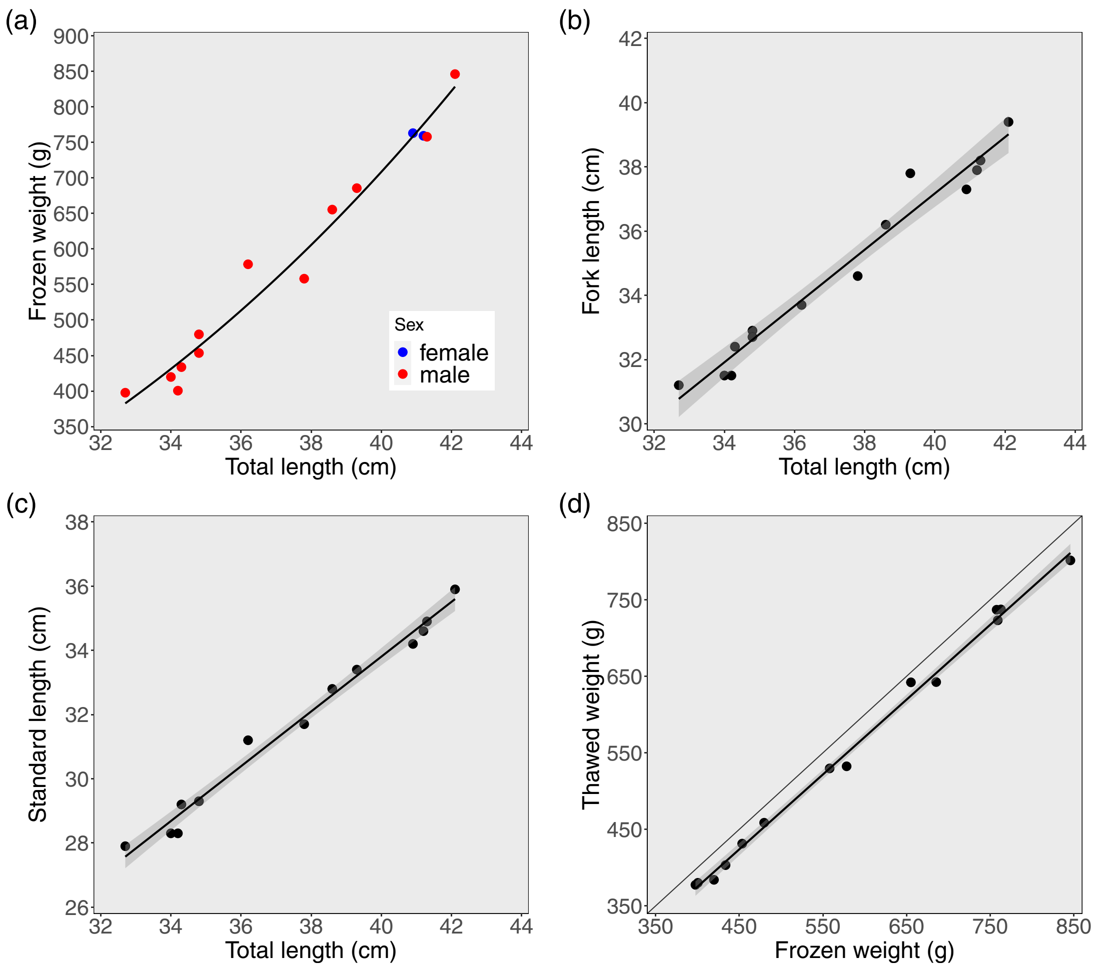

FIGURE 7 Total length *v.* (a) frozen weight, (b) fork length, (c) and standard length and frozen weight *v.* (d) thawed weight for black ruff *Centrolophus niger* (Gmelin, 1789). (a) Nonlinear and (b–d) linear regression models are shown (a–d) as well as $x = y$ line (d).

TABLE 3 Model equations and residual sum of squares for total length *v.* weight, fork length, and standard length and frozen weight *v.* thawed weight.

Model	R^2	Note
Frozen weight = 0.01 × total length 3.06		
Fork length = 2.1 + 0.88 total length	0.96	Current study only
Fork length = −1.19 + 0.95 total length	0.99	Current and published data
Standard length = −0.34 + 0.85 total length	0.98	
Thawed weight = −16.21 + 0.98 frozen weight	1.00	

immature. The maturity stage of these dissected individuals, and the size range of the other individuals caught during the survey (29–45 cm with only two individuals >57 cm), indicates that the majority of the fish caught during the survey from 2009 to 2021 were likely to be immature. Adult *C. niger* is reported to live deeper in the water column than juveniles (Haedrich, 1986a), and our results are in line with this in that very few large individuals had been caught during the surface trawls, which sample the upper 35 m of the water column. Some of the records of *C. niger* describe their specimen(s) as juvenile or adult but do not exclusively mention that they examined the gonads to determine maturity (Akyol, 2008; Ayas et al., 2018; Čolić et al., 2020). The gonads were examined for one specimen in Mackay (1972). This specimen was a female of 45.4 cm total length and was described as in a "non-spawning state." Therefore, there is essentially no information in the literature at what size *C. niger* mature.

Although the difference in the relationship between fork and standard lengths between the current and previous studies was significant, the difference was small and likely to be a statistical artifact due to differences in the length range of the fish. Visual examination of the data shows most of the observations from the current study are very similar to those of the previous studies. However, although the relationship between total length and standard length exhibits a similar slope between the current and previous studies, there is a clear, albeit small, difference in the intercept. The reason for this difference is not entirely clear but could be due to slight differences in methodology when identifying the last vertebrae given that the

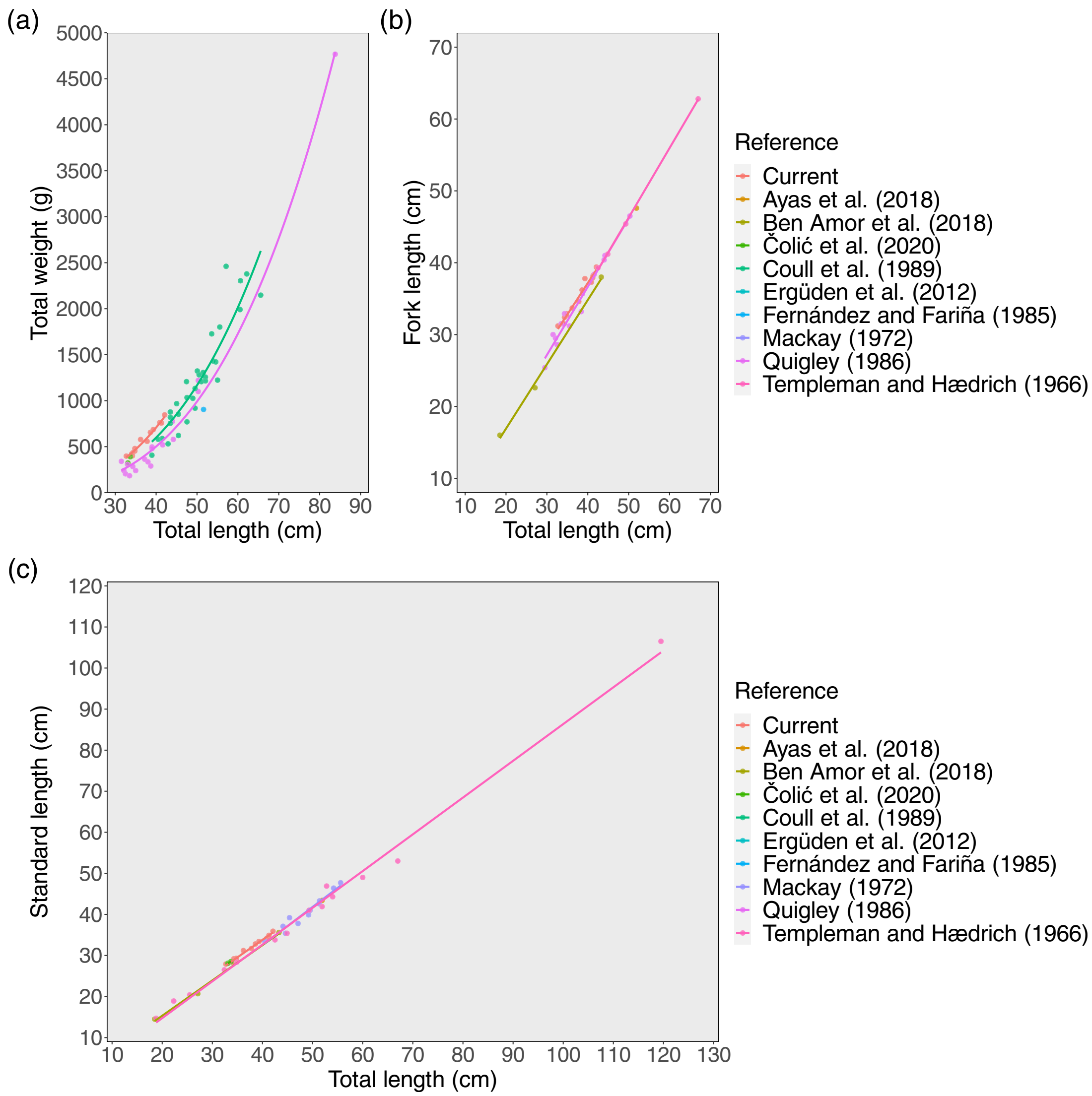

FIGURE 8 Total length *v.* (a) total weight, (b) fork length, and (c) standard length for black ruff *Centrolophus niger* (Gmelin, 1789) from the current and previous studies. The origin of the previous data is indicated in the legend. (a) Nonlinear and (b, c) linear regression models are shown. Note that total weight corresponds to frozen weight for measurements in the current study, whereas for previous studies, corresponds to the weight given in the respective study.

TABLE 4 The intercept, slope, residual sum of squares, and *p*-value (* = <0.05, ** = <0.01, *** = <0.001) for the linear models of total length *v.* otolith length (mm), width (mm), and area (mm^2) for the left and right otoliths.

Attribute	Otolith	Intercept	Slope	R^2	*p*-Value
Length	Left	7.52	0.19	0.51	**
Length	Right	7.98	0.18	0.44	**
Width	Left	3.62	0.09	0.36	*
Width	Right	2.30	0.13	0.61	***
Area	Left	−18.18	2.50	0.62	***
Area	Right	−8.85	2.25	0.60	***

slope is similar. The difference in weight at length between the current and previous studies is not entirely surprising. In the current study, the fish were frozen within ~1 h of capture and then weighed before they were defrosted so the frozen weight will be close to live weight. In the previously published data, the fish came from a variety of sources and not weighed fresh. The data from fish in Coull et al. (1989) were unlikely to be fresh when weighed given the methodology they described for rare fish. The data presented in Quigley (1986) were fish that had been caught by fishers and brought to the laboratory, so the fish were likely to have been at least 1 day old, sufficient time for water loss. The data presented in the current study on weight at length are probably the most accurate published for *C. niger* so far.

As expected, otolith size was positively correlated with fish size, and the information we present can therefore be used to give an indication of the fish size from the size of the otolith. If only one otolith is recovered, whether this is from the left or right side is inconsequential, as there was no difference in any measurement between the two otoliths. Otolith area had the lowest confidence intervals and was

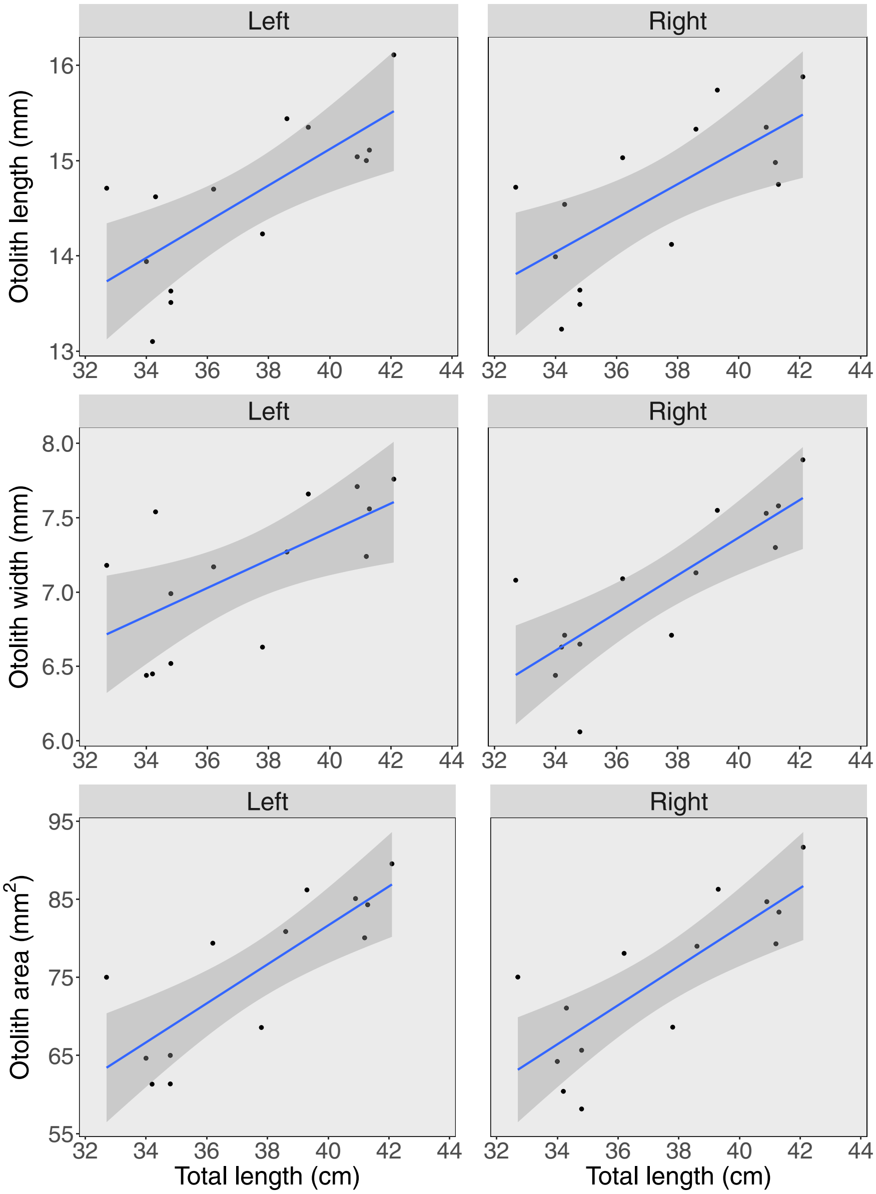

FIGURE 9 Total length *v.* length, width, and area of left and right otoliths from black ruff *Centrolophus niger* (Gmelin, 1789). Linear regression lines are shown together with 0.95 confidence interval.

likely to give the most accurate estimate of fish size; however, measuring the area is the more labor intensive than measuring length or width. So far, relationships between otolith size or area and fish size were not available for *C. niger*. Now the information collected during the present study can be used during stomach content analysis of potential predators of *C. niger*. The pictures of the left and right otoliths also present the characteristic structure of the *C. niger* otolith. Unfortunately, the otoliths seemed to be particularly fragile when extracted from the fish, and it is likely that their structure will not be conserved in the digestive system of predators, although this is speculative.

Unfortunately, only a small amount of the prey items within the stomach content could be identified. However, the obtained information did give an insight into the feeding habits of *C. niger* during the juvenile stage. The diversity of prey items suggests that *C. niger* does not target specific prey but feeds more like a generalist, feeding on any available prey items of suitable size, and is likely to feed on smaller fishes if they are present. Two studies have previously examined the diet of *C. niger*, one in the Mediterranean Sea and one in the coastal waters of Namibia (Battaglia et al., 2014; Macpherson & Roel, 1987). In Namibian waters, prey items consisted of Medusae and Ctenophores (Macpherson & Roel, 1987), whereas in the Mediterranean Sea, the prey items were more diverse with Chaetognatha, Copepoda, and Amphipoda making up the bulk of the prey, but other prey items were also present, including the jellyfish *Pelagia noctiluca* (Battaglia et al., 2014). In the current study, no gelatinous zooplankton were detected within the stomachs. However, these items are rapidly digested and may also have been damaged during the freezing and thawing of the fish and could have been unidentifiable within the stomach content. There

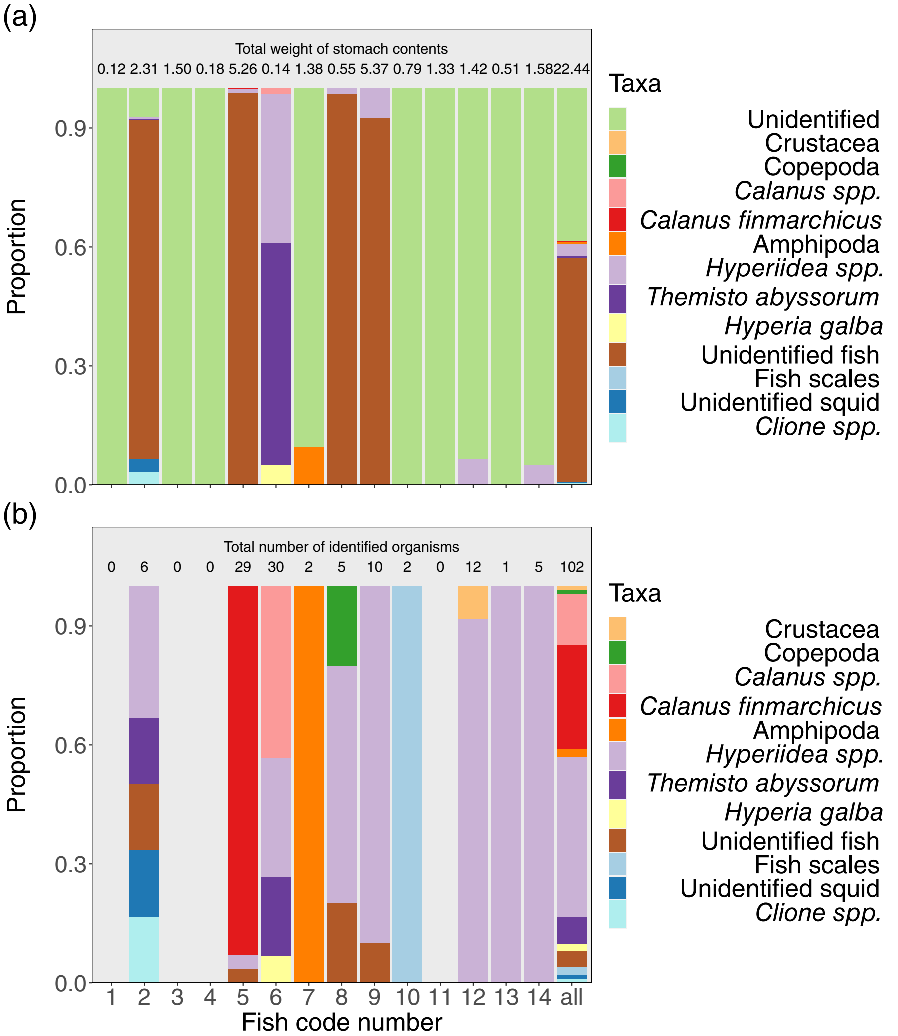

FIGURE 10 Proportion of each prey item found in the stomachs of black ruff *Centrolophus niger* (Gmelin, 1789) as a function of (a) weight and (b) number in the stomach. Count data do not account for unidentified organisms. Bar labeled "all" is all the stomach data combined, numbers at the top of the graph show (a) total weight [g] of the stomach contents and (b) total number of identified organisms in the stomach (bottom).

was a significant amount of unidentifiable remains within the stomach, which could be the remains of gelatinous zooplankton. If this is the case, it suggests that such organisms are an important prey item for *C. niger*.

In conclusion, our results indicate that, when present in Icelandic waters, the distribution of *C. niger* is limited to the south and southwest of Iceland, where temperature is higher and which is likely to be the northern limit for *C. niger*. The occurrence of *C. niger* in Icelandic waters has increased in recent years, but whether this increase is the result of fish migrating further north, an increase in population size or a result of another unknown factors, or a combination of multiple factors is unclear. The fish that are present in the surface waters are mostly juveniles that feed on zooplankton and smaller fishes that are present in the area.

AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Fish were dissected by Anna Heiða Ólafsdóttir, Christophe Pampoulie, Svandís Eva Aradóttir, and Svanhildur Egilsdóttir. Svandís Eva Aradóttir and Svanhildur Egilsdóttir performed the stomach analysis. James Kennedy performed the otolith analysis and statistical analysis of the data. The first draft of the manuscript was written by James Kennedy, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

ACKNOWLEDGMENTS

The authors would like to thank the crew and scientific personnel aboard R./V. Árni Friðriksson during the IESSNS surveys.

FUNDING INFORMATION

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement no. 817806.

CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

The station data where the dissected individuals were caught, individual measurements, stomach content data, and photographs of dissected individuals and their otoliths are available from Pangaea (Kennedy et al., 2023).

ORCID

James Kennedy https://orcid.org/0000-0002-5466-2814
Anna Heiða Ólafsdóttir https://orcid.org/0000-0001-5048-2659
Christophe Pampoulie https://orcid.org/0000-0001-6425-9060

REFERENCES

Akyol, O. (2008). New record of the juvenile blackfish, *Centrolophus Niger* (Centrolophidae), from the Aegean Sea (Izmir Bay, Turkey). *Cybium*, *32*, 91–92.

Ayas, D., Erguden, D., Çiftçi, N., & Bakan, M. (2018). The new locality record of *Centrolophus Niger* (Gmelin, 1789), from Büyükeceli coast (North-Eastern Mediterranean Sea). *Comu Journal of Marine Science and Fisheries*, *1*, 48–52.

Battaglia, P., Musolino, S., Esposito, V., Ammendolia, G., Consoli, P., Andaloro, F., & Romeo, T. (2014). Feeding habits of juvenile fishes belonging to three medusivorous species (Centrolophidae and Nomeidae) from the strait of Messina (Central Mediterranean Sea). *Marine Biology Research*, *10*, 927–933.

Ben Amor, M. M., Ounifi-Ben Amor, K., & Capapé, C. (2018). Additional records and extension of the range of blackfish, *Centrolophus Niger* (osteichthyes: Centrolophidae) from the Tunisian coast (Central Mediterranean Sea). *Annales: Series Historia Naturalis*, *28*, 123–128.

Blindheim, J., & Østerhus, S. (2005). In H. Drange, T. Dokken, T. Furevik, R. Gerdes, & W. Berger (Eds.), *The Nordic seas: An integrated perspective* (pp. 11–37). American Geophysical Union (AGU).

Capapé, C., Rafrafi-Nouira, S., & El Kamel-Moutalibi, O. (2017). On the occurrence of blackfish *Centrolophus Niger* (Osteichthyes: Centrolophidae) from the Tunisian coast (Central Mediterranean). *Cahiers de Biologie Marine*, *58*, 117–120.

Cengiz, Ö., Parug, S. S., & Kizilkaya, B. (2019). Occurrence of rudderfish (*Centrolophus Niger* Gmelin, 1789) in Saroz Bay (northern) Aegean Sea, Turkey. *Turkish Journal of Agriculture-Food Science and Technology*, *7*, 799–801.

Ceyhan, T., & Akyol, O. (2011). Occurrence of the blackfish, *Centrolophus Niger* (Gmelin 1789) (Osteichthyes: Centrolophidae), in Izmir Bay, Aegean Sea. *Journal of Applied Ichthyology*, *27*, 139–140.

Čolić, S., Nikolić, M., & Čolić, V. (2020). The first record of blackfish, *Centrolophus Niger* (Gmelin,1788) in Montenegrin coastal waters. *Agriculture & Forestry*, *66*, 237–239.

Coull, K. A., Jermyn, A. S., Newton, A. W., Henderson, G. I., & Hall, W. B. (1989). Length/weight relationships for 88 species of fish encountered in the north East Atlantic. *Scottish Fisheries Research Report* (Vol. 43). Department of Agriculture and Fisheries for Scotland.

Ergüden, D., Yağlıoğlu, D., Gürlek, M., & Turan, C. (2012). An occurrence of the blackfish, *Centrolophus Niger* (Gmelin, 1789), in Iskenderun Bay, (north eastern Mediterranean, Turkey). *Journal of the Black Sea/-Mediterranean Environment*, *18*, 97–101.

Farrag, M. M. S. (2016). Deep-sea ichthyofauna from eastern Mediterranean Sea, Egypt: Update and new records. *The Egyptian Journal of Aquatic Research*, *42*, 479–489.

Fernández, A., & Fariña, A. C. (1985). Cita de la especie *Centrolophus Niger* Gmelin, 1789, para aguas de Galicia. *Boletin del Instituto Espanol de Oceanografia*, *2*, 69–72.

Fowler, H. W. (1936). *The marine fishes of West Africa based on the collection of the American museum Congo expedition, 1909-1915* (Vol. 70). Bulletin American Museum of Natural History.

Froese, R., & Pauly, D. (2022). FishBase. World Wide Web electronic publication. www.fishbase.org, version (06/2022) accessed May 20, 2022

Granquist, S. M., & Hauksson, E. (2016). Diet of harbour seals in a salmon estuary in north-West Iceland. *Icelandic Agricultural Sciences*, *29*, 7–19.

Haedrich, R. L. (1986a). Centrolophidae. In P. J. P. Whitehead, M. L. Bauchot, J.-C. Hureau, J. Nielsen, & E. Tortonese (Eds.), *Fishes of the North-Eastern Atlantic and the Mediterranean* (pp. 1177–1182). UNESCO.

Haedrich, R. L. (1986b). Stromateidae. In M. M. Smith & P. C. Heemstra (Eds.), *Smiths' sea fishes* (pp. 842–846). Springer-Verlag.

Haedrich, R. L. (1990). Centrolophidae. In J. C. Quero, J. C. Hureau, C. Karrer, A. Post, & L. Saldanha (Eds.), *Check-list of the fishes of the eastern tropical Atlantic (CLOFETA)* (Vol. 2, pp. 1011–1013). JNICT, Lisbon; SEI; UNESCO.

ICES. (2015). Manual for international pelagic surveys (IPS). In *Series of ICES Survey Protocols SISP 9 – IPS* (p. 92).

Kennedy, J., Ólafsdóttir, A. H., Aradóttir, S. E., Egilsdóttir, S., & Pampoulie, C. (2023). *Centrolophus niger south of Iceland in July 2017 and July 2021*. PANGAEA.

Kloppmann, M., Mohn, C., & Bartsch, J. (2001). The distribution of blue whiting eggs and larvae on porcupine Bank in relation to hydrography and currents. *Fisheries Research*, *50*, 89–109.

Laptikhovsky, V., Bell, J. B., Benedet, R., Glass, J., Glass, W., Green, R., Robson, G. R., … Collins, M. A. (2020). Feeding habits of bluenose warehou, *Hyperoglyphe Antarctica* (Carmichael, 1819) (Centrolophidae) at seamounts of the southern Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers*, *156*, 103182.

Mackay, K. T. (1972). Further Records of the Stromateoid Fish *Centrolophus Niger* from the northwestern Atlantic, with comments on body proportions and behavior. *Copeia*, *1972*, 185–187.

Macpherson, E., & Roel, B. A. (1987). Trophic relationships in the demersal fish community off Namibia. *South African Journal of Marine Science*, *5*, 585–596.

Mianzan, H. W., Mari, N., Prenski, B., & Sanchez, F. (1996). Fish predation on neritic ctenophores from the Argentine continental shelf: A neglected food resource? *Fisheries Research*, *27*, 69–79.

Nye, J. A., Link, J. S., Hare, J. A., & Overholtz, W. J. (2009). Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series*, *393*, 111–129.

Olafsdottir, A. H., Rong, K., Arge, J., Jansen, T., Óskarsson, G. J., Nøttestad, L., Elvarsson, B., … Slotte, A. (2018). Geographical expansion of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic seas from 2007 to 2016 was primarily driven by stock size and constrained by low temperatures. *Deep-Sea Research Part*, *159*, 152–168.

Pálsson, Ó. K. (2005). An analysis of by-catch in the Icelandic blue whiting fishery. *Fisheries Research*, *73*, 135–146.

Quigley, D. T. G. (1986). Blackfish *Centrolophus Niger* (Gmelin, 1789) (C. Pompilus Cuv. & Val.) in Irish waters: A further record and a review of Irish records. *The Irish Naturalists' Journal*, *22*, 97–101.

Reyes, P., Hüne, M., & Ruiz, V. H. (2007). Mesopelagic fish *Centrolophus Niger* (gmelin 1789) (pisces:Perciformes) recorded in Chilean continental slopewaters of south American plate. *Gayana*, *71*, 96–101.

Rohatgi, A. (2022). Webplotdigitizer: Version 4.6. https://automeris.io/WebPlotDigitizer

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675.

Sørlie, M., Nilssen, K. T., Bjørge, A., & Freitas, C. (2020). Diet composition and biomass consumption of harbour seals in Telemark and Aust-Agder, Norwegian Skagerrak. *Marine Biology Research*, *16*, 299–310.

Staby, A., Skjæraasen, J. E., Geffen, A. J., & Howell, D. (2018). Spatial and temporal dynamics of European hake (*Merluccius merluccius*) in the North Sea. *ICES Journal of Marine Science*, *75*, 2033–2044.

Templeman, W., & Haedrich, R. L. (1966). Distributions and comparisons of *Centrolophus Niger* (Gmelin) and *Centrolophus britannicus* Günther (Centrolophidae) from the North Atlantic. *Journal of the Fisheries Research Board of Canada*, *23*, 1161–1185.

Went, A. E. J. (1963). Rare fishes taken in irish waters in 1962. *The Irish Naturalists' Journal*, *14*, 105–109.
Went, A. E. J. (1966). Rare fishes taken in irish waters in 1965. *The Irish Naturalists' Journal*, *15*, 159–163.
Went, A. E. J. (1968). Rare fishes taken in irish waters in 1967. *The Irish Naturalists' Journal*, *16*, 35–39.
Went, A. E. J. (1969). Rare fishes taken in Irish waters in 1968. *The Irish Naturalists' Journal*, *16*, 147–150.
Went, A. E. J. (1971). Interesting fishes from Irish waters in 1970. *The Irish Naturalists Journal*, *17*, 41–45.

How to cite this article: Kennedy, J., Ólafsdóttir, A. H., Aradóttir, S. E., Egilsdóttir, S., & Pampoulie, C. (2023). Biological information on a rare pelagic fish, black ruff *Centrolophus niger*, caught in Icelandic waters: Distribution, feeding, and otoliths. *Journal of Fish Biology*, 1–13. https://doi.org/10.1111/jfb.15611