

RESEARCH ARTICLE

Diet and feeding strategy of Northeast Atlantic mackerel (*Scombrus scomber*) in Icelandic waters

Cecilia Kvaavik^{1,2,3*}, Gudmundur J. Óskarsson¹, Anna Kristín Daniélsdóttir³, Guðrún Marteinsdóttir²

1 Pelagic Division, Marine and Freshwater Research Institute, Skulagata, Reykjavik, Iceland, **2** Institute of Biology, University of Iceland, Sturlugata, Reykjavik, Iceland, **3** Matis, Vinlandsleið, Reykjavik, Iceland

* cecilia.kvaavik@hafogvatn.is



OPEN ACCESS

Citation: Kvaavik C, Óskarsson GJ, Daniélsdóttir AK, Marteinsdóttir G (2019) Diet and feeding strategy of Northeast Atlantic mackerel (*Scombrus scomber*) in Icelandic waters. PLoS ONE 14(12): e0225552. <https://doi.org/10.1371/journal.pone.0225552>

Editor: Geir Ottersen, Havforskningsinstituttet, NORWAY

Received: June 3, 2019

Accepted: November 6, 2019

Published: December 30, 2019

Copyright: © 2019 Kvaavik et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All the data underlying the present study is available at: <https://issues.pangaea.de/browse/PDI-20828>.

Funding: This research was funded by the Icelandic Centre for Research (grant number: 163371-051), the Marine and Freshwater Institute of Iceland and Matis as a part of a PhD project on the ecosystem impact of mackerel in Icelandic waters.

Competing interests: The authors have declared that no competing interests exist.

Abstract

Predator-prey relations, as well as the trophic ecology of highly migratory marine species, is important to understand their impact on the ecosystem. Conventional methods were used to study the diet composition and feeding strategy of the Northeast Atlantic mackerel (*Scombrus scomber*), during their summer feeding migration to Icelandic waters in 2009–2014. In addition, generalised additive modelling (GAM) was used to determine which biological and environmental factors contribute to the variation of their stomach weight in the years 2011–2014. From the dietary analysis, we found that calanoid copepods (especially *Calanus finmarchicus*) were the most important contributor to the overall diet of mackerel in the years studied. Although in some years and areas, they also preyed heavily on larger prey items such as euphausiids, amphipods and megalopa larvae of crab and shrimp. The GAM showed that temperature and the time the day of sampling were significant explanatory variables for the stomach weight, while zooplankton biomass did not seem to have much influence. The Northeast Atlantic mackerel are ferocious feeders upon copepods, as well as exhibiting an overall opportunistic feeding strategy. During their feeding migration in Icelandic waters, they were found to feed on the most dominant species available to them.

Introduction

Marine ecosystems are under an increasing threat from climate changes on top of environmental variability. Highly migratory pelagic fish species occupying large and different marine ecosystems might respond to such changes by altering migration patterns, distribution and feeding habits. These responses will impact the ecosystems inhabited through predator-prey interactions, which can be difficult to predict and observe [1,2]. Hence, understanding these impacts requires studying fish diets and feeding habits (i.e. prey selection and specialisation). Such studies provide the basis for understanding trophic interactions in marine food webs and the effect the predator has on the ecosystem as a whole [3,4] and are crucial for more ecosystem-based fishery management.

Recent warming of sea surface temperatures around Iceland has opened up new habitats for more migratory temperate species, such as the Northeast Atlantic mackerel (*Scombrus scomber*) [5–7]. The reason for the expansion of the Northeast Atlantic mackerel (hereafter called “mackerel”) feeding migration in the last decade to the north and northwest is not evident. However, this migration is postulated to be the result of many co-contributing factors such as; increased stock size (170% from 2002–2013 [8]), gradual increase in temperature [5], decline in zooplankton biomass in the Norwegian Sea [9] and possible competition with other major pelagic fish stocks such as herring (*Clupea harengus*) [5,8]. This expansion has meant that mackerel are now found in large numbers within Icelandic waters during the summer [10–12]. At this time of year, the surface water is above 7°C in Icelandic waters, which seems to restrict the mackerel distribution during its summer feeding migration, as they prefer water temperatures within the range 9–13°C [10,12–15].

Studying the diet composition of mackerel in the marine ecosystem around Iceland is crucial for understanding its position and trophic interactions in the marine food web and how it might differ from other ecosystems. Information on mackerel feeding ecology, provides much-needed information on mackerel growth conditions, feeding competition and distributional shifts [8,16,17]. Mackerel has proven to be a very ferocious predator and exhibits both particle and filter feeding [18,19], and while feeding in Icelandic waters during the summer, it has been reported to gain about 43% in body weight on average [20]. This example, signifying its massive feeding activity, together with the fact that the mackerel stock is one of the largest pelagic fish stocks in Northeast Atlantic [21] means that mackerel is a major component in the epi-pelagic ecosystems, including Icelandic waters [10]. Further knowledge on its feeding habits and diet composition is therefore highly relevant for a better understanding of the ecosystems’ functioning.

Previous stomach content analysis of mackerel in the Northwest Atlantic has shown that their diet consists, for the most part, of mesozooplankton (i.e. calanoid copepods, euphausiids and amphipods). Additionally, some studies have also shown mackerel to feed heavily on larger prey items such as juvenile fish (e.g. herring, sandeel *Ammodytes* spp. and capelin *Mallotus villosus*), fish eggs as well as larger crustaceans and squid [13,16,20,22–27]. A potential increase in predation of crustaceans, fish eggs and larvae by mackerel in Icelandic waters can have a detrimental effect on the survival of native populations of seabirds, marine mammals and fish, even to the point of affecting the recruitment rates of these species, who rely on these prey items as their primary food source [28–31]. It is therefore imperative to conduct more studies on the feeding habits and potential impact of mackerel in Icelandic waters and elsewhere.

The objective of this study is to examine the diet composition and feeding strategy (e.g. prey selectivity) of mackerel during their summer feeding in Icelandic waters in 2009–2014 through stomach content analysis. It includes examining the effects of predator size as well as temporal and spatial variation in stomach contents. This will be done by using generalised additive modelling (GAM) to estimate which environmental factors contribute to this variation. All this will provide more comprehensive knowledge on the biology and trophic ecology of this species and expand our understanding of the possible impact mackerel can have on similar native species in this ecosystem and elsewhere.

Materials and methods

Study area

Iceland is situated where two submarine ridges meet, the Mid-Atlantic Ridge and the Greenland-Scotland Ridge, just below the Arctic Circle [32,33]. These ridges affect the flow of surface

waters around Iceland, with more saline and warm Atlantic water flowing along the south, southwest and southeast coast following the North Atlantic—and Irminger Current and more fresh and cold Arctic water masses flowing towards the north and east coast originating from the East Iceland—and East Greenland Current [6,7,32]. Consequently, the area south and west of Iceland contains warm Atlantic water while colder mixed Atlantic and Arctic waters are north and east of Iceland. During the summers, warming of the surface waters creates a thermocline at around 30m depth, so the surface waters of the north- and east coast of Iceland can be above 7°C and are thereby at a suitable temperature range for mackerel [12,34–36]. The stomach sampling covered these different water masses around Iceland (Fig 1).

Stomach sampling

Mackerel stomachs were collected in the International Ecosystem Summer Survey in Nordic Seas (IESSNS), which is coordinated by ICES (International Council for the Exploration of the Seas) and took place from July to August in 2009–2014 (Fig 1). During this survey, a total of 18601 mackerel were collected for further analysis in Icelandic waters, ranging from 18–46 cm in length (S1 Table and S1 Fig). Of those, 3777 stomachs were sampled for dietary analysis. In 2009 and 2010 the samples were taken in an epipelagic trawl, whereas from 2011 and onwards a specially designed pelagic Multpelt 832 trawl was used. The trawl hauls were taken in the surface waters at predefined locations around Iceland [11]. The vertical opening of the trawls varied from 16.5m (2009 and 2010) to 30–35 m (from 2011 onwards) [10]. Trawl catches were sorted and weighed, and the fish were identified to species level and other taxa to higher taxonomic levels. Total length (L; 1.0 cm), whole body weight (W; 0.1 g), weight of gonads (0.1 g), sex, maturity stage and age were recorded for all mackerel. Where possible, ten mackerel

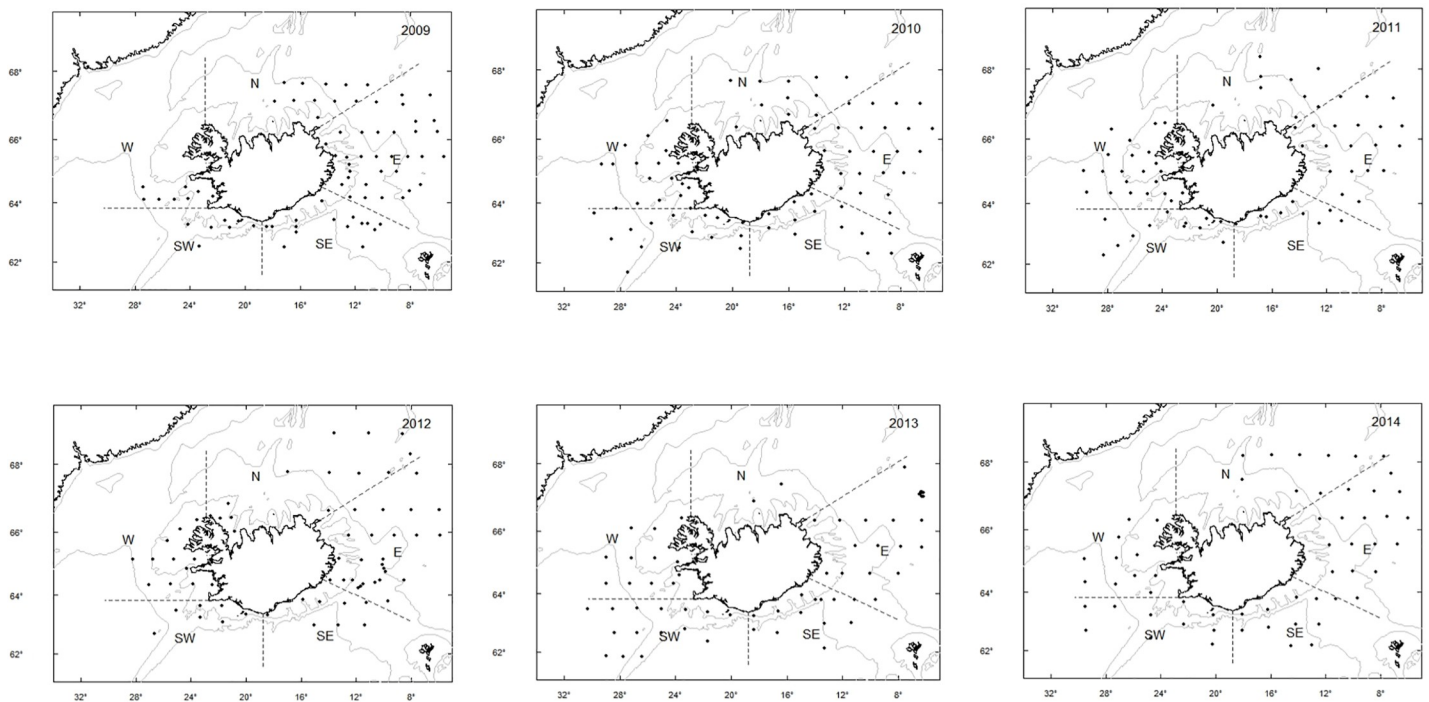


Fig 1. Study area. Sampling stations for Northeast Atlantic mackerel, plankton and CDT in Icelandic waters in 2009–2014, separated into five sub-areas: north (N), east (E), southeast (SE), southwest (SW) and west (W).

<https://doi.org/10.1371/journal.pone.0225552.g001>

stomachs were collected from each station, and the stomach weight (including the stomach content) was recorded (0.1 g) and frozen immediately to -20°C for later analyses ashore. In the laboratory, the stomach content from individual fish was analysed by use of a microscope and the prey items were grouped into the lowest taxonomic group, excluding parasitic animals and unidentified objects (these were weighed but not counted). Small prey individuals within a taxonomic group were counted and weighed together (wet weight to nearest 0.01 g) and for larger prey items (i.e. fish) the total length was also measured (mm). For stomachs containing large amounts of zooplankton, a sub-sample was taken, by mixing the sample and removing 1–2 mL of the mixture to a counting chamber with a pipette. Prey items that were much digested (e.g. fish otoliths or euphausiid eyes) were all identified to the lowest taxonomic level.

The total length of mackerel examined ranged from 19–48 cm. To evaluate variation in food habits as a function of predator size, mackerel were divided into three length groups (≥ 33 cm (S); 34–38 cm (M); ≤ 39 cm (L)), with a minimum of 50 fish in each group. A separation into five sub-areas (south, southeast, southwest, west and north) within Icelandic waters (Fig 1) was done to examine if there was a difference in diet composition between these areas. So, within each area, individual mackerel stomachs from all stations were pooled. This separation was based on oceanographic boundaries (SE vs. E and W vs. N; see description of study area above) and more arbitrary boundaries related to geographical features (W vs. SW), migration distance for mackerel coming from southeast (N vs. E and W vs. SW), size of the continental shelf and size of the areas (SE vs. SW) [20,37,38].

Our study did not involve any endangered or protected species and no experimentation with live animals was performed. No other ethical issues applied to the present research project. Special permissions or rules for sacrificing fish from an animal ethics committee, are at present non-existing in Iceland for the scientific sampling of fish. Usually, trawling and handling of the fish onboard the vessels, including sorting and sampling leads to high mortality. Therefore the fish collected as part of this research were killed as rapidly as possible. Hence, all the fish were dead before any surgical procedure occurred.

Environmental and ecological measurements

Zooplankton were sampled during the IESSNS survey in 2009–2014 using a WP2-net with a mesh size of $200\mu\text{m}$ at the same locations as the trawl hauls were taken. The nets were hauled vertically from a depth of 200 m, or from the near bottom at shallower stations, to the surface at a speed of 0.5 m/s. All samples were split in two, where one half was preserved in formalin for species identification the other half was dried and weighed for biomass estimation. Temperature, salinity and depth were also measured during the surveys at the same locations by a SEABIRD CTD sensor from the surface down to 500 m or to the sea bottom (at shallower depths). However, the analyses below are limited to the uppermost 50 meters and applied as average temperature and salinity over 0–50 m for each station. In the Nordic Seas, the thermocline is generally at 20–40 m depth during summer [39]. The mackerel is typically found in this layer [10], and the trawling takes place there, thereby the stomach sampling. Instead of limiting the environmental variables to this layer (~ 40 m) it was decided to use 0–50 m. The reasons are: (1) mackerel can be expected to feed near and below the thermocline to some degree, especially within the Atlantic waters where the temperature below the thermocline is $>7^{\circ}\text{C}$ (SE, SW and W; Fig 1); (2) The mackerel can be expected to feed and occupy the whole well-mixed water column above the thermocline so using average temperature and salinity sounds logical; (3) The salinity is relatively unconnected to the thermocline so the average value over 50 m represents mainly the type of water masses (Atlantic, Arctic, mixture or coastal).

Dietary analysis

In this study, different indices previously used in dietary studies were applied to the stomach content data to address the different objectives by following Hyslop [40]. Numerical (%N) and gravimetric (%W) composition were calculated together with the frequency of occurrence (FOi), for all stomachs. To estimate the feeding activity of mackerel the Vacuity Index (Vi) was calculated;

$$V_i = \frac{E_s}{T_s} \times 100$$

where E_s is the number of empty stomachs and T_s the total number of stomachs. The Prey-Specific Index of Relative Importance (PSIRI) was used to quantify the importance of each prey category in the diet [41]. PSIRI is ideal for comparisons between predators and prey because its values are not dependent upon the taxonomic level and act as a balanced treatment of the relative measures of prey quantity. PSIRI was calculated as:

$$PSIRI = (FO_i \times (PW_i + PN_i))/2$$

were the prey-specific abundance PW_i (weight) and PN_i (number) were needed for this calculation: $PW_i = \sum W_i / \sum SW_i$; $PN_i = \sum N_i / \sum SN_i$ where W_i is the weight of prey i and N_i is the number of prey i . SW_i and SN_i are the total stomach content in weight and number, respectively, of individual predators with prey i in their stomachs. Feeding strategy was assessed graphically with a two-dimensional representation of prey-specific abundance (P_i) and FO_i of the various preys [42]. The prey-specific abundance of prey i (P_i) was defined as the percentage a prey taxon comprises of all prey items in only those predators in which the actual prey occurs. For this study, we used weight to describe P_i , or in mathematical terms:

$$P_i = (\sum SW_i / \sum PW_i) \times 100$$

Statistical analysis

For statistical testing of diet contribution, fourth-root gravimetric data were assessed, using permutational multivariate analysis of variance (PERMANOVA; [43]) using a Bray-Curtis similarity index or a Kruskal Wallis followed by Dunn's post hoc if significant. All statistical analyses were performed in PAST v3.20 [44] using a significance level of $p < 0.05$. Spatial differences in diet were also examined using the Bray-Curtis similarity index on fourth-root gravimetric data between areas for all years, and hierarchical agglomerative clustering was applied to the similarity matrix [45–47], where clustering was based on the group average cluster mode and visualised in a dendrogram using PAST v3.20 software.

The variation of stomach weight of mackerel was analysed using a generalised additive model (GAM) [48]. A GAM is simply a generalised linear model (GLM) with a linear predictor that is composed of a sum of smooth functions of the covariates, and thus particularly effective at modelling complex ecological relationships [49]. A GAM structure can be written as:

$$g(E(Y)) = \beta_0 + s_1(x_1) + s_2(x_2) + \dots + s_p(x_p)$$

Where Y is the dependent variable, $E(Y)$ denotes the expected value and $g(Y)$ signifies the link function that links the expected value to the explanatory variables x_1, \dots, x_p (Table 1). The terms $s_1(x_1), \dots, s_p(x_p)$ refer to smooth nonparametric functions.

To examine which of the variables were significant in explaining the stomach weight of mackerel, we used data collected from each trawl station containing mackerel. Here the stomach weight is considered to represent feeding success. In our data, most of the stomachs

Table 1. Variables and model selection.

A)								
Variables	Description							
Depth	Measured from sea surface to the ocean floor (meters)							
Sea surface salinity (SSS)	Average salinity from each station from 0–50 meters (parts "per mille"—ppt)							
Sea surface temperature (SST)	Average temperature from each station from 0–50 meters (°C)							
Zooplankton biomass	Dry weight from WP2 hauls at each station (mg/m ³)							
Fulton's K	Fulton's condition factor ($K = 100(W/L^3)$)							
Latitude and longitude	Geographical marker of stations							
Total catch	Log transformed total mackerel catch (ton) per station							
Week	week number during the survey							
Time of day	Day divided into four time periods with 6 hours in each (00:00–05:00, 06:00–11:00, 12:00–17:00, 18:00–23:00)							
Year	Data collected from 2011–2014							
Distance to shore	From isobath lines ($\leq 100m, \leq 200m, \leq 500, > 501m$)							
B)								
Model #	Response variable Explanatory variable	Factorial variables	AIC	ΔAIC	w_i	Deviance explained	R ² adjusted	DF
1	log(stomach weight) zooplankton + (longitude,latitude) + Fulton's K+ depth + SSS + SST + log(total catch)	time period+distance to shore+week+year	-1854	8.92	0.007	48.50%	0.44	153
2	log(stomach weight) zooplankton + (longitude,latitude) + depth + SSS + SST + log(total catch)	time period+distance to shore	-1863	0	0.58	48.60%	0.44	150
3	log(stomach weight) zooplankton + (longitude,latitude) + SSS + SST + log(total catch)	time period	-1862	1	0.35	48.50%	0.44	148
4	log(stomach weight) zooplankton + (longitude,latitude) + depth+ SSS + SST	time period	-1860	4.4	0.06	48.30%	0.42	147

A) List of explanatory variables considered in analyses of Northeast Atlantic mackerel stomach weight in Icelandic waters in 2011–2014 using generalised additive models (GAMs). B) GAMs selection table, the model marked in bold was found to be the best-fitted model based on Akaike Information Criterion (AIC) from the R package "MuMIn" (see Table 6).

<https://doi.org/10.1371/journal.pone.0225552.t001>

contained prey, which suggests that mackerel that can feed continuously are in better condition and thus have better feeding success [50,51]. The explanatory variables included in the modelling were; time of sampling (four time periods (00:00–05:00, 06:00–11:00, 12:00–17:00, 18:00–23:00), week number and year), location (station and distance to shore (0–200m, 201–500m, 501–1000m, >1001m), environmental variables (bottom depth, average temperature from 0–50m and average salinity from 0–50m) and biological variables (zooplankton dry weight biomass, Fulton's K ($K = W / L^3 \times 100$) of individual mackerel, total catch of mackerel) (Table 1A). Only years from 2011–2014 (S1 Table) were used in the GAMs since no zooplankton biomass data was available in 2009 and 2010. Also, only stations with > 9 individual stomachs were selected for all years for more robust comparisons. Furthermore, small fish (< 25 cm) were not included in the analysis because they were not well represented for all years in the dataset (S1 Fig). Before modelling, data were checked for collinearity.

The GAMs were fitted to a Gaussian distribution with an identity link function in the R package "mgcv" v. 1.8–26 [49], using Restricted Maximum Likelihood (REML) as smoothing selection [52]. The best-fitting GAM was selected by computing models with every possible combination of the variables using the "MuMIn" package v. 1.42.1 [53], as well as using visual

assessment of the residual—and smooth plots and Akaike Information Criterion (AIC), delta (Δ) AIC and Akaike weight (w_i) [54]. Variables were excluded if their inclusion did not belong within the 95% confidence set of the model (Table 1B).

Results

Diet composition and feeding strategy

The vacuity index (VI) was between 2–22% (average $VI = 8.3\%$), with no statistical difference between years (Kruskal- Wallis; $H = 5$, $p = 0.42$) and overall, 92% of the mackerel stomachs contained food, meaning that almost all stomachs contained prey items to a varying degree. A total of 42 prey species were identified and are listed in Table 2. For further analysis, the prey species found in the stomachs were grouped into the ten following taxon groups; molluscs, copepods, amphipods, euphausiids, large crustaceans, small crustaceans, fish, appendicularians, chaetognaths and ova. All unidentified prey matter and parasites found in the stomachs were excluded from further analysis.

The overall prey specific index of relative importance ($PSIRI$) showed that the most common prey group that occurred in all mackerel stomachs for all the years was the copepod group (Fig 2), constituting a $PSIRI$ between 48.7% to 86.6% in the years studied. Other important prey groups varied more among years in $PSIRI$ with euphausiids ranging from 1.4–5.8%, large crustaceans 0.01–14.7%, amphipods 1.1–6.2% and fish 0.5–2.0%. The remaining prey groups, which had lower $PSIRI$ values, were thus considered of lesser importance.

To assess the feeding strategy of mackerel, the prey-specific abundance (P_i) was plotted against the frequency of occurrence (FO_i) (Fig 3A), which was done for the whole surveyed area in Icelandic waters pooling all years. Almost all prey groups were located to the lower left of the diagram, i.e. a region of low prey importance (Fig 3B). Copepods was the dominated prey group and its location at the upper right corner of the diagram (Fig 3A) signifies its importance and specialisation by the mackerel.

Results from the two-way PERMANOVA indicated a statistical difference in gravimetric weight of prey among areas and years ($Pseudo F_{4,5} = 5.3$, $p < 0.001$; $Pseudo F_{4,5} = 13.8$, $p < 0.001$). It also revealed that most prey groups varied among years and areas (Tables 3 and 4). Exceptions to this pattern include euphausiids among years and molluscs, large crustaceans, and chaetognaths among areas.

The difference between the three length groups of mackerel in the relative measure of total stomach content, indicated by the gravimetric index, was only significant in 2011 ($H = 52.1$, $p < 0.001$) and in 2012 ($H = 10.9$, $p < 0.005$). Dunn's post hoc test showed a difference between all length groups in 2011 (S-M, $p < 0.001$; S-L, $p < 0.001$; M-L, $p < 0.005$) while in 2012 there was a difference between the largest mackerel and the two other length groups (L-S, $p < 0.005$; L-M, $p < 0.01$). When analysing differences in prey composition among length groups combined over all the years, there was only difference with the fish prey group ($H = 13.1$, $p < 0.005$), where a Dunn's post hoc revealed that larger mackerel preyed more on fish than smaller mackerel did (S-M, $p < 0.05$; S-L, $p < 0.001$).

Diet variation between areas

Results from the one-way PERMANOVA analysis of prey composition in the stomachs showed that there was some diet variation between areas within the years (Table 5 and Supplementary S2 and S3 Tables). Hierarchical clustering of the five areas based on the diet variation resulted in three groups that were clearly separated but still showed a high percentage of similarity (Fig 4A). One of the groups consisted of west, southwest and southeast areas with 85–92% similarity, the second group (north) revealed slightly lower similarity (78%) and the

Table 2. Prey species observed in the stomach content of Northeast Atlantic mackerel in Icelandic waters in 2009–2014.

Group		PWi%	PNi%	FOi%	PSIRI%
Molluscs		3.80%	1.20%	17.90%	0.40%
	<i>Planktomya</i> spp.				
	<i>Limacina helicina</i>				
	<i>Limacina retroversa</i>				
	<i>Prosobranchia</i> spp.				
	<i>Todarodes sagittatus</i>				
Copepods		72.90%	97.30%	81.30%	69.20%
	<i>Calanus finmarchicus</i>				
	<i>Calanus hyperboreus</i>				
	<i>Acartia clausi</i>				
	<i>Temora longicornis</i>				
	<i>Centropages hamatus</i>				
	<i>Metridia longa</i>				
	<i>Oithona similis</i>				
	<i>Microcalanus</i> spp.				
	<i>Pseudocalanus</i> spp.				
	<i>Euchaeta</i> spp.				
	<i>Caligidae</i> spp.				
Amphipods		15.60%	2.20%	35.40%	3.10%
	<i>Themisto abyssorum</i>				
	<i>Hyperia medusarum</i>				
	<i>Gammaridae</i> spp.				
Euphausiids		18.60%	1.30%	40.10%	4.00%
	<i>Thysanoessa inermis</i>				
	<i>Thysanoessa longicaudata</i>				
	<i>Meganyctiphanes norvegica</i>				
Large crustaceans		42.10%	9.80%	21.20%	5.50%
	<i>Leucon (Leucon) nasica</i>				
	<i>Carcinus maenas</i>				
	<i>Hymenodora glacialis</i>				
	<i>Eusegestes arcticus</i>				
Small crustaceans		16.10%	4.40%	7.60%	0.80%
	<i>Balanidae</i> spp.				
	<i>Ostracoda</i> spp.				
	<i>Podon</i> spp.				
	<i>Evadne</i> spp.				
Fish		26.70%	0.30%	7.80%	1.10%
	<i>Ammodytes</i> spp.				
	<i>Clupea harengus</i>				
	<i>Gadus morhua</i>				
	<i>Melanogrammus aeglefinus</i>				
	<i>Micromesistius poutassou</i>				
	<i>Merlangius merlangus</i>				
	<i>Maulisia maui</i>				
	<i>Mallotus villosus</i>				
	<i>Anarhichas minor</i>				
Appendicularia		16.30%	32.00%	1.40%	0.30%

(Continued)

Table 2. (Continued)

Group		PWi%	PNi%	FOi%	PSIRI%
	<i>Oikopleura</i> spp.				
Chaetognaths		16.20%	0.80%	1.00%	0.10%
	<i>Sagitta</i> spp.				
Ova		0.20%	1.20%	13.60%	0.10%
	<i>Actinopteri</i> spp.				

Observed prey and categorisation across species, showing prey-specific weight ($PW_i\%$) and number ($PN_i\%$), Frequency of Occurrence ($FO_i\%$) and Prey-Specific Index of Relative Importance ($PSIRI_i\%$) of all years combined.

<https://doi.org/10.1371/journal.pone.0225552.t002>

lowest being east (70%). These similarities were also recognised by a graphical representation of the diet composition in each area (Fig 4B).

Variation in stomach weight

The results from the GAMs, show that the stomach weight of mackerel was primarily affected by zooplankton biomass, temperature, salinity, depth as well as spatial and temporal variables, in this order, which together explains over 48% of the deviance. All predictor variables, except total catch per station, contributed to the overall model by having a smoothing term significantly different from zero (Table 6). Increase in zooplankton biomass had a positive effect on

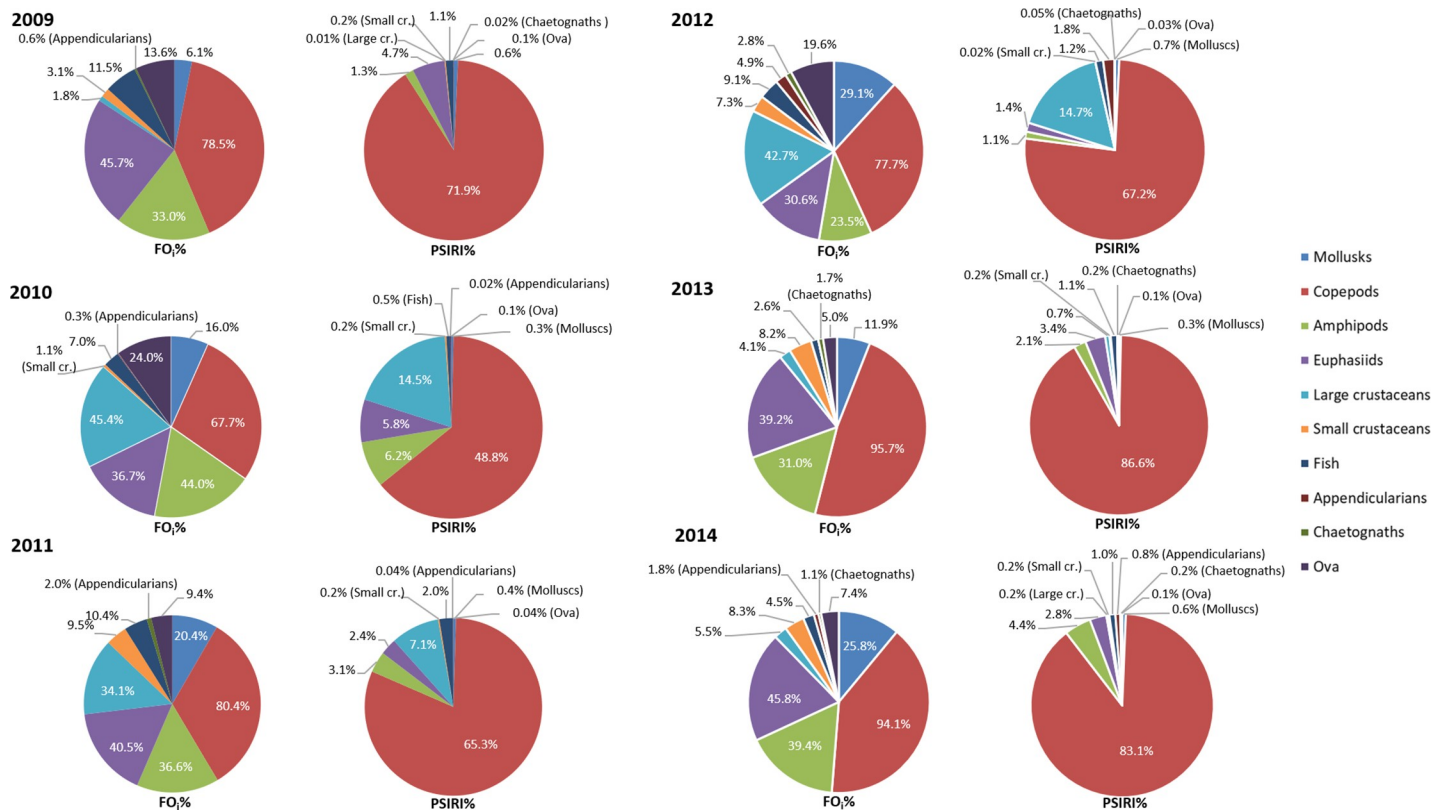


Fig 2. Frequency of Occurrence (FOi%) and Prey-Specific Index of Relative Importance (PSIRI%) for different prey groups of Northeast Atlantic mackerel in Icelandic waters in the years 2009–2014.

<https://doi.org/10.1371/journal.pone.0225552.g002>

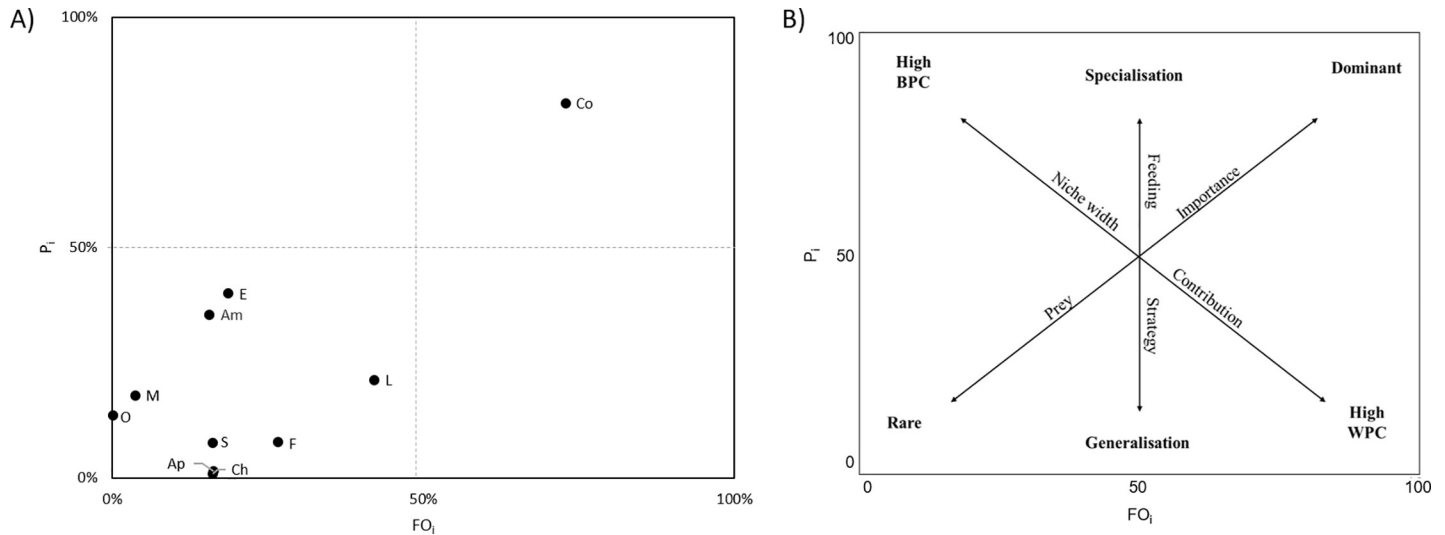


Fig 3. Graphical representation of feeding strategy from the stomach composition of Northeast Atlantic mackerel in Icelandic waters in 2019–2014. A) Feeding strategy shown by plotting frequency of occurrence (FO_i%) and prey-specific abundance (P_i%) of prey in diet of fish collected where the prey groups are: M = molluscs; Co = copepods; Am = amphipods; E = euphausiids; L = large crustaceans; S = small crustaceans; F = fish; Ap = appendicularians; Ch = chaetognaths; O = ova. B) Explanatory diagram for interpretation of feeding strategy, prey importance and niche width contribution for mackerel (adapted from Amundsen et al. [42]); BPC, between-phenotype component; WPC, within-phenotype component.

<https://doi.org/10.1371/journal.pone.0225552.g003>

stomach weight, while a negative trend, with a wide confidence interval, was detected in the higher end of the zooplankton biomass based on few samples (Fig 5). Depth had an overall positive effect on the stomach weight of mackerel, whereas the positive relationship between salinity and stomach weight was largely driven by a single station with low values for both variables. Temperature had a more mixed effect but became positive when it exceeded 9°C. The total catch had both a negative and positive effect on stomach weight. Regarding the factorial variables, some significant effects were revealed, both regarding the distance to the shore (depth profiles) and time of day (time period).

Discussion

The variation in prey composition

The results showed that mackerel’s main food source while feeding in Icelandic waters, were calanoid copepods, which constituted (on average) >60% of the total content weight of the stomachs. Over 70% of the copepods by weight consisted of *C. finmarchicus*. This finding is in accordance with studies done on the zooplankton community in Icelandic waters, which have identified *C. finmarchicus* to be the most abundant calanoid species (50–80%) [55,56]. Other diet studies of mackerel from other areas in the Northeast Atlantic showed similar results, where *C. finmarchicus* was found to be the most dominant copepod species in mackerel stomachs [16,20,26,57,58]. Smaller copepods, such as *T. longicornis* and *Oithona* spp., were also found in large amounts in mackerel stomachs during their summer feeding, especially from those fish caught close to and on the shelf area to the south and southeast. This coincides with similar diet studies of mackerel from the Norwegian Sea [57] and in the Gulf of St. Lawrence [59,60] and characterises their more coastal distribution [7,61–63]. Mackerel are mainly planktivores, using both filter and particulate methods of feeding when faced with different prey assemblages in order to maximise their net intake [18]. Studies have shown that mackerel may feed on zooplankton by primarily filter feeding and then shift to particulate feeding when prey

Table 3. Summary of two-way PERMANOVA for the analysis of differences between areas and years.

Source	df	SS	MS	Pseudo-F	P
<i>Molluscs</i>					
Area	4	1.26	0.32	1.15	>0.1
Year	5	6.68	1.34	5.00	<0.001
Residual	363	99.00	0.27		
<i>Copepods</i>					
Area	4	1.12	0.28	3.40	<0.001
Year	5	1.53	0.31	3.70	<0.001
Residual	363	30.00	0.08		
<i>Amphipods</i>					
Area	4	4.82	1.20	4.37	<0.001
Year	5	3.76	0.75	2.74	<0.01
Residual	363	99.91	0.28		
<i>Euphausiids</i>					
Area	4	2.96	0.74	3.00	<0.01
Year	5	1.39	0.28	1.10	>0.1
Residual	363	92.68	0.26		
<i>Large crustaceans</i>					
Area	4	0.74	0.18	0.95	>0.1
Year	5	38.86	7.77	40.17	<0.001
Residual	363	70.23	0.19		
<i>Small crustaceans</i>					
Area	4	2.08	0.52	2.60	0.01
Year	5	4.64	0.93	4.63	<0.001
Residual	363	72.70	0.20		
<i>Fish</i>					
Area	4	2.55	0.64	9.08	<0.001
Year	5	0.54	0.11	1.54	>0.1
Residual	363	25.48	0.07		
<i>Appendicularians</i>					
Area	4	0.84	0.21	4.51	0.001
Year	5	0.60	0.12	2.56	<0.01
Residual	363	17.00	0.05		
<i>Chaetognaths</i>					
Area	4	0.23	0.06	1.13	>0.1
Year	5	0.93	0.19	3.61	0.001
Residual	363	18.64	0.05		
<i>Ova</i>					
Area	4	1.71	0.43	1.51	0.1
Year	5	13.72	2.74	9.69	<0.001
Residual	363	102.80	0.28		

Based on Bray–Curtis dissimilarities of the fourth-root gravimetric weight of prey groups of mackerel in 2009–2014 in Icelandic waters. Significant results are shown in bold.

<https://doi.org/10.1371/journal.pone.0225552.t003>

size and the size distribution of available prey changes [18,19], which probably allows them to make more extensive use of the available prey. Therefore, the feeding behaviour of mackerel can be size-selective and is probably based upon the efficiency of retention of different-sized particles by the gill rakers.

Table 4. Pairwise comparisons from the results of the two-way PERMANOVA (Table 3).

A)					Large Crustaceans	Small Crustaceans		Appen-dicularians	Chaet-ognaths	
	Molluscs	Copepods	Amphipods	Euphausiids			Fish			Ova
2009–2010	0.001	< 0.001	< 0.01	>0.5	< 0.001	>0.1	< 0.05	0.5	< 0.01	>0.1
2009–2011	< 0.001	< 0.05	>0.1	>0.5	< 0.001	0.001	>0.5	0.01	>0.1	>0.05
2009–2012	< 0.001	>0.5	>0.1	>0.05	< 0.001	>0.5	>0.1	0.01	>0.1	>0.1
2009–2013	< 0.05	< 0.05	>0.5	>0.5	0.01	>0.1	0.001	1	0.05	< 0.001
2009–2014	0.001	>0.5	>0.1	>0.5	< 0.05	>0.1	< 0.001	0.01	>0.1	< 0.001
2010–2011	>0.1	>0.05	>0.1	>0.5	0.01	< 0.001	>0.1	>0.1	1	0.01
2010–2012	0.02	< 0.01	< 0.001	>0.1	>0.05	>0.1	>0.5	>0.1	< 0.001	>0.05
2010–2013	>0.1	< 0.001	< 0.01	>0.5	< 0.001	< 0.05	>0.05	>0.5	< 0.01	< 0.001
2010–2014	>0.1	0.001	>0.05	>0.1	< 0.001	0.01	>0.05	>0.1	>0.1	< 0.001
2011–2012	>0.1	>0.05	< 0.05	>0.1	>0.1	0.001	>0.1	1	< 0.001	>0.1
2011–2013	>0.1	0.001	>0.1	>0.5	< 0.001	< 0.05	< 0.01	0.01	< 0.01	< 0.001
2011–2014	>0.5	< 0.05	>0.5	>0.1	< 0.001	< 0.05	< 0.01	>0.5	>0.1	0.01
2012–2013	0.01	0.01	>0.1	>0.05	< 0.001	>0.1	< 0.05	>0.05	>0.5	< 0.001
2012–2014	>0.05	>0.05	< 0.5	< 0.05	< 0.001	>0.1	< 0.05	>0.5	< 0.05	< 0.01
2013–2014	0.5	>0.1	>0.1	>0.5	>0.5	>0.5	>0.5	>0.05	0.01	>0.05
B)					Large Crustaceans	Small Crustaceans		Appen-dicularians	Chaet-ognaths	
	Molluscs	Copepods	Amphipods	Euphausiids			Fish			Ova
W-SW	>0.5	>0.1	< 0.001	>0.5	>0.1	>0.1	>0.1	0.01	>0.1	>0.1
W-SE	>0.5	>0.1	0.01	>0.1	>0.5	0.01	>0.5	< 0.01	>0.5	>0.05
W-E	>0.1	0.01	0.001	>0.05	>0.5	>0.1	>0.5	0.01	>0.1	>0.5
W-N	>0.05	< 0.001	>0.1	< 0.01	>0.1	>0.1	0.001	>0.5	>0.5	>0.5
SW-SE	>0.5	>0.5	>0.05	>0.1	>0.1	>0.1	>0.05	1	>0.5	>0.5
SW-E	>0.1	>0.1	< 0.05	>0.05	>0.1	>0.1	>0.1	>0.1	0.05	>0.1
SW-N	>0.1	0.01	< 0.01	0.01	>0.5	>0.05	< 0.001	< 0.05	>0.1	>0.1
SE-E	>0.5	>0.1	>0.1	0.05	>0.5	< 0.05	>0.1	>0.1	>0.1	< 0.05
SE-N	>0.1	>0.05	>0.1	0.01	>0.1	0.001	< 0.05	< 0.05	>0.5	< 0.05
E-N	>0.1	0.01	>0.1	>0.1	>0.1	>0.1	< 0.001	>0.1	>0.1	>0.5

Based on Bray–Curtis dissimilarities of fourth-root transformed values of gravimetric weight of prey between years (A) and between areas (B) for all years combined. Significant results are shown in bold.

<https://doi.org/10.1371/journal.pone.0225552.t004>

Table 5. One-way PERMANOVA of species composition from stomachs between areas within years.

Prey groups	2009	2010	2011	2012	2013	2014
Molluscs	>0.5	>0.1	< 0.001	< 0.05	>0.1	>0.1
Copepods	>0.5	>0.05	< 0.01	0.01	>0.1	>0.5
Amphipods	0.05	>0.1	>0.05	0.01	>0.05	>0.5
Euphausiids	0.01	>0.1	>0.1	>0.5	< 0.01	>0.1
Large crustaceans	>0.1	< 0.01	>0.05	>0.5	>0.5	>0.5
Small crustaceans	0.1	>0.05	>0.1	>0.1	>0.5	< 0.05
Fish	>0.1	< 0.05	0.01	>0.1	>0.1	0.5
Appendicularians	NA	< 0.05	>0.1	>0.05	NA	>0.05
Chaetognaths	>0.5	NA	NA	>0.1	>0.5	>0.1
Ova	>0.1	>0.1	>0.05	>0.1	>0.1	>0.5

Based on Bray–Curtis dissimilarities of fourth-root gravimetric weight of prey. Significant results are shown in bold.

<https://doi.org/10.1371/journal.pone.0225552.t005>

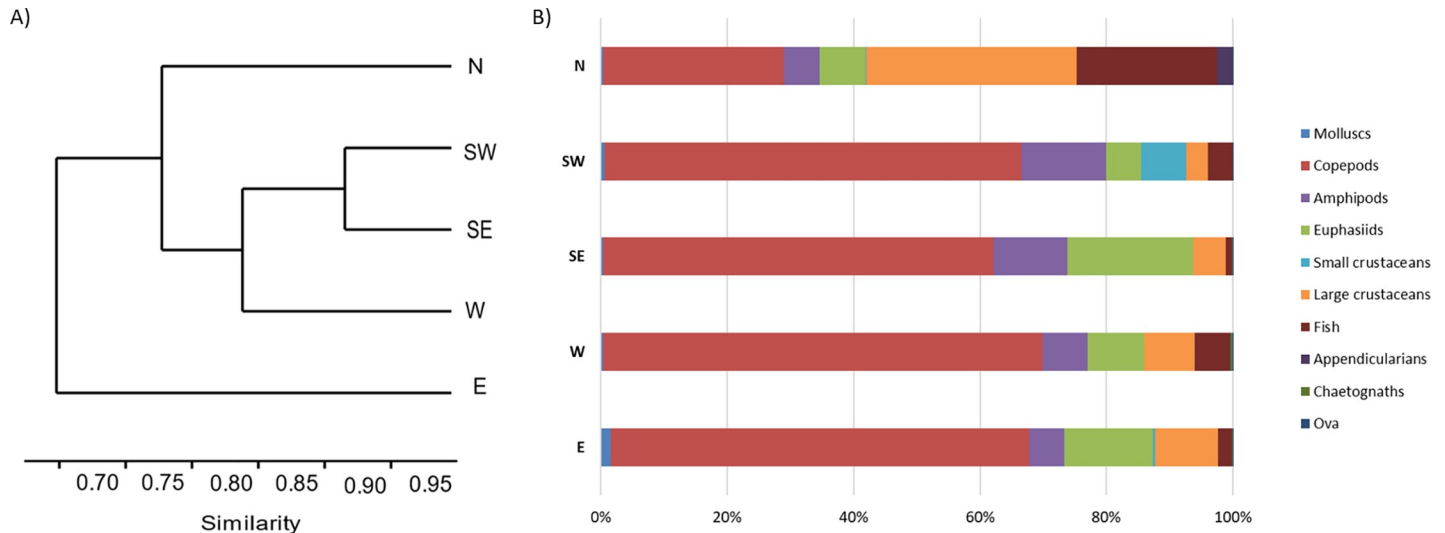


Fig 4. Diet variation between areas. A) Dendrogram for hierarchical clustering of the prey composition of mackerel according to sampling locations (Fig 1) using Bray-Curtis similarities calculated on fourth-root transformed values of the gravimetric weight of prey. B) Composition of mackerel diet by area, based on the gravimetric weight of prey (W%).

<https://doi.org/10.1371/journal.pone.0225552.g004>

This study revealed that euphausiids, amphipods and large crustaceans play an essential role as food for mackerel. Of the four euphausiid species found in Icelandic waters, *Thysanoessa inermis* occurs all over the Icelandic shelf, *T. longicaudata* is most abundant in offshore waters, *T. raschi* is mainly confined to fjords and bays and *Meganyctiphanes norvegica* is most common near the shelf edge off the south and west coasts [64,65]. The euphausiid species identified in the analysed stomachs was, to a large extent *T. inermis* and to some extent *M. norvegica*. *Themisto abyssorum* was the most abundant amphipod species in the stomachs, which concurs very well with zooplankton studies finding *T. abyssorum* to be the most common amphipod species in Icelandic waters [66]. In 2010–2012, megalopa larvae of large crustaceans

Table 6. Summary statistics from the general additive model (GAM).

A) Parametric coefficients	Estimate	Std. error	t-value	p-value
Intercept	1.00986	0.05624	17.955	<0.001
Distance to shore2 (depth 200–500m)	-0.07544	0.0306	-2.465	<0.05
Distance to shore3 (depth 501–1000m)	-0.14472	0.06793	-2.13	<0.05
Distance to shore4 (depth > 1000m)	-0.20338	0.09313	-2.184	<0.05
Time period 2 (06:00–11:00h)	-0.02611	0.01839	-1.42	>0.1
Time period 3 (12:00–17:00h)	-0.02054	0.01763	-1.165	>0.1
Time period 4 (18:00–23:00h)	-0.06468	0.01583	-4.086	<0.001
B) Smooth terms	Est. DF	F	p-value	
s(zooplankton biomass)	3.174	4.376	<0.01	
s(bottom depth)	3.227	4.818	<0.01	
s(salinity)	3.594	3.803	<0.01	
s(temperature)	116.947	5.897	<0.001	
s(longitude, latitude)	6.48	3.286	<0.01	
s(total catch)	3.183	2.85	>0.05	

Showing the parametric coefficients of factorial variables (A) together with the approximate significance of smooth terms used in the model (B). Significant p-values are in bold.

<https://doi.org/10.1371/journal.pone.0225552.t006>

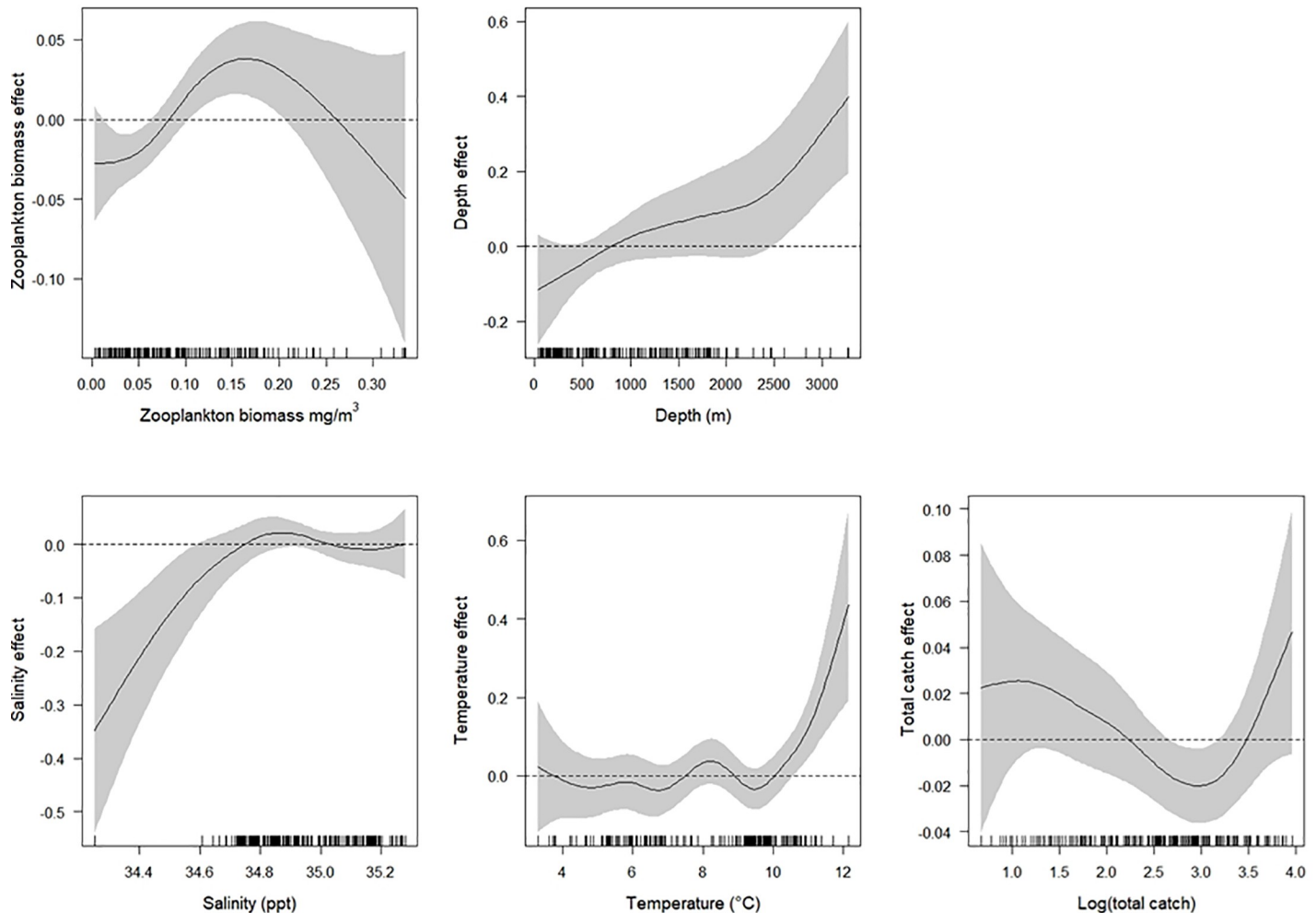


Fig 5. Generalised additive model (GAM). Results from the GAM of the effects of different explanatory variables on Northeast Atlantic mackerel stomach weights in the summers of 2011–2014 in Icelandic waters, where the solid lines are smoother estimates of the covariates according to the model. The shaded grey area represents the 95% confidence interval of the smoothers, and vertical dashes at the bottom of the plots show the distribution of data points entering the model.

<https://doi.org/10.1371/journal.pone.0225552.g005>

(mostly crab and shrimp), were found to a greater extent (second most important prey item (*PSIRI*) Fig 2) in the stomach content than other years. It is difficult to say why this prey group was represented in greater abundance in those three years, than in the other years. The only shrimp and crab species fished commercially, and thus monitored regularly, in Icelandic waters are the Northern shrimp (*Pandalus borealis*) that are found all around Iceland but more abundance in the north and east [67] and Norway lobster (*Nephrops norvegicus*) which is, however, limited to the south and west coast of Iceland [64]. We cannot tell with the data at hand, if and how much of these observed megalopa larvae belong to these species, and thereby if, for example, the mackerel predation could be impacting the Norway lobster recruitment success, which has been failing for many years [68]. However, this is of both ecological and economic interest and requires further investigation through, for example, genetic analysis of stomach content, to assess the potential impact.

Fish were the only prey group that varied among length groups, where large mackerel (≥ 39 cm) tended to consume more fish than smaller mackerel. Experiments on mackerel foraged on fish larvae revealed that adult mackerel actively shifted preference towards larger prey

to achieve a higher rate of energy intake, and thus preyed more heavily on large larvae than the smaller mackerel [19,24]. This strategy could be more profitable for larger fish, who could endure the extra energy it takes, to actively feed on more mobile prey. Otherwise, there was not much difference in diet composition between the length groups, which could be because most mackerel caught in Icelandic waters during the summer are relatively large (>33cm) (S1 Fig). Smaller and younger mackerel occasionally observed in Icelandic waters (<25 cm [69]), were not part of this study.

The results of prey composition in mackerel stomachs between areas revealed some subtle differences (Fig 4) and these differences reflect the zooplankton distribution pattern around Iceland to some degree. Past studies have shown that the mean annual zooplankton biomass in the surface layers are more than two times higher in the warm Atlantic water south of Iceland than in the subarctic waters to the north and that species composition varies greatly among areas as well [7,38]. In the uppermost water mass around Iceland *C. finmarchicus* is the most dominant zooplankton species, followed by *Oithona* spp. [38,63]. Other species like *T. longicornis*, *Centropages hamatus*, *Acartia* spp., *Podon* spp., cirripede larvae, bivalves and polychaetes dominate the biomass to the southeast, south and southwest [7,38,63,64]. To the north and northeast of Iceland, there seem to be relatively high zooplankton biomass of *C. hyperboreus*, *C. glacialis*, *Metridia longa*, *Pseudocalanus* spp., euphausiids and appendicularia (*Oikopleura* spp.) [7,38,63–65]. Although *C. finmarchicus* was the dominant copepod species found in mackerel stomachs for all areas, smaller copepod species such as *T. longicornis* and *Arcatia clausi* were especially abundant in samples from the coastal areas to the southwest and southeast. As were small crustaceans (i.e. cirripede larvae and *Podon* spp). In the northern area, the diet was also dominated by large crustaceans and fish, where euphausiids were more commonly found in stomachs from the east and southeast.

Feeding strategy of mackerel

The vacuity index (VI) (or empty stomachs' ratio), is an inverse indicator of feeding intensity which varies according to variations in the abundance of fish as well as seasonal changes in water temperature and food items available [70]. The low value of the vacuity index (VI) for all years indicate that mackerel feed continuously while in Icelandic waters during the summer. Mackerel is a visual predator, and experiments have shown that mackerel have a greater feeding activity during the day than at night. At the time they are foraging in Icelandic waters, there is daylight almost for 24 hours, which allows them a more continuous feeding time frame [19,59]. Our findings from the GAM modelling supports this where the time of the day had only small impacts on the variation in the stomach weight. Only time period 4 (from 18:00–23:00 hours) was found significant, with a tendency for less stomach weight indicating, surprisingly, a less feeding in the afternoon (Table 6). Study of mackerel feeding behaviour from the Irminger Sea by Jansen et al. (2019) [50] during the summer, found that mackerel had some diel aspects in their feeding dynamics, where they consumed larger zooplankton prey during dusk hours, even though copepods were still numerous in the surface layers. Our data on stomach composition did not allow for analyses of the diurnal differences.

Our general findings from the GAM indicated that the weight of mackerel stomachs were affected by several explanatory variables. The positive impact of the sea temperature was not surprising since mackerel prefer higher temperatures. In the same way, zooplankton biomass had a positive effect on the stomach weight up to a certain degree, where it started to have a negative effect according to the model. The positive effect seems like logical, where higher density of zooplankton causes higher feeding success and thereby greater stomach weight. This negative effect was, however, caused by few samples, had wide confidence interval, and is

therefore considered to have little significance. There are some shortcomings in our approach that should be mentioned regarding the zooplankton biomass. It was obtained from WP2 plankton nets, and thus not fully representative of the zooplankton community, since larger zooplankton species, like euphausiids, tend to evade capture [71]. The results from the GAM are interesting enough for further exploration regarding the feeding of mackerel in Icelandic waters concerning shifts in time of day as well as the waters they occupy (coastal, shelf or oceanic).

Analyses of the feeding strategy of mackerel showed that it is a specialised predator during the summer feeding, that relies heavily upon copepods as its main prey while eating other prey groups to a varying degree when encountering them. Since mackerel has the option to both filter and particulate feed, it can switch between methods readily, in order to utilise the searched area (Macy et al. 1998; Darbyson et al. 2003). Feeding experiments have shown that when mackerel were introduced to high concentrations of large copepods, they switched from particulate feeding to filter feeding (Macy et al. 1998). This was also true when offered intermediate and smaller prey items at relatively high concentrations, and when the concentration of smaller size zooplankton is low, mackerel shift back to particulate feeding [19]. The shift in feeding method can be explained by the energy cost of filter feeding [72] as well as a lower energy density of *C. finmarchicus* [73]. Thus, mackerel can shift to larger and more energy-rich food sources when available. This has also been observed in nature, where mackerel switched to particulate feeding of large zooplankton even though copepods were available [50]. These types of behaviour responses are also thought to be common within mackerel schools, because differences in the size and abundance of prey at the front and rear end of schools may vary [18]. Studies have also shown that mackerel tend to slow their swimming speed when encountering highly concentrated patches of zooplankton [14,18], probably as they do not need to “chase” their prey. Higher swimming speeds are then associated with larger prey and reflect a higher energy intake [18,19]. Thus, mackerel increase their swimming speed as zooplankton abundance decreases, and thereby tend to have high clearance rates of a variety of prey sizes within the plankton community, which then again can affect the density of less abundant prey such as fish larvae. In summary, the literature implies that mackerel is an opportunistic predator, meaning that is generally not selective in its feeding but more or less feeds on the biomass available. Our results indicate that mackerel is a specialised predator on copepods, although this can also be interpreted as support to the opportunistic feeding strategy since the most abundant biomass of zooplankton prey in Icelandic waters are calanoid copepods.

Studies limitations

Evacuation studies have shown that adult mackerel can clear their stomachs within 28 hours at 17°C but longer evacuation time is needed at lower temperatures [74,75]. Furthermore, mackerel evacuate stomach content at a continuous rate, and smaller prey items are evacuated faster than large ones [75]. Therefore, visual analysis of stomach contents alone can be biased, because often the contents are so digested that there is only “soup”, or bits and pieces left visible. This makes it hard to quantify and identify the prey down to species level.

Consequently, a more comprehensive and alternative analysis of a fish’s diet can be informative and relevant, not only in strengthening and widening the results, but also to discover if there are prey species that were not detectable by visual analysis alone. These methods could be in the form of stable isotope analysis of different fish tissues [76,77], fatty acid profiling [78,79] or genetic analysis of stomach content [80]. In this study, conventional methods were used to evaluate the feeding strategy of the Northeast Atlantic mackerel from stomach content

analyses, which showed that mackerel is a specialised feeder upon copepods while in Icelandic waters. These findings correspond very well with similar studies on mackerel diet in the North-east Atlantic during the summer. However, applying different methods might give a different perception and more holistic information on the temporal and spatial variability on the prey field of Northeast Atlantic mackerel across its distribution area.

Ecological considerations

Mackerel, being a ferocious feeder and capable of sustaining high clearance rates of prey items in their vicinity, can most likely have significant impacts on the marine ecosystem around Iceland and elsewhere [20,73]. Even though there are presently no documented cases of direct ecological impacts of mackerel in Icelandic waters, it seems logical to suggest that the relative recent massive influx of mackerel into Icelandic waters during their feeding migration, has altered the food web structure by top-down forcing, adding pressure on other planktivorous fish species as well. For example, the Norwegian spring spawning herring undertakes an extensive feeding migration in the early summer, from its spawning grounds along the Norwegian coast into the Norwegian Sea and to the waters east and north of Iceland, feeding mainly on overwintering *C. finmarchicus* [26,81]. As the summer progresses, herring tend to shift their diet to include more euphausiids and amphipods, although copepods are still an essential part of their diet [20,56]. Mackerel, on the other hand, arrives into Icelandic waters later and are mainly feeding on the first generation of *C. finmarchicus*, which is the main proportion of their diet throughout the summer [16,20,57]. Therefore, not only are mackerel competing with other species, (e.g. herring) for food, they have the potential to overgraze on the zooplankton community [73]. This could lead to a decline in zooplankton abundance, especially of *C. finmarchicus*, which in turn can have detrimental effects on the food-web structure, as well as the survival of many marine fish, bird and whale species [29,30,82–84]. Studies have shown, that mackerel on several occasions seem to prefer fish larvae to zooplankton [24,27], and reports say that mackerel readily feed on juvenile herring, capelin, sand eel among others [27,57,73,85]. Mackerel could, therefore, impact the survival of small fish and larvae in Icelandic waters as well. On the other hand, the increase of mackerel has also shown some positive effects on top predators such as seals, whales and northern gannets [29,83,86,87]. The ecological consequences of mackerel entering into Icelandic waters during their summer feeding migration are unknown, but given that they are avid foragers on the zooplankton community, the potential impact is imminent and should be taken into consideration for future research.

Supporting information

S1 Table. Sample sizes from the years 2009–2014 used in this study.
(DOCX)

S2 Table. Results of the Permutational Analysis of Variance (PERMANOVA) based on Bray–Curtis dissimilarities of fourth-root transformed values of gravimetric weight of the prey within each year, between the five areas. Significant values are marked in grey
(DOCX)

S3 Table. Results of pairwise comparison of the PERMANOVA (S2 Table), based on Bray–Curtis dissimilarities of fourth-root transformed gravimetric weight of prey between areas within each year. Only prey groups that were significant from the PERMANOVA are listed. Significant values are marked in grey
(DOCX)

S1 Fig. The size distribution of mackerel caught in Icelandic waters from 2009–2014 during the summer.

(TIF)

Acknowledgments

Special thanks go to the ISSENS survey crew on R.V. Árni Friðriksson as well as lab and student workers at the Marine and Freshwater Research Institute (MFRI) in Iceland for help in analysing stomach samples. We also want to thank Teresa Silva (MFRI) for helping with the data analysis and insight on large zooplankton species, and to Ástþór Gíslason (MFRI) for providing personal insights on small zooplankton and assistance with obtaining data on them.

Author Contributions

Conceptualization: Cecilia Kvaavik, Gudmundur J. Óskarsson.

Data curation: Cecilia Kvaavik.

Formal analysis: Cecilia Kvaavik.

Funding acquisition: Cecilia Kvaavik.

Methodology: Cecilia Kvaavik, Gudmundur J. Óskarsson.

Supervision: Gudmundur J. Óskarsson, Anna Kristín Daniélsdóttir, Guðrún Marteinsdóttir.

Visualization: Cecilia Kvaavik.

Writing – original draft: Cecilia Kvaavik.

Writing – review & editing: Cecilia Kvaavik, Gudmundur J. Óskarsson, Anna Kristín Daniélsdóttir, Guðrún Marteinsdóttir.

References

1. Simenstad C, Cailliet GM. Contemporary studies on fish feeding. Springer Science & Business Media; 2013.
2. Strøm JF, Rikardsen AH, Campana SE, Righton D, Carr J, Aarestrup K, et al. Ocean predation and mortality of adult Atlantic salmon. Scientific reports. Nature Publishing Group; 2019; 9(1):7890. <https://doi.org/10.1038/s41598-019-44041-5> PMID: 31133666
3. Navarro J, Coll M, Preminger M, Palomera I. Feeding ecology and trophic position of a Mediterranean endemic ray: consistency between sexes, maturity stages and seasons. Environmental Biology of Fishes. Springer; 2013;1–14.
4. Chipps SR, Garvey JE. Assessment of food habits and feeding patterns. Analysis and interpretation of freshwater fisheries data American Fisheries Society, Bethesda. 2007;473–514.
5. Astthorsson OS, Valdimarsson H, Gudmundsdottir A, Óskarsson GJ. Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. ICES Journal of Marine Science: Journal du Conseil. Oxford University Press; 2012;fss084.
6. Valdimarsson H, Astthorsson OS, Pálsson J. Hydrographic variability in Icelandic waters during recent decades and related changes in distribution of some fish species. ICES Journal of Marine Science: Journal du Conseil. Oxford University Press; 2012; 69(5):816–25.
7. Astthorsson OS, Gíslason A, Jonsson S. Climate variability and the Icelandic marine ecosystem. Deep Sea Research Part II: Topical Studies in Oceanography. Elsevier; 2007; 54(23):2456–77.
8. Olafsdottir AH, Slotte A, Jacobsen JA, Óskarsson GJ, Utne KR, Nøttestad L. Changes in weight-at-length and size-at-age of mature Northeast Atlantic mackerel (*Scomber scombrus*) from 1984 to 2013: effects of mackerel stock size and herring (*Clupea harengus*) stock size. ICES Journal of Marine Science: Journal du Conseil. Oxford University Press; 2015;fsv142.

9. ICES. Interim Report of the Working Group on Integrated Ecosystem Assessments for the Norwegian Sea (WGINOR). ICES WGINOR REPORT 2018. 26–30 November 2018. Reykjavik, Iceland.: ICES CM 2018/IEASG: 10; 2019;
10. Nøttestad L, Utne KR, Óskarsson GJ, Jónsson SP, Jacobsen JA, Tangen Ø, et al. Quantifying changes in abundance, biomass, and spatial distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic seas from 2007 to 2014. *ICES Journal of Marine Science*. Oxford University Press; 2015; 73(2):359–73.
11. ICES. Cruise report from the International Ecosystem Summer Survey in the Nordic Seas (IESSNS) 30th of June–6th of August 2018. Working Document to ICES Working Group on Widely Distributed Stocks (WGWIDE). Havstovan, Tórshavn, Faroe Islands, 28 August–3 September 2018. 2018;39.
12. Olafsdóttir AH, Utne KR, Jacobsen JA, Jansen T, Óskarsson GJ, Nøttestad L, et al. 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 II: Topical Studies in Oceanography*. Elsevier; 2019; 159:152–68.
13. Utne KR, Huse G, Ottersen G, Holst JC, Zabavnikov V, Jacobsen JA, et al. Horizontal distribution and overlap of planktivorous fish stocks in the Norwegian Sea during summers 1995–2006. *Marine Biology Research*. Taylor & Francis; 2012; 8(5–6):420–41.
14. Nøttestad L, Diaz J, Penã H, Søyland H, Huse G, Fernö A. Feeding strategy of mackerel in the Norwegian Sea relative to currents, temperature, and prey. *ICES Journal of Marine Science*. Oxford University Press; 2015; 73(4):1127–37.
15. Nikolioudakis N, Skaug H, Olafsdóttir A, Jansen T, Jacobsen J, Enberg K. Drivers of the summer-distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic Seas from 2011 to 2017; a Bayesian hierarchical modelling approach. *ICES Journal of Marine Science*. 2018; <https://doi.org/10.1093/icesjms/fsx225>
16. Bachiller E, Skaret G, Nøttestad L, Slotte A. Feeding Ecology of Northeast Atlantic Mackerel, Norwegian Spring-Spawning Herring and Blue Whiting in the Norwegian Sea. *PloS one*. Public Library of Science; 2016; 11(2):e0149238. <https://doi.org/10.1371/journal.pone.0149238> PMID: 26895485
17. Jansen T. Pseudocollapse and rebuilding of North Sea mackerel (*Scomber scombrus*). *ICES Journal of Marine Science: Journal du Conseil*. Oxford University Press; 2014; 71(2):299–307.
18. Pepin P, Koslow J, Pearre S Jr. Laboratory study of foraging by Atlantic mackerel, *Scomber scombrus*, on natural zooplankton assemblages. *Canadian Journal of Fisheries and Aquatic Sciences*. NRC Research Press; 1988; 45(5):879–87.
19. Macy WK, Sutherland SJ, Durbin EG. Effects of zooplankton size and concentration and light intensity on the feeding behavior of. *Marine Ecology Progress Series*. 1998; 172:89–100.
20. Óskarsson GJ, Gudmundsdóttir A, Sveinbjörnsson S, Sigurdsson T. Feeding ecology of mackerel and dietary overlap with herring in Icelandic waters. *Marine Biology Research*. Taylor & Francis; 2016; 12(1):16–29.
21. ICES. Working Group on Widely Distributed Stocks (WGWIDE). ICES Scientific Reports [Internet]. 2019;36:948 pp. Available from: <http://doi.org/10.17895/ices.pub.5574>
22. Mehl S, Westgård T. The diet and consumption of mackerel in the North Sea (a preliminary report). 1983;
23. Dahl K, Kirkegaard E. Stomach contents of mackerel, horse mackerel and whiting in the eastern part of the North Sea in July 1985. *Danmarks Fiskeri-og Havundersøgelser*; 1986.
24. Pepin P, Pearre S Jr, Koslow J. Predation on Larval Fish by Atlantic Mackerel *Scomber scombrus*, with a Comparison of Predation by Zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences*. NRC Research Press; 1987; 44(11):2012–8.
25. Langøy H, Nøttestad L, Skaret G, Broms C, Fernö A. Feeding ecology of Atlantic mackerel (*Scomber scombrus*) in the Norwegian Sea. 2006.
26. Debes H, Homrum E, Jacobsen JA, Hátún H, Danielsen J. The feeding ecology of pelagic fish in the southwestern Norwegian Sea-Inter species food competition between Herring (*Clupea harengus*) and mackerel (*Scomber scombrus*). *ICES CM*. 2012; 1000:07.
27. Skaret G, Bachiller E, Langøy H, Stenvik EK. Mackerel predation on herring larvae during summer feeding in the Norwegian Sea. *Ices Journal of Marine Science*. 2015;
28. Engelhard GH, Peck MA, Rindorf A, Smout SC, van Deurs M, Raab K, et al. Forage fish, their fisheries, and their predators: who drives whom? *Ices Journal of Marine Science*. 2014;
29. Vikingsson GA, Pike DG, Valdimarsson H, Schleimer A, Gunnlaugsson T, Silva T, et al. Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? *Frontiers in Ecology and Evolution*. *Frontiers*; 2015; 3:6.

30. Vigfusdottir F, Gunnarsson TG, Gill JA. Annual and between-colony variation in productivity of Arctic Terns in West Iceland. *Bird study*. Taylor & Francis; 2013; 60(3):289–97.
31. Bailey K, Houde E. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in marine biology*. Elsevier; 1989. p. 1–83.
32. Jonsson S, Valdimarsson H. Recent developments in oceanographic research in Icelandic waters. Caseldine C, Russell A, Hardardottir J, Knudsen O., editor. *Iceland—Modern Processes and Past Environments*. Elsevier, Amsterdam; 2005;pp. 79–92.
33. Valdimarsson H, Malmberg S-A. Near-surface circulation in Icelandic waters derived from satellite tracked drifters. *Rit Fiskideild*. 1999; 16:23–40.
34. Jónsson S. Sources of fresh water in the Iceland Sea and the mechanisms governing its interannual variability. *ICES mar Sci Symp*. 1992; 195:62–7.
35. Hanna E, Jónsson T, Ólafsson J, Valdimarsson H. Icelandic Coastal Sea Surface Temperature Records Constructed: Putting the Pulse on Air Sea Climate Interactions in the Northern North Atlantic. Part I: Comparison with HadISST1 Open-Ocean Surface Temperatures and Preliminary Analysis of Long-Term Patterns and Anomalies of SSTs around Iceland. *Journal of Climate*. 2006; 19:5652–66.
36. Godø OR, Hjellvik V, Iversen SA, Slotte A, Tenningen E, Torkelsen T. Behaviour of mackerel schools during summer feeding migration in the Norwegian Sea, as observed from fishing vessel sonars. *ICES Journal of Marine Science: Journal du Conseil*. Oxford University Press; 2004; 61(7):1093–9.
37. Stefánson U. North Icelandic waters. *Atvinnudeild Háskólans, Fiskideild*; 1962.
38. Astthorsson OS, Gislason A. Long-term changes in zooplankton biomass in Icelandic waters in spring. *ICES Journal of Marine Science: Journal du Conseil*. Oxford University Press; 1995; 52(3–4):657–68.
39. Nilsen JE, Falck E. Variations of mixed layer properties in the Norwegian Sea for the period 1948–1999. *Progress in Oceanography*. Elsevier; 2006; 70(1):58–90.
40. Hyslop EJ. Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology*. Wiley Online Library; 1980; 17(4):411–29.
41. Brown SC, Bizzarro JJ, Cailliet GM, Ebert DA. Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). *Environmental Biology of Fishes*. Springer; 2012; 95(1):3–20.
42. Amundsen PA, Gabler HM, Staldvik FJ. A new approach to graphical analysis of feeding strategy from stomach contents data—Modification of the Costello (1990) method. *Journal of Fish Biology*. 1996; 48(4):607–14.
43. Anderson MJ. A new method for non-parametric multivariate analysis of variance. *Austral Ecol*. Wiley Online Library; 2001; 26(1):32–46.
44. Hammer Ø, Harper D, Ryan P. PAST—Palaeontological statistics. www.uv.es/~pardomv/pe/2001/_1/past/pastprog/past.pdf, accessed em. 2001;25(07):2009.
45. Santić M, Rađa B, Pallaoro A. Diet and feeding strategy of thornback ray *Raja clavata*. *J Fish Biol*. 2012; 81(3):1070–84. <https://doi.org/10.1111/j.1095-8649.2012.03382.x> PMID: 22880738
46. Clarke K, Warwick R. An approach to statistical analysis and interpretation. *Change in marine communities*. 1994; 2:117–43.
47. Sneath PH, Sokal RR, others. *Numerical taxonomy. The principles and practice of numerical classification*. 1973.
48. Hastie T, Tibshirani R. *Generalized Additive Models*. Chapman & Hall/CRC. Monographs on Statistics & Applied Probability Chapman and Hall/CRC. 1990;1.
49. Wood SN. *Generalized additive models: an introduction with R*. Chapman and Hall/CRC; 2017.
50. Jansen T, Post S, Olafsdottir AH, Reynisson P, Óskarsson GJ, Arendt KE. Diel vertical feeding behaviour of Atlantic mackerel (*Scomber scombrus*) in the Irminger current. *Fisheries Research*. Elsevier; 2019; 214:25–34.
51. Hall SJ, Gurney WS, Dobby H, Basford DJ, Heaney SD, Robertson MR. Inferring feeding patterns from stomach contents data. *Journal of Animal Ecology*. JSTOR; 1995;39–62.
52. Wood SN. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*. 2011; 73(1):3–6.
53. Barton K. MuMIn: Multi-Model Inference [Internet]. R package v. 1.42.1. 2018. Available from: <https://cran.r-project.org/web/packages/MuMIn/index.html>
54. Anderson D, Burnham K. *Model selection and multi-model inference*. Second NY: Springer-Verlag. 2004;

55. Gislason A. Seasonal and spatial variability in egg production and biomass of *Calanus finmarchicus* around Iceland. *Marine ecology Progress series*. Inter-Research; 2005; 286:177–92.
56. Gislason A, Astthorsson OS. The food of Norwegian spring-spawning herring in the western Norwegian Sea in relation to the annual cycle of zooplankton. *Sarsia: North Atlantic Marine Science*. 2002; 87(3):236–47.
57. Prokopchuk I, Sentyabov E. Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. *ICES Journal of Marine Science: Journal du Conseil*. Oxford University Press; 2006; 63(1):117–27.
58. Langøy H, Nøttestad L, Skaret G, Broms C, Fernö A. Overlap in distribution and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea during late summer. *Marine biology research*. Taylor & Francis; 2012; 8(5–6):442–60.
59. Darbyson E, Swain D, Chabot D, Castonguay M. Diel variation in feeding rate and prey composition of herring and mackerel in the southern Gulf of St Lawrence. *Journal of Fish Biology*. Wiley Online Library; 2003; 63(5):1235–57.
60. Plourde S, Grégoire F, Lehoux C, Galbraith PS, Castonguay M. Effect of environmental variability on the Atlantic Mackerel (*Scomber scombrus* L.) stock dynamics in the Gulf of St. Lawrence. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2014/092. 2014.
61. Astthorsson OS, Gislason A. Investigations on the ecology of the zooplankton community in Isafjord-deep, northwest Iceland. *Sarsia*. Taylor & Francis; 1992; 77(3–4):225–36.
62. Beare DJ, Gislason A, Astthorsson OS, E. M. Assessing long-term changes in early summer zooplankton communities around Iceland. *ICES Journal of Marine Science*. 2000; 57(6):1545–61.
63. Gislason A, Petursdóttir H, Astthorsson OS, Gudmundsson K, Valdimarsson H. Inter-annual variability in abundance and community structure of zooplankton south and north of Iceland in relation to environmental conditions in spring 1990–2007. *Journal of Plankton Research*. 2009; 31(5):541–51.
64. Gislason A, Astthorsson OS. Distribution patterns of zooplankton communities around Iceland in spring. *Sarsia: North Atlantic Marine Science*. Taylor & Francis; 2004; 89(6):467–77.
65. Silva T, Gislason A, Astthorsson OS, Marteinsdóttir G. Abundance and distribution of early life stages of krill around Iceland during spring. *Marine Biology Research*. Taylor & Francis; 2016; 12(8):864–73.
66. Gislason A, Silva T. Abundance, composition, and development of zooplankton in the Subarctic Iceland Sea in 2006, 2007, and 2008. *ICES Journal of Marine Science: Journal du Conseil*. 2012; 69:1263–76.
67. Jónsdóttir IG, Björnsson H, Skuladóttir U. Predation by Atlantic cod *Gadus morhua* on northern shrimp *Pandalus borealis* in inshore and offshore areas of Iceland. *Marine Ecology Progress Series*. 2012; 469:223–32.
68. Eiríksson H, Jónasson JP. The fishery and stock assessment of Norway lobster (*Nephrops norvegicus*) in Icelandic waters during 1950–2016. *Haf- og vatnarannsóknir HV2018-25*; 2018.
69. Gunnarsson B, Jónasson JP, Logemann Kai, Marteinsdóttir G, Óskarsson GJ. Recent occurrence and origin of juvenile Atlantic mackerel (*Scomber scombrus* L.) in Icelandic waters. *Haf- og vatnarannsóknir HV 2019–03*; 2019.
70. Sakamoto T. Studies on fishery biology of the ribbon fish, *Trichiurus lepturus*, Linne, in the Kii channel. *Wakayama pref Fish Sta.* 1982;111–5.
71. Brinton E. Vertical Migration and Avoidance Capability of Euphausiids in the California Current. *Limnology and Oceanography*. 1967; 12(3):451–83.
72. Gibson RN, Ezzi IA. The relative profitability of particulate- and filter-feeding in the herring, *Clupea harengus* L. *Journal of Fish Biology*. 1992; 40:577–90.
73. Bachiller E, Utne KR, Jansen T, Huse G. Bioenergetics modeling of the annual consumption of zooplankton by pelagic fish feeding in the Northeast Atlantic. *PLoS one*. Public Library of Science; 2018; 13(1):e0190345.
74. Lambert TC. Gastric emptying time and assimilation efficiency in Atlantic mackerel (*Scomber scombrus*). *Canadian journal of zoology*. NRC Research Press; 1985; 63(4):817–20.
75. Temming A, Bøhle B, Skagen D, Knudsen F. Gastric evacuation in mackerel: the effects of meal size, prey type and temperature. *Journal of Fish Biology*. Wiley Online Library; 2002; 61(1):50–70.
76. Weidner T, Hirons A, Leavitt A, Kerstetter D. Combined gut-content and stable isotope trophic analysis of the pelagic stingray *Pteroplatytrygon violacea* (Bonaparte, 1832) diet from the western North Atlantic Ocean. *Journal of Applied Ichthyology*. Wiley Online Library; 2017; <https://doi.org/10.1111/jai.13371>
77. McClain-Counts JP, Demopoulos AW, Ross SW. Trophic structure of mesopelagic fishes in the Gulf of Mexico revealed by gut content and stable isotope analyses. *Marine Ecology*. Wiley Online Library; 2017; 38(4):e12449.

78. Young T, Pincin J, Neubauer P, Ortega-García S, Jensen OP. Investigating diet patterns of highly mobile marine predators using stomach contents, stable isotope, and fatty acid analyses. *ICES Journal of Marine Science*. Oxford University Press; 2018; 75(5):1583–90.
79. Madgett AS, Yates K, Webster L, McKenzie C, Moffat CF. Understanding marine food web dynamics using fatty acid signatures and stable isotope ratios: Improving contaminant impacts assessments across trophic levels. *Estuarine, Coastal and Shelf Science*. Elsevier; 2019; 227:106327.
80. Harms-Tuohy CA, Schizas NV, Appeldoorn RS. Use of DNA metabarcoding for stomach content analysis in the invasive lionfish *Pterois volitans* in Puerto Rico. *Marine Ecology Progress Series*. 2016; 558:181–91.
81. Broms C, Melle W, Horne JK. Navigation mechanisms of herring during feeding migration: the role of ecological gradients on an oceanic scale. *Marine Biology Research*. Taylor & Francis; 2012; 8(5–6):461–74.
82. Frederiksen M, Anker-Nilssen T, Beaugrand G, Wanless S. Climate, copepods and seabirds in the boreal Northeast Atlantic—current state and future outlook. *Glob Chang Biol*. 2013; 19(2):364–72. <https://doi.org/10.1111/gcb.12072> PMID: 23504776
83. Guillemette M, Grégoire F, Bouillet D, Rail J-F, Bolduc F, Caron A, et al. Breeding failure of seabirds in relation to fish depletion: Is there one universal threshold of food abundance? *Marine Ecology Progress Series*. 2018; 587:235–45.
84. Stige LC, Kvile KØ, Bogstad B, Langangen Ø. Predator-prey interactions cause apparent competition between marine zooplankton groups. *Ecology*. Wiley Online Library; 2018; 99(3):632–41. <https://doi.org/10.1002/ecy.2126> PMID: 29281755
85. Berge J, Heggland K, Lønne OJ, Cottier F, Hop H, Gabrielsen GW, et al. First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway, with possible explanations for the extension of its distribution. *Arctic*. 2015; 68:54–61.
86. Nøttestad L, Sivle LD, Krafft BA, Langård L, Anthonypillai V, Bernasconi M, et al. Prey selection of offshore killer whales *Orcinus orca* in the Northeast Atlantic in late summer: spatial associations with mackerel. *Marine Ecology Progress Series*. 2014; <https://doi.org/10.3354/meps10820>
87. Nilssen KT, Lindstrøm U, Westgaard JI, Lindblom L, Blencke T-R, Haug T. Diet and prey consumption of grey seals (*Halichoerus grypus*) in Norway. *Marine Biology Research*. Taylor & Francis; 2019; 15(2):137–49.