Comparison Between Trophic Positions in the Barents Sea Estimated From Stable Isotope Data and a Mass Balance Model

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The trophic position concept is central in system ecology, and in this study, trophic position (TP) estimates from stable-isotopes and an Ecopath mass-balance food web model for the Barents Sea were compared. Two alternative models for estimating TP from stable isotopes, with fixed or scaled trophic fractionation were applied. The mass-balance model was parametrized and balanced for year 2000, was comprised of 108 functional groups (Gs), and was based on biomass and diet data largely based on predator stomach data. Literature search for the Barents Sea Large Marine Ecosystem revealed 93 sources with stable isotope data (δ^{15}N values) for 83 FGs, and 25 of the publications had trophic position estimated from nitrogen stable isotopes. Trophic positions estimated from the mass-balance model ranged to 5.1 TP and were highly correlated with group mean δ^{15}N values, and also highly correlated with the original literature estimates of trophic positions from stable isotopes. On average, TP from the mass-balance model was 0.1 TP higher than the original literature TP estimates (TP$_{SIR}$) from stable isotopes. A trophic enrichment factor (TEF) was estimated assuming fixed fractionation and minimizing differences between trophic positions from Ecopath and TP predicted from δ^{15}N values assuming a baseline value for δ^{15}N calculated for pelagic particulate organic matter at a baseline TP of 1.0. The estimated TEF of 3.0‰ was lower than the most commonly used TEF of 3.4 and 3.8‰ in the literature. The pelagic whales and pelagic invertebrates functional groups tended to have higher trophic positions from Ecopath than from stable isotopes while benthic invertebrate functional groups tended to show an opposite pattern. Trophic positions calculated using the scaled trophic fractionation approach resulted in lower TP than from Ecopath for intermediate TPs and also a larger TP range in the BS. It is concluded that TPs estimated from δ^{15}N values using a linear model compared better to the Ecopath model than the TPs from scaled fractionation approach.

Keywords: ecosystem structure, trophic enrichment factor, Arctic ecosystem, ecosystem comparison, polar bear, food web

INTRODUCTION

Following the introduction of integer trophic levels by Lindeman (1942) and fractional trophic levels by Odum and Heald (1975), the use of trophic levels has developed and it has become a conceptual pillar in ecosystem analysis. Fractional trophic levels have also been termed trophic positions (TP) in the literature (Odum and Heald, 1975; Vander Zanden and Rasmussen, 2001; Hussey et al., 2014a). TP is included in the theoretical basis and calculation of many ecosystem metrics and indicators such as trophic efficiency, transfer efficiency and omnivory index (Shannon et al., 2014). Furthermore, TP is an important predictor of trophic enrichment of pollutants in food webs (Hop et al., 2002; Jæger et al., 2009). TP estimates have been used in analysis of ecosystem structure, effects of harvesting, trophic control mechanisms, and how trophic cascades propagate within an ecosystem (Pauly et al., 1998; Frank et al., 2007). Trophic position estimates may be useful for evaluation of fisheries exploitation and management strategies, and it is important to evaluate methods used to estimate trophic positions and factors affecting uncertainty in these estimates.

Trophic position has been estimated from methods based on body size (Basedow et al., 2010), stomach content (Odum and Heald, 1975), stable isotopes (Hobson and Welch, 1992; Hobson et al., 2002), combination of stable-isotope and body size (Jennings et al., 2008), binary diet matrices (Blanchet et al., 2019) and mass-balance food web models (Polovina, 1985; Christensen, 1995). There are relatively few studies comparing results from different methods, but a common approach to evaluate the parametrization of mass-balance models has been to compare the TPs from the mass-balance models with independent TP estimates from stable isotopes (Kline et al., 1998; Nilsen et al., 2008; Navarro et al., 2011; Du et al., 2020). McCormack et al. (2019) reviewed comparisons of TP estimates from stable isotope (SI) and mass-balance models and suggested that comparison of food web model attributes with measures of stable isotopes composition of taxa, has a potential for improving ecosystem model parameterization.

The use of stable isotopes for estimating TP is based on the assumption of an enrichment (increase) in the heavier ^{15}N isotope relative to the lighter ^{14}N isotope between consumer and food source (Post, 2002). The ratio of stable isotopes of nitrogen (δ^{15}N) may be enriched by about 2 to 4‰ per trophic level and this increase has been termed trophic fractionation, diet–tissue discrimination factor or trophic enrichment factor (TEF) (Post, 2002; Hussey et al., 2014a; Linnebjerg et al., 2016).

Two alternative methods for estimating TP from SIR, fixed fractionation and scaled fractionation, have been applied (Post, 2002; Hussey et al., 2014a). In the fixed fractionation approach, TP can be estimated from stable isotope values (δ^{15}N) from a δ^{15}N baseline value (δ^{15}N$_{base}$) of a group at baseline TP (TP$_{base}$) (**Table 1**). The baseline organism is typically a primary producer, a copepod, or an invertebrate suspension feeder, and a constant trophic enrichment factor (TEF) describes the increase in δ^{15}N per

trophic level (Post, 2002) (Eq. 1). This is termed the linear model in this study.

$$\text{TP}_{lin} = \text{TP}_{base} + (\delta^{15}\text{N} - \delta^{15}\text{N}_{base})/\text{TEF} \qquad (1)$$

The choice of baseline organism and baseline trophic position vary between studies (Casey and Post, 2011). In the Barents Sea, several baseline groups and organisms have been selected; pelagic particulate organic matter (pPOM) at TP = 1 and copepods and bivalves at TP = 2 (Hop et al., 2002; Hallanger et al., 2011a; Fuhrmann et al., 2017). Consistent strong spatial gradients in δ^{15}N values of lower trophic level organisms and δ^{15}N baseline values have been observed within the West-Greenland and in the North Sea ecosystems (Jennings et al., 2008; Hansen et al., 2012; MacKenzie et al., 2014). Such spatial gradients in δ^{15}N baseline values (isoscapes) have been used when inferring trophodynamics from stable isotopes (Jennings et al., 2008; MacKenzie et al., 2014), but isoscapes have so far not been established for the Barents Sea. The Barents Sea Large Marine Ecosystem comprise both open water habitat and numerous fjords and these habitats differ with regard to environmental conditions which may influence stable isotope patterns of organisms (**Figure 1**; Fuhrmann et al., 2017; McGovern et al., 2020).

In Arctic marine ecosystems, a TEF in the range 3.4–3.8‰ has been commonly applied to most ecological groups (Hobson et al., 2002; Søreide et al., 2006), but a lower TEF (e.g., 2.4‰) has been applied to some areas and to birds in some studies (Hobson and Clark, 1992; Hop et al., 2002; Hoondert et al., 2021). Experimental studies indicate that TEF may depend on taxonomic class (Caut et al., 2009) and on diet quality, and thus vary between trophic groups such as herbivores, carnivores, and detritivores (McCutchan et al, 2003; Vanderklift and Ponsard, 2003; Martínez del Rio et al., 2009; McMahon et al., 2015). For the BS, it is uncertain if a common TEF for all FGs would be applicable given that there are many taxonomic and functional groups.

The fixed fractionation model (Eq. 1) has been questioned and an alternative scaled fractionation suggested (Hussey et al., 2014a). In the scaled fractionation approach (Hussey et al., 2014a), alternative TP values are calculated assuming that TEF decreases with increasing diet δ^{15}N values resulting in lower δ^{15}N value increments per TP at high δ^{15}N values. Application of the scaled model results in a larger range of TP than assuming a constant TEF (Hussey et al., 2014a). The scaled model has been applied to a cephalopod species in the Barents Sea (Golikov et al., 2019), but it is uncertain how it will perform for other FGs.

Mass-balance models, such as Ecopath, estimate trophic positions of functional groups based on input data on biomass, production per biomass, consumption per biomass, assimilation efficiency, diet, and fisheries catches (Christensen et al., 2005). Ecopath models usually represent an annual average of mass flows in an ecosystem (Christensen et al., 2005). When comparing TPs from mass-balance models and SI, there is a need to match season, space, and ontogeny for the data input for two methods (McCormack et al., 2019). Ontogenetic changes in δ^{15}N

TABLE 1 | Overview of definition of acronyms in alphabetical order.

Acronym	Definition
BS	Barents Sea
DC	Weight proportion (carbon) of prey in diet
$\delta^{15}N_{base}$ value	Baseline $\delta^{15}N$ value for group at TP_{base}
$\delta^{15}N_{lim}$ value	The highest $\delta^{15}N$ value with positive trophic enrichment factor used in the scaled model, see Hussey et al. (2014a)
$\delta^{15}N_{TP}$ value	Observed $\delta^{15}N$ value for an organism for which a trophic position (TP_{sca}) will be calculated using a scaled model (Eq. 4)
FG	Functional group (see list of FGs in **Table 2**)
iPOM	Ice algal particulate organic matter
pPOM	Pelagic particulate organic matter
POM	Particulate organic matter
RMSD	Root mean squared deviation (Eq. 3) is a measure of deviation between observed and model predicted values
r	Pearson correlation coefficient
r_s	Spearman correlation coefficient
sPOM	Surface sediment particulate organic matter
TEF	Trophic enrichment factor (‰) per trophic position
TP_{base}	Baseline TP for lower TP group
TP	Trophic position
TP_{ec}	Trophic positions for various functional groups estimated from the Ecopath mass balance model for the Barents Sea (Pedersen et al., 2021) (Eq. 2)
TP_{lin}	Trophic position calculated from a linear model with fixed fractionation (constant trophic enrichment factor) according to Eq. (1).
TP_{sca}	Trophic position calculated from a scaled trophic fractionation model assuming a decrease in trophic enrichment factor with increasing trophic position according to Eq. (4).
TP_{SIR}	Trophic positions calculated from fixed fractionation models and published in the literature sources

values of organisms may coincide with seasonal food-pulses and $\delta^{15}N$ values have been found to change with stage or body size in a number of taxa (Jennings et al., 2008; Ramsvatn and Pedersen, 2012; Jennings and Van Der Molen, 2015). When structuring mass-balance models (e.g., Ecopath models) it is common to use size and age structured multi-stanza groups to represent ontogenetic changes in diet composition, TP, growth and mortality rates (Ahrens et al., 2012).

Several mass-balance models with varying functional group resolution has been parametrized for the Barents Sea and Norwegian Sea (Blanchard et al., 2002; Dommasnes et al., 2002; Skaret and Pitcher, 2016; Bentley et al., 2017; Berdnikov et al., 2019; Pedersen et al., 2021), but so far no TP-comparisons between model and stable-isotope data have been performed for the area. For other ecosystems, comparisons between TP estimated from SI and mass-balance models generally show positive correlations between TPs estimated by the two methods (Kline et al., 1998; Milessi et al., 2010; Navarro et al., 2011; McCormack et al., 2019; Hoover et al., 2021). For Ullsfjord, a fjord area at 70°N within the Barents Sea Large Marine Ecosystem (LME), TPs from a mass-balance model and SI have been compared and correlated well (Nilsen et al., 2008). Previous estimates of trophic positions of organisms in the Barents Sea from stable isotopes have been based on various baseline organisms and values for $\delta^{15}N$ baseline and trophic enrichment factors. In this study, TPs from a recently developed mass-balance model (Ecopath) for the Barents Sea with high trophic resolution (Pedersen et al., 2021), will be compared with published data on stable isotopes and TP.
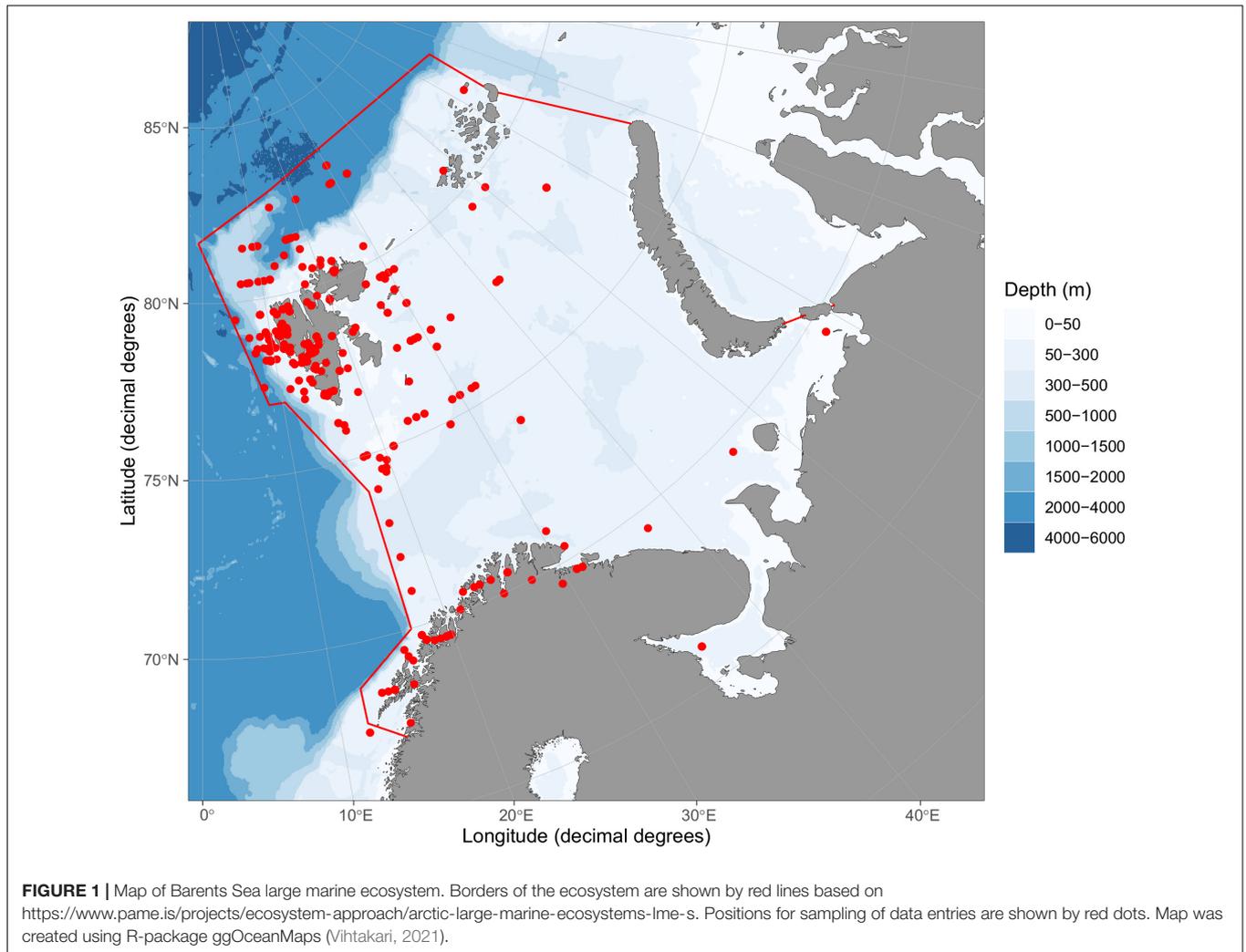
The specific aims of this study were to investigate:

(i) If $\delta^{15}N$ values for functional groups differ between open water and fjords and change with latitude within the Barents Sea.
(ii) If TPs from the Ecopath model and published TPs from SI correspond.
(iii) If TPs estimated from stable isotope using a fixed fractionation model or a scaled fractionation model show better correspondence to TPs from Ecopath.
(iv) The range of trophic positions in the Barents Sea ecosystem.

MATERIALS AND METHODS

Study Area

The study area included the Barents Sea Large Marine Ecosystem (BS) and only data sampled from within this area were included (**Figure 1**). The Barents Sea Large Marine Ecosystem is a shelf-ecosystem (area 2,010,000 km) with an average depth of 230 m and is characterized by inflow of warm nutrient-rich Atlantic water from the southwest (Loeng, 1991; Loeng and Drinkwater, 2007; Skjoldal and Mundy, 2013). In the north and northeast BS, cold Arctic water dominates and BS is partially ice-covered with a seasonal change in ice coverage. Phytoplankton is the dominant primary producer but ice algae are also important in ice-covered waters (Sakshaug et al., 1994). Primary production is highest in the warmer Atlantic ice-free part of the BS. Copepods and krill are major grazers on phytoplankton, and there is a rich and diverse fauna of benthic invertebrates (Jørgensen et al., 2017).

FIGURE 1 | Map of Barents Sea large marine ecosystem. Borders of the ecosystem are shown by red lines based on https://www.pame.is/projects/ecosystem-approach/arctic-large-marine-ecosystems-lme-s. Positions for sampling of data entries are shown by red dots. Map was created using R-package ggOceanMaps (Vihtakari, 2021).

Both pelagic and demersal fishes, sea birds, seals, and whales are abundant, and polar bears is present in the northern part of the BS (Sakshaug et al., 1994). There are several distinct carbon flow pathways from lower to higher trophic FGs; the copepod pathway, the krill pathway, the microbial food web pathway, and the benthic invertebrate pathway (Pedersen et al., 2021). The large stocks of planktivorous fishes, e.g., capelin, polar cod, and small herring are major prey sources for whales, seals, birds, and large demersal and benthic fish FGs (Bogstad et al., 2015; Pedersen et al., 2021).

A few studies have reported average SI values, from locations both within and outside BS, and these values were included if there were no statistical significant differences between values within and outside BS. Data from fjord areas within the BS were included.

Mass-Balance Model for the Barents Sea

A trophically highly resolved mass-balance model for the Barents Sea for year 2000 has been developed (Pedersen et al., 2021) and was used to provide model based estimates of TPs. The model comprises 108 functional groups (FGs) (**Table 2**). Nineteen FGs

were multi-stanza FGs, i.e., groups were divided into adult/large and juvenile/small groups with separate input values, diet compositions, and TPs (**Table 2**). When parametrizing Ecopath mass-balance models, the major input to the mass-balance model are biomass (g C m^{-2}), production/biomass (year^{-1}) and consumption/biomass ratios (year^{-1}), ecotrophic efficiency, proportion of unassimilated food, catches, and diet compositions (Christensen et al., 2005). Ecotrophic efficiency is the proportion of the production of a group that is consumed within the model. Data on biomass were taken from stock assessments for exploited fish and mammal FGs and from literature for other FGs (Pedersen et al., 2021). The Ecopath model is balanced to assure that the production of each FG is sufficient to match the demands from predation, fishery, and other losses. During the balancing process, the initial values of the diet matrix may be modified.

Ecopath calculates trophic position (TP$_{ec}$) of the FGs and the TPec,$_j$ of each predator group **j** using the equation:

$$TPec,j = 1 + \sum_{i=1}^{n} DC_{ij} TPec,i \qquad (2)$$

TABLE 2 | Overview of functional groups for which output values from Ecopath were aggregated into major categories.

Aggregated category	Ecopath groups within the category
Polar bears	**(1) Polar bears**
Whales	**(2) Minke whale, (3) Fin whale, (4) Blue whale,** (5) Bowhead, (6) Humpback whale, (7) White whale, (8) Narwhale, (9) Dolphins, **(10) Harbor porpoise, (11) Killer whales,** (12) Sperm whale
Seals	**(13) Harp seal, (14) Harbor seal,** (15) Grey seal, **(16) Ringed seal, (17) Bearded seal, (18) Walrus**
Birds	**(19) Northern fulmar, (20) Black legged kittiwake, (21) Other gulls and surface feeders, (22) Little auk, (23) Brunnich guillemot,** (24) Common guillemot and razorbill, (25) Atlantic puffin, **(26) Benthic feeding piscivorous birds, (27) Benthic invertebrate feeding birds**
Benthic and demersal fishes	**(28) Greenland shark, (29) Northeast Arctic cod (3+), (30) Northeast Arctic cod (0–2), (31) Coastal cod (2+), (32) Coastal cod (0–1), (33) Saithe (3+), (34) Saithe (0–2), (35) Haddock (3+), (36) Haddock (0–2), (37) Other small gadoids, (38) Large Greenland halibut, (39) Small Greenland halibut, (40) Other piscivorous fish, (41) Wolffishes, (42) Stichaeidae, (43) Other small benthivorous fishes, (44) Other large benthic invertebrate feeding fish, (45) Thorny skate, (46) Long rough dab, (47) Other benthivore flatfish, (59) Large redfish, (60) Small redfish**
Pelagic fishes	**(48) Large herring, (49) Small herring, (50) Capelin (3+), (51) Capelin (0–2), (52) Polar cod (2+), (53) Polar cod (0–1), (54) Blue whiting,** (55) Sand eel, **(56) Other pelagic planktivorous fish, (57) Lumpfish,** (58) Mackerel, **(61) Atlantic salmon**
Pelagic invertebrates	**(62) Cephalopods, (63) Scyphomedusae, (64) Chaetognaths, (65) *Thysanoessa*, (66) Large krill, (67) Ctenophora, (68) Pelagic amphipods, (69) Symphagic amphipods, (70) Pteropods, (71) Medium sized copepods, (72) Large calanoids,** (73) Small copepods, **(74) Other large zooplankton,** (75) Appendicularians, (76) Ciliates, (77) Heterotrophic dinoflagellates, (78) Heterotrophic nanoflagellates
Benthic predatory invertebrates	**(79) Northern shrimp (*Pandalus borealis*), (80) Crangonid and other shrimps, (81) Other large crustaceans, (82) Crinoids, (83) Predatory asteroids, (84) Predatory gastropods, (85) Predatory polychaetes, (86) Other predatory benthic invertebrates, (101) Snow crab,** (102) Large red king crab, **(103) Medium red king crab,** (104) Small red king crab
Benthic detritivorous invertebrates	**(87) Detritivorous polychaetes, (88) Small benthic crustaceans, (89) Small benthic molluscs, (90) Large bivalves, (91) Detritivorous echinoderms, (92) Large epibenthic suspension feeders, (93) Other benthic invertebrates, (94) Meiofauna, (96)** Benthic foraminifera
Primary producers	**(97) Diatoms*, (98) Autotroph flagellates*, (99) Ice algae**, (100) Macroalgae**

*Included in pPOM. **Included in iPOM. Functional group numbers are shown in brackets. Groups with $\delta^{15}N$ values are shown in bold.

Where DC_{ij} is the proportion of prey, *i* in the diet of predator *j*, and $TPec_{,i}$ is the trophic position of FG *i*. In Ecopath it is assumed that all the detritus groups have trophic position 1 (Christensen et al., 2005).

Stable Isotope Data, Sources and Overview

Literature was searched for sources containing $\delta^{15}N$ values for organisms and/or trophic position (TP_{SIR}) estimated from $\delta^{15}N$ values for the Barents Sea LME area (**Figure 1**), resulting in a total of 93 sources with data (**Supplementary Table 1**). The SI-data included values from living groups and on $\delta^{15}N$ values from organic matter in surface sediment samples. TP and $\delta^{15}N$ values were registered for the lowest taxonomic level reported in the publication and were allocated to FGs that matched the Ecopath functional groups (**Table 2**).

For each data entry with SI values, the variables registered included: the year or time period and month of sampling, geographical sampling area, location, whether data were sampled in a fjord (binary habitat variable; fjord = 1, open water = 0). Position or geographic range of sampling (latitude and longitude of sampling were registered). The sampling location was registered by entering either the exact latitude and longitude when reported, or the midpoint of the geographical area of sampling represented by the lowest and highest integer latitude and longitude including the sampling area. The species

name or higher taxonomic level, or if the sample comprised particulate organic matter (POM) of three categories; pPOM (pelagic particulate organic matter), sPOM (POM from surface sediment), iPOM (ice algal particulate organic matter) was registered. If data on size or stage were available, it was recorded. The entries were allocated to FGs based on the feeding category (i.e., herbivore, detritivorous or predatory), and the number of replicates the $\delta^{15}N$ value were based on and the $\delta^{15}N$ value were noted (**Supplementary Table 2**).

To obtain model independent values for TEF that could help to explain deviations from model predicted TPs, literature was searched to obtain estimated values on TEF from experiments and field studies with known diet source for organisms in FGs that are distributed within the BS. It was required that at least the genus of the species is distributed within the BS.

Data Analysis, Trophic Position-Stable Isotope Relationships and Statistical Analysis

Data that were only available in plots were digitized using a digitizer (WebPlotDigitizer[1]). Data entries represented by average values for $\delta^{15}N$ and TP_{SIR} were calculated for given taxa when there were several values for the same taxa, sampling position, and time. Separate data entries were recorded for

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[1]https://automeris.io/WebPlotDigitizer/

different sampling positions or sampling times. Values for separate size or stage groups within a taxa, and for various sampling times (seasons), locations, and sampling years were kept in their original format. Data entries were allocated to functional groups (FGs) matching the Ecopath groups based on information from literature (i.e., Kędra et al., 2010; Planque et al., 2014; Sokołowski et al., 2014; Jumars et al., 2015; Renaud et al., 2015; Pedersen et al., 2021). Ontogenetic effects are partly included in the Ecopath model by the specification of groups for small and large individuals (multi-stanza FGs) for a number of species; Northeast arctic cod, coastal cod, saithe, haddock, Greenland halibut, redfish, capelin, polar cod and red king crab (**Table 2**). Data entries were allocated to the multi-stanza FGs based on information about age and body size given in the source. $\delta^{15}N$ or TP_{SIR} values reported for broad categories (e.g., "copepods") that were too broad to match the FGs (e.g., three copepod FGs in the Ecopath model, **Table 2**) were not included in the further analysis. All taxa names were checked to be in accordance with the accepted names in World Register of Marine Species[2] (accessed 20 June 2021) and presently unaccepted names in the original sources were corrected (**Supplementary Table 2**).

Further analysis of the isotope data were made in several major steps corresponding to the aims (I–IV) given in the introduction. Since the Ecopath mass-balance model give TPs for an average state of the BS ecosystem, the stable isotope data were treated to represent average conditions.

(I) The total data set was unbalanced with regard to geographic position and season of sampling (**Figure 1** and **Supplementary Table 3**). There were few samples from open water in the southern part of the Barents Sea and most samples were taken during the summer months (**Figure 1** and **Supplementary Table 3**). A large proportion (61%) of the total number of $\delta^{15}N$ values were from samples taken in fjord habitats. It was considered inappropriate to apply statistical methods that were dependent on balanced designs. For FGs with sufficient number ($n > 5$) of $\delta^{15}N$ values, $\delta^{15}N$ values were plotted versus latitude and month-values with different plotting symbols for open water and fjord habitats to assess if there were obvious spatial or seasonal trends. Whether $\delta^{15}N$ values were correlated with latitude was examined using the Spearman rank correlation coefficient (r_s) applying the cor.test in package stats in R. P-values for multiple tests were adjusted according to Benjamini and Hochberg (1995) using p.adjust in package stats in R. Values deviating more than 3 SD from the mean of the FG were identified as outliers.

The FG mean $\delta^{15}N$ values and the difference between the mean-values for fjord and open water habitat for each FG were calculated. Whether the frequency distributions of $\delta^{15}N$ values for each habitat (open water or fjord) deviated from normal distributions was examined using Shapiro-Wilks test (shapiro.test in package stats in R), and for distributions not deviating from normality, two-group t-tests with separate variances were applied to test if the mean were equal in fjords and open-water habitats. For groups where $\delta^{15}N$ values from at least one habitat deviated from normality, a two-sample non-parametric Mann–Whitney

test was applied to test if central tendency differed for δ15N values between habitats.

(II) Average $\delta^{15}N$ and TP values were calculated for each FG with values on $\delta^{15}N$ and/or trophic position value from stable isotopes given in literature sources (TP_{SIR}), For FGs with only one $\delta^{15}N$ and TP_{SIR} value, this value was used to represent the FG. A total of 83 and 65 FGs had $\delta^{15}N$ and TP_{SIR} values, respectively. In addition to the living functional groups, values of $\delta^{15}N$ measured from sediment sampled particulate organic matter (sPOM) were entered as representative for the FG "detritus from other sources" which is a functional group in Ecopath and a major food source for benthic detritivorous invertebrates and bacteria.

Values of TP_{ec} and TP_{SIR} were compared in bi-scatter plots and the Pearson correlation coefficient was estimated. TP_{ec} and TP_{SIR} values for each FG were compared and whether there was a significant difference between TP_{ec} and TP_{SIR} was examined using a Wilcoxon two-sample paired sample test (Zar, 1999). The significance level was set to 5% in all statistical tests.

The root mean squared deviation (RSMD) (Piñeiro et al., 2008), represent the mean deviation of model predicted TP values (yp_i) with respect to the observed ones here taken as TP_{ec} ($yo_i = TP_{ec}$).

$$RMSD = \sqrt{\frac{1}{n-1} \sum_{i=1}^{n} \left(ypi - yoi \right)^2} \qquad (3)$$

where n is the number of pairs of observed and predicted values. RMSD has unit trophic position and lower RMSD values indicate better fit of model predictions to observations than do higher RMSD values.

(III) Since there is a range of possible TEF values, a linear best-fit model was estimated to represent the average relationship between TP and $\delta^{15}N$ values. The model was fitted to two alternative sets of data; (i) from open water and fjord habitat, and (ii) from only open water data. This was chosen because open water represent the majority of the area in the BS and because most of the Ecopath background data is from open water. The model estimated TEF by minimizing the sum of squared differences between values for TP_{ec} and TP predicted from $\delta^{15}N$ values (TP_{lin}) using Eq. (1). The baseline TP was set to 1.0 and the $\delta^{15}N$ baseline value was set to the average $\delta^{15}N$ value for pPOM representing phytoplankton which is the dominating primary producer in BS (Sakshaug et al., 1994). The model was fitted to the data (TP_{ec} and the average $\delta^{15}N$ values for each FG) applying the nls function with least-squares estimation in package stats in R. The values for TP_{base} and $\delta^{15}N_{base}$ were kept fixed during the estimation.

Pelagic particulate organic matter-samples may contain heterotrophic organisms such as bacteria and protozoa in addition to phytoplankton (Stowasser et al., 2012), and the effects of choosing an alternative TP_{base} of 1.2 in the linear best-fit model for data from both open water and fjord habitats were tested.

A scaled model for calculating TP was based on the description by Hussey et al. (2014a,b) (Eq. 4). The scaled model requires that a primary consumer (base) is selected with its $\delta^{15}N$ value ($\delta^{15}N_{base}$

value) and its trophic position (TP_{base}). The TP (TP_{sca}) of an organism with known $\delta^{15}N$ value ($\delta^{15}N_{TP}$) can then be calculated

$$TP_{sca} = \left(\frac{log\,(\delta^{15}N_{lim} - \delta^{15}N_{base}) - log\,(\delta^{15}N_{lim} - \delta^{15}N_{TP})}{k} \right) + TP_{base} \quad (4)$$

where

$$k = -log(\frac{\beta 0 - \delta^{15}N_{lim}}{-\delta^{15}N_{lim}}) \quad (5)$$

and

$$\delta^{15}N_{lim} = -\frac{\beta 0}{\beta 1} \quad (6)$$

The approach adapted to Arctic ecosystems by Linnebjerg et al. (2016) and Golikov et al. (2019) was followed and $\delta^{15}N_{base}$ was set to the $\delta^{15}N$ value of 7.20‰ for *Calanus glacialis* in the Barents Sea and assuming TP_{base} to be 2.0. β0 and β1 are coefficients used to calculate $\delta^{15}N_{lim}$ which is the highest $\delta^{15}N$ value with positive TEF. The values of β0 (5.92) and β1 (−0.27) were estimated in a meta-analysis by Hussey et al. (2014a). In this study, TP_{sca} values were calculated for individual $\delta^{15}N$ values at the data entry level before average TP_{sca} values were calculated for each FG.

The residual TPs ($TP_{ec}-TP_{lin}$) from the linear best-fit model and the deviations ($TP_{ec}-TP_{sca}$) for the scaled model (Eqs 2 and 3) for the 83 FGs were calculated and inspected visually in plots. RMSD (Eq. 3) was calculated taking TP_{ec} as observed and TP_{lin} or TP_{sca} as predicted values. The 83 FGs were aggregated into 10 categories (**Table 2**) based on previous assignment of functional groups into aggregated categories in the Ecopath model (Pedersen et al., 2021) and TP residuals for FGs were plotted in box plots. Whether residuals differed significantly between FGs of these aggregated categories was examined using a Kruskal–Wallis test (Zar, 1999). Polar bears were not included in this test since the test needs more than one value in each category.

(IV) Maximum TP of FGs for the various methods were recorded to indicate range of TP for the BS ecosystem.

RESULTS

Overview
A total of 83 functional groups of organisms had a total of 1,832 $\delta^{15}N$ values. The number of $\delta^{15}N$ values per FG varied from 1 to 126 (**Table 2** and **Supplementary Table 4**). Many of the $\delta^{15}N$ values had not been used to calculate TP_{SIR} values in the original sources and 759 TP_{SIR} values from 65 functional groups were published in the original sources. In addition, the material included a total of 87 $\delta^{15}N$ values from samples of sediment organic matter (sPOM) (**Supplementary Table 3**).

Latitude and Habitat Effects
For $\delta^{15}N$ values from both habitats and including pPOM, iPOM and sPOM, $\delta^{15}N$ values and latitude were significantly correlated for few (12%) FGs (**Supplementary Table 5**), with negative correlations for large bivalves ($r_s = -0.32$,

$n = 113$; $p = 0.009$), large suspension feeders ($r_s = -0.66$, $n = 23$; $p = 0.009$) and polar cod (age 2+) ($r_s = -0.70$, $n = 15$; $p = 0.04$). For data from only open water, no FGs had significant correlations between $\delta^{15}N$ values and latitude (**Supplementary Table 5**).

A large majority, with 22 of 26 of the living FGs with sufficient number of $\delta^{15}N$ values to compare (n for both habitats > 5), had higher mean $\delta^{15}N$ values in open water than in fjord habitat (**Supplementary Table 5**). The proportion of the FGs with higher $\delta^{15}N$ values in open water than in fjords was 85% and the median $\delta^{15}N$ values of the FGs were higher for open water than for fjord habitat (Wilcoxon two-sample paired-samples test; $p = 0.001$). Tests for equality between $\delta^{15}N$ values in fjord or open water habitat within separate FGs in normally distributed groups (mean) or for groups deviating from normal distributions (central tendency) showed significantly lower $\delta^{15}N$ values in fjord habitat for sPOM (**Supplementary Table 5**). Average sPOM and pPOM $\delta^{15}N$ values were 1.1 and 1.5‰ lower in fjords than for open water, respectively (**Supplementary Table 5**). Both sPOM and pPOM had largest variability in some Svalbard fjords at 77–80°N (**Supplementary Figure 1**). Detrivorous echinoderms and small benthic mollusks also showed significant habitat differences with $\delta^{15}N$ values that were 1.3 to 2.0‰ lower in fjords than in open water (**Supplementary Table 5**).
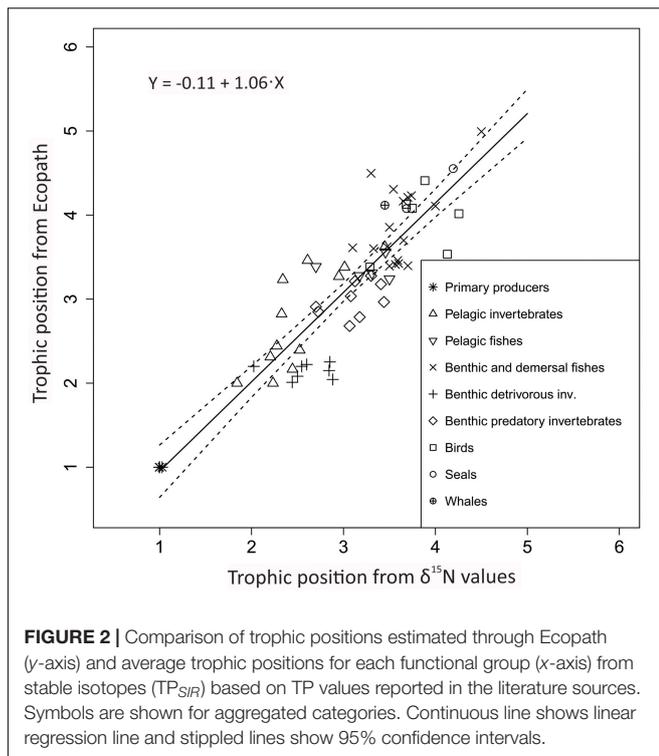
Benthic predatory invertebrate FGs, other small benthivorous fishes, and Stichaeidae had $\delta^{15}N$ values that were 0.3 to 2.0‰ lower in fjords than in open water, but the differences were not significant for single FGs (**Supplementary Table 5**). For pelagic invertebrates and fish groups, the $\delta^{15}N$ values did not differ significantly between the open water and fjord habitat (**Supplementary Table 5**).

$\delta^{15}N$ values from the methane seep areas in the western part of the BS were included in the material (Åström et al., 2019; **Supplementary Table 1**) and, among the taxa sampled, the chemosymbiotic polychaetes *Siboglinidae* had low deviating $\delta^{15}N$ values in the range of – 3.7 to 4.5‰ (Åström et al., 2019). Some deviating low $\delta^{15}N$ values for pPOM and some benthic invertebrates from a spring bloom situation were observed in the data set (Silberberger et al., 2018; **Supplementary Table 1**) from the Vesterålen area (68°N) (Silberberger et al., 2018; **Supplementary Figure 1**). The values above were included in the analysis.

Comparison of Trophic Position From Ecopath and From Isotopes
On average, TP_{ec} was slightly higher than the original TP_{SIR} reported in the literature sources with an average pairwise difference of 0.10 TL (**Supplementary Table 4**), but the difference was not significant (Wilcoxon two-sample paired test, $n = 65$; $p = 0.07$). TP_{ec} were strongly positively correlated with the original TP_{SIR} values in the papers ($r = 0.89$; $p < 0.0001$, $n = 65$) (**Figure 2**). RMSD was 0.4 TP (**Table 3**).

On the FG level and for data pooled from both habitats, TP_{ec} was strongly positively correlated with FG mean $\delta^{15}N$ values ($r = 0.90$, $n = 83$) (**Figure 3A** and **Supplementary Figure 2**). The average $\delta^{15}N$ values for the three primary producer FGs were

FIGURE 2 | Comparison of trophic positions estimated through Ecopath (*y*-axis) and average trophic positions for each functional group (*x*-axis) from stable isotopes (TP$_{SIR}$) based on TP values reported in the literature sources. Symbols are shown for aggregated categories. Continuous line shows linear regression line and stippled lines show 95% confidence intervals.

similar: phytoplankton (pPOM) (4.4‰, SD = 2.0, *n* = 78), ice algae (iPOM) (4.2‰, SD = 1.4, *n* = 24) and macroalgae (4.6‰, SD = 1.2, *n* = 63) (**Supplementary Table 4**). The average δ^{15}N value of sPOM (av. 5.0‰, SD = 1.7, *n* = 87) was also similar to the values for the primary producers.

The δ^{15}N value of 4.4‰ for pPOM was chosen as δ^{15}N baseline at TP of 1.0 for the linear best-fit model since phytoplankton is the major primary producer FG in the ecosystem (Sakshaug et al., 1994). The fit of the linear model for both open water and fjord data (TP$_{lin}$ = 1 + (δ^{15}N − 4.4)/TEF), resulted in a TEF of 3.0‰ (95% CI 2.9, 3.1). RMSD was 0.4 TP (**Table 3**). The TEF from the linear best-fit model was within the range of 2.7 to 3.8‰ published for the BS ecosystem (**Supplementary Table 6**) (**Figure 4**). The linear best-fit model was intermediate compared to published linear TP-SI models for BS that were based on various values for TP$_{base}$ (1, 2, or 3), δ^{15}N$_{base}$ values, and TEF values (**Figure 4**).

For the linear model for both open water and fjord data, the median of the residuals for TP of FGs (Polar bears was not included) differed significantly between aggregated categories (Kruskal–Wallis, χ^2 = 21.8, df = 8; *p* = 0.005) (**Figure 5**). Whales and the pelagic invertebrate FGs had predominantly positive residuals (TP$_{lin}$ < TP$_{ec}$) while the benthic detritivorous- and predatory invertebrate FGs had predominantly negative residuals (TP$_{lin}$ > TP$_{ec}$) (**Figure 5**). Seals, birds, benthic, demersal, and pelagic fish FGs had residuals centered approximately around zero (**Figure 5**).
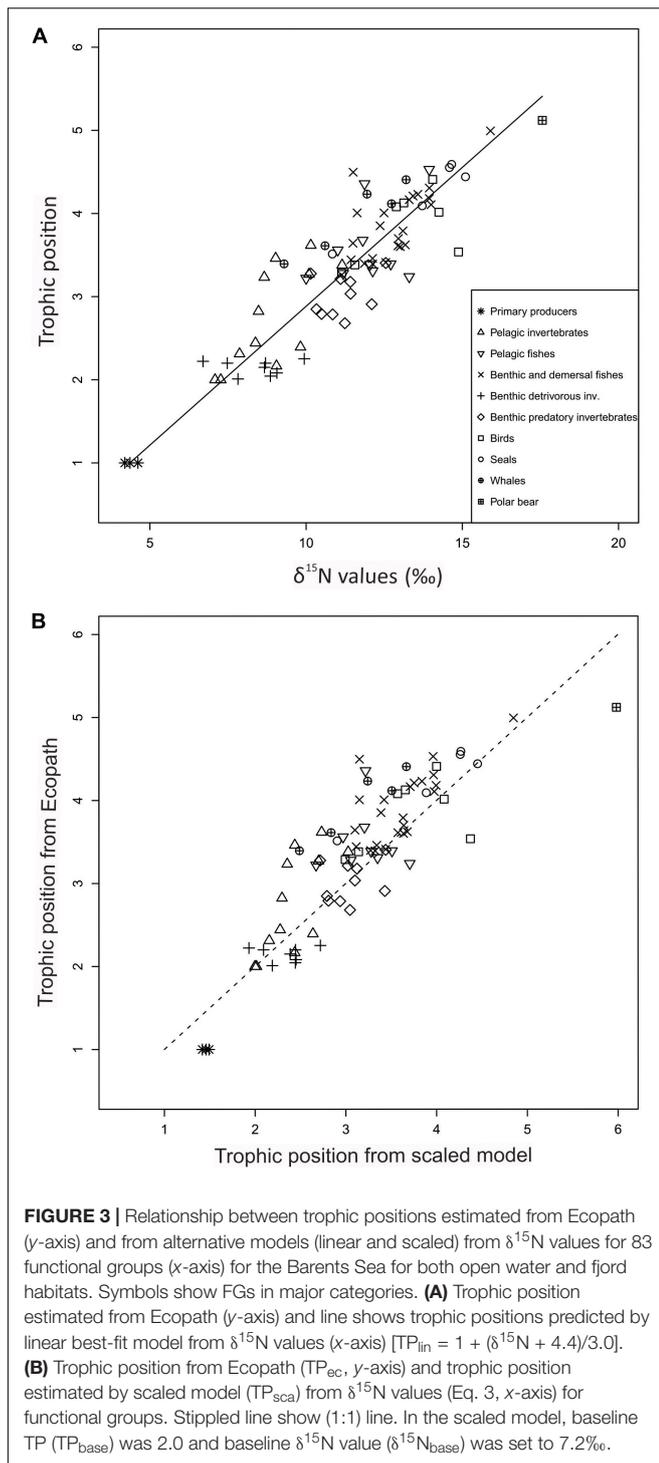
At the FG-level, the five FGs with the highest positive residuals were: small Greenland halibut (1.1 TP), Ctenophora (0.9 TP), Atlantic salmon (0.9 TP), pelagic amphipods (0.8 TP), and blue whales (0.7 TP). The groups with the five most negative residuals were: other gulls and surface feeders (−1.0 TP), capelin (3+) (−0.8 TP), predatory asteroids (−0.7 TP), predatory gastropods (−0.6 TP), and detrivorous echinoderms (−0.6 TP).

The alternative linear model for all habitats with pPOM as N$_{base}$ assuming a TP$_{base}$ of 1.2 resulted in a TEF of 3.2‰ (95% CI 3.1, 3.4) and a RMSD of 0.4 TP (**Table 3**). To test if inclusion

TABLE 3 | Overview of major results from comparison of trophic positions from Ecopath and calculation of trophic positions using fixed fractionation (linear model) and scaled fractionation.

Model	Data	TP$_{base}$, δ^{15}N$_{base}$	Measure and/or variables	Value (*n*)
Linear	Both habitats, published TP$_{SIR}$	Various	*r* for TP$_{ec}$ vs. TP$_{SIR}$	0.89 (65)
			RMSD	0.4 TP
	Both habitats	1.0, 4.4‰	*r* for TP$_{ec}$ vs. δ^{15}N values	0.90 (83)
			TEF	3.0‰
			RMSD	0.4 TP
			Maximum TP$_{lin}$	5.4
		1.2, 4.4‰	*r* for TP$_{ec}$ vs. δ^{15}N values	0.90 (83)
			TEF	3.2‰
			RMSD	0.4 TP
			Maximum TP$_{lin}$	5.3
	Only open water	1.0, 4.9‰	*r* for TP$_{ec}$ vs. δ^{15}N values	0.82 (68)
			TEF	2.9‰
			RMSD	0.5 TP
			Maximum TP$_{lin}$	5.4*
Scaled	Both habitats	2.0	RMSD	0.6 TP
			Maximum TP$_{sca}$	6.0
	Only open water	2.0	RMSD	0.6 TP
			Maximum TP$_{sca}$	6.0*

All polar bears were assumed to belong to open water habitat.TP, trophic position; r, Pearson correlation coefficient; n, number of functional groups.

FIGURE 3 | Relationship between trophic positions estimated from Ecopath (y-axis) and from alternative models (linear and scaled) from $\delta^{15}N$ values for 83 functional groups (x-axis) for the Barents Sea for both open water and fjord habitats. Symbols show FGs in major categories. **(A)** Trophic position estimated from Ecopath (y-axis) and line shows trophic positions predicted by linear best-fit model from $\delta^{15}N$ values (x-axis) [$TP_{lin} = 1 + (\delta^{15}N + 4.4)/3.0$]. **(B)** Trophic position from Ecopath (TP_{ec}, y-axis) and trophic position estimated by scaled model (TP_{sca}) from $\delta^{15}N$ values (Eq. 3, x-axis) for functional groups. Stippled line show (1:1) line. In the scaled model, baseline TP (TP_{base}) was 2.0 and baseline $\delta^{15}N$ value ($\delta^{15}N_{base}$) was set to 7.2‰.

of the SI data from fjords had a major influence on the results, an analysis with only open water data were undertaken. The data from open water comprised 708 $\delta^{15}N$ values from 68 living functional groups and in addition, there was 52 $\delta^{15}N$ values from sediment samples. The average $\delta^{15}N$ value for pPOM of 4.9‰ (SD = 1.7), based on 39 values for open water, was higher than the value for the total material (4.4‰). At the FG level, $\delta^{15}N$

values were strongly correlated to TP from Ecopath ($r = 0.82$, $n = 68$). The value for pPOM was used as baseline ($N_{base} = 4.9‰$) and the fit of the linear model for the open water material ($TP_{lin} = 1 + (\delta^{15}N - 4.9)/TEF$) resulted in a TEF of 2.9‰ (95% CI 2.7, 3.0) which was very similar to the TEF estimated for the total material from both habitats. The fit of the linear model to the average FG values and the test for differences in residuals between categories (Kruskal–Wallis, $\chi^2 = 24.8$, df = 8; $p = 0.002$) and the residual patterns for open water data was also very similar to the fit for the data from both habitats (**Supplementary Figure 3**). RMSD was 0.5 TP (**Table 3**). This imply that the major patterns in between FG variability of TP were similar for the two data sets (both habitats vs. open water only).

Trophic Positions From Scaled Model and Range of Trophic Position

Trophic positions for FGs calculated by the scaled model with a reference TP of 2.0 for the total material from both habitats showed a curved relationship between TP_{sca} and $\delta^{15}N$ values (**Figure 6**). TP_{sca} were lower than the TP_{ec} for most FGs with the largest differences for TP_{sca} between ca. 2.5 to 4.5 (**Figure 3B**). RMSD was 0.6 TP (**Table 3**). The results when applying the scaled model on open water $\delta^{15}N$ values were very similar to the results from the scaled model for all habitats (**Supplementary Figure 4**) and RMSD was 0.6 TP (**Table 3**).

Trophic positions from Ecopath ranged from 1.0 for primary producers to 5.1 for polar bears. The maximum TP_{lin} estimated by the linear best-fit model for the total material was 5.4 for polar bears. The TP_{sca} for polar bears from the scaled model TP was 6.0 (SD = 1.6, $n = 43$) which is 0.9 higher than the TP_{ec} for polar bears (**Figure 3B** and **Table 3**). Among the original published TP_{SIR} values, Greenland shark had the maximum FG average with a TP of 4.5 but there was no TP estimate for polar bears.

Trophic Enrichment Factors From Published Experiments and Field Studies With Known Diet

Median TEF was 3.5‰ ($n = 7$) and 2.7‰ ($n = 12$) for detritivorous invertebrates and for vertebrates, respectively (**Supplementary Table 7**). The TEF values of detritivorous invertebrate FGs were significantly higher than for vertebrates (whales, seals, polar bear and fish FGs) (**Figure 7**) (Mann–Whitney, $U = 13$; $p = 0.02$). Polar bears had a relatively low TEF of 2.0‰.

DISCUSSION

Variability in Trophic Positions and $\delta^{15}N$ Values Related to Latitude and Habitat

The limited range in $\delta^{15}N$ values for both sPOM and pPOM in BS open water habitat along the latitudinal gradient, suggest that there were small changes with latitude for $\delta^{15}N$ values at the base of the food web. In a meta-analysis based on $\delta^{15}N$ values for a number of species from the Svalbard area, Hoondert et al. (2021) found no latitudinal effect. Phytoplankton is the main primary
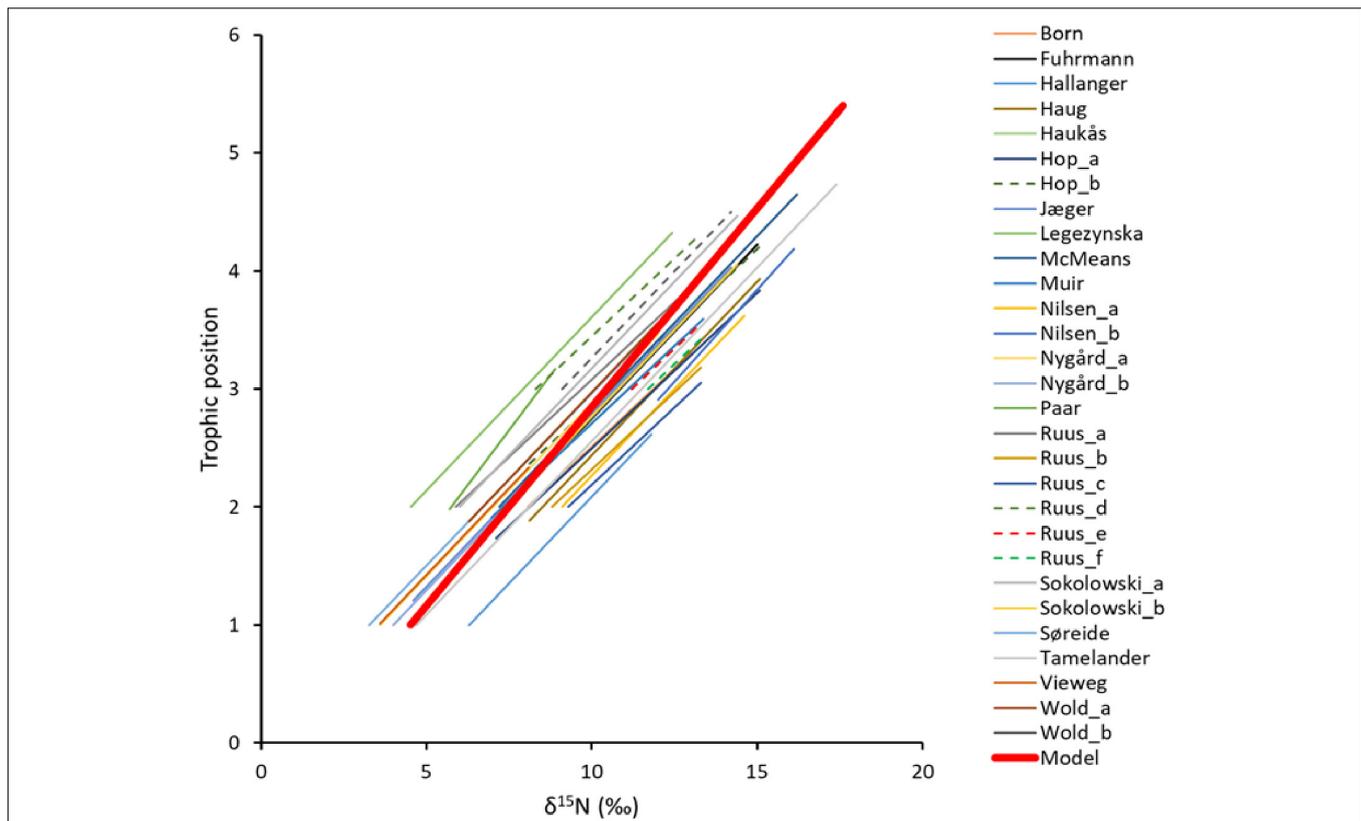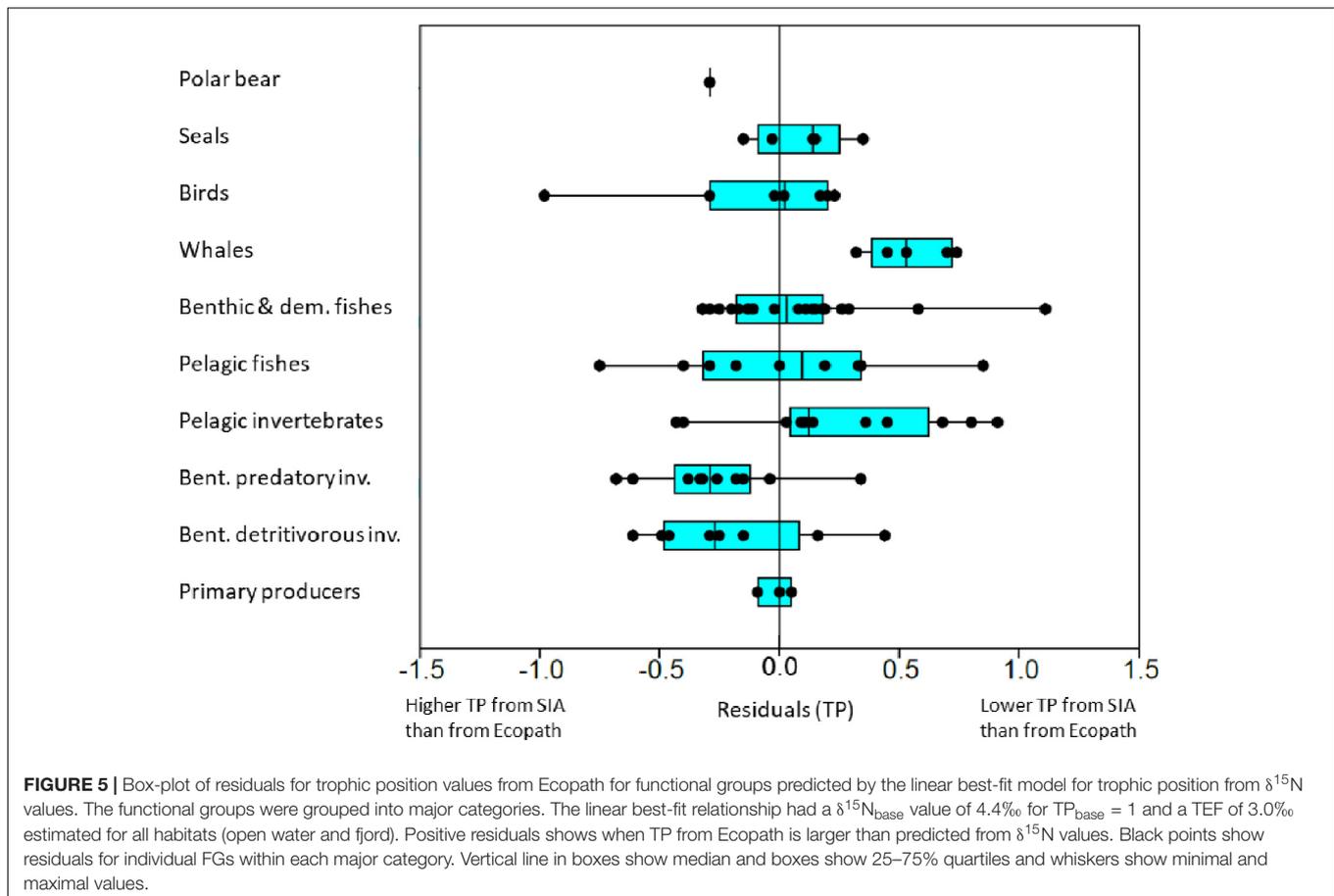
FIGURE 4 | Comparison of 29 published linear relationships between trophic positions (TP) and $\delta^{15}N$ values from literature from the Barents Sea Large Marine Ecosystem. Red bold line show the linear best-fit model for the TP- $\delta^{15}N$ value relationship estimated in this study for all habitats. The linear best-fit relationship had a $\delta^{15}N_{base}$ value of 4.4‰ for $TP_{base} = 1$ and a TEF of 3.0‰. Values for the published SI-TP relationships are given in **Supplementary Table 6**. Sources for short-names in the figure legend; Born (Born et al., 2003), Fuhrmann (Fuhrmann et al., 2017), Hallanger (Hallanger et al., 2011b), Haug (Haug et al., 2017), Haukås (Haukås et al., 2007), Hop a and b (Hop et al., 2002), Jæger (Jæger et al., 2009), Legeżyńska (Legeżyńska et al., 2012), McMeans (McMeans et al., 2013), Muir (Muir et al., 2003), Nilsen a and b (Nilsen et al., 2008), Nygård a and b (Nygård et al., 2012), Paar (Paar et al., 2019), Ruus a–f (Ruus et al., 2015), Sokołowski a and b (Sokołowski et al., 2014), Tamelander (Tamelander et al., 2006), Vieweg (Vieweg et al., 2012), Wold a and b (Wold et al., 2011).

producer in the BS (Sakshaug et al., 1994), and nitrate is the major source of nitrogen for phytoplankton during the spring/summer bloom in the BS (Tamelander et al., 2009). In support of limited range in baseline $\delta^{15}N$ value at both low and high latitudes within the BS, seawater nitrate $\delta^{15}N$ had stable values of c. 5.1‰ for both Atlantic and Arctic water in the BS (Tuerena et al., 2020). Tuerena et al. (2020) found no clear trend in $\delta^{15}N$ values for nitrate or for particulate nitrogen with increasing latitude in the BS. This apparent stability in BS in lower TP $\delta^{15}N$ values is in contrast to persistent latitudinal gradients in $\delta^{15}N$ values in the North Sea and at West-Greenland (Jennings et al., 2008; Hansen et al., 2012; MacKenzie et al., 2014).

That only a few FGs showed a change in $\delta^{15}N$ values with latitude in the BS may be a result of a relatively stable baseline $\delta^{15}N$ value. The decrease in $\delta^{15}N$ values with increasing latitude observed in some FGs [large bivalves, large epibenthic suspension feeders, and polar cod (2+)] reflect effects on $\delta^{15}N$ values that hypothetically may be caused by changes in temperature or diet composition and quality with latitude. The decreasing trend in $\delta^{15}N$ values with latitude in the BS for the three FGs is opposite to the increase in $\delta^{15}N$ values with increasing latitude found in open

water at West-Greenland for *Calanus finmarchicus* and the krill species *Thysanoessa raschii* (Hansen et al., 2012). The latitudinal trend at West-Greenland was explained as a result of high $\delta^{15}N$ values in high Arctic blooms due to partial depletion of the nitrate pool and higher renewal by deep nitrate resulting in lower $\delta^{15}N$ values further south (Hansen et al., 2012). Carroll et al. (2014) observed that $\delta^{15}N$ values of the large bivalve *Ciliatocardium ciliatum* was lower in Artic than in Atlantic waters in the BS and this is consistent with the trend in the total material in this study. The authors suggested that this difference may be due to higher rates of primary production, recycling in the pelagic and heterotrophy in Atlantic than in Arctic waters (Carroll et al., 2014). When large bivalves are used as baseline organisms for estimation of TP from $\delta^{15}N$, spatial trends in their $\delta^{15}N$ values will affect TP estimates for higher TPs.

For polar cod, the decrease in $\delta^{15}N$ values with latitude may be caused by a change in diet composition with increasing latitude. Polar cod inhabiting drift ice in the northernmost area of the BS feed, to a large degree, on symphagic fauna (Lønne and Gulliksen, 1989) while the diet of polar cod in open water may be more varied including copepods, pelagic amphipods, krill and
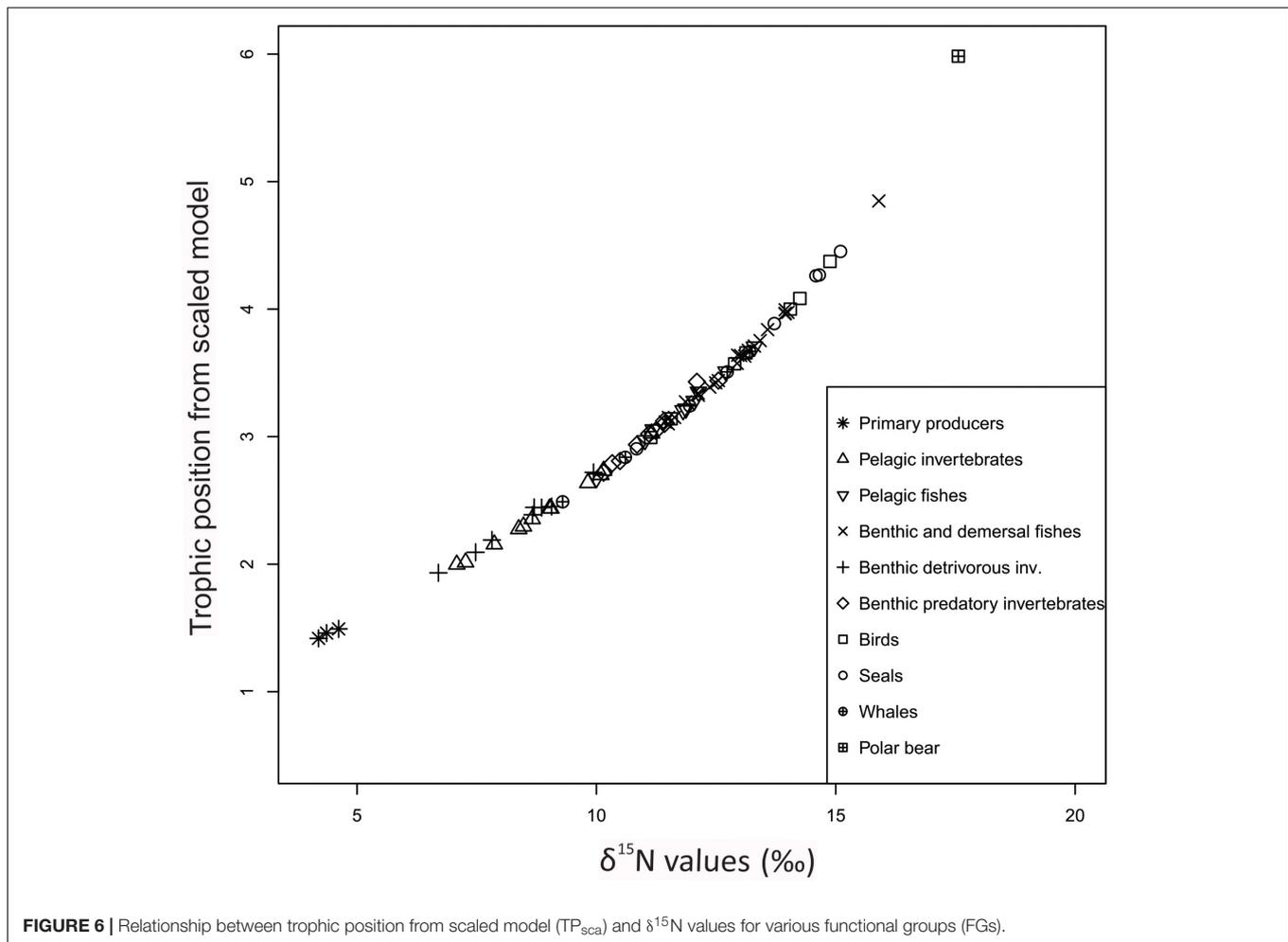
FIGURE 5 | Box-plot of residuals for trophic position values from Ecopath for functional groups predicted by the linear best-fit model for trophic position from $\delta^{15}N$ values. The functional groups were grouped into major categories. The linear best-fit relationship had a $\delta^{15}N_{base}$ value of 4.4‰ for $TP_{base} = 1$ and a TEF of 3.0‰ estimated for all habitats (open water and fjord). Positive residuals shows when TP from Ecopath is larger than predicted from $\delta^{15}N$ values. Black points show residuals for individual FGs within each major category. Vertical line in boxes show median and boxes show 25–75% quartiles and whiskers show minimal and maximal values.

fish (Aune et al., 2021). Symphagic fauna in the drift ice may have lower TP than diet sources in open water which may cause the observed trend. In support of this, the symphagic amphipod *Apherusa glacialis* which is a dominating prey source for polar cod in ice covered habitats had very low mean $\delta^{15}N$ values in the study (5.4‰) compared to iPOM (4.8‰) (Kohlbach et al., 2016), and consumption of these amphipods may have contributed to the low $\delta^{15}N$ values of polar cod at high latitudes.

The difference between open water and some fjords at Svalbard which had lower $\delta^{15}N$ values for sPOM than in open water have also earlier been observed by Knies et al. (2007). There is freshwater supply of particulate terrestrial organic nitrogen with low $\delta^{15}N$ values in some high Arctic fjords at Svalbard (Koziorowska et al., 2016; McGovern et al., 2020). Low $\delta^{15}N$ values in particles in freshwater runoff to inner fjord areas at Svalbard may contribute to low $\delta^{15}N$ values for lower TP benthic invertebrate FGs in fjord areas at Svalbard (McGovern et al., 2020). The very low $\delta^{15}N$ values both in sediments (sPOM), pelagic POM (pPOM) and benthic invertebrates from some fjord areas at Svalbard, suggest a bottom-up effect propagating from phytoplankton and detritus to benthic invertebrate detritivores and benthic invertebrate predators. The lack of a clear fjord-effect for major zooplankton FGs (e.g., medium sized copepods and *Thysanoessa*) may be caused by advection of these FGs into fjord areas from open water areas. The effect of the lower $\delta^{15}N$ value for

pPOM used as baseline value (4.4‰ for both habitats compared to 4.9‰ for open water habitat) for the linear model results was low since the estimates of TEF (2.9 vs. 3.0‰) for the two data sets were similar (**Table 3**). This suggest that the overall effect of the terrestrial input of light nitrogen to the fjords on the results for FGs at higher trophic positions is low.

In this study, the fjord areas, especially in the Svalbard area, generally had a high density of samples and data entries per unit area compared to the large open water area (**Figure 1**). Despite the variability in pPOM, the isotopic baselines for the total material comprising both open water and fjord (4.4‰) and the open water habitat (4.9‰) were similar (**Table 3**). Thus, the fjord-open water habitat effect did not largely affect the linear best-fit estimates of TEF, RMSD and maximum TP. This suggests that this habitat-difference does not markedly affect the results from the comparison of TPs from SI and Ecopath.

That open water had higher $\delta^{15}N$ values than some fjords for sPOM and benthic invertebrates in the Barents Sea is in contrast to the pattern observed along the coast of Greenland, where higher $\delta^{15}N$ values were observed in pelagic groups in fjords than offshore (Hansen et al., 2012). The inshore-open water gradient in lower trophic level $\delta^{15}N$ values in the Barents Sea are also in contrast to the large gradient in the North Sea with high $\delta^{15}N$ values in the southern shallow part with large freshwater input than the lower $\delta^{15}N$ values in the deeper northern North

FIGURE 6 | Relationship between trophic position from scaled model (TP$_{sca}$) and δ^{15}N values for various functional groups (FGs).

Sea (Jennings et al., 2008; MacKenzie et al., 2014). The habitat gradient in δ^{15}N values from the Barents Sea resembles the pattern in the Beaufort Sea with low δ^{15}N values in terrestrial organic material from river input (Bell et al., 2016).
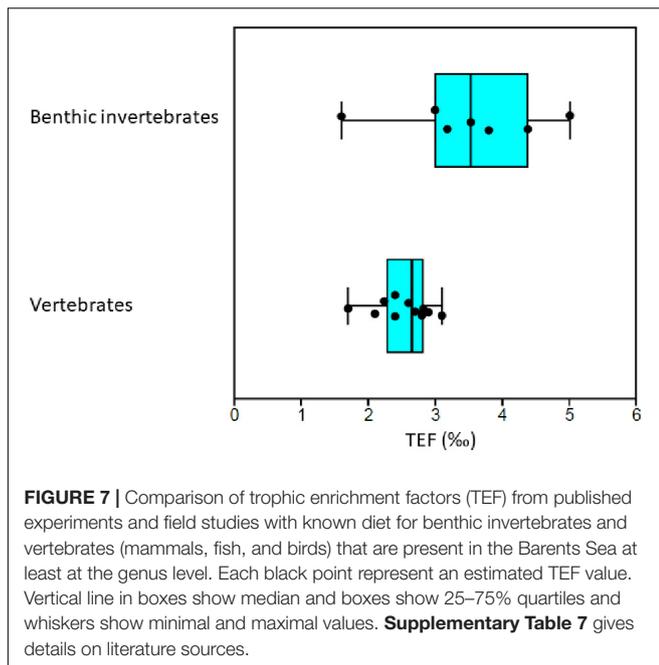
The deviating low δ^{15}N values for some FGs from areas with methane seeps in the western part of the BS have been well described by Åström et al. (2019). The few deviating low δ^{15}N values for pPOM and some benthic invertebrates from the southern part of the BS LME (Silberberger et al., 2018), probably indicate local effects that did not markedly affect the overall results because of the low number of entries identified as outliers (Silberberger et al., 2018).

Comparison of Trophic Positions Estimated From Ecopath and Linear Trophic Position-SI Relationship

The TP$_{ec}$ values from Ecopath and the original TP$_{SIR}$ from stable isotopes were similar for most FGs in the BS ecosystem. TP$_{SIR}$ was calculated using linear TP-SI relationships were based on a various baseline organisms, baseline δ^{15}N value and TEF values, and were calculated for different purposes. The strong correlation

between TP$_{ec}$ and TP$_{lin}$ estimated using the linear best-fit model, also indicates a good correspondence between the two methods.

The deviations from the linear best –fit linear TP- SI relationship estimated in this study may be caused by factors affecting both the TPs from Ecopath and from δ^{15}N values. That most pelagic invertebrate FGs had higher TP$_{ec}$ than TP$_{lin}$ (positive residuals), may indicate that these FGs had low TEF values. Microzooplankton FGs are included in the Ecopath model with the FGs heterotrophic nanoflagellates, ciliates, and heterotrophic dinoflagellates, but no SI values were available for these FGs. Experiments indicate that protists may be isotopically "invisible" using bulk stable isotopes due to their very low bulk δ^{15}N value enrichment (Gutiérrez-Rodríguez et al., 2014; Landry and Décima, 2017; Park et al., 2021). The microzooplankton FGs are active and have a large production in the BS, and ciliates and dinoflagellates are important prey groups for a number of pelagic invertebrate FGs (Rat'kova and Wassmann, 2002; De Laender et al., 2010; Pedersen et al., 2021). In the Ecopath model used in this study for the BS, microzooplankton amounted to 7–32% of the diet of the copepods FGs, krill (*Thysanoessa*) and pelagic amphipods (Pedersen et al., 2021). Thus, a low TEF of the microzooplankton FGs may contribute to low δ^{15}N values

FIGURE 7 | Comparison of trophic enrichment factors (TEF) from published experiments and field studies with known diet for benthic invertebrates and vertebrates (mammals, fish, and birds) that are present in the Barents Sea at least at the genus level. Each black point represent an estimated TEF value. Vertical line in boxes show median and boxes show 25–75% quartiles and whiskers show minimal and maximal values. **Supplementary Table 7** gives details on literature sources.

for their predator FGs and hence low TP_{lin} values and positive residuals. There are few experimental data on TEF for pelagic invertebrates. That the predominantly herbivorous pelagic FGs (copepod groups and krill groups) had small residuals indicate higher TEF values than for the pelagic planktonic predators such as pelagic amphipods, cephalopods, Ctenophora, and Scyphozoa which had high residuals, and this may fit with the diet-quality hypothesis.

The positive residuals from the linear TP-SI relationship for whales may suggest that this group also had relatively low TEF compared to other groups, and the low values for TEF from literature sources for whales may give support to this explanation. The whale FGs with SI data in this study included baleen and toothed whales and long distance seasonal migrants (blue whales, fin whales, minke whales) and all-year resident whales in the Barents Sea (e.g., harbor porpoise and killer whales). Individual feeding specialization was found for killer whales and polar bears (Blévin et al., 2019; Jourdain et al., 2020). Some killer whales specialize in feeding on coastal seals and show high $\delta^{15}N$ values while the majority of the individuals feed on herring (Jourdain et al., 2020), and have relatively low $\delta^{15}N$ values and low standard deviation of $\delta^{15}N$ value (SD = 0.05) (**Supplementary Table 4**).

Benthic detritivorous and benthic predatory invertebrate FGs were the other aggregated categories deviating most from the linear average TP- SI model with higher TP_{lin} than TP_{ec}. It is possible that the diet composition of benthic detritivorous FGs in Ecopath generally contain too little heterotrophic FGs (e.g., bacteria and other microorganisms) and this may contribute to relative low TP_{ec} of these FGs compared to TP from stable isotopes. In Ecopath, all detritus are assigned to TP = 1.0 by convention, while the $\delta^{15}N$ values of detritus from organisms at higher TPs are likely to correspond to the TP of the organisms

producing detritus. This may contribute to a reduce TPs from Ecopath compared to TPs from SI.

The higher TP_{lin} than TP_{ec} of benthic invertebrate FGs could also indicate relatively high values for TEF for these FGs in the BS. This interpretation is supported by the relatively high TEF values from experiments with detritivorous invertebrates. Vanderklift and Ponsard (2003) found that mollusks and crustaceans had lower TEF and related this to the mode of nitrogen excretion. Crustaceans and mollusks excrete ammonia (i.e., are ammonotelic) and had lower TEF than taxonomic groups that were ureotelic or uricotelic. However, in this study, the two other important taxa dominating among benthic detritivorous FGs, polychaetes and echinoderms, also excrete ammonia to a large degree (Davoult et al., 1991; Thiel et al., 2017). Thus, it is more likely that the low TEF values of the benthic detritivorous FGs in this study are related to diet composition than to nitrogen excretion mode.

Fractionation is dependent on diet quality and Adams and Sterner (2000) found that TEF of a zooplankton species (*Daphnia magna*) increased with increasing carbon:nitrogen ratio in the food. In the marine fish *Fundulus heteroclitus*, TEF was largest for diets with low $\delta^{15}N$ values, i.e., a larger difference between consumer and diet $\delta^{15}N$ values (Elsdon et al., 2010). In this study, it seems most likely that the negative residuals for most benthic invertebrate FGs are due to high TEF values for detritivorous FGs feeding on low quality detritus (i.e., high C:N ratio) and that predatory benthic invertebrates get relatively high $\delta^{15}N$ values because their benthic detritivorous invertebrate prey have high $\delta^{15}N$ values.

Seasonal variation in $\delta^{15}N$ values are common in aquatic invertebrates (Woodland et al., 2012), and seasonal variability in baseline $\delta^{15}N$ value may potentially affect the usefulness of TP-SI models. The pelagic primary production in Arctic ecosystems is highly seasonal and food pulses propagate to higher trophic levels with time delay (Falk-Petersen et al., 2007). The spring phytoplankton bloom is based on nitrate as its main nutrient, but after the bloom phytoplankton production is, to a large degree, based on regenerated nutrients (Kristiansen et al., 1994; Tamelander et al., 2009). This may contribute to seasonal variations in $\delta^{15}N$ values and computed trophic position for species and FGs (Hoondert et al., 2021). Some FGs (e.g., copepod FGs) are omnivorous and change diet seasonally from phytoplankton in spring and summer to protozoa and detritus during summer (De Laender et al., 2010; Kohlbach et al., 2021). Generally, high $\delta^{15}N$ values of have been observed in several FGs during winter and spring when feeding at lower trophic levels are reduced (Olive et al., 2003; Hertz et al., 2015). Hertz et al. (2015) found an average increase in $\delta^{15}N$ values of fasting of 0.5‰, and in the BS, Carroll et al. (2014) found higher $\delta^{15}N$ values (ca. 0.5–1.0‰) in the large bivalve *Ciliatocardium ciliatum* during spring than in fall. That the majority of stable isotope samples in the material analyzed in this paper were sampled during spring, summer, and autumn suggest that they were representative of the most productive season.

Other factors, such as ontogeny and gender, may also influence $\delta^{15}N$ values. Ontogenetic effects are partly included in the Ecopath model by the specification of multi-stanza FGs for

a number of fish species with separate groups for small and large fishes. Hoondert et al. (2021) found a clear effect of sex with females having higher $\delta^{15}N$ values than males, but it is unlikely that a gender – biased sampling would have affected this study markedly.

The TEF of 3.0‰ estimated by the linear best-fit model with TP_{base} of 1.0 was lower than the most commonly used TEF of 3.4 and 3.8‰ in the literature, but seems reasonable compared to the TEF values from experiments and field studies with known diet for organisms that occur in BS. The value (3.0‰) is also close to the average TEF of 3.1‰ calculated for four Arctic pelagic food webs including data from Svalbard (Hoondert et al., 2021). The corresponding TEF for benthic food webs was higher (3.4‰) (Hoondert et al., 2021). The TP of the pPOM used as TP_{base} is uncertain because POM contain heterotrophic organisms, but assuming a TP_{base} of 1.2 resulted in a TEF of 3.2‰ which is in the middle of the range of 2.7 to 3.8‰ commonly applied for TEF in the BS. The RMSD values were identical for linear models with TP_{base} of 1.0 and 1.2 but were lower than the RMSD for the scaled model indicating a better correspondence with Ecopath TPs for TPs from the linear model than from the scaled model.

The average pairwise difference of 0.10 TP between TP_{SIR} from stable isotopes and TP_{ec} from the Ecopath model in this study is in the same range as differences for FGs in TP between published mass-balance models for the BS. The average pairwise differences between TPs for FGs estimated by the Ecopath model in this study for minke whales, harp seals, fish and pelagic invertebrate FGs and corresponding TPs from four other mass-balance models for the Barents Sea and the Barents Sea and Norwegian Sea area varied from +0.25 to −0.25 TP (Pedersen et al., 2021).

Trophic Positions From the Scaled Model and Range of Trophic Positions

That TPs from the scaled model differed systematically from TP from Ecopath for intermediate TP in the range of 2.5 to c. 4.5 ($TP_{sca} < TP_{ec}$) and above 5 TP ($TP_{sca} > TP_{ec}$), is caused by the assumed decrease in TEF with increasing TP underlying the scaled method. In Ecopath, TPs of specific FGs at intermediate TPs were affected by diet compositions of their food source FGs at lower TPs. Uncertainty in diet composition vary between FGs and this uncertainty may affect uncertainty of TPs for single groups. The maximum TP of 6.0 for the scaled model for the Barents Sea was higher than the maximum TP from the linear model for both habitats ($TP_{lin} = 5.4$) and TP from Ecopath ($TP_{ec} = 5.1$) and the linear best-fit model, showing that the maximum TP for the BS is sensitive to choice of method.

The values for maximum TP for the BS from the linear model ($TP_{lin} = 5.4$) and Ecopath ($TP_{ec} = 5.1$) are similar to maximum TP values for most other Arctic ecosystems using linear models (Linnebjerg et al., 2016; Hoondert et al., 2021). Hoondert et al. (2021) found a maximum TP of 4.9 for the Svalbard area within the BS using a linear model with TEF of 3.39 and 3.44‰ for the pelagic and benthic part of the food web, respectively. Maximum TP values of 4.8 to 5.3 were reported for three other Arctic ecosystems (Hoondert et al., 2021). Polar bears has the highest TP value among the FGs in ecosystems where polar bears was

present (Hoondert et al., 2021). Earlier published Ecopath models for the BS did not include polar bears as FG. In the Barents Sea, some polar bears also prey on terrestrial prey and birds which have lower $\delta^{15}N$ values than seals (Lippold et al., 2019). Blanchet et al. (2019) estimated TP for polar bears to 5.2 in the BS based on a binary diet matrix and this value is close to the value from the Ecopath model (TP = 5.1).

The difference of 0.6 TP between maximum TP from the scaled and the linear method for BS was much less than the corresponding differences for the West-Greenland ecosystem. Here the scaled model resulted in a much larger maximum TP_{sca} value of 8.6 compared to maximum TPs calculated by linear TP-SI models of 5.2 and 5.6 assuming TEFs of 3.4‰ 3.2‰, respectively (Linnebjerg et al., 2016). The fish-based scaling relationship from Hussey et al. (2014a,b) may not capture the TEF patterns for invertebrate and mammal FGs that are important in Arctic ecosystems. This suggests that, for the BS, a linear model may be sufficient to predict TP from $\delta^{15}N$ values for most purposes. Further improvement in TP-prediction for specific FGs or categories and ecosystem range in TP may be achieved by conducting experiments with organisms feeding on known diet to estimate both bulk TEF and compound specific (amino acid, fatty acid) SI-analysis.

Limitations of the Study

The data set used in this study was not balanced with regard to environmental factors such as season (month), latitude, bottom depth, and geographic regions within the BS. All these factors may influence $\delta^{15}N$ values and hence TP estimates. Furthermore, the sampled tissue and treatment (i.e., lipid extraction, acid treatment) of the samples varied, potentially affecting the $\delta^{15}N$ values used in this study (Sotiropoulos et al., 2004; Canseco et al., 2021). It is known that lipid extraction may affect $\delta^{15}N$ values but effects seem to vary between studies. Lipid extraction caused a ca. 1‰ increase in $\delta^{15}N$ values in fish muscle (Elsdon et al., 2010). Cloyed et al. (2020) found no effect of lipid extraction $\delta^{15}N$ values in dolphins and Caut et al. (2009) found that discrimination factors for nitrogen did not differ in samples from many types of organisms with and without lipid extraction. It was not attempted to correct for effects of various treatment and tissues since it was difficult to find relevant conversion factors.

For some FGs, $\delta^{15}N$ values were based on few entries, and lower number of entries could have contributed to high residuals for some FGs with few entries (n) such as capelin (3+) ($n = 1$) and blue whale ($n = 1$). That the $\delta^{15}N$ averages for multi-species FGs were calculated without weighting species-specific $\delta^{15}N$ values by the biomass of species will give more influence to species with many entries but with low biomass than less-studied species with higher biomass but less entries. This approach was chosen since biomasses of some species are uncertain.

CONCLUSION

Few FGs had $\delta^{15}N$ values that were correlated with latitude. Sediment POM, pelagic POM and some benthic detritivorous and benthic predatory invertebrate FGs had lower $\delta^{15}N$ values

in some fjords at Svalbard than in open water. This was likely caused by freshwater supply of POM of terrestrial origin with low $\delta^{15}N$ values. TPs from the mass-balance model (Ecopath) corresponded well with published TPs based on $\delta^{15}N$ values. TPs from Ecopath and linear best-fit model for TP-SI relationship also corresponded well with an estimate of TEF of 3.0‰. The linear model predicted lower TPs from $\delta^{15}N$ values than from Ecopath for pelagic invertebrates and whales and higher TPs for benthic invertebrates, and this was likely a result of lower TEF for pelagic groups and whales than for benthic invertebrates. A scaled model approach resulted in generally lower TPs than from Ecopath for TP in the range from ca. 2.5 to 4.5 The range of TP in the BS ecosystem varied when estimated by Ecopath, linear and scaled models with maximum TPs of 5.1, 5.4 and 6.0, respectively. It is concluded that the TPs from Ecopath and from a linear TP-SI model corresponded better than between TPs from Ecopath and the scaled approach.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article **Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the study was done using published information and did not involve new experiments or sampling.

AUTHOR CONTRIBUTIONS

TP has done all work with the manuscript except the checking of scientific species names which was done by Johanna Hovinen.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.813977/full#supplementary-material

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