Received 4 February 2016

Accepted 3 March 2016

A trans-Atlantic examination of haddock *Melanogrammus aeglefinus* food habits

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RUNNING HEADLINE: TRANS-ATLANTIC EXAMINATION OF ***M. AEGLEFINUS*** DIET

The food habits of *Melanogrammus aeglefinus* were explored and contrasted across multiple north-eastern and north-western Atlantic Ocean ecosystems, using databases that span multiple decades. The results show that among all ecosystems echinoderms are a consistent part of *M. aeglefinus* diet, but patterns emerge regarding where and when *M. aeglefinus* primarily eat fishes *v*. echinoderms. *Melanogrammus aeglefinus* does not regularly exhibit the increase in piscivory with ontogeny that other gadoids often show, in several ecosystems there is a lower occurrence of piscivory. There is an apparent inverse relationship between the consumption of fishes and echinoderms in *M. aeglefinus* over time, where certain years show high levels of one prey item and low levels of another. This apparent binary choice can be viewed as part of a gradient of prey options, contingent upon a suite of factors external to *M. aeglefinus* dynamics. The energetic consequences of this prey choice are discussed, noting that in some instances it may not be a choice at all.

Key words: echinoderms; ecosystem-based fisheries management; piscivory; prey choice.

INTRODUCTION

An integral part of managing commercial fish stocks from an ecosystems-based fisheries management (EBFM) perspective is understanding trophic linkages and the nature of feeding choices in target species (Pauly *et al.*, 1998; Link *et al.*, 2002). For predatory species, prey selection defines their ecological role and offers insight into how these species can and should be managed (Greenstreet *et al.*, 1997; Link *et al.*, 2009; Branch *et al.*, 2010). For historically harvested fish stocks, such as gadoids and Pleuronectiformes in the North Atlantic Ocean, it is important to understand their functional roles and what ecological buffers exist (in terms of functional redundancies, where multiple species contribute in equal ways to ecosystem function) against direct and indirect effects of overexploitation (Bellwood *et al.*, 2003; Link, 2007). In the case of geographically-widespread, opportunistic predators, populations of the same species can develop differing dietary strategies and specializations. This has been well documented in marine mammals where species such as harbour seals *Phoca vitulina* and killer whales *Orcinus orca* exhibit a variety of prey specializations between their geographically widespread populations even though they are able to eat a substantial range of prey (Ford *et al.*, 1998, 2010; Tollit *et al.*, 1998). Fewer such comparisons are made between fish populations, but examinations of fisheries literature indicates that dietary specializations occur in opportunistic fish predators. For example, the spiny dogfish *Squalus acanthias* L. 1758 is a widespread commercial fish that appears to consume proportionately more benthic invertebrates around New Zealand (Hanchet, 1991), teleosts in the North Atlantic Ocean (Holden, 1966; Link *et al.*, 2002) and large proportions of euphausiids in the eastern Pacific Ocean (Jones & Geen, 1977; Tanasichuk *et al.*, 1991). This can have strong implications on how target species are managed in different parts of the world as local abundances of preferred prey can dictate the stock size of the predator and subsequent functional redundancies may differ from place to place (ecosystem to ecosystem).

Haddock *Melanogrammus aeglefinus* (L. 1758) is an important species in the North Atlantic, with a long history of commercial exploitation (Jensen, 1965; Bergstad *et al.*, 1987; Pope & Macer, 1996; Hedger *et al.*, 2004). *Melanogrammus aeglefinus* is a widespread species with fisheries on the east coast of North America and in many parts of northern Europe and the British Isles (Aleev, 1944; Jensen, 1965; Albert, 1994; Jiang & Jørgensen, 1996; Temming *et al.*, 2004; Bogstad *et al.*, 2013). Juvenile *M. aeglefinus* move after 3 to 5 months from living in the upper reaches of the water column to living on muddy, sandy or gravel substrata (Platt *et al.*, 2003; Sell & Kröncke, 2013). As demersal fish, they spend their adult life in close association with the benthic habitat. Like other gadoids, they are opportunistic, higher-trophic-level feeders and prey on a variety of fishes and invertebrates (Schückel *et al.*, 2010; Smith & Link, 2010). Although *M. aeglefinus* is an abundant species in many ecosystems and its feeding behaviour is extensively studied in specific locales (Sonina, 1969; Dolgov *et al.*, 2007), overviews about its diet or how its diet may change throughout its life history or across its geographic range have not been carried out in a comparative way.

Echinoderms have been relatively well studied in marine ecology, primarily as consumers. Notable examples are crown-of thorns *Acanthaster planci* decimating corals in the Indo-Pacific (Moran *et al.*, 1992; Vogler *et al.*, 2008), purple sea stars *Pisaster ochraceus* as a keystone predator on North Pacific Ocean intertidal communities (Paine, 1966; 1969) and green sea urchins *Strongylocentrotus droebachiensis* denuding temperate areas entirely of macrophytes (Watanabe & Harrold, 1991; Gagnon *et al.*, 2004; Lauzon-Guay & Scheibling, 2007). Outside of the sea otter–urchin–macrophyte feeding dynamic (Estes & Palmisano, 1974; Dayton, 1975), however, studies of predation on echinoderms seldom occur, some exceptions being Pinnegar *et al.* (2000) and Schückel *et al.* (2010. Furthermore, the trophic role of echinoderms in deeper, subtidal communities is undervalued commercially as well as ecologically and not well studied compared with the role of fish prey, particularly in the northern Atlantic Ocean.

A unique aspect of *M. aeglefinus* feeding is that echinoderms can make up a significant part of their diet in the north-western Atlantic Ocean (Mahon & Neilson, 1987; Link, 2004; Shackell *et al.*, 2010; Smith & Link, 2010). This is rare among gadoids and from an energetic perspective would appear to be counterintuitive (Dauvin & Joncourt, 1989). With the exception of sea cucumbers, echinoderms are mainly composed of thick, calcareous exoskeletons that are only slowly digested by most fishes and contain less energy g^{-1} than other invertebrate diets items including worms, gastropods, bivalves and crustaceans (Steimle & Terranova, 1980). Survey observations of fish stomach contents in the north-west Atlantic Ocean has shown that several species consume echinoderms at some point in their life histories (Link, 2004; Smith & Link, 2010; Bundy *et al.*, 2011). The fact that commercially important fishes, like *M. aeglefinus*, choose to eat echinoderms is rarely addressed in fisheries management and ecosystem modelling even though echinoderms appear to play a large role in regulating energy flow in marine food webs (Steimle & Terranova, 1980; Zamarro, 1992).

What is unclear is the level of consistency across *M. aeglefinus* populations throughout their range in consuming echinoderms as a significant food source. There are indications that the diet of *M. aeglefinus* differs between areas and time periods. As a consequence, the functional redundancies to *M. aeglefinus* remain unknown. This study aims to examine the diet similarities of *M. aeglefinus* populations throughout their distributional range, at different stages during their life history and across several decades. This is an important step in understanding the dynamics in feeding ecology of *M. aeglefinus* and the role of echinoderms in benthic ecosystems.

MATERIALS AND METHODS

STUDY AREAS AND DATA COLLECTION

Melanogrammus aeglefinus stomachs were collected from nine ecosystems in the North Atlantic Ocean (Fig. 1). In the Gulf of Maine, Georges Bank, Scotian Shelf, Rockall Bank, North Sea and Barents Sea diet composition was assessed as the mass of the diet item relative to the total mass of the stomach contents. In the Celtic Sea, Irish Sea and Spitzbergen (Svalbard), frequency of occurrence (F_O; the number of stomachs containing the diet item relative to the total number of stomachs) was used to assess the diet (Hyslop, 1980; Ahlbeck *et al.*, 2012). The sampling primarily occurred from the 1970s to present, but extended to earlier decades for some regions (Table I).

Stomach contents were collected from length-stratified samples during fishery-independent and fishery-dependent surveys and prey were quantified by mass or number depending on where and what type sampling occurred (Table I). Where possible, prey items were identified to species level, but owing to varying levels of digestion, prey were often identified to genus, class or family levels (Smith & Link, 2010; Cook & Bundy, 2012; Bundy *et al.*, 2011).

DATA ANALYSIS

Data were parsed to include only the dominant prey of *M. aeglefinus* diet. Because they have been described elsewhere in detail for given ecosystems (Table I), non-echinoderm invertebrates (worms, gastropods, bivalves and crustaceans) were not considered in the analyses. As each ecosystem may contain a different selection of prey species and given the aims of this study, prey were grouped according to rough taxonomic classification of echinoderm, fishes or other prey item. To determine if *M. aeglefinus* undergo similar ontogenetic shifts in diet composition across regions, *M. aeglefinus* were also grouped into the following total length (L_T) groups: 10–29, 30–49 and > 50 cm, where data were available. These sizes are consistent with observed major ontogenetic shifts in diet (Link & Garrison, 2002*a*). Where time-series data were available (Georges Bank, Gulf of Maine, U.S. Scotian Shelf and Barents Sea), *M. aeglefinus* diet was plotted in 5 year blocks to examine consistency in food choice over time.

Given that the diet of *M. aeglefinus* was recorded differently between ecosystems, Kendall's τ (Fredricks & Nelsen, 2007) was used to examine the non-parametric, rank-order relationship between the proportion of echinoderm and fishes in the diet of *M. aeglefinus* in differing ecosystems. This statistical method is the non-parametric equivalent of measures of association or correlation .This analysis determined if there was any consistent and significant association between the amount of fishes and echinoderms in the diet of *M. aeglefinus* for all ecosystems examined. Within ecosystem differences between echinoderms and fishes in *M. aeglefinus* diet were determined using χ^2 analysis. To explore and test for relationships within ecosystems of *M. aeglefinus* diet between L_T classes, χ^2 analysis of the proportion of each diet item in the stomachs of fish across L_T classes was used. To examine trends in prey selection of *M. aeglefinus* at each ecosystem over time, a generalized linear model was used with per cent of the diet item as the dependent variable and time as the independent variable. This determined if *M. aeglefinus* showed general shifts in their prey selection over time. For each 5 year block within each ecosystem, a χ^2 analysis was performed to determine significant differences between the percentage of echinoderms and fishes in *M. aeglefinus* diet and reveal any changes in the feeding pattern of *M. aeglefinus* over time.

RESULTS

There was no significant relationship between echinoderms and fishes in the diet of *M. aeglefinus* that could be applied to all ecosystems according to the Kendall's *Ä*analysis (Fig. 2; *Ä* = 0.33, *Z*-score = 1.25, $P > 0.05$). The North Sea and Rockall Bank populations of *M. aeglefinus* showed significantly higher piscivory, while all other ecosystems showed significantly higher echinoderms consumed or else no dominant prey (Table II).

Differing patterns of ontogenetic shifts towards piscivory were apparent in *M. aeglefinus* among ecosystems based on L_T class data (Fig. 3). In several ecosystems there was a significantly lower occurrence of piscivory (*i.e.* eggs and larvae) with increasing L_T (Georges Bank: Ç^2 = 30.52, d.f. = 2, P <0.001; Gulf of Maine: Ç^2 = 15.91, d.f. = 2, P <0.001). In the North Sea and Rockall Bank there was a higher occurrence of piscivory (*i.e.* small pelagic fishes) with increasing size class (Ç^2 = 38.34, 23.90, d.f. = 2, 2, P < 0.001, <0.001, respectively), but the proportion of echinoderms in the diet of *M. aeglefinus* remained constant. Through their life history, *M. aeglefinus* diet comprised a high proportion of echinoderms in most ecosystems. Echinoderms were a proportionally consistent component of *M. aeglefinus* diet throughout their life cycle except in the Gulf of Maine and Scotian Shelf, where echinoderms increased in frequency with increasing size (Ç^2 = 22.29, 17.82, d.f. = 2, 2, P <0.001, <0.001, respectively).

There was no consistent temporal shift in the diet of *M. aeglefinus* in either echinoderms or fishes within ecosystems ($F_{1,4}$ = 0.18, P > 0.05). Long-term stomach content data indicated that echinoderms were consistently a part of *M. aeglefinus* diet over time, but neither diet item exhibited any linear trend, indicating that there was no shift in diet related to an external pressure (*i.e*. environment or habitat). Despite the lack of trend, the Ç^2 analyses indicated that there were significant differences in the consumption of echinoderms and fishes by *M. aeglefinus* within time periods (Table III). There appeared to be an inverse relationship between the consumption of fishes and echinoderms by *M. aeglefinus* over time. Periods of high and low fish consumption by *M. aeglefinus* coincided with respective periods of low and high echinoderm consumption (Fig. 4). During the late 1980s and early 2000s there appeared to be peaks in echinoderm consumption by *M. aeglefinus*.

DISCUSSION

It is unusual for a gadoid species to consistently maintain a high proportion of benthic invertebrates in its diet throughout its life history. Most gadoids are known to be opportunistic, *e.g.* Atlantic cod *Gadus morhua* L. 1758 is a generalist feeder, saithe *Pollachius virens* (L. 1758) and some hake species consume more of a pelagic diet (Smith & Link, 2010). *Gadus morhua* have shown a clear ontogenetic shift in diet, with smaller *G. morhua* feeding more on benthic prey and larger *G. morhua* showing a strong shift towards piscivory (Link & Garrison, 2002*b*; Smith *et al.*, 2007; Rowlands *et al.*, 2008). In contrast, *M. aeglefinus* exhibit no ontogenetic shift towards piscivory with the exception of the North Sea and Rockall Bank, where echinoderms still occur in their diets throughout their lives. This difference in ontogenetic diet shift between *M. aeglefinus* and *G. morhua* can be explained by the smaller gape size and body size of *M. aeglefinus* that is not able to eat as many larger prey fish compared with *G. morhua* (Løkkeborg *et al.*, 1989).

Melanogrammus aeglefinus consistently consume echinoderms across the range of environmental conditions examined. In ecosystems where *M. aeglefinus* appear to be more piscivorous or predominantly eat a combination of other invertebrates, echinoderms still make up at least 10% of their diet. Since the early 2000s *M. aeglefinus* stocks have experienced an increase in abundance in all regions studied with the exception of the Scotian Shelf and, thus, do not appear to be suffering from reduced productivity due to their reliance on low-nutrient food sources (Brodziak *et al.*, 2008; Bogstad *et al.*, 2013; Pecuchet *et al.*, 2014). Eating food of high calcium carbonate and low energy may have developed in *M. aeglefinus* to reduce competition with other gadoids by obtaining a consistent, albeit low-energy food source.

While it may not seem like a successful strategy to consume large proportions of echinoderms due to their low nutritional value compared with prey fishes, their relatively high abundances and relatively low defences (slow moving) make them a very accessible prey to *M. aeglefinus*. Echinoderms in the north-western Atlantic Ocean make up a large proportion of the biomass in benthic habitats (up to 500 g m^{-2} and up to 90% of the total grab sample) with sand dollar sea urchins *Echinarachnius parma* in shallower regions and brittle stars *Amphioplus* spp. and sea cucumbers dominating deeper areas of Georges Bank and the Gulf of Maine basins (Steimle, 1990). In Atlantic Canada, echinoderms at times have made up to 35% of the total energy m^{-2} of benthic habitat even though they are relatively low in energy content compared with other invertebrate phyla (Brawn *et al.*, 1968). In the North Sea, the brittle star *Amphiura filiformis* dominates the benthic system and lives in densities up to 2250 individuals m^{-2} (Skold *et al.*, 1994; Wood *et al.*, 2009) and other important species include the sea potato sea urchin *Echinocardium cordatum*, the pea sea urchin *Echinocyamus pusillus*, the red-brown brittle star *Ophiura albida* and *Ophiocten affinis* and that are also common components of the benthos . These high abundances of echinoderms in benthic communities support the hypothesis that *M.*

aeglefinus exhibit ambient feeding in some regions to perhaps sustain the populations while supplementing their diet with other prey.

In this study the diet of *M. aeglefinus,* consistently included echinoderms across ecosystems and over time, even in regions where the dominant prey is fish. This indicates that echinoderms are an important food source throughout their distribution. While there does not appear to be long-term, multi-decadal shifts in the diet of *M. aeglefinus*, there is an indication of shorter-term changes in *M. aeglefinus* feeding habits (Fig. 4). At 5 year intervals in the Georges Bank, Gulf of Maine, Scotian Shelf and Barents Sea there is evidence of an inverse relationship between the contribution of echinoderms and fish prey to the diet of *M. aeglefinus* (Antipova *et al.*, 1980). Foraging fishes are known to be able to alter their behaviour in response to variations in food availability and the threat of competition (Dill, 1983). *Melanogrammus aeglefinus* probably consume lower quality food choices when faced with adversity in acquiring a preferred resource (Vinyard, 1980; McNamara & Houston, 1987). Feeding on echinoderms could be a strategy for *M. aeglefinus* to maintain constant energy levels during periods of low prey fish abundance and high competition with other gadoids that may occur on a multi-annual cycle (Temming *et al.*, 2004). Intra-annual abundances for all prey items of *M. aeglefinus* from the ecosystems surveyed in this study, however, were not examined and it would be a useful avenue for future research to measure selectivity across time in all of these populations.

An opportunistic feeding mode for *M. aeglefinus* has been demonstrated in several earlier studies (Mattson, 1992; Schückel *et al.*, 2010) and current observations from the different ecosystems reveals that high amounts of fishes in the diet of larger North Sea *M. aeglefinus* are likely to be a consequence of prey availability rather than an ontogenetic shift (*i.e.* the high abundance of sandeels *Ammodytes* spp.). This is supported by observations on Dogger Bank (55° N; 03° E) in the North Sea, where Sell & Kröncke (2013) found the distribution of *M. aeglefinus* to be more strongly correlated with abiotic habitat variables (depth, temperature and sediment composition) than with biotic factors, including the availability of potential mud dwelling prey. It has also been shown that *M. aeglefinus* adapt their diets based on prey availability due to benthic disturbance from fishing gear, with less benthos and slightly more fish consumed in disturbed habitats (Smith *et al.*, 2013).

There is some indication that echinoderms have higher nutrition and energy content than expected, but past studies have shown that the caloric content of fish to be higher than echinoderms. Brawn *et al.* (1968) found that prey fishes contained two to three times more kJ g^{-1} than echinoderms in St Margaret's Bay in Nova Scotia, Canada (44° 302N; 64° 002W). Other studies have found lower energy content in sea stars and brittle stars compared with fishes (19.10 kJ g^{-1} ash-free dried for echinoderms and 22.96–24.22 kJ g^{-1} ash-free dried mass for fishes), while sea urchins had a higher energy content (25.82 kJ g^{-1} ash-free dried mass) than both demersal or pelagic fishes (Steimle & Terranova, 1980; Packer *et al.*, 1994). Inconsistencies in the values of energy contents drawn from these studies may be due to the different species contributing to the sample groups. There may also be a seasonal element to the appeal of echinoderms as *M. aeglefinus* prey. When echinoderms are gravid they are more nutritionally valuable and contain a higher lipid and protein content. Steimle & Terranova (1980) found that the energy content in *E. parma* doubled during autumn spawning periods compared with spring values. Certain conditions in timing and availability may make echinoderms a logical food choice for *M. aeglefinus*.

There is some evidence that hard shelled invertebrates, such as echinoderms and bivalves, digest more slowly and less efficiently than other, soft-tissue prey such as fishes and polychaetes (MacDonald *et al.*, 1982; Tibbetts *et al.*, 2004; Jaworski & Ragnarsson, 2006). Preliminary calculations indicate that the digestibility of hard shelled invertebrates are only *c.* 10% less than that of soft bodied prey such as fishes and polychaetes in gadoid diets and respective evacuation rates could be on the order of one to two times slower (MacDonald *et al.*, 1982; Tibbetts *et al.*, 2006). If this is the case, the relative importance of echinoderms in the diet of *M. aeglefinus* could potentially be amplified by a similar factor. If, however, the per cent diet composition of echinoderms in the diet of *M. aeglefinus* is lower, the fact remains that echinoderms still remain a notable, consistent and regular component of the diet of *M. aeglefinus*. In contrast, there is evidence that the test in echinoderms may actually promote more efficient digestion in predatory fishes. Mattson (1992) indicates that the calcareous trst of echinoderms act as a grinding element and can enhance digestion as well as ingestion. This increased maceration may compensate for the low nutritional value inherent in echinoderm prey and could ultimately improve the digestion of all hard-shelled organisms in *M. aeglefinus* diet.

The implications of understanding the diets of target fish species span far beyond just knowing what they are eating. Assessing food habits in fishes, particularly in opportunistic feeders, can give insight into habitats and prey species distributions that are difficult to survey (Link, 2004; Cook & Bundy, 2012). In determining that *M. aeglefinus* consume large proportions of echinoderms in many regions, this study has identified an important link between the benthos and harvested fishes. This is a mechanism that is rarely considered in management decisions and implies that impacts to the benthic habitat in certain regions will probably affect *M. aeglefinus* more than other harvested gadoid species. From an EBFM perspective, the functional redundancies of *M. aeglefinus* lie alongside other echinoderm consumers such as American plaice *Hippoglossoides platessoides* (Fabricius 1780) and ocean pout *Macrozoarces americanus* (Bloch & Schneider 1801) rather than species of the same family group (Zamarro, 1992; Packer *et al.*, 1994; Link, 2007).

While traditional conservation strategies, such as fisheries closures, are not always effective at increasing target fish stocks (Fisher & Frank, 2002; Kelly *et al.*, 2006), *M. aeglefinus* have historically responded well to these management options (Brodziak *et al.*, 2008). In the mid-1990s, *M. aeglefinus* stocks in the north-west Atlantic Ocean were the lowest on record (Hutchings, 2000). After strict closures as a response to the declining stock status, *M. aeglefinus* stocks increased dramatically (Murawski *et al.*, 2000; Brodziak *et al.*, 2008). *Melanogrammus aeglefinus* are also known to have a restricted daily ambit compared with other gadoids, indicating a strong association with local habitats (Perry & Smith, 1994; Fogarty *et al.*, 2001). Reduced impacts on the benthic habitat compounded with the high proportion of echinoderms in *M. aeglefinus* diet, in part, explain why *M. aeglefinus* stocks have successfully responded to fisheries closures and marine protected areas (Smith *et al.*, 2013). In areas where *M. aeglefinus* exhibited a high frequency of piscivory, such as the North Sea, fishery closures did not improve their abundances nearly as much (FSBI, 2001; Fisher & Frank, 2002) . These differences in feeding habits between populations can complicate management efforts because species may not respond the same way in all regions of their distributional range. Thus, conservation methods need to take into account the biology of the ecosystem as well as species-specific life histories to ensure positive and efficient management outcomes.

The importance of the benthic habitat to harvested fishes is becoming increasingly apparent. The interconnectedness and complexity of food webs is an important consideration in sustainable fisheries management (Pauly *et al.*, 1998; Link, 2011; Cook & Bundy, 2012; Link & Auster, 2013). To complicate the understanding of trophic webs in fisheries even further, comparative studies such as this one are revealing that populations of the same fish species can interact with their local habitat differently between regions. This emphasizes the need for ecosystem-level management that will improve the resiliency and long-term economic viability of harvested fish throughout their distributions.

We would like to thank the research vessel crews at NOAA and DFO whose hard work has made studies such as this possible. We also thank the International Council for the Exploration of the Sea (ICES) and the Institute for Marine Resource and Ecosystem Studies (IMARES) for making this stomach data available. Partial support for data collection was provided by E.U. FP7 project BENTHIS (KBBE.2012.1.2-09) (J.K.P.). We would like to thank internal reviewers K.

Holsman, R. Heintz and K. Osgood for their helpful comments and suggestions. This work was supported by a NOAA Postdoctoral Fellowship to J.C.T.

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TABLE I. Data collection methods and sources. Frequency of occurrence was measured as the number of each diet item relative to the total number of stomachs in per cent. Diet composition was measured as the mass of the diet items relative to the total mass of *Melanogrammus aeglefinus* stomachs in percentages

Ecosystem	Time of sampling	Type of data collected	*M. aeglefinus* stomachs sampled (*n*)	Collection method	Source
Gulf of Maine	1973–1982, 1984–2011	Diet composition	3629	Data compiled from U.S. Northeast Fisheries Science Center (NEFSC) surveys through random stratified bottom trawl surveys.	(NEFSC, 1988; Smith & Link, 2010)
Georges Bank	1973–1982, 1984–1992, 1994–2011	Diet composition	5825	Data compiled from NESFC surveys through random stratified bottom trawl surveys.	(NEFSC, 1988; 1998; Smith & Link, 2010)
Scotian Shelf	1995–2009	Diet composition	2690	Data compiled from Department of Fisheries and Oceans Canada trawl surveys.	(Cook & Bundy, 2010; 2012; Bundy *et al.*, 2011)
North Sea	1981, 1991	Diet composition	4452	Data collected during the ICES coordinated International Bottom Trawl	(Daan, 1989; ICES, 1997; 2010)

				Surveys of the North Sea	
Rockall Bank	2004–2007, 2009–2010	Diet composition	3746	Data compiled from the Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Russia.	(Antipova *et al.*, 1980)
Barents Sea	1984–1991, 1993–2011	Diet composition	11064	Data compiled by the Institute of Marine Research, Norway, and PINRO.	(Antipova *et al.*, 1980; Dolgov *et al.*, 2007)
Irish Sea	1894, 1981–1983, 2008, 2010	Frequency of occurrence	653	Data compiled from the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) U.K. (England).	(Pinnegar, 2014)
Celtic Sea	1977, 1978, 1981–1988, 1991–1993	Frequency of occurrence	971	Data compiled from CEFAS.	(Pinnegar, 2014)
Spitzbergen	1930, 1936, 1937, 1949, 1950, 1954, 1964	Frequency of occurrence	735	Data compiled from CEFAS.	(Pinnegar, 2014)

TABLE II. Results of the χ^2 analysis examining the relationship between echinoderms and fishes in *Melanogrammus aeglefinus* diet within each ecosystem

Ecosystem	X^2	*P*	Dominant prey
Gulf of Maine	3.79	>0.05	None
Georges Bank	0.12	>0.05	None
Scotian Shelf	2.80	>0.05	None
North Sea	6.92	< 0.01	Fishes
Rockall Bank	22.11	< 0.01	Fishes
Barents Sea	0.02	>0.05	None
Irish Sea	3.77	>0.05	None
Celtic Sea	22.54	< 0.01	Echinoderms
Spitzbergen	43.67	< 0.01	Echinoderms

TABLE III. Results of the χ^2 analysis (*P*-values) examining the relationship between echinoderms and fishes in *Melanogrammus aeglefinus* diet at each five year block within ecosystems

Year	Georges Bank	Gulf of Maine	Scotian Shelf	Barents Sea
1975	< 0.01	< 0.01		
1980	< 0.01	< 0.01		
1985	< 0.01	< 0.01		<0.05
1990	< 0.01	< 0.01		>0.05
1995	>0.05	< 0.01		< 0.01
2000	< 0.01	< 0.01	< 0.01	>0.05
2005	< 0.01	>0.05	< 0.01	>0.05
2010	>0.05	>0.05	< 0.01	>0.05
2015	>0.05	>0.05		>0.05

TABLE I. Data collection methods and sources. Frequency of occurrence was measured as the number of each diet item relative to the total number of stomachs in per cent. Diet composition was measured as the mass of the diet items relative to the total mass of *Melanogrammus aeglefinus* stomachs in percentages

Ecosystem	Time of sampling	Type of data collected	*M. aeglefinus* stomachs sampled (*n*)	Collection method	Source
Gulf of Maine	1973–1982, 1984–2011	Diet composition	3629	Data compiled from U.S. Northeast Fisheries Science Center (NEFSC) surveys through random stratified bottom trawl surveys.	(NEFSC, 1988; Smith & Link, 2010)
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Celtic Sea	1977, 1978, 1981–1988, 1991–1993	Frequency of occurrence	971	Data compiled from CEFAS.	(Pinnegar, 2014)
Spitzbergen	1930, 1936, 1937, 1949, 1950, 1954, 1964	Frequency of occurrence	735	Data compiled from CEFAS.	(Pinnegar, 2014)

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1975	< 0.01	< 0.01		
1980	< 0.01	< 0.01		
1985	< 0.01	< 0.01		<0.05
1990	< 0.01	< 0.01		>0.05
1995	>0.05	< 0.01		< 0.01
2000	< 0.01	< 0.01	< 0.01	>0.05
2005	< 0.01	>0.05	< 0.01	>0.05
2010	>0.05	>0.05	< 0.01	>0.05
2015	>0.05	>0.05		>0.05

Received 4 February 2016

Accepted 3 March 2016

A trans-Atlantic examination of haddock *Melanogrammus aeglefinus* food habits

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The food habits of *Melanogrammus aeglefinus* were explored and contrasted across multiple north-eastern and north-western Atlantic Ocean ecosystems, using databases that span multiple decades. The results show that among all ecosystems echinoderms are a consistent part of *M. aeglefinus* diet, but patterns emerge regarding where and when *M. aeglefinus* primarily eat fishes *v*. echinoderms. *Melanogrammus aeglefinus* does not regularly exhibit the increase in piscivory with ontogeny that other gadoids often show, in several ecosystems there is a lower occurrence of piscivory. There is an apparent inverse relationship between the consumption of fishes and echinoderms in *M. aeglefinus* over time, where certain years show high levels of one prey item and low levels of another. This apparent binary choice can be viewed as part of a gradient of prey options, contingent upon a suite of factors external to *M. aeglefinus* dynamics. The energetic consequences of this prey choice are discussed, noting that in some instances it may not be a choice at all.

Key words: echinoderms; ecosystem-based fisheries management; piscivory; prey choice.

INTRODUCTION

An integral part of managing commercial fish stocks from an ecosystems-based fisheries management (EBFM) perspective is understanding trophic linkages and the nature of feeding choices in target species (Pauly *et al.*, 1998; Link *et al.*, 2002). For predatory species, prey selection defines their ecological role and offers insight into how these species can and should be managed (Greenstreet *et al.*, 1997; Link *et al.*, 2009; Branch *et al.*, 2010). For historically harvested fish stocks, such as gadoids and Pleuronectiformes in the North Atlantic Ocean, it is important to understand their functional roles and what ecological buffers exist (in terms of functional redundancies, where multiple species contribute in equal ways to ecosystem function) against direct and indirect effects of overexploitation (Bellwood *et al.*, 2003; Link, 2007). In the case of geographically-widespread, opportunistic predators, populations of the same species can develop differing dietary strategies and specializations. This has been well documented in marine mammals where species such as harbour seals *Phoca vitulina* and killer whales *Orcinus orca* exhibit a variety of prey specializations between their geographically widespread populations even though they are able to eat a substantial range of prey (Ford *et al.*, 1998, 2010; Tollit *et al.*, 1998). Fewer such comparisons are made between fish populations, but examinations of fisheries literature indicates that dietary specializations occur in opportunistic fish predators. For example, the spiny dogfish *Squalus acanthias* L. 1758 is a widespread commercial fish that appears to consume proportionately more benthic invertebrates around New Zealand (Hanchet, 1991), teleosts in the North Atlantic Ocean (Holden, 1966; Link *et al.*, 2002) and large proportions of euphausiids in the eastern Pacific Ocean (Jones & Geen, 1977; Tanasichuk *et al.*, 1991). This can have strong implications on how target species are managed in different parts of the world as local abundances of preferred prey can dictate the stock size of the predator and subsequent functional redundancies may differ from place to place (ecosystem to ecosystem).

Haddock *Melanogrammus aeglefinus* (L. 1758) is an important species in the North Atlantic, with a long history of commercial exploitation (Jensen, 1965; Bergstad *et al.*, 1987; Pope & Macer, 1996; Hedger *et al.*, 2004). *Melanogrammus aeglefinus* is a widespread species with fisheries on the east coast of North America and in many parts of northern Europe and the British Isles (Aleev, 1944; Jensen, 1965; Albert, 1994; Jiang & Jørgensen, 1996; Temming *et al.*, 2004; Bogstad *et al.*, 2013). Juvenile *M. aeglefinus* move after 3 to 5 months from living in the upper reaches of the water column to living on muddy, sandy or gravel substrata (Platt *et al.*, 2003; Sell & Kröncke, 2013). As demersal fish, they spend their adult life in close association with the benthic habitat. Like other gadoids, they are opportunistic, higher-trophic-level feeders and prey on a variety of fishes and invertebrates (Schückel *et al.*, 2010; Smith & Link, 2010). Although *M. aeglefinus* is an abundant species in many ecosystems and its feeding behaviour is extensively studied in specific locales (Sonina, 1969; Dolgov *et al.*, 2007), overviews about its diet or how its diet may change throughout its life history or across its geographic range have not been carried out in a comparative way.

Echinoderms have been relatively well studied in marine ecology, primarily as consumers. Notable examples are crown-of thorns *Acanthaster planci* decimating corals in the Indo-Pacific (Moran *et al.*, 1992; Vogler *et al.*, 2008), purple sea stars *Pisaster ochraceus* as a keystone predator on North Pacific Ocean intertidal communities (Paine, 1966; 1969) and green sea urchins *Strongylocentrotus droebachiensis* denuding temperate areas entirely of macrophytes

(Watanabe & Harrold, 1991; Gagnon *et al.*, 2004; Lauzon-Guay & Scheibling, 2007). Outside of the sea otter–urchin–macrophyte feeding dynamic (Estes & Palmisano, 1974; Dayton, 1975), however, studies of predation on echinoderms seldom occur, some exceptions being Pinnegar *et al.* (2000) and Schückel *et al.* (2010. Furthermore, the trophic role of echinoderms in deeper, subtidal communities is undervalued commercially as well as ecologically and not well studied compared with the role of fish prey, particularly in the northern Atlantic Ocean.

A unique aspect of *M. aeglefinus* feeding is that echinoderms can make up a significant part of their diet in the north-western Atlantic Ocean (Mahon & Neilson, 1987; Link, 2004; Shackell *et al.*, 2010; Smith & Link, 2010). This is rare among gadoids and from an energetic perspective would appear to be counterintuitive (Dauvin & Joncourt, 1989). With the exception of sea cucumbers, echinoderms are mainly composed of thick, calcareous exoskeletons that are only slowly digested by most fishes and contain less energy g^{-1} than other invertebrate diets items including worms, gastropods, bivalves and crustaceans (Steimle & Terranova, 1980). Survey observations of fish stomach contents in the north-west Atlantic Ocean has shown that several species consume echinoderms at some point in their life histories (Link, 2004; Smith & Link, 2010; Bundy *et al.*, 2011). The fact that commercially important fishes, like *M. aeglefinus*, choose to eat echinoderms is rarely addressed in fisheries management and ecosystem modelling even though echinoderms appear to play a large role in regulating energy flow in marine food webs (Steimle & Terranova, 1980; Zamarro, 1992).

What is unclear is the level of consistency across *M. aeglefinus* populations throughout their range in consuming echinoderms as a significant food source. There are indications that the diet of *M. aeglefinus* differs between areas and time periods. As a consequence, the functional redundancies to *M. aeglefinus* remain unknown. This study aims to examine the diet similarities of *M. aeglefinus* populations throughout their distributional range, at different stages during their life history and across several decades. This is an important step in understanding the dynamics in feeding ecology of *M. aeglefinus* and the role of echinoderms in benthic ecosystems.

MATERIALS AND METHODS

STUDY AREAS AND DATA COLLECTION

Melanogrammus aeglefinus stomachs were collected from nine ecosystems in the North Atlantic Ocean (Fig. 1). In the Gulf of Maine, Georges Bank, Scotian Shelf, Rockall Bank, North Sea and Barents Sea diet composition was assessed as the mass of the diet item relative to the total mass of the stomach contents. In the Celtic Sea, Irish Sea and Spitzbergen (Svalbard), frequency of occurrence (F_O; the number of stomachs containing the diet item relative to the total number of stomachs) was used to assess the diet (Hyslop, 1980; Ahlbeck *et al.*, 2012). The sampling primarily occurred from the 1970s to present, but extended to earlier decades for some regions (Table I).

Stomach contents were collected from length-stratified samples during fishery-independent and fishery-dependent surveys and prey were quantified by mass or number depending on where and what type sampling occurred (Table I). Where possible, prey items were identified to species level, but owing to varying levels of digestion, prey were often identified to genus, class or family levels (Smith & Link, 2010; Cook & Bundy, 2012; Bundy *et al.*, 2011).

DATA ANALYSIS

Data were parsed to include only the dominant prey of *M. aeglefinus* diet. Because they have been described elsewhere in detail for given ecosystems (Table I), non-echinoderm invertebrates (worms, gastropods, bivalves and crustaceans) were not considered in the analyses. As each ecosystem may contain a different selection of prey species and given the aims of this study, prey were grouped according to rough taxonomic classification of echinoderm, fishes or other prey item. To determine if *M. aeglefinus* undergo similar ontogenetic shifts in diet composition across regions, *M. aeglefinus* were also grouped into the following total length (L_T) groups: 10–29, 30–49 and > 50 cm, where data were available. These sizes are consistent with observed major ontogenetic shifts in diet (Link & Garrison, 2002*a*). Where time-series data were available (Georges Bank, Gulf of Maine, U.S. Scotian Shelf and Barents Sea), *M. aeglefinus* diet was plotted in 5 year blocks to examine consistency in food choice over time.

Given that the diet of *M. aeglefinus* was recorded differently between ecosystems, Kendall's τ (Fredricks & Nelsen, 2007) was used to examine the non-parametric, rank-order relationship between the proportion of echinoderm and fishes in the diet of *M. aeglefinus* in differing ecosystems. This statistical method is the non-parametric equivalent of measures of association or correlation .This analysis determined if there was any consistent and significant association between the amount of fishes and echinoderms in the diet of *M. aeglefinus* for all ecosystems examined. Within ecosystem differences between echinoderms and fishes in *M. aeglefinus* diet were determined using χ^2 analysis. To explore and test for relationships within ecosystems of *M. aeglefinus* diet between L_T classes, χ^2 analysis of the proportion of each diet item in the stomachs of fish across L_T classes was used. To examine trends in prey selection of *M. aeglefinus* at each ecosystem over time, a generalized linear model was used with per cent of the diet item as the dependent variable and time as the independent variable. This determined if *M. aeglefinus* showed general shifts in their prey selection over time. For each 5 year block within each ecosystem, a χ^2 analysis was performed to determine significant differences between the percentage of echinoderms and fishes in *M. aeglefinus* diet and reveal any changes in the feeding pattern of *M. aeglefinus* over time.

RESULTS

There was no significant relationship between echinoderms and fishes in the diet of *M. aeglefinus* that could be applied to all ecosystems according to the Kendall's *Ä*analysis (Fig. 2; *Ä* = 0.33, *Z*-score = 1.25, $P > 0.05$). The North Sea and Rockall Bank populations of *M. aeglefinus* showed significantly higher piscivory, while all other ecosystems showed significantly higher echinoderms consumed or else no dominant prey (Table II).

Differing patterns of ontogenetic shifts towards piscivory were apparent in *M. aeglefinus* among ecosystems based on L_T class data (Fig. 3). In several ecosystems there was a significantly lower occurrence of piscivory (*i.e.* eggs and larvae) with increasing L_T (Georges Bank: *Ç*^{2} = 30.52, d.f. = 2, $P < 0.001$; Gulf of Maine: *Ç*^{2} = 15.91, d.f. = 2, $P < 0.001$). In the North Sea and Rockall Bank there was a higher occurrence of piscivory (*i.e.* small pelagic fishes) with increasing size class (*Ç*^{2} = 38.34, 23.90, d.f. = 2, 2, $P < 0.001$, <0.001, respectively), but the proportion of echinoderms in the diet of *M. aeglefinus* remained constant. Through their life history, *M. aeglefinus* diet comprised a high proportion of echinoderms in most ecosystems. Echinoderms were a proportionally consistent component of *M. aeglefinus* diet throughout their life cycle except in the Gulf of Maine and Scotian Shelf, where echinoderms increased in frequency with increasing size (*Ç*^{2} = 22.29, 17.82, d.f. = 2, 2, $P < 0.001$, <0.001, respectively).

There was no consistent temporal shift in the diet of *M. aeglefinus* in either echinoderms or fishes within ecosystems ($F_{1,4} = 0.18$, $P > 0.05$). Long-term stomach content data indicated that echinoderms were consistently a part of *M. aeglefinus* diet over time, but neither diet item exhibited any linear trend, indicating that there was no shift in diet related to an external pressure (*i.e*. environment or habitat). Despite the lack of trend, the $Ç^2$ analyses indicated that there were significant differences in the consumption of echinoderms and fishes by *M. aeglefinus* within time periods (Table III). There appeared to be an inverse relationship between the consumption of fishes and echinoderms by *M. aeglefinus* over time. Periods of high and low fish consumption by *M. aeglefinus* coincided with respective periods of low and high echinoderm consumption (Fig. 4). During the late 1980s and early 2000s there appeared to be peaks in echinoderm consumption by *M. aeglefinus*.

DISCUSSION

It is unusual for a gadoid species to consistently maintain a high proportion of benthic invertebrates in its diet throughout its life history. Most gadoids are known to be opportunistic, *e.g.* Atlantic cod *Gadus morhua* L. 1758 is a generalist feeder, saithe *Pollachius virens* (L. 1758) and some hake species consume more of a pelagic diet (Smith & Link, 2010). *Gadus morhua* have shown a clear ontogenetic shift in diet, with smaller *G. morhua* feeding more on benthic prey and larger *G. morhua* showing a strong shift towards piscivory (Link & Garrison, 2002*b*; Smith *et al.*, 2007; Rowlands *et al.*, 2008). In contrast, *M. aeglefinus* exhibit no ontogenetic shift towards piscivory with the exception of the North Sea and Rockall Bank, where echinoderms still occur in their diets throughout their lives. This difference in ontogenetic diet shift between *M. aeglefinus* and *G. morhua* can be explained by the smaller gape size and body size of *M. aeglefinus* that is not able to eat as many larger prey fish compared with *G. morhua* (Løkkeborg *et al.*, 1989).

Melanogrammus aeglefinus consistently consume echinoderms across the range of environmental conditions examined. In ecosystems where *M. aeglefinus* appear to be more piscivorous or predominantly eat a combination of other invertebrates, echinoderms still make up at least 10% of their diet. Since the early 2000s *M. aeglefinus* stocks have experienced an increase in abundance in all regions studied with the exception of the Scotian Shelf and, thus, do not appear to be suffering from reduced productivity due to their reliance on low-nutrient food sources (Brodziak *et al.*, 2008; Bogstad *et al.*, 2013; Pecuchet *et al.*, 2014). Eating food of high calcium carbonate and low energy may have developed in *M. aeglefinus* to reduce competition with other gadoids by obtaining a consistent, albeit low-energy food source.

While it may not seem like a successful strategy to consume large proportions of echinoderms due to their low nutritional value compared with prey fishes, their relatively high abundances and relatively low defences (slow moving) make them a very accessible prey to *M. aeglefinus*. Echinoderms in the north-western Atlantic Ocean make up a large proportion of the biomass in benthic habitats (up to 500 g m^{-2} and up to 90% of the total grab sample) with sand dollar sea urchins *Echinarachnius parma* in shallower regions and brittle stars *Amphioplus* spp. and sea cucumbers dominating deeper areas of Georges Bank and the Gulf of Maine basins (Steimle, 1990). In Atlantic Canada, echinoderms at times have made up to 35% of the total energy m^{-2} of benthic habitat even though they are relatively low in energy content compared with other invertebrate phyla (Brawn *et al.*, 1968). In the North Sea, the brittle star *Amphiura filiformis* dominates the benthic system and lives in densities up to 2250 individuals m^{-2} (Skold *et al.*, 1994; Wood *et al.*, 2009) and other important species include the sea potato sea urchin *Echinocardium cordatum*, the pea sea urchin *Echinocyamus pusillus*, the red-brown brittle star *Ophiura albida* and *Ophiocten affinis* and that are also common components of the benthos .

These high abundances of echinoderms in benthic communities support the hypothesis that *M. aeglefinus* exhibit ambient feeding in some regions to perhaps sustain the populations while supplementing their diet with other prey.

In this study the diet of *M. aeglefinus,* consistently included echinoderms across ecosystems and over time, even in regions where the dominant prey is fish. This indicates that echinoderms are an important food source throughout their distribution. While there does not appear to be long-term, multi-decadal shifts in the diet of *M. aeglefinus*, there is an indication of shorter-term changes in *M. aeglefinus* feeding habits (Fig. 4). At 5 year intervals in the Georges Bank, Gulf of Maine, Scotian Shelf and Barents Sea there is evidence of an inverse relationship between the contribution of echinoderms and fish prey to the diet of *M. aeglefinus* (Antipova *et al.*, 1980). Foraging fishes are known to be able to alter their behaviour in response to variations in food availability and the threat of competition (Dill, 1983). *Melanogrammus aeglefinus* probably consume lower quality food choices when faced with adversity in acquiring a preferred resource (Vinyard, 1980; McNamara & Houston, 1987). Feeding on echinoderms could be a strategy for *M. aeglefinus* to maintain constant energy levels during periods of low prey fish abundance and high competition with other gadoids that may occur on a multi-annual cycle (Temming *et al.*, 2004). Intra-annual abundances for all prey items of *M. aeglefinus* from the ecosystems surveyed in this study, however, were not examined and it would be a useful avenue for future research to measure selectivity across time in all of these populations.

An opportunistic feeding mode for *M. aeglefinus* has been demonstrated in several earlier studies (Mattson, 1992; Schückel *et al.*, 2010) and current observations from the different ecosystems reveals that high amounts of fishes in the diet of larger North Sea *M. aeglefinus* are likely to be a consequence of prey availability rather than an ontogenetic shift (*i.e.* the high abundance of sandeels *Ammodytes* spp.). This is supported by observations on Dogger Bank (55° N; 03° E) in the North Sea, where Sell & Kröncke (2013) found the distribution of *M. aeglefinus* to be more strongly correlated with abiotic habitat variables (depth, temperature and sediment composition) than with biotic factors, including the availability of potential mud dwelling prey. It has also been shown that *M. aeglefinus* adapt their diets based on prey availability due to benthic disturbance from fishing gear, with less benthos and slightly more fish consumed in disturbed habitats (Smith *et al.*, 2013).

There is some indication that echinoderms have higher nutrition and energy content than expected, but past studies have shown that the caloric content of fish to be higher than echinoderms. Brawn *et al.* (1968) found that prey fishes contained two to three times more kJ g^{-1} than echinoderms in St Margaret's Bay in Nova Scotia, Canada (44° 302N; 64° 002W). Other studies have found lower energy content in sea stars and brittle stars compared with fishes (19.10 kJ g^{-1} ash-free dried for echinoderms and 22.96–24.22 kJ g^{-1} ash-free dried mass for fishes), while sea urchins had a higher energy content (25.82 kJ g^{-1} ash-free dried mass) than both demersal or pelagic fishes (Steimle & Terranova, 1980; Packer *et al.*, 1994). Inconsistencies in the values of energy contents drawn from these studies may be due to the different species contributing to the sample groups. There may also be a seasonal element to the appeal of echinoderms as *M. aeglefinus* prey. When echinoderms are gravid they are more nutritionally valuable and contain a higher lipid and protein content. Steimle & Terranova (1980) found that the energy content in *E. parma* doubled during autumn spawning periods compared with spring values. Certain conditions in timing and availability may make echinoderms a logical food choice for *M. aeglefinus*.

There is some evidence that hard shelled invertebrates, such as echinoderms and bivalves, digest more slowly and less efficiently than other, soft-tissue prey such as fishes and polychaetes (MacDonald *et al.*, 1982; Tibbetts *et al.*, 2004; Jaworski & Ragnarsson, 2006). Preliminary calculations indicate that the digestibility of hard shelled invertebrates are only *c.* 10% less than that of soft bodied prey such as fishes and polychaetes in gadoid diets and respective evacuation rates could be on the order of one to two times slower (MacDonald *et al.*, 1982; Tibbetts *et al.*, 2006). If this is the case, the relative importance of echinoderms in the diet of *M. aeglefinus* could potentially be amplified by a similar factor. If, however, the per cent diet composition of echinoderms in the diet of *M. aeglefinus* is lower, the fact remains that echinoderms still remain a notable, consistent and regular component of the diet of *M. aeglefinus*. In contrast, there is evidence that the test in echinoderms may actually promote more efficient digestion in predatory fishes. Mattson (1992) indicates that the calcareous trst of echinoderms act as a grinding element and can enhance digestion as well as ingestion. This increased maceration may compensate for the low nutritional value inherent in echinoderm prey and could ultimately improve the digestion of all hard-shelled organisms in *M. aeglefinus* diet.

The implications of understanding the diets of target fish species span far beyond just knowing what they are eating. Assessing food habits in fishes, particularly in opportunistic feeders, can give insight into habitats and prey species distributions that are difficult to survey (Link, 2004; Cook & Bundy, 2012). In determining that *M. aeglefinus* consume large proportions of echinoderms in many regions, this study has identified an important link between the benthos and harvested fishes. This is a mechanism that is rarely considered in management decisions and implies that impacts to the benthic habitat in certain regions will probably affect *M. aeglefinus* more than other harvested gadoid species. From an EBFM perspective, the functional redundancies of *M. aeglefinus* lie alongside other echinoderm consumers such as American plaice *Hippoglossoides platessoides* (Fabricius 1780) and ocean pout *Macrozoarces americanus* (Bloch & Schneider 1801) rather than species of the same family group (Zamarro, 1992; Packer *et al.*, 1994; Link, 2007).

While traditional conservation strategies, such as fisheries closures, are not always effective at increasing target fish stocks (Fisher & Frank, 2002; Kelly *et al.*, 2006), *M. aeglefinus* have historically responded well to these management options (Brodziak *et al.*, 2008). In the mid-1990s, *M. aeglefinus* stocks in the north-west Atlantic Ocean were the lowest on record (Hutchings, 2000). After strict closures as a response to the declining stock status, *M. aeglefinus* stocks increased dramatically (Murawski *et al.*, 2000; Brodziak *et al.*, 2008). *Melanogrammus aeglefinus* are also known to have a restricted daily ambit compared with other gadoids, indicating a strong association with local habitats (Perry & Smith, 1994; Fogarty *et al.*, 2001). Reduced impacts on the benthic habitat compounded with the high proportion of echinoderms in *M. aeglefinus* diet, in part, explain why *M. aeglefinus* stocks have successfully responded to fisheries closures and marine protected areas (Smith *et al.*, 2013). In areas where *M. aeglefinus* exhibited a high frequency of piscivory, such as the North Sea, fishery closures did not improve their abundances nearly as much (FSBI, 2001; Fisher & Frank, 2002) . These differences in feeding habits between populations can complicate management efforts because species may not respond the same way in all regions of their distributional range. Thus, conservation methods need to take into account the biology of the ecosystem as well as species-specific life histories to ensure positive and efficient management outcomes.

The importance of the benthic habitat to harvested fishes is becoming increasingly apparent. The interconnectedness and complexity of food webs is an important consideration in sustainable fisheries management (Pauly *et al.*, 1998; Link, 2011; Cook & Bundy, 2012; Link & Auster, 2013). To complicate the understanding of trophic webs in fisheries even further, comparative studies such as this one are revealing that populations of the same fish species can interact with their local habitat differently between regions. This emphasizes the need for ecosystem-level management that will improve the resiliency and long-term economic viability of harvested fish throughout their distributions.

We would like to thank the research vessel crews at NOAA and DFO whose hard work has made studies such as this possible. We also thank the International Council for the Exploration of the Sea (ICES) and the Institute for Marine Resource and Ecosystem Studies (IMARES) for making this stomach data available. Partial support for data collection was provided by E.U. FP7 project BENTHIS (KBBE.2012.1.2-09) (J.K.P.). We would like to thank internal reviewers K. Holsman, R. Heintz and K. Osgood for their helpful comments and suggestions. This work was supported by a NOAA Postdoctoral Fellowship to J.C.T.

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