A trans-Atlantic examination of haddock Melanogrammus aeglefinus food habits

Tam, J.C.; Link, J.S.; Large, S.I.; Bogstad, B.; Bundy, A.; Cook, A.M.; Dingsør, G.E.; Dolgov, A.V.; Howell, D.; Kempf, A.; Pinnegar, J.K.; Rindorf, Anna; Schückel, S.; Sell, Anne F.; Smith, B.E.

Published in:
Journal of Fish Biology

Link to article, DOI:
0.1111/jfb.12983

Publication date:
2016

Document Version
Peer reviewed version

Link back to DTU Orbit

Citation (APA):
TITLE: A Trans-Atlantic Examination of Haddock (Melanogrammus aeglefinus) Food Habits


ADDRESSES:
1 NOAA-Fisheries, 166 Water Street, Woods Hole, MA 02543, USA
2 International Council for the Exploration of the Seas (ICES), Copenhagen V 1553, Denmark
3 Institute of Marine Research (IMR), 5817, Bergen, Norway
4 Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, NS, B2Y 4A2, Canada
5 Polar Research Institute of Marine Fisheries and Oceanography (PINRO), 6, Knipovich-St., Murmansk, 183038, Russia
6 Thünen Institute of Sea Fisheries, Palmaille 9, 22767 Hamburg, Germany
7 Centre for Environment, Fisheries & Aquaculture Science (Cefas), Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK
8 National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Slot, DK-2920 Charlottenlund, Denmark
9 BioConsult, Reeder-Bischoff Str. 54, 28757 Bremen, Germany

*Corresponding author: jamie.tam@noaa.gov +01 508 495 2083

RUNNING HEADLINE: Trans-Atlantic examination of haddock diet
Haddock (*Melanogrammus aeglefinus*) is a commercially and ecologically important gadoid in the food webs and economies of regional ecosystems across the North Atlantic. *Melanogrammus aeglefinus* is reported to be primarily piscivorous in some cases and primarily an echinoderm feeder in others. Often, the species exhibits ontogenetic dietary shifts, focusing on a specific prey at small sizes and on different prey at larger sizes. Here we explore and contrast the food habits of *M. aeglefinus* across multiple northeastern and northwestern Atlantic 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 do emerge regarding where and when *M. aeglefinus* primarily eat fishes versus 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. We view this apparent binary choice as part of a gradient of prey options, contingent upon a suite of factors external to *M. aeglefinus* dynamics. We discuss the energetic consequences of this prey choice, noting that in some instances it may not be a choice at all.

**KEY WORDS:** haddock, prey choice, echinoderms, piscivory, ecosystem-based fisheries management
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, 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 acantbias* is a widespread commercial fish that appears to consume proportionately more benthic invertebrates in New Zealand (Hanchet, 1991), teleost fishes in the North Atlantic (Holden, 1966; Link et al., 2002) and large proportions of Euphausiids in the Eastern Pacific (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* 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 in 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* transition after 3-5 months from living in the upper reaches of the water column to living on muddy, sandy or gravel substrate (Platt *et al*., 2003; Sell & Kröncke, 2013). As demersal fish, they spend their adult life in close association with 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 (Tseeb, 1964; 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 executed comparatively.

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), seastars *Pisaster ochraceus* as a keystone predator on North Pacific intertidal communities (Paine, 1966, 1969) and sea urchins *Strongylocentrotus droebachiensis* denuding temperate areas entirely of macrophytes (Watanabe & Harrold, 1991;
Gagnon et al., 2004; Lauzon-Guay & Scheibling, 2007). However, outside of the sea otter-
urchin-macrophyte feeding dynamic (Estes & Pal misano, 1974; Dayton, 1975), studies of
predation on echinoderms seldom occur (but see Pinnegar et al., 2000; 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 to the role of fish prey,
particularly in the northern Atlantic.

A unique aspect of *M. aeglefinus* feeding is that echinoderms can make up a significant part
of their diet in the Northwestern Atlantic (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 per gram than other invertebrate diets items
including worms, gastropods, bivalves and crustaceans (Steimle & Terranova, 1980). Survey
observations of fish stomach contents in the Northwest Atlantic 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**

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

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

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, we grouped prey according to rough taxonomic classification of echinoderm, fish, or other
prey item. To determine if *M. aeglefinus* undergo similar ontogenetic shifts in diet composition
across regions, we also grouped *M. aeglefinus* into the following size 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, 2002a). Where time series data was available (Georges Bank,
Gulf of Maine, US 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 tau (Fredricks & Nelsen, 2007) was used to examine the non-parametric, rank-order
relationship between the proportion of echinoderm and fish 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 Chi-square analysis. To explore and test for relationships within ecosystems of *M. aeglefinus* diet between size classes, Chi-square analysis of the proportion of each diet item in the stomachs of fish across size classes was used. To examine trends in prey selection of *M. aeglefinus* at each ecosystem over time, a generalized linear model was used with percent 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.

At each 5 year block within each ecosystem, a Chi-square 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 of echinoderms and fishes in the diet of *M. aeglefinus* that could be applied to all ecosystems according to the Kendall’s tau analysis (Figure 2; $\tau = 0.33$, $Z$-score = 1.25, $p = 0.21$). 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 size class data (Figure 3). In several ecosystems there was a significantly lower occurrence of piscivory (i.e. eggs and larvae) with increasing size (Georges Bank: $X^2 = 30.52$, df = 2, $p = <0.001$; Gulf of Maine: $X^2 = 15.91$, df = 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 ($X^2 = 38.34, 23.90$, df = 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, $M. aeglefinus$ ate a large proportion of echinoderms in most ecosystems. Echinoderms were a proportionately 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 ($X^2 = 22.29, 17.82$, df = 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 ($F_{1,4} = 0.18$, $p = 0.95$). Long-term stomach content data indicated that echinoderms were consistently a part of $M. aeglefinus$ diet over time, but neither diet item exhibited any positive or negative 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 Chi-square 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 (Figure 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:
Atlantic cod *Gadus morhua* being a generalist feeder, saithe *Pollachius virens* and some hake species consuming 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, 2002b; 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 are not able to eat as many larger prey fish compared to *G. morhua* (Løkkeborg *et al.*, 1989).

*M. 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 to prey fish, their relatively high
abundances and relatively low defenses (slow moving) make them a very accessible prey to *M. aeglefinus*. Echinoderms in the northwestern Atlantic 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 dollars *Echinarchachinus parma* in shallower regions and brittlestars *Amphiopus* spp. and sea cucumbers *Echinocardium cordatum* 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 cal m\(^{-2}\) of benthic habitat even though they are relatively low in energy content compared to other invertebrate phyla (Brawn *et al.*, 1968). In the North Sea, the brittlestar *Amphiura filiformis* dominates the benthic system and lives in densities up to 2250 indv m\(^{-2}\) (Skold *et al.*, 1994; Wood *et al.*, 2009), and other important species include *Echinocyamus pusillus, Ophiura albida, Ophiura affinis* and *Echinocardium cordatum* 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 include 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 (Figure 4). At five year intervals in 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 fish 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* likely 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). However, intra-annual abundances for all prey items of *M. aeglefinus* from the ecosystems surveyed in this study 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 fish in the diet of larger North Sea *M. aeglefinus* is 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 in the North Sea, where Sell and Kröncke (2013) found the distribution of *M. aeglefinus* to be more strongly correlated with abiotic habitat parameters (depth, temperature, 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 fish contained 2-3 times more cal g\(^{-1}\) than echinoderms in St. Margaret’s Bay in Nova Scotia, Canada. Other studies have found lower energy content in seastars and brittlestars compared to fish (19.10 kJ g\(^{-1}\) for echinoderms and 22.96-24.22 kJ g\(^{-1}\) for fish; ash-free dried weight), while sea urchins had a higher energy content (25.82 kJ g\(^{-1}\); ash-free dried weight) 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 and Terranova (1980) found that the energy content in *E. parma* doubled during autumn spawning periods compared to 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 approximately 10% less than that of soft bodied prey such as fish and polychaetes in gadoid diets, and respective evacuation rates could be on the order of 1-2 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 percent 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.*
In contrast, there is evidence that the shells in echinoderms may actually promote more efficient digestion in predatory fish. Mattson (1992) indicates that the calcareous shell 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 organism 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 fish. This is a mechanism that is rarely considered in management decisions and implies that impacts to the benthic habitat in certain regions will likely 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* and ocean pout *Macrozoarces americanus* 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 northwest Atlantic were the lowest on record (Hutchings, 2000). After strict closures as a response by 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 to other gadoids, indicating a strong association with local habitats (Perry & Smith, 1994; Fogarty et al., 2001). Reduced impacts to 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 MPAs (Smith et al., 2013). In areas where *M. aeglefinus* exhibited a high frequency of piscivory, such as the North Sea, fisheries 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 fish 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 our 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.

ACKNOWLEDGEMENTS
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 ICES and IMARES for making this stomach data available. Partial support for data collection was provided by EU FP7 project BENTHIS (KBBE.2012.1.2-09) (J.K.P.). We would like to thank internal reviewers Kristin Holsman, Ron Heintz and Kenric Osgood for their helpful comments and suggestions. This work was supported by a NOAA Postdoctoral Fellowship to JCT.

REFERENCES


Løkkeborg, S., Bjordal, A. & Fernö, A. (1989) Responses of Cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) to baited hooks in the natural environment. Canadian Journal of Fish and Aquatic Sciences, 46, 1478–1483.

MacDonald, J.S., Waiwood, K.G. & Green, R.H. (1982) Rates of digestion of different prey in Atlantic Cod (Gadus morhua), Ocean Pout (Macrozoarces americanus), Winter Flounder (Pseudopleuronectes americanus), and American Plaice (Hippoglossoides platessoides). Canadian Journal of Fisheries and Aquatic Sciences, 39, 651–659.


Melanogrammus aeglefinus to benthic prey availability in three different areas of the northern
North Sea. *Journal of Fish Biology, 77*, 98–118.

assemblages — A case study on the Dogger Bank (North Sea). *Journal of Sea Research, 80*, 12–
24.

predator body size and changing climate alter trophic structure in an oceanic ecosystem.

Skold, M., Loo, L. & Rosenberg, R. (1994) Production, dynamics and demography of an


cod: insights from tri-monthly, localized scales of sampling. *Journal of Fish Biology, 71*, 749–
762.

Smith, B.E. & Link, J.S. (2010) *The Trophic Dynamics of 50 Finfish and 2 Squid Species on the
Northeast US Continental Shelf*. Woods Hole, MA. USA.

Research Board of Canada, 1924*, 1–154.

Steimle, F.W. (1990) *Benthic Macrofauna and Habitat Monitoring on the Continental Shelf of*
the Northeastern United States. Washington, DC. USA.


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 percent. Diet composition was measured as the weight of the diet items relative to the total weight of *M. aeglefinus* stomachs in percent.

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>Time of sampling</th>
<th>Type of data collected</th>
<th><em>M. aeglefinus</em> stomachs sampled (#)</th>
<th>Collection method</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scotian Shelf</td>
<td>1995-2009</td>
<td>Diet composition</td>
<td>2690</td>
<td>Data compiled from Department of Fisheries and Oceans trawl surveys.</td>
<td>(Cook &amp; Bundy, 2010, 2012; Bundy et al., 2011)</td>
</tr>
</tbody>
</table>
Table II. Results of the Chi-square analysis examining the relationship between echinoderms and fish in *M. aeglefinus* diet within each ecosystem. Bold numbers indicate significant differences.

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>$\chi^2$</th>
<th>p-value</th>
<th>Dominant prey</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gulf of Maine</td>
<td>3.79</td>
<td>0.05</td>
<td>None</td>
</tr>
<tr>
<td>Georges Bank</td>
<td>0.12</td>
<td>0.73</td>
<td>None</td>
</tr>
<tr>
<td>Scotian Shelf</td>
<td>2.80</td>
<td>0.09</td>
<td>None</td>
</tr>
<tr>
<td><strong>North Sea</strong></td>
<td><strong>6.92</strong></td>
<td>&lt; 0.01</td>
<td>Fish</td>
</tr>
<tr>
<td>Rockall Bank</td>
<td>22.11</td>
<td>&lt; 0.01</td>
<td>Fish</td>
</tr>
<tr>
<td>Barents Sea</td>
<td>0.02</td>
<td>0.89</td>
<td>None</td>
</tr>
<tr>
<td>Irish Sea</td>
<td>3.77</td>
<td>0.05</td>
<td>None</td>
</tr>
<tr>
<td><strong>Celtic Sea</strong></td>
<td><strong>22.54</strong></td>
<td>&lt; 0.01</td>
<td>Echinoderms</td>
</tr>
<tr>
<td>Spitzbergen</td>
<td>43.67</td>
<td>&lt; 0.01</td>
<td>Echinoderms</td>
</tr>
</tbody>
</table>
Table III. Results of the Chi-square analysis (p-values) examining the relationship between echinoderms and fish in *M. aeglefinus* diet at each five year block within ecosystems. Bold numbers indicate significant differences.

<table>
<thead>
<tr>
<th>Year</th>
<th>Georges Bank</th>
<th>Gulf of Maine</th>
<th>Scotian Shelf</th>
<th>Barents Sea</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1985</td>
<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>1990</td>
<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
<td>0.90</td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td>0.08</td>
<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
<td>0.85</td>
</tr>
<tr>
<td>2005</td>
<td>&lt; 0.01</td>
<td>0.82</td>
<td>&lt; 0.01</td>
<td>0.09</td>
</tr>
<tr>
<td>2010</td>
<td>0.29</td>
<td>0.11</td>
<td>&lt; 0.01</td>
<td>0.10</td>
</tr>
<tr>
<td>2015</td>
<td>0.56</td>
<td>0.71</td>
<td></td>
<td>0.59</td>
</tr>
</tbody>
</table>
FIGURE CAPTIONS

Figure 1. Map of different ecosystems sampled.

Figure 2. Percent contribution of echinoderms and fish to *M. aeglefinus* from different ecosystems. Diet from Celtic Sea, Irish Sea and Spitzbergen were measured in frequency of occurrence (number of stomachs containing the diet item relative to the total number of stomachs), diet from the Barents Sea, North Sea, Rockall Bank, Scotian Shelf, Georges Bank and Gulf of Maine was measured in diet composition (weight of the diet items relative to the total weight of *M. aeglefinus* stomachs in percent).

Figure 3. Percent contribution of echinoderms and fish to the diet of different size classes (cm) of *M. aeglefinus* in different ecosystems where size class data was available.

Figure 4. Percent contribution of echinoderm (grey dotted line) and fish (black solid line) over time (year) in different ecosystems where time series data was available.
Figure 1. Map of different ecosystems sampled.
Figure 2. Diet of *M. aeglefinus* in different ecosystems.
Figure 3. Diet of different size class of *M. aeglefinus*.
Figure 4. Diet of *M. aeglefinus* over time.