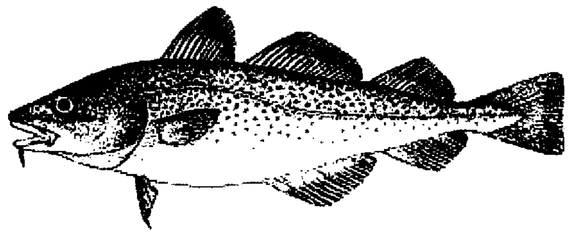

The Trophic Ecology of Atlantic Cod: Insights from Tri-monthly, Localized Scales of Sampling

FINAL REPORT

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Period of Performance: October 2001 through June 2004

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ABSTRACT

The effects of oversfishing, environmental change, fish community dynamics, and other factors that have altered the trophic ecology of Atlantic cod (*Gadus morhua*) are generally not well understood. Most of the research on cod trophic ecology has been either broad-scale oceanic studies or *in vivo* laboratory studies. We examined the small-scale variation of cod feeding based upon tri-monthly stomach sample collections from a nearshore, localized region off Cape Cod, Massachusetts. We had two major objectives for this work: 1) to relate any change in cod diet and amount of food eaten to changes in temperature, spawning, prey abundance, and major weather events, filling the "information gap" between broad-scale and lab studies, and 2) to work cooperatively with the fishing industry to transform previously "anecdotal" information into quantitative data available for fisheries science and management. Final results suggest that the amount of food eaten by cod is generally stable throughout the year, except when pelagic forage fish migrate through the area. This corresponds to critical periods in the life history of cod. The temporal variation in diet composition remained remarkably consistent each year over the 28-months of the project, suggesting important feeding periods for cod which correspond to environmental and biological queues. The diet is comprised primarily of several species of forage fish (e.g., Atlantic herring (*Clupea harengus*), sand lance (*Ammodytes sp.*), and Atlantic mackerel (*Scomber scombrus*)), ophiuroids, *Cancer* crabs, and other small crustaceans. Additionally, these results confirm the preference cod exhibit for prey such as herring, sand lance, and crabs. We infer that cod generally eat local forage fish and benthic macro-invertebrates and then supplement their diet by gorge feeding upon migrating pelagic species.

INTRODUCTION

The diet of Atlantic cod has been well chronicled (reviewed in Palsson 1994, Methven 1999). There have been several broad-scale studies of cod feeding ecology in the U.S. Atlantic and other ecosystems (Langton and Bowman 1980, Langton 1982, Bowman and Michaels 1984, Vinogradov 1984, Mattson 1990, Palsson 1994, Grunwald and Koester 1994, Hoines and Bergstad 1999, Methven 1999, Link and Almeida 2000, Link and Garrison 2002a, Link and Garrison 2002b). There have also been numerous *in vivo* studies of cod feeding (e.g. dos Santos and Jobling 1991, Bjornsson 1993, Jobling et al. 1994, Grant et al. 1998, Kjesbu et al. 1998, Grant and Brown 1999, Puvanendrum and Brown 1999, Dutil and Lambert 2000, Lambert and Dutil 2000, Purchase and Brown 2001). From these studies we can infer numerous rates, processes, and relationships about cod, cod prey, and oceanographic conditions.

There have been however, only a limited number of studies conducted on cod feeding at small temporal (month) and spatial (approximately 300 mi^2 or 777 km^2) scales. In a sense, there is a gap between the small scale laboratory experiments and the broad scale studies. Data acquired from a localized area two or three times a month over a two-year period would help to fill this gap. The data collected at this scale would provide a new perspective on cod feeding habits with particular respect to short-term and seasonal temperature changes, pre-spawning, spawning, and post spawning events, migration of key prey, cod migration, and intense episodic weather events. It has been hypothesized, but is still unclear, that cod feeding (i.e. diet composition, amount of food eaten, consumption rates, etc.) can alter in response to those factors (e.g. Konstantinov et al. 1985, Methven and Piatt 1989, Lilly 1991, 1994, Sparholt 1991, Kjesbu

1994, Uzars 1994, Burton et al. 1997, Lambert and Dutil 1997, 2000, Swain 1999, Lee and Khan 2000, Link and Garrison 2002b).

The information collected on monthly and local scale cod feeding can have broad implications for fisheries management. It may be that forage fish are most important during the pre-spawning/spawning period and should not be over-exploited in general or removed at that time to preserve cod spawning. It may also be that cod aggregate to feed on a temperature induced increase in benthic invertebrate populations, implying that the habitat where this phenomenon occurs is critical during that time.

The human element behind the rationale for the proposed research should not be discounted. This project is an opportunity for fishermen and scientists to do collaborative research that may otherwise not occur. Fishermen are often frustrated when their knowledge is considered "anecdotal" and not useful in a quantitative fisheries management and science context. This project has already provided a way to help quantify observational information and as such has been beneficial to both the scientific and fishing communities.

REVIEW OF PREVIOUS WORK

The primary source of data regarding cod food habits in the northeast U.S. continental shelf ecosystem comes from the NMFS, Northeast Fisheries Science Center (NEFSC) broad scale survey from the past forty years (Link and Almeida 2000). These data were collected on bottom trawl surveys from Cape Hatteras, NC to Nova Scotia in depths of approximately 27 to 366 m primarily during the spring and autumn each year. From the research trawl catch, subsamples of cod have been eviscerated to examine the stomach contents, both prey type and amount, across the time series. These results generally indicate that cod are opportunistic generalists, feeding on a variety of fish and invertebrate prey along a gradient from the pelagia to the benthos.

Several other studies have been conducted (Langton and Bowman 1980, Langton 1982, Bowman and Michaels 1984, Vinogradov 1984, Mattson 1990, Palsson 1994, Grunwald and Koester 1994, Hoines and Bergstad 1999, Methven 1999) and document that cod is an important invertebrate and fish predator in numerous continental shelf ecosystems. Cod are, or once were, the dominant piscivore in many ecosystems. Several models have estimated that the magnitude of cod predation on other fish and invertebrate populations can be significant (e.g. Andersen and Ursin 1977, Helgason and Gislason 1979, Daan and Sissenwine 1991, Collie and Tsou 1996, Bogstad et al. 1997, Overholtz et al. 2000, Link and Garrison 2002).

The degree of spatio-temporal overlap between cod and its prey is usually reflected in the diet. Changes in the prey field between geographic regions or across time are seen in the diet, having been documented for several ecosystems (e.g. Konstantinov et al. 1985, Methven and Piatt 1989, Lilly 1991, 1994, Sparholt 1991, Uzars 1994, Lee and Khan 2000). For example, Lee and Khan (2000) show a shift from fish to crustacean dominance from south to north along the Labrador Coast, reflecting the distribution and abundance of capelin in the south and snow crabs in the north. In fact, cod have been used as a "sampler" to assess the distribution, abundance, and size structure of various prey (Lilly and Parsons 1991, Fahrig et al. 1993, Link 2004). We intended to further refine our understanding of this phenomenon by more intensive sampling at a local scale.

Several other studies have been executed in the laboratory (dos Santos and Jobling 1991, Bjornsson 1993, Jobling et al. 1994, Grant et al. 1998, Kjesbu et al. 1998, Grant and Brown

1999, Lindholm et al. 1999, Morgan et al. 1999, Puvanendrum and Brown 1999, Dutil and Lambert 2000, Lambert and Dutil 2000, Winger et al. 2000, Purchase and Brown 2001) which generally elucidate behavior, vital rates, and related processes at the scale of individual fish. Many of these works have been extended and hence scaled up to conditions that infer processes occurring in the field. Many of these results are used in key models of cod biology.

Some studies indicate that a more "balanced" diet, specific diet components, or simply more available food will increase cod growth (Brown et al. 1989, Mehl and Sunnana 1991, Lambert and Dutil 1997, Jobling et al. 1994, Clark et al. 1995, Krohn et al. 1997, Dutil and Lambert 2000). Others indicate that spawning ceases or is curtailed if inadequate food is present (Kjesbu 1994, Burton et al. 1997, Lambert and Dutil 2000). Lambert and Dutil (1997) and Swain (1999) suggest that combined with overfishing, changes in cod diet are responsible for declines in cod stocks and distribution shifts. However, Lilly (1991, 1994) suggests that changes in cod distribution and inferred differences in growth rate at locales with different temperatures may not be related to changes in capelin distribution and abundance (and hence, their proportion of cod diet). Additionally, the growth and mean size of cod in the northeast U.S. continental shelf ecosystem has remained relatively constant across time (Mayo et al. 1998, O'Brien 1999, O'Brien and Munroe 2000), and the severe declines in cod abundance are primarily attributed to intense fishing pressure (Serchuk and Wigley 1992, Serchuk et al. 1994, Murawski et al. 1997, Fogarty and Murawski 1998). Whether food type or amount influences cod spawning, fecundity, juvenile survival, or recruitment in the northeast U.S. continental shelf ecosystem is unknown. Thus, whether changes in cod trophic dynamics have broad implications for cod populations remains a key question.

PROJECT OBJECTIVES AND SCIENTIFIC HYPOTHESIS

Our principal objective was to study the short-term monthly changes in cod feeding habits at a local scale, hypothesizing that there is no change in cod feeding across a two year timescale at a given locale.

The study examined the timing of expected shifts in cod diet with respect to seasons, temperature, prey (fish and invertebrate) abundance, spawning, and major weather events. Our goals were to:

1. Examine cod stomachs three times per month for two years in one general area (see Figure 1 for location);

2. Collect basic oceanographic data (e.g. temperature, depth, etc.) at the same sampling intensity and locales;

3. Estimate consumption rates of cod for this time scale;

4. Determine if any patterns exist in the diet composition and amount of food eaten by cod;

5. If any patterns of cod feeding exist, attempt to relate such patterns to oceanographic conditions, prey field (obtained from other studies), fish biology (e.g. spawning) or related factors.

This approach allowed us to evaluate "anecdotal" observations in a quantitative fashion. For example, fishermen have noted that cod change their behavior (schooling, distribution, migration, etc.) in the winter and are no longer found in shoal waters (16-20 fathoms; 30-37 m) where they were once common at this time of year but rather in deeper waters (30-50 fathoms; 55-90 m). Fishermen speculate that these differences are due to a change in temperature, the loss of population genetic memory as a result of many of the fish simply being caught, removal of key seasonal prey (e.g. brittle stars) by storm events, or other declines in the availability of prey which form a large part of the cod diet. For instance, fishermen note that herring and mackerel are a large part of the diet of cod right before and during cod spawning. Noting the importance of these forage fish would be valuable from both the perspective of cod fishermen and multi-species management considerations. Fishermen also observe large amounts of sand lance in the diet of cod in late spring and early summer, and conclude that sand lance allow cod to grow through the summer. As such, fishermen speculate that sand lance are an important seasonal food item that allow cod "to maintain themselves" until schools of herring and mackerel arrive. Associated anecdotes relating cod distribution or abundance to cod feeding, and by extension cod feeding to storm events, bad "health of the bottom", gear effects on the ocean bottom, changes in prey availability, and other "habitat" issues could be further explored by the study.

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METHODS

Fish were collected using hand lines during routine research days at sea. The depth fished ranged from approximately 50-300 ft of water (15-92 m). The general gear used for sampling included 150 lb (68 kg) test line with a 100-lb (45 kg) test leader, having a 26 oz (737 g) jig with approximately 4 lures (aka "bugs") spaced at 2¼ ft (69 cm) intervals above the jig. Bait was not used to obtain research samples. When fished in 230 ft (70 m) of water or more, and/or sea-state conditions were rough electric reels were used.

The vessel used was the *F/V Reina Marie* (USCG Doc. #926302, Federal Permit #221764), owned and operated by Theodore J. Ligenza. The vessel is a 31 ft BHM, with a draft of 3½ ft, and is powered with a 225 hp John Deere diesel engine. The boat is equipped with a color depth sounder, radar, loran, GPS, and VHS radio.

Our sampling area encompassed a 300 mi^2 (777 km^2) region off Cape Cod, Massachusetts (Figure 1). Specific fishing locations included Nauset ground SW to Crab Ledge, Southeast to Great Hill grounds, to "The Lemons" and then to "The Mussels", east to "The Inshore Figs" and "The Figs". The particular fish sampling locales were determined within the general area on an *ad hoc* basis by Mr. Ligenza to ensure the highest probably of capturing fish. We note that jig fishermen cannot fish in certain areas due to potential gear conflicts.

Stomach samples were collected approximately every ten days (two or three times a month) for two years and 4 months, beginning in October of 2001 and ending January 2004. At sea, fish were separated into 20 cm size classes, starting at 20 cm. Stomachs from five to ten fish were taken from each size class. The preliminary target was approximately 30 fish per trip.

While removing each stomach, cod showing signs of regurgitation (i.e. flaccid or inverted stomach) were discarded. Collected stomachs were then placed in an individual plastic jar with 95% ethanol. Each jar received a tag recording date, location where the fish was caught, fish length, sex, and sexual maturity.

Upon returning to the dock, the stomach samples were transported to Marine Research, Inc. (MRI) in Falmouth, MA for processing following standard NEFSC stomach processing protocols. Very briefly, each stomach was emptied, the stomach contents weighed (nearest 0.01 g), the prey separated and identified to the lowest taxon feasible, and any fish prey lengths measured (nearest 1.0 mm).

DATA

We completed 94 sampling trips aboard the *F/V Reina Marie* (Table 1) during the project. During these trips, a total of 2481 stomachs were sampled with an average of about 89 stomachs/month. All stomachs were analyzed and prey identified by MRI and resulting data entered and archived. Table 1 provides a summary of the sampling trips completed, including the number of cod stomachs excised and preserved for laboratory analysis during each trip and samples collected for other researchers. The data collected during 2001 and 2002 are grouped individually by year while data collected during 2003 is detailed for each month. The audited data from our project has been incorporated into the Northeast Fisheries Science Center, Food Web Dynamics Program Food Habits Database (http://www.nefsc.noaa.gov/femad/pbio/fwdp/FWDP.htm).

RESULTS AND CONCLUSIONS

The data were characterized by the presence of recurrent temporal feeding patterns occurring across the 28-month timescale of the project (Figure 2). There was a general increase in mean stomach content from a low of about 13.6 g/stomach from October to early December, 2001. After a peak in mid-December to about 57.5 g/stomach, mean content dropped to low levels during mid to late winter (January to March 2002) when stomachs averaged only about 7.7g. In April 2002, there was a second peak followed by a decline, but to an average level of 25.1 g, greater than in the previous late autumn. This apparent seasonality in the total amount of food eaten corresponds to both migrations of Atlantic herring and Atlantic mackerel (since the peaks in consumption in December and April were made up largely of these species) (Figure 3). Throughout the second year and the final 4 months of the project, this seasonality in the total amount of food consumed by cod was also apparent, revealing similar predation upon Atlantic herring and Atlantic mackerel, although the total amount of prey consumed by cod appears to be reduced in comparison to the first year.

The diet was made up primarily of benthic macroinvertebrates (i.e. various crustaceans, and ophiuroids), sand lance, and other small fish (Figures 3 & 4). Cod are opportunistic generalist feeders and appear to switch to Atlantic herring, and mackerel when these species migrate through the local area. Cod appear to prefer fish when available, particularly migratory pelagics, than crabs and other benthos. It is also apparent that cod may prefer a diet of fish as they age and mature. In an analysis of diet in relation to length, it was noted that only about 40% of the diet of cod less than 40 cm was fish, whereas cod greater than 40 cm averaged 64% fish in their stomachs (Figure 5). This apparent ontogenetic shift in diet suggests cod less than 40 cm are more dependent upon the benthos (i.e. benthic macroinvertebrates).

The annual reproductive cycle of Atlantic cod also coincides with a relatively key feeding period. When stomach contents were related to maturity stage, a confirming pattern emerged (Figure 6). Cod whose gonads were developing or ripe and running (spawning) averaged about 17.8 g/stomach and 12.6 g/stomach respectively. However, those that had recently completed their annual spawning activity (their gonads in the spent stage) averaged over twice as much food in their stomachs at 37.6 g. This indicates that in the period immediately after spawning cod tend to feed heavily, but during the portion of the cycle leading up to and including spawning, feeding is limited. The timing of this post-spawning event (spent stage) begins approximately around the initial migration period of Atlantic herring and Atlantic mackerel when a relatively larger abundance of prey is available. Across the second year of sampling (2002-2003), an absence of herring was detected during this initial migration period (Figure 4), although a general increase in mean stomach content still occurred relevant to this post-spawning cycle.

We conclude the seasonal variation in cod feeding habits is consistent, recurrent, linked to key bioenergetic processes, and is timed to coincide with a major influx of energy to the area. Cod primarily feed on benthic macroinvertebrates during the year, but actively "gorge-feed" upon migratory pelagic fish when available. These temporal feeding patterns are related to prey availability, prey abundance, changes in water temperature, and spawning time. One of the most important observations is that these patterns remained consistent each year of the study. Our results are generally similar, but more refined in scale, to broad-scale studies surrounding Atlantic cod trophic dynamics in the north Atlantic. The additional value of our local-scale project offers an image with greater detail for detecting subtle feeding variation (i.e. ecosystem-level changes) throughout the year and suggests critical feeding periods as well as critical prey for Atlantic cod. This information could prove beneficial for supporting ecosystem-based approaches to fisheries management.

PARTNERSHIPS

The high quality and far-reaching extent of the fisherman-scientist relationship was an important aspect of our research project. The demanding nature of the project's field sampling detail could not have been accomplished without strong interests from the fisherman and the scientists involved. As a result, a relationship of trust was built, allowing for enhanced participation from each party. On many levels, the fisherman and scientists were able to share their own expertise, teaching and learning from one another over the duration of the project. There were many lessons learned over the course of the project, including:

1. Fishermen expect, and tend to be, jacks-of-all-trades; scientists tend to be specialists.

2. Fishermen are very observant, however, not all observations are useful nor all questions or hypotheses worth pursuing. Open discussions between participants and an understanding of all points of view are critical to making decisions and 'buying into' those decisions.

3. Experiences, observations, and anecdotes do not necessarily mean data. The collection of data to support the experiences, observations, and anecdotes is often laborious and complicated.

4. Trust needs to be earned by listening, by considering and including all opinions and ideas, by demonstrating competency and consistency, and by following through on commitments.

5. Fishermen and scientists both like to tell stories, but we often use different styles and methods.

6. To a fisherman, catch is $$; to a scientist, time is $$. We have found that we needed to devote more time to the planning and execution of the project than we expected. Our fishing industry partner was more likely to have his schedule revolve around the project than the scientists.

7. Flexibility is a key to the success of any cooperative project.

8. Safety is important - period.

9. A day fishing does not necessarily equal a research day. It is important to consider all aspects of the fishery regulations and how they impact not only the fisherman but also the ability of the cooperating scientists to carry out the project.

10. Our fishing industry partner is extremely curious and observant.

11. Our fishing industry partner is very enthusiastic about learning and conducting scientific research on fish ecology.

12. Scientists have had difficulty understanding how much pressure fishermen are under to make a living at their job while complying with often complicated fishery regulations - and - Fishermen often do not understand how complicated and involved doing science can be.

COLLABORATION WITH OTHER PROJECTS

Table 1. lists other samples collected for other projects. Whenever possible, we tried to accommodate these requests and were particularly successful with two colleagues. One of these resulted in additional research proposals.

IMPACTS ON END-USERS

See "PARTNERSHIPS" above.

PRESENTATIONS

Smith, B.E., Ligenza, T.J., Almeida, F.P. and Link, J.S. The use of Atlantic Cod to sample the benthos at a localized region of Georges Bank. Benthic Ecology Meeting 2003, Mystic-Groton, CT. March 2003.

Ligenza, T.J., Smith, B.E., Almeida, F.P., and Link, J.S. The Trophic Ecology of Atlantic Cod: Preliminary Insights from Localized Sampling. NEC Annual Participants Meeting. Durham, NH. October 2002.

Smith, B.E., Ligenza, T.J., Almeida, F.P. and Link, J.S. The Trophic Ecology of Atlantic Cod: Preliminary Insights from Localized Sampling. Southern New England Chapter, American Fisheries Society, Summer Meeting. Bristol, RI. June 2002. (http://www.nefsc.noaa.gov/femad/pbio/fwdp/BsmithLocCod_files/frame.htm)

PUBLISHED REPORTS AND PAPERS

Currently there are two publications in preparation and the project has been the subject of three newsletter articles. The Cape Cod Commercial Hook Fishermen's Association published an article entitled "Collaborative Science In Action on the Reina Marie" in their newsletter "Hooked on Cod". A second article, "What are cod eating?" was published in the NAMA Collaborations, August 2002 issue (this article can be found at: http://www.namanet.org/collaborations.htm). The third article, published in the Island Institute newsletter, Working Waterfront, was titled "Hook fisherman, scientists study what cod eat" (http://www.workingwaterfront.com/article.asp?storyID=20021209).

FUTURE RESEARCH

After the project began, the question of how feeding affects the reproductive cycle of cod was raised by the cooperating fisherman in the study. In order to study this, we began to collect female gonad weights and livers to calculate gonadosomatic and hepatosomatic indices in July 2002. These indices have been found useful in studying the reproductive cycles of several species as indices of the physiological tradeoffs between spawning and non-spawning periods. Although this was not an original objective of the project, we will analyze the data to determine whether this is a good index of cod reproduction and whether changes in cod diet are related to these indices.

Further expansion into a more complete bioenergetic set of studies is merited. For now, estimates of cod consumption will be calculated.

A closer examination of how feeding differences are related to benthic habitat is a possible follow-up study that could be conducted. Could we use cod to index benthic communities by determining what was in their diets and relating them to the habitat? Benthic sampling techniques, including underwater video, combined with intense stomach sampling like we are conducting in this study, could assist in characterizing benthic habitat and potentially restricting destructive gear in sensitive habitats.

All of these issues/ideas have been developed since the project began. The observational expertise of our cooperating fisherman, combined with the scientific skills and experience of the NEFSC cooperating scientists have made this project a much greater learning experience than any of us expected when the project first began.

LITERATURE CITED

Andersen KP, Ursin E (1977) A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorous circulation and primary production. Medd. Danm. Fish.-og. Havunders. N.S. 7:319-435.

Bjornsson B (1993) Swimming speed and swimming metabolism of Atlantic cod (*Gadus morhua*) in relation to available food: A laboratory study. Can. J. Fish. Aquat. Sci. 50:2542-2551.

Bogstad B, Hauge KH, Ulltang O (1997) MULTSPEC- a multi-species model for fish and marine mammals in the Barents Sea. J. Northw. Atl. Fish. Sci. 22:317-341

Bowman RE, Michaels WL (1984) Food of seventeen species of northwest Atlantic fish. NOAA Tech. Memo. NMFS-F/NEC.

Brown JA, Pepin P, Methven DA, Somerton DC (1989) The feeding, growth and behaviour of juvenile cod, *Gadus morhua* L., in cold environments. J. Fish. Biol. 35:373-380.

Burton MPM, Penney RM, Biddiscombe S (1997) Time course of gametogenesis in northwest Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 54 (Suppl. 1):122-131.

Collie JS, Tsou TS (1996) Multispecies virtual population analysis of the Georges Bank fish community. ICES CM 1996/G:28 16 pp.

Clark DS, Brown JA, Goddard SJ, Moir J (1995) Activity and feeding behavior of Atlantic cod (*Gadus morhua*) in sea pens. Aquaculture 131:49-57.

Daan N, Sissenwine MP (eds.) (1991) Multispecies models relevant to management of living resources. ICES Mar. Sci. Symp. 193.

dos Santo J, Jobling M (1991) Factors affecting gastric evacuation in cod, *Gadus morhua* L., fed single meals of natural prey. J. Fish. Biol. 38:697-713.

Dutil JD, Lambert Y (2000) Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 57:826-836.

Fahrig L, Lilly GR, Miller DS (1993) Predator stomachs as sampling tools for prey distribution: Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 50:1541-1547.

Fogarty MJ, Murawski SA (1998) Large-scale disturbance and the structure of marine ecosystems: fishery impacts on Georges Bank. Ecol. Appl. 8(1):S6-S22.

Grant SM, Brown JA (1999) Variation in condition of coastal Newfoundland 0-group Atlantic cod (*Gadus morhua*): Field and laboratory studies using simple condition indices. Mar. Biol. 133:611-620.

Grant SM, Brown JA, Boyce DL (1998) Enlarged fatty livers of small juvenile cod: a comparison of laboratory-cultured and wild juveniles. J. Fish Biol. 52:1105-1114.

Grunwald E, Koester F (1994) Feeding habits of Atlantic cod in West-Greenland waters. ICES CM 1994/P:5 19 pp.

Helgason T, Gislason H (1979) VPA-analysis with species interaction due to predation. ICES CM 1979/G:52 10 pp.

Hoines AS, Bergstad OA (1999) Resource sharing among cod, haddock, saithe, and pollock on a herring spawning ground. J. Fish Biol. 55:1233-1257.

Jobling M, Meloey OH, dos Santos J, Christiansen B (1994) The compensatory growth response of the Atlantic cod: Effects of nutritional history. Aquacult. Int. 2:75-90.

Kjesbu OS (1994) Time of start of spawning in Atlantic cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. J. Fish. Biol. 45:719-735.

Kjesbu OS, Witthames PR, Solemdal P, Walker MG (1998) Temporal variations in the fecundity of Arcto-Norwegian cod *(Gadus morhua)* in response to natural changes in food and temperature. J. Sea Res. 40:303-321.

Konstantinov KG, Turuk TN, Plekhanova NA (1985) Food links of some fishes and invertebrates on Flemish Cap. NAFO Sci. Coun. Studies 8:39-48.

Krohn M, Reidy S, Kerr S (1997) Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 54 (suppl. 1):113-121.

Lambert Y, Dutil JD (1997) Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. Can. J. Fish. Aquat. Sci. 54:2388-2400.

Lambert Y, Dutil JD (2000) Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Can. J. Fish. Aquat. Sci. 57:815-825.

Langton RW, Bowman RE (1980) Food of fifteen northwest Atlantic gadiform fishes. NOAA Tech. Rep. NMFS-SSRF-740.

Langton RW (1982) Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other Northwest Atlantic finfish. Fish. Bull. 80:745-759.

Lee EM, Khan RA (2000) Length-weight-age relationships, food, and parasites of Atlantic cod (*Gadus morhua*) off coastal Labrador within NAFO Divisions 2H and 2J-3K. Fish. Res. 34:65-72.

Lilly GR (1991) Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. ICES Mar. Sci. Symp. 193:133-146.

Lilly GR (1994) Predation by Atlantic cod on capelin on the southern Labrador and northeast Newfoundland shelves during a period of changing spatial distributions. ICES Mar. Sci. Symp. 198:600-611.

Lilly GR, Parsons DG (1991) Distributional patterns of the northern shrimp (*Pandalus borealis*) in the Northwest Atlantic as inferred from stomach contents of cod (*Gadus morhua*). ICES CM 1991/K:41 15 pp.

Lindholm JB, Auster PJ, Kaufman LS (1999) Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 180:247-255.

Link JS (2004) Using fish stomachs as samplers of the benthos: integrating long-term and broad scales. Mar. Ecol. Prog. Ser. 269:265-275.

Link JS, Garrison LP (2002a) Changes in piscivory associated with fishing induced changes to the finsfish community on Georges Bank. Fish. Res. 55:71-86.

Link JS, Garrison LP (2002b) Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US continental shelf. Mar. Ecol. Prog. Ser. 277:109-123.

Link JS, Almeida FP (2000) An overview and history of the food web dynamics program of the Northeast Fisheries Science Center, Woods Hole, Massachusetts. NOAA Tech. Memo. NMFS-NE-159. 60pp.

Mattson S (1990) Food and feeding habits of fish species over a sublittoral bottom in the northeast Atlantic. 1. Cod (*Gadus morhua* L.) (Gadidae). Sarsia 75:247-260.

Mayo RK, O'Brien L, Wigley SE (1998). Assessment of the Gulf of Maine Atlantic Cod Stock for 1998. NEFSC CRD 98-13.

Mehl S, Sunnana K (1991) Changes in growth of northeast Arctic cod in relation to food consumption in 1984-1988. ICES Mar. Sci. Symp. 193:109-112.

Methven DA (1999) Annotated bibliography of demersal fish feeding with emphasis on selected studies from the Scotian Shelf and Grand Banks of the northwestern Atlantic. Can. Tech. Rep. Fish. Aquat. Sci. no. 2267, 110 pp.

Methven DA, Piatt JF (1989) Seasonal and annual variation in the diet of Atlantic cod (*Gadus morhua*) in relation to the abundance of capelin (*Mallotus villosus*) off eastern Newfoundland, Canada. J. Cons. Ciem. 45:223-225.

Morgan MJ, Wilson CE, Crim LW (1999) The effect of stress on reproduction in Atlantic cod. J. Fish Biol 54:477-488.

Murawski SA, Maguire JJ, Mayo RK, Serchuk FM (1997) Groundfish stocks and the fishing industry. *In*: Boreman J, Nakashima BS, Wilson JA, Kendall RL (eds.) Northwest Atlantic groundfish: perspectives on a fishery collapse. American Fisheries Society, Bethesda, Maryland, USA.

O'Brien L (1999) Factors influencing rates of maturation in the Georges Bank and Gulf of Maine Atlantic Cod stocks. J. Northw. Atl. Fish. Sci. 25:179-203.

O'Brien L, Munroe N (2000) Assessment of the Georges Bank Atlantic Cod stock for 2000. NEFSC CRD-00-17.

Overholtz WJ, Link JS, Suslowicz LE (2000) The impact and implications of fish predation on pelagic fish and squid on the eastern USA shelf. ICES J. Mar. Sci. 57:1147-1159.

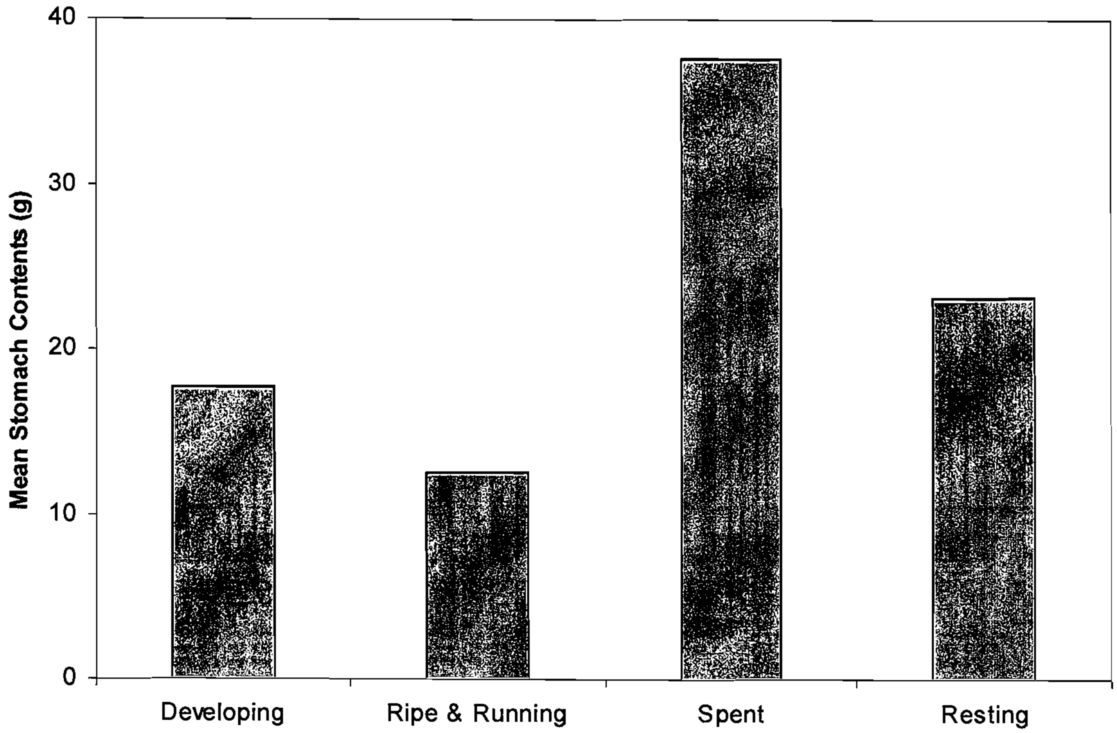

Figure 6. Mean Stomach Contents (g) Across the Maturity Stages