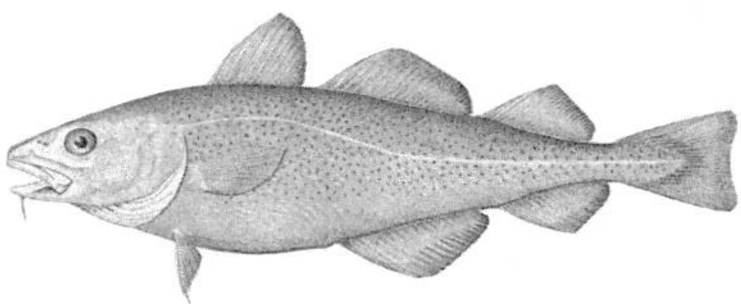
COSEWIC
Assessment and Status Report

on the

Atlantic Cod
Gadus morhua

Laurentian North population
Laurentian South population
Newfoundland and Labrador population
Southern population
Arctic Lakes population
Arctic Marine population

in Canada



Laurentian North population - ENDANGERED
Laurentian South population - ENDANGERED
Newfoundland and Labrador population - ENDANGERED
Southern population - ENDANGERED
Arctic Lakes population - SPECIAL CONCERN
Arctic Marine population - DATA DEFICIENT
2010

COSEWIC
Committee on the Status
of Endangered Wildlife
in Canada

COSEPAC
Comité sur la situation
des espèces en péril
au Canada

COSEWIC status reports are working documents used in assigning the status of wildlife species suspected of being at risk. This report may be cited as follows:

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Previous report(s):

COSEWIC. 2003. COSEWIC assessment and update status report on the Atlantic Cod *Gadus morhua* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xi + 76 pp.

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Atlantic Cod — Line drawing of Atlantic Cod *Gadus morhua* by H.L. Todd. Image reproduced with permission from the Smithsonian Institution, NMNH, Division of Fishes.

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COSEWIC
Assessment Summary

Assessment Summary – April 2010

Common name
Atlantic Cod - Laurentian North population

Scientific name
Gadus morhua

Status
Endangered

Reason for designation
Populations in this designatable unit (DU) have declined 76-89% in the past 3 generations. The main cause of the decline in abundance was overfishing and there is no indication of recovery. This DU includes the cod management units 3Ps and 3Pn4RS. A limit reference point (LRP) has been estimated for the 3Pn4RS management unit. The abundance for this management unit has been relatively stable over the past decade, but it is well below the LRP, and directed fisheries continue. Abundance in southern Newfoundland (3Ps) is declining. The assessment indicates that this management unit is at the LRP, and directed fisheries continue.

Occurrence
Atlantic Ocean

Status history
The species was considered a single unit and designated Special Concern in April 1998. When the species was split into separate populations in May 2003, the Laurentian North population was designated Threatened. Status re-examined and designated Endangered in April 2010.

Assessment Summary – April 2010

Common name
Atlantic Cod - Laurentian South population

Scientific name
Gadus morhua

Status
Endangered

Reason for designation
Populations in this designatable unit (DU) have declined by 90% in the past 3 generations. The main cause of the rapid decline in abundance during the early 1990s was overfishing. Commercial fisheries were curtailed in 1993 and the abundance stabilized for a number of years. However, increased natural mortality and continued small catches have caused the abundance to decline again. Quantitative analysis of population demographic parameters indicate the population will continue to decline in the absence of fishing if the current elevated level of natural mortality persists. This DU includes the cod management units 4TVn (November – April), 4Vn (May – October) and 4VsW. A limit reference point (LRP) has been estimated for the 4TVn management unit and the current status is assessed to be well below the LRP. An LRP has not been estimated for the 4VsW management unit; however, it is considered to be at a critically low level.

Occurrence
Atlantic Ocean

Status history
The species was considered a single unit and designated Special Concern in April 1998. When the species was split into separate populations in May 2003, the Maritimes population was designated Special Concern. When the Maritimes population was further split into two populations (Laurentian South population and Southern population) in April 2010, the Laurentian South population was designated Endangered, and the original Maritimes population was de-activated.

Assessment Summary – April 2010

Common name
Atlantic Cod - Newfoundland and Labrador population

Scientific name
Gadus morhua

Status
Endangered

Reason for designation
This designatable unit (DU) includes the cod management units 2GH, 2J3KL and 3NO, located in the inshore and offshore waters of Labrador and eastern Newfoundland, and the Grand Banks. Cod in this area have declined 97-99% in the past 3 generations and more than 99% since the 1960s. The area of occupancy declined considerably as the stock collapsed in the early 1990s. The main cause of the decline in abundance was overfishing, and there has been a large reduction in the fishing rate since 1992. However, the population has remained at a very low level with little sign of substantive recovery. The most recent surveys indicate an increase in abundance over the past 3 years; however, this change in abundance is very small compared to the measured decline over the past 3 generations. The extremely low level of abundance and contracted spatial distribution makes the population vulnerable to catastrophic events, such as abnormal oceanographic conditions. Threats from fishing, predation, and ecosystem changes persist. There is no limit reference point (LRP) for the 2J3KL management unit but the population in this area is considered to be well below any reasonable LRP value. The offshore 2J3KL fishery is under moratorium and there is an inshore stewardship fishery with no formal total allowable catch (TAC). The fishery in the 3NO management unit is also under moratorium. There is an LRP for this management unit and the population is well below this value.

Occurrence
Atlantic Ocean

Status history
The species was considered a single unit and designated Special Concern in April 1998. When the species was split into separate populations in May 2003, the Newfoundland and Labrador population was designated Endangered. Status re-examined and confirmed in April 2010.

Assessment Summary – April 2010

Common name
Atlantic Cod - Southern population

Scientific name
Gadus morhua

Status
Endangered

Reason for designation
Populations in this designatable unit (DU) have declined by 64% in the past 3 generations and the decline is continuous. Commercial fishing is ongoing and is an important contributor to the decline. As well, there is evidence of an unexplained increase in natural mortality in the 4X portion of the DU. Rescue from the US population is unlikely given the low abundance of the species in that area. This DU includes the cod management units 4X5Y and 5Zjm. There is a directed fishery for the species in the 4X5Y area, and although there is no limit reference point (LRP), recent fishery management advice indicates that this management unit is at a critically low level. There is also a directed fishery in the 5Zjm management unit and this fishery is co-managed with the United States.

Occurrence
Atlantic Ocean

Status history
The species was considered a single unit and designated Special Concern in April 1998. When the species was split into separate populations in May 2003, the Maritimes population was designated Special Concern. When the Maritimes population was further split into two populations (Laurentian South population and Southern population) in April 2010, the Southern population was designated Endangered, and the original Maritimes population was de-activated.

Assessment Summary – April 2010

Common name
Atlantic Cod - Arctic Lakes population

Scientific name
Gadus morhua

Status
Special Concern

Reason for designation
This designatable unit (DU) exists in 3 isolated lakes on Baffin Island, Nunavut. The combined surface area of the 3 lakes is less than 20 km^2. Rescue from other DUs is not possible. One of the lakes, Ogac Lake, is accessible for fishing and large numbers of the species may be removed from the lake if fishing increases.

Occurrence
NU

Status history
The species was considered a single unit and designated Special Concern in April 1998. When the species was split into separate populations in May 2003, the Arctic population was designated Special Concern. When the Arctic population was further split into two populations (Arctic Lakes population and Arctic Marine population) in April 2010, the Arctic Lakes population was designated Special Concern, and the original Arctic population was de-activated.

Assessment Summary – April 2010

Common name
Atlantic Cod - Arctic Marine population

Scientific name
Gadus morhua

Status
Data Deficient

Reason for designation
Information to establish any COSEWIC status category with assurance is not available. Data on distribution, abundance, habitat, and changes over time are insufficient.

Occurrence
Arctic Ocean, Atlantic Ocean

Status history
The species was considered a single unit and designated Special Concern in April 1998. When the species was split into separate populations in May 2003, the Arctic population was designated Special Concern. When the Arctic population was further split into two populations (Arctic Lakes population and Arctic Marine population) in April 2010, the Arctic Marine population was designated Data Deficient, and the original Arctic population was de-activated.

COSEWIC
Executive Summary

Atlantic Cod
Gadus morhua

Laurentian North population
Laurentian South population
Newfoundland and Labrador population
Southern population
Arctic Lakes population
Arctic Marine population

Species information

Class:	Actinopterygii
Order:	Gadiformes
Family:	Gadidae
Latin binomial:	*Gadus morhua* Linnaeus 1758

Common names: English – Atlantic Cod
French – morue franche
Inuktitut – ogac (Nunavut); ovak, ogac (Ungava Bay); uugak, ugak (Innu, Labrador) (McAllister *et al.* 1987)

Distribution

Atlantic Cod inhabit all waters overlying the continental shelves of the Northwest and the Northeast Atlantic Ocean. On a global scale, the historical distribution of cod probably differs relatively little from that of its present distribution. In Canada, Atlantic Cod are found contiguously along the east coast from Georges Bank and the Bay of Fundy in the south, northward along the Scotian Shelf, throughout the Gulf of St. Lawrence, around the island of Newfoundland, and finally along the eastern shores of Labrador and Baffin Island, Nunavut. There are also three landlocked populations of Atlantic Cod on Baffin Island. Outside Canadian waters in the Northwest Atlantic, cod can be found on the northeast and southeast tips of Grand Bank and on Flemish Cap, lying immediately northeast of Grand Bank, and in the waters east of Baffin Island extending to western Greenland.

Habitat

During the first few weeks of life, cod exist as eggs, and then as larvae, in the upper 50 metres of the ocean. The primary factors affecting habitat suitability for cod during these early stages of life are probably the oceanographic retention of pelagic eggs and larvae, food availability, and temperature. The most essential habitat characteristics for Atlantic Cod may be those required during the juvenile stage when cod have settled to the bottom for the first 1 to 4 years of their lives. Evidence suggests that a heterogeneous habitat, notably in the form of vertical structures, such as eelgrass, *Zostera marina*, in nearshore waters, is favoured by juvenile cod because it reduces the risk of predation and may also allow for increased growth. As adults, the habitat requirements of cod become increasingly diverse. Indeed, it is not clear that older cod have particular depth or bottom-substrate requirements. The primary factors affecting the distribution and habitat of older cod are probably temperature and food supply. From a spawning perspective, it is not known if cod have specific habitat requirements. Cod spawn in waters ranging from tens to hundreds of metres in depth. Perhaps the factor most beneficial to the survival of offspring is the presence of physical oceanographic features that would serve to entrain the buoyant eggs and prevent them from being dispersed to waters poorly suited to larval cod, e.g., waters off the continental shelf. Currently, it is highly unlikely that spawning habitat is limiting for Atlantic Cod.

Biology

The life history of cod varies a great deal throughout the species' range. In the relatively warm waters at the southern end of its Canadian range (Georges Bank, off the state of Maine) and in the Bay of Fundy, cod commonly attain maturity at 2 to 3 years of age. By contrast, cod inhabiting the Northeast Newfoundland Shelf, eastern Labrador, and the Barents Sea typically mature between ages 5 and 7 yr. Size at maturity ranges from between 35 to 85 cm in length. The number of eggs produced by a single female in a single breeding season typically ranges from between 300,000 and 500,000 at maturity to several million eggs for females greater than 75 cm in length. Egg diameter, which can show a weak, positive association with body size, ranges between 1.25 and 1.75 mm.

Atlantic Cod typically spawn over a period of less than three months in water that may vary in depth from tens to hundreds of metres. Cod are described as batch spawners because of the observation that only 5 to 25% of a female's egg complement is released at any given time (approximately every 2 to 6 days) during a 3- to 6-week spawning period. During the larval stage, the young feed on phytoplankton and small zooplankton in the upper 10 to 50 metres of the water column. After the larval stage, the juveniles swim, or 'settle', to the bottom, where they appear to remain for a period of 1 to 4 years. These settlement areas are known to range from very shallow (< 10 m to 30 m) coastal waters to moderately deep (50 to 150 m) waters on offshore banks. After this settlement period, it is believed that the fish begin to undertake the often-seasonal movements (apparently undirected swimming in coastal waters) and migrations (directed movements to and from specific, highly predictable locations) characteristic of adults.

Populations and designatable units

Estimates of the size of the breeding part of the population for Atlantic Cod are available from two sources: (1) abundance estimates of the mature part of the population, as derived from a fisheries-dependent model called a Virtual Population Analysis (VPA), and (2) catch rates of fish of reproductive age as determined from fisheries-independent research surveys. Surveys provide an index which must be scaled to get the true population size. Models like VPA may extend further back in time and have the potential to smooth trends (year effects) and scale the index using catch data. Fisheries and Oceans Canada (DFO) is the primary source of these abundance data.

Based on COSEWIC's guidelines for assigning status below the species level, six DUs are identified in the present report and, when data are available, trends in the numbers of breeding individuals are described for each. Each of the DUs includes cod from one or more management unit, as delineated by geographical areas defined by the Northwest Atlantic Fisheries Organization (NAFO). These areas are used to identify the cod stocks managed by Fisheries and Oceans Canada.

Arctic Lakes DU

Cod in this DU are confined to coastal lakes along the eastern coast of Baffin Island, Nunavut (three have been documented) that receive intermittent tidal intrusions of salt water. These are Ogac Lake, Qasigialiminiq Lake and Tariujarusiq Lake.

Arctic Marine DU

Cod in this DU inhabit the marine environment east and southeast of Baffin Island, Nunavut (NAFO 0A, 0B). Although little is known about cod inhabiting the marine waters in this area, they are rarely caught in abundance, and may be an extension of cod stocks found in the waters around western Greenland.

Newfoundland and Labrador DU

Cod in this DU inhabit the waters ranging from immediately north of Cape Chidley (the northern tip of Labrador) southeast to Grand Bank off eastern Newfoundland. For management purposes, cod in this DU are treated as three separate stocks by DFO: (1) Northern Labrador cod (NAFO 2GH), (2) "Northern" cod, i.e., those found off southeastern Labrador, the Northeast Newfoundland Shelf, and the northern half of Grand Bank (NAFO 2J3KL), and (3) Southern Grand Bank cod (NAFO 3NO). Approximately 75 to 80% of the Atlantic Cod in Canadian waters were located within this population in the early 1960s.

Laurentian North DU

Cod in this DU combine the stocks identified for management purposes by DFO as (1) St. Pierre Bank (NAFO 3Ps) and (2) Northern Gulf of St. Lawrence (NAFO 3Pn4RS). These stocks are located north of the Laurentian Channel, bordering the south and west coast of Newfoundland and south coast of Quebec.

Laurentian South DU

Cod in this DU comprise three DFO-recognized management units (1) Southern Gulf of St. Lawrence (NAFO 4TVn Nov. to April), (2) Cabot Strait (NAFO 4Vn May to October), (3) Eastern Scotian Shelf (NAFO 4VsW). These stocks range from the southern Gulf of St. Lawrence to the eastern Scotian shelf and many overwinter along the southern slope of the Laurentian Channel.

Southern DU

Cod in this DU combine two stocks identified for management purposes by DFO: (1) Bay of Fundy/Western Scotian Shelf (NAFO 4X and the Canadian portion of NAFO 5Y), and (2) Eastern Georges Bank ($5Z_{jm}$). The latter stock is transboundary and is managed jointly by Canada and the USA. Geographically, this DU is located in the waters adjacent to Nova Scotia and New Brunswick, extending from southern Nova Scotia and the Bay of Fundy, to the Canadian portion of Georges Bank 5Z.

Limiting factors and threats

The primary historical cause of the reduction of Atlantic Cod range-wide was over-exploitation. The rate of decline was likely exacerbated by life history changes such as reductions in individual growth and age at maturation. Current threats to the stability and recovery of Atlantic Cod populations associated with exploitation include directed commercial fishing (quota-regulated harvest), recreational or "food fisheries", indirect fishing (a consequence of illegal fishing, catch misreporting, discarding), and bycatch from other fisheries for bottom-dwelling species (e.g., Greenland halibut, northern shrimp, haddock, lobster, winter flounder). However, increased natural mortality of older cod now surpasses exploitation as the primary threat and source of mortality south of the Laurentian Channel particularly in the Laurentian South DU. Sources of high natural mortality remain unknown but may include changes to the magnitude and types of species interactions, and unfavourable environmental conditions. Selection against late maturity and rapid growth rate, induced by previously high rates of exploitation, may also be contributing to the higher mortality and slower growth observed in some areas today. The influence of marine climatic variation on cod population productivity remains poorly understood, but it seems likely that periods of cold water and high North Atlantic Osciliation anomalies are associated with reduced productivity in some populations.

DU status and trends

The report suggests that, for designation purposes, Atlantic Cod in Canada be recognized as six DUs, in accordance with known genetic, ecological, and demographic data, and in accordance with the guidelines detailed by COSEWIC (Nov. 2008). Regarding the assignment of risk, the primary cause of the reduction in Atlantic Cod (fishing) has not ceased in any of the DUs (although it is restricted in some regions). In the Laurentian North DU, excessive fishing mortality has reduced the breeding part of the population, particularly in the Northern Gulf section of this DU. In the Laurentian South DU and Southern DU, high natural mortality rates and not fishing pressure seem the dominant threat and are resulting in projections of unprecedented declines and functional extinction within decades. For the Newfoundland and Labrador DU, it is evident, based on harvest rates estimated by Fisheries and Oceans Canada, that fishing may be a significant impediment to recovery in parts of this population's range and increasing declines in others. The populations, their 3-generaton rates of decline, and threats to their recovery are summarized in the table below.

Designatable Unit	NAFO Areas	Three-Generation Rate of Decline (VPA/RV)	Threats
1.Arctic Lakes		Unknown	Increased angling pressure in some lakes.
2.Arctic Marine	0A and 0B	Unknown	Bycatch, though magnitude of stock and threat remains unknown.
3.Newfoundland and Labrador	2G, 2H, 2J, 3K, 3L, 3N, 3O	97% / 99%	1. Fishing (including legal, illegal, and unreported catches). 2. Fishing-induced and natural changes to the ecosystem, resulting in altered levels of inter-specific competition and predation, notably predation by Harp Seals and fish on northern cod. 3. Marine climatic variation and its correlation with population productivity. 4. Alteration of bottom habitat by fishing gear and genetic changes to life history represent potential but unevaluated threats.
4.Laurentian North	3Ps, 3Pn, 4R, 4S	89% / 76%	1. Fishing (including legal, illegal, and unreported catches), representing a greater threat to Northern Gulf cod. 2. Fishing-induced and natural changes to the ecosystem, resulting in altered levels of inter-specific competition and predation, notably predation by Harp Seals and fish on Northern Gulf cod. 3. Marine climatic variation and its correlation with population productivity. 4. Alteration of bottom habitat by fishing gear and genetic changes to life history represent potential but unevaluated threats.
5.Laurentian South	4T, 4Vn, 4Vs, 4W	90% / 90%	1. Fishing-induced and natural changes to the ecosystem, resulting in elevated levels of natural mortality through inter-specific competition and predation, notably Grey Seal predation. 2. Fishing (including legal, illegal, and unreported catches). 3. Marine climatic variation and its correlation with population productivity. 4. Alteration of bottom habitat by fishing gear and genetic changes to life history represent potential but unevaluated threats.
6. Southern	4X, Canadian portions of 5Y and 5Z	64% / 67%	1. Fishing (including legal, illegal, and unreported catches). 2. Fishing-induced and natural changes to the ecosystem. 3. Marine climatic variation and its correlation with population productivity. 4. Alteration of bottom habitat by fishing gear and genetic changes to life history.

Special significance of the species

Given its historical and contemporary importance to society, few species have been of greater significance in Canada. After the short-lived Viking-based settlements on Newfoundland's Northern Peninsula in the late tenth century, it was cod that brought the first Europeans to Newfoundland waters in the late fifteenth century, an economic venture that spawned one of the first permanent settlements in British North America (1612; Cupids, Newfoundland). Until the early 1990s, Atlantic Cod was the economic mainstay for Newfoundland and Labrador, as it was for a large part of the population in the Maritimes and along Quebec's north shore and Gaspé Peninsula. From a biological perspective, the Atlantic Cod, which numbered approximately 2.5 billion spawning individuals as recently as the early 1960s, was one of the top predators of the marine food web in the Northwest Atlantic.

Existing protection or other status designations

In Canada, the Atlantic Cod is protected federally by the *Fisheries Act* and by the *Oceans Act*. At present, Conservation Harvesting Plans are in place for the Southern Gulf of St. Lawrence, and three Federal/Provincial Cod Action Teams have been established (Newfoundland and Labrador, Maritimes, Quebec) with a mandate to promote recovery. In addition, several of the cod DUs in Canadian waters are managed jointly with other countries. For example, the Eastern Georges Bank cod stock is jointly managed by Fisheries and Oceans Canada and the National Marine Fisheries Service in the United States; and cod in the NAFO 3Ps area of the Laurentian North DU are managed bilaterally by Canada and France (on behalf of Saint Pierre and Miquelon). In most regions, quotas as well as seasonal and gear restrictions have been incorporated into the management framework (Worcester *et al*. 2009). Although biologically relevant reference points for stock abundance have been identified in several areas, these are currently not used in the management of these stocks, and fisheries management can essentially be described as ad hoc with respect to the setting of annual TACs. At present, several stocks remain under commercial moratoria and the remaining are under quota restrictions with respect to historic levels.

Other Status Designations for Atlantic Cod

IUCN: Vulnerable
Global Heritage Status Rank: G5

COSEWIC HISTORY

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) was created in 1977 as a result of a recommendation at the Federal-Provincial Wildlife Conference held in 1976. It arose from the need for a single, official, scientifically sound, national listing of wildlife species at risk. In 1978, COSEWIC designated its first species and produced its first list of Canadian species at risk. Species designated at meetings of the full committee are added to the list. On June 5, 2003, the *Species at Risk Act* (SARA) was proclaimed. SARA establishes COSEWIC as an advisory body ensuring that species will continue to be assessed under a rigorous and independent scientific process.

COSEWIC MANDATE

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assesses the national status of wild species, subspecies, varieties, or other designatable units that are considered to be at risk in Canada. Designations are made on native species for the following taxonomic groups: mammals, birds, reptiles, amphibians, fishes, arthropods, molluscs, vascular plants, mosses, and lichens.

COSEWIC MEMBERSHIP

COSEWIC comprises members from each provincial and territorial government wildlife agency, four federal entities (Canadian Wildlife Service, Parks Canada Agency, Department of Fisheries and Oceans, and the Federal Biodiversity Information Partnership, chaired by the Canadian Museum of Nature), three non-government science members and the co-chairs of the species specialist subcommittees and the Aboriginal Traditional Knowledge subcommittee. The Committee meets to consider status reports on candidate species.

DEFINITIONS
(2010)

Wildlife Species	A species, subspecies, variety, or geographically or genetically distinct population of animal, plant or other organism, other than a bacterium or virus, that is wild by nature and is either native to Canada or has extended its range into Canada without human intervention and has been present in Canada for at least 50 years.
Extinct (X)	A wildlife species that no longer exists.
Extirpated (XT)	A wildlife species no longer existing in the wild in Canada, but occurring elsewhere.
Endangered (E)	A wildlife species facing imminent extirpation or extinction.
Threatened (T)	A wildlife species likely to become endangered if limiting factors are not reversed.
Special Concern (SC)*	A wildlife species that may become a threatened or an endangered species because of a combination of biological characteristics and identified threats.
Not at Risk (NAR)**	A wildlife species that has been evaluated and found to be not at risk of extinction given the current circumstances.
Data Deficient (DD)***	A category that applies when the available information is insufficient (a) to resolve a species' eligibility for assessment or (b) to permit an assessment of the species' risk of extinction.

* Formerly described as "Vulnerable" from 1990 to 1999, or "Rare" prior to 1990.

** Formerly described as "Not In Any Category", or "No Designation Required."

*** Formerly described as "Indeterminate" from 1994 to 1999 or "ISIBD" (insufficient scientific information on which to base a designation) prior to 1994. Definition of the (DD) category revised in 2006.

Environment Canada / Environnement Canada
Canadian Wildlife Service / Service canadien de la faune

Canada

The Canadian Wildlife Service, Environment Canada, provides full administrative and financial support to the COSEWIC Secretariat.

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in Canada

2010

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SPECIES INFORMATION

Name and classification

Class:	Actinopterygii
Order:	Gadiformes
Family:	Gadidae
Latin binomial:	*Gadus morhua* Linnaeus 1758

Common names: English – Atlantic Cod
French – morue franche
Inuktitut – ogac (Nunavut); ovak, ogac (Ungava Bay); uugak, ugak (Innu, Labrador) (McAllister *et al.* 1987)

Morphological description

The Atlantic Cod is a medium to large marine fish (Figure 1), inhabiting cold (10° to 15° C) and very cold waters (less than 0° to 5° C) in coastal areas and in offshore waters overlying the continental shelf throughout the Northwest and Northeast Atlantic Ocean (Figure 2). Morphologically, the feature that distinguishes them from most other fishes (a feature shared by other gadids) is the presence of three dorsal fins and two anal fins. Otherwise, cod have the "classic", streamlined, fusiform shape characteristic of fish that are able to sustain moderate speed over relatively long distances. The colour of cod varies a great deal throughout Canadian waters, having been described by fishermen as near-black, brown, and red, depending on the location of capture (Neis *et al.* 1999). The flesh of cod is comprised of firm, non-oily, white tissue that deteriorates relatively slowly after death, and is easily preserved by drying, salting, or some combination thereof.

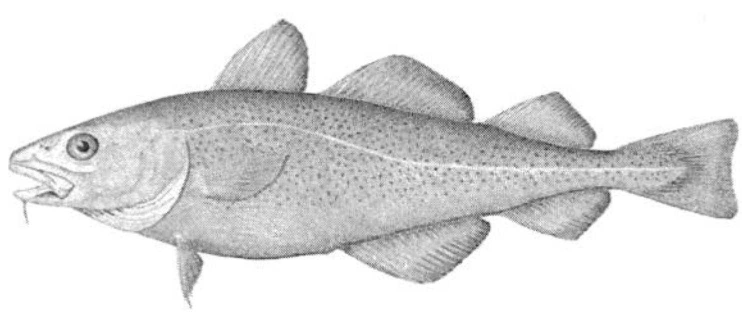


Figure 1. Line drawing of Atlantic Cod, or morue franche, *Gadus morhua*, by H.L. Todd. Image reproduced with permission from the Smithsonian Institution, NMNH, Division of Fishes.

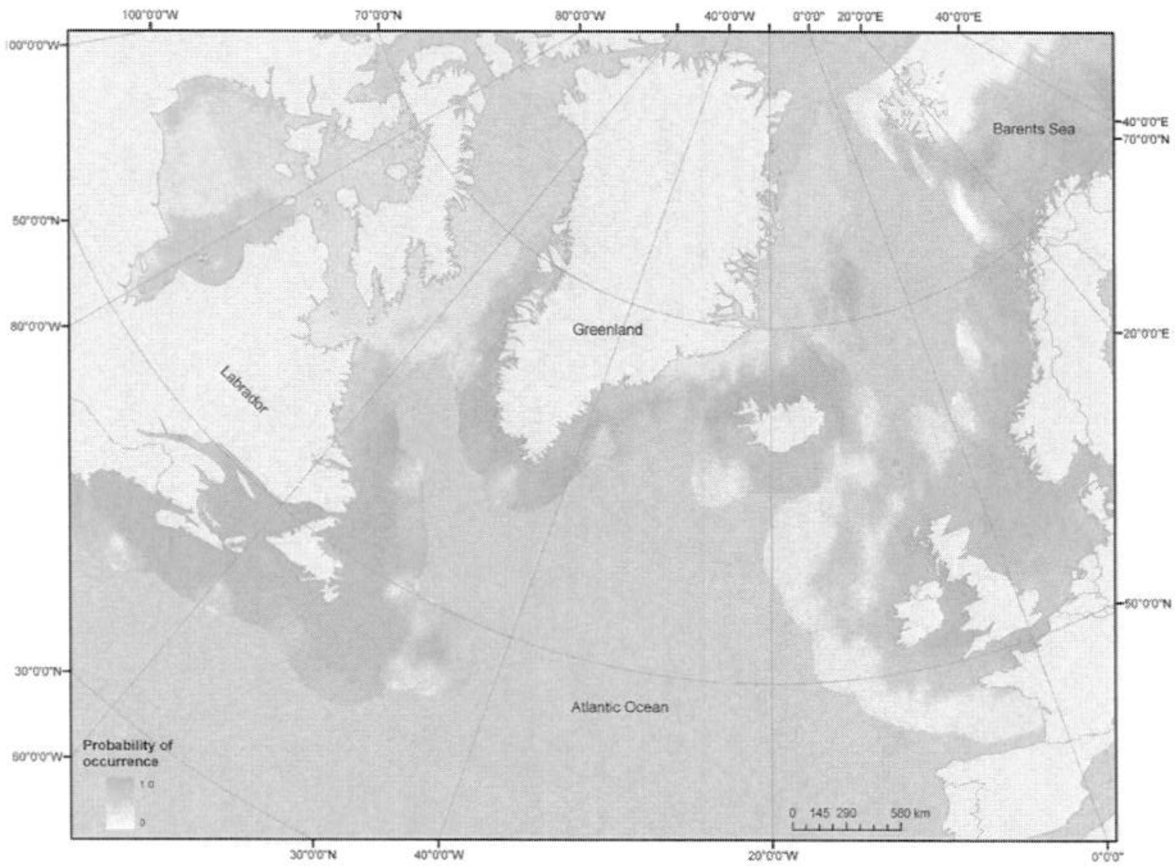


Figure 2. Global distribution of Atlantic Cod, *Gadus morhua*. Data from Fishbase.org.

Spatial population structure

The approach for defining the level of spatial structuring recognized by COSEWIC for Atlantic Cod has changed over the last decade. Presently, COSEWIC defines a DU by two criteria: 1) it must be substantially reproductively isolated from other populations, as evidenced by genetic distinctiveness, spatial disjunction, or occupation of different ecogeographic regions, and 2) it must represent a significant component of the evolutionary legacy of the species (Waples 1991). Accordingly, DUs are generally more reproductively isolated over a longer period of time than are the subpopulations within them, and multiple types of information (e.g., genetic structure, life history variation) are often required to address both significance and discreteness. In 1998, COSEWIC assigned cod to the Special Concern (Vulnerable) category and assigned a single designation to cod throughout their entire Canadian range. For a single designation to be valid, this requires the absence of significant variation in genetic and life history or adaptive variation throughout the species' range. However, as recent genetic and ecological data are consistent with the hypothesis that Atlantic Cod can be distinguished as separate DUs, in 2003 COSEWIC identified 4 designatable units (DUs) for cod in Canadian waters. Integrating information from genetic, ecological, and life history research, there is substantial evidence of population differentiation among Atlantic Cod in the Northwest Atlantic. However, while differences among recognized cod stocks are sufficiently high to warrant their separate treatment from a management perspective, it is not clear how populations might best be designated from an evolutionary perspective, given that genetic and life history data are not available for all stocks. Nonetheless, there is ever-increasing and substantive evidence of restricted dispersal and adaptive differences among cod at spatial scales considerably smaller than the geographical range of the species in Canada. From the general perspective, relevant studies include those on:

1. Genetic analyses of neutral genetic variation: Bentzen *et al.* 1996; Ruzzante *et al.* 1996, 1997, 1998, 1999, 2000a,b, 2001; Pogson *et al.* 1995, 2001; Beacham *et al.* 2002; Lage *et al.* 2004; Hardie *et al.* 2006; Bradbury *et al.* submitted; Bradbury *et al.* unpublished. In addition see Carr *et al.* 1995; Carr and Crutcher 1998; Carr and Marshall 2008 for mtDNA analyses.

2. Tagging studies such as mark-recapture, telemetry data, and natural tags: Thompson 1943; McKenzie 1956; McCracken 1959; Martin and Jean 1964; Templeman 1962; Lear 1984; Taggart *et al.* 1995; Hunt *et al.* 1999; Campana *et al.* 1999; Green and Wroblewski 2000; Swain and Frank 2000; Cote *et al.* 2001; Robichaud and Rose 2004; Windle and Rose 2005; Brattey *et al.* 2008a.

3. Spatio-temporal variation in reproduction: such as spawning period, location and the distribution of early life history stages (Hjort 1919; Frost 1938; Bulatova 1962; Postolaky 1974; Gagne and O'Boyle 1984; O'Boyle *et al.* 1984; Campana *et al.* 1989; Suthers *et al.* 1989; Frank *et al.* 1994; Myers *et al.* 1993; Hutchings *et al.* 1993; Lough *et al.* 1994; DeYoung and Davidson 1994; Pepin and Helbig 1997; Bradbury *et al.* 2000, 2002, 2008; Bradbury and Snelgrove 2001).

4. Life history variation: Pinhorn 1984; Trippel *et al.* 1997; McIntyre and Hutchings 2003; Fudge and Rose 2008.

5. Spatial differences in vertebral number variation demonstrated to have a genetic basis in fishes (e.g., Billerbeck *et al.* 1997) and to be adaptively significant (e.g., Templeman 1962; Templeman 1981; Swain 1992; Swain *et al.* 2001).

6. Genetically based adaptive differences: Puvanendran and Brown 1998; Goddard *et al.* 1999; Purchase and Brown 2000; Purchase and Brown 2001; Marcil *et al.* 2006a; Marcil *et al.* 2006b; Hutchings *et al.* 2007; Bradbury *et al.* submitted.

7. Geographical correlations and differences in demography (i.e. recruitment, natural mortality and growth): Myers *et al.* 1995; Swain and Castonguay 2000.

Designatable units and populations

COSEWIC identifies DUs as discrete and evolutionarily significant units, where "significant" means that the DU is important to the evolutionary legacy of the species as a whole and if lost would likely not be replaced over ecological time scales. Discreteness is considered of primary importance, and may refer to genetic isolation, habitat discontinuity, or ecological isolation. Significance may refer to deep phylogenetic divergence (e.g., glacial races), adaptive (e.g., life history variation), or ecological uniqueness, and its inclusion in the definition reflects the opinion that isolation in and of itself is not deemed sufficient for designation. In this context, it is important to acknowledge that a DU may contain multiple smaller subpopulations, each of which may be connected by some migration (McElhany *et al.* 2000), but migration is not necessary, as discrete subpopulations which lack demonstrable adaptive differences (i.e. significance) may be combined to a single DU. It is also worth noting that as the data are collected as part of the regular Fisheries and Oceans Canada (DFO) assessment process, the finest scale available for designation is at the scale of the DFO-recognized stock on which assessments are based. Nonetheless, these management units have a long history and generally represent a finer spatial scale than most major demographically independent populations. Therefore, evolutionarily significant structure below this scale seems unlikely, but also remains to be tested in many instances. Based on COSEWIC's guidelines for assigning status below the species level, six designatable units are identified in the present report and, when data are available, trends in the numbers of breeding individuals are described for each. Each of the DUs includes cod found in more than one management unit (with the exception of the Arctic Lakes DU), as delineated by NAFO (Northwest Atlantic Fisheries Organization) Divisions (Figure 7). These divisions also identify the cod stocks managed by Fisheries and Oceans Canada.

Arctic Lakes DU

Cod in this DU are those confined to coastal lakes along the eastern coast of Baffin Island, Nunavut (three have been documented) that receive intermittent tidal intrusions of salt water. These are Ogac Lake, Qasigialiminiq Lake and Tariujarusiq Lake.

Arctic Marine DU

Cod in this DU inhabit the marine environment east and southeast of Baffin Island, Nunavut (NAFO 0A, 0B). Although little is known about cod inhabiting the marine waters in this area, they are rarely caught in abundance, and may be an extension of cod stocks found in the waters around western Greenland.

Newfoundland and Labrador DU

Cod in this DU inhabit the waters ranging from immediately north of Cape Chidley (the northern tip of Labrador) southeast to Grand Bank off eastern Newfoundland. For management purposes, cod in this DU are treated as three separate stocks by DFO:

(1) Northern Labrador cod (NAFO 2GH), (2) "Northern" cod, i.e., those found off southeastern Labrador, the Northeast Newfoundland Shelf, and the northern half of Grand Bank (NAFO 2J3KL), and (3) Southern Grand Bank cod (NAFO 3NO). Approximately 75 to 80% of the Atlantic Cod in Canadian waters were located within this DU in the early 1960s.

Laurentian North DU

Cod in this DU combine the stocks identified for management purposes by DFO as (1) St. Pierre Bank (NAFO 3Ps) and (2) Northern Gulf of St. Lawrence (NAFO 3Pn4RS). These stocks are located north of the Laurentian Channel, bordering the south and west coast of Newfoundland and south coast of Quebec.

Laurentian South DU

Cod in this DU comprise three DFO-recognized management units (1) Southern Gulf of St. Lawrence (NAFO 4TVn Nov. to April), (2) Cabot Strait (NAFO 4Vn May to Oct.), (3) Eastern Scotian Shelf (NAFO 4VsW). These stocks range from the southern Gulf of St. Lawrence to the eastern Scotian shelf and many overwinter along the southern slope of the Laurentian Channel.

Southern DU

Cod in this DU combine two stocks identified for management purposes by DFO: (1) Bay of Fundy/Western Scotian Shelf (NAFO 4X and the Canadian portion of NAFO 5Y), and (2) Eastern Georges Bank ($5Z_{jm}$). The latter stock is transboundary and is managed jointly by Canada and the USA. Geographically, this DU is located in the waters adjacent to Nova Scotia and New Brunswick, extending from southern Nova Scotia and the Bay of Fundy, to the Canadian portion of Georges Bank 5Z.

Scientific Basis for Distinguishing the Newfoundland & Labrador, Laurentian North, Laurentian South and Southern Dus

These DUs can be identified as "distinct" and "significant" by a combination of different types of available data. These include age at maturity, maximum population growth rate (r_{max}), temporal trends in abundance, tagging returns, genetic variability at selectively neutral loci, and genetic differences among selectively important traits.

Age at maturity

Age at maturity (represented as the age at which 50% of females are reproductive) differs among the populations, and it likely reflects both environmental (e.g., temperature), and genetic influences and may be subject to strong selection associated with fishing pressure. To compare ages at maturity, the average pre-collapse age across all stocks within each DU was calculated, weighting the average age for each stock by the highest estimated abundance of mature individuals in that stock (as determined by VPA abundance data; see POPULATION SIZES AND TRENDS below). Cod are oldest at maturity in the Newfoundland & Labrador DU in which both stocks mature at 6 years, and youngest in the Southern DU in which the 2 stocks mature at 2.5 years (Figure 3). The clearest difference in age at maturity occurs in the Southern DU where cod mature at 2-3 yrs, considerably younger than in other DUs.

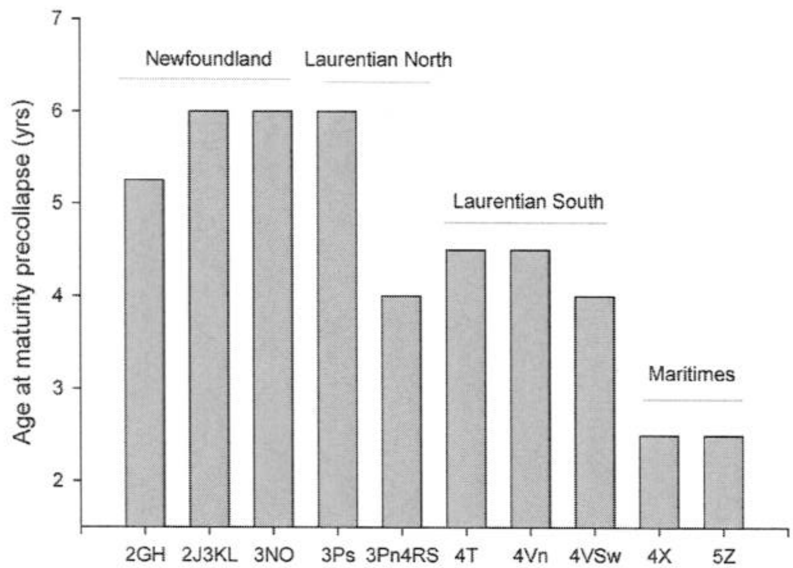


Figure 3. Age at maturities (pre-collapse) for each of the 10 recognized stocks of Atlantic Cod in Canadian waters.

Designatable Unit	Number of stocks	Age at maturity (range among stocks)	Reference(s)
Newfoundland & Labrador	2	6.0 (6-6 yr)	Lilly *et al.* (2001); Trippel *et al.* (1997); Stansbury *et al.* (2001); COSEWIC 2003
Laurentian North	2	4.5 (4-6 yr)	Brattey *et al.* (2001a); COSEWIC 2003
Laurentian South	3	4.5 (4.0-4.5 yr)	Doug Swain, personal communication 2009; Worcester *et al.* 2009
Southern	2	2.5 (2.5-2.5 yr)	Trippel *et al.* (1997); Hunt and Hatt (2002)

Maximum population growth rate (r_{max})

Based on data available in the mid-1990s, one can compare estimates of maximum population growth for the population identified here. The estimate for northern cod is available from Hutchings (1999); the remaining estimates are reported by Myers *et al.* (1997a; revised Table 1; pers. comm.). Estimates of r_{max} are made using the slope of the stock-recruitment relationship near the origin and subject to the caveat that r_{max} may have changed since the mid-1990s as has been observed in some regions (e.g., Swain and Chouinard 2008). However, what is important here is the question of whether r_{max} is likely to differ among the DUs, even for data restricted to the pre-collapse and immediate post-collapse periods for each stock. To compare r_{max} among populations, the average r_{max} across all stocks within each DU was calculated, weighting the r_{max} estimate for each stock by the highest known abundance of mature individuals in that stock (as determined by VPA abundance data; see POPULATION SIZES AND TRENDS below). As predicted based on their differences in age at maturity, the Newfoundland & Labrador DU has a lower maximum population growth rate than its more southerly counterparts. Note, under recent productivity conditions the Laurentian South DU has exhibited extremely low productivity even though it extends farther south than some of the other populations (see Shelton *et al.* 2006).

Designatable Unit	**Number of stocks**	**Maximum population growth rate, r_{max} (range among stocks)**	**Reference(s)**
Newfoundland & Labrador	2	0.15 (0.13-0.35)	Myers *et al.* (1997a, revised Table 1); Hutchings (1999)
Laurentian North	2	0.32 (0.29-0.39)	Myers *et al.* (1997a, revised Table 1)
Laurentian South	3	0.36 (0.24-0.50)	Myers *et al.* (1997a, revised Table 1)
Southern	2	0.51 (0.47-0.67)	Myers *et al.* (1997a, revised Table 1)

Temporal abundance trends

Myers *et al.* (1995) examined the spatial scale of correlation in recruitment to the various Canadian stocks and observed correlations at scales <500km. Accordingly, certain stocks have displayed similar rates of decline. For instance, stocks that comprise the Newfoundland & Labrador DU (2J3KL and 3NO) have experienced steady declines across most of the time period of available data (>90% declines, see POPULATION SIZES AND TRENDS below).

Tagging and Telemetry Data

Tagging studies have been conducted in Canadian waters on cod since the 1930s. The general consensus is that tagged individuals rarely move more than 500 km. An evaluation of almost 50 years of tagging experiments off Newfoundland (Taggart 1995, see Movements/Dispersal section) indicates a clear decline in straying rates with distance and high rates of annual site fidelity (Figure 4A). Furthermore, across studies the evidence for strong site fidelity of cod in Canadian waters is accumulating (Green and Wroblewski 2000; Cote *et al.* 2001; Windle and Rose 2005; Brattey *et al.* 2008a). Brattey *et al.* (2008a) document annual rates of homing to Smith Sound Trinity Bay ranging from 65-100%. Robichaud and Rose (2004) suggest that 40% of all cod stocks worldwide are resident non-migratory populations. Moreover, although some stocks undergo large-scale migrations, such as in the Gulf of St. Lawrence, the degree of mixing and straying may be quite limited (e.g., Campana *et al.* 1999).

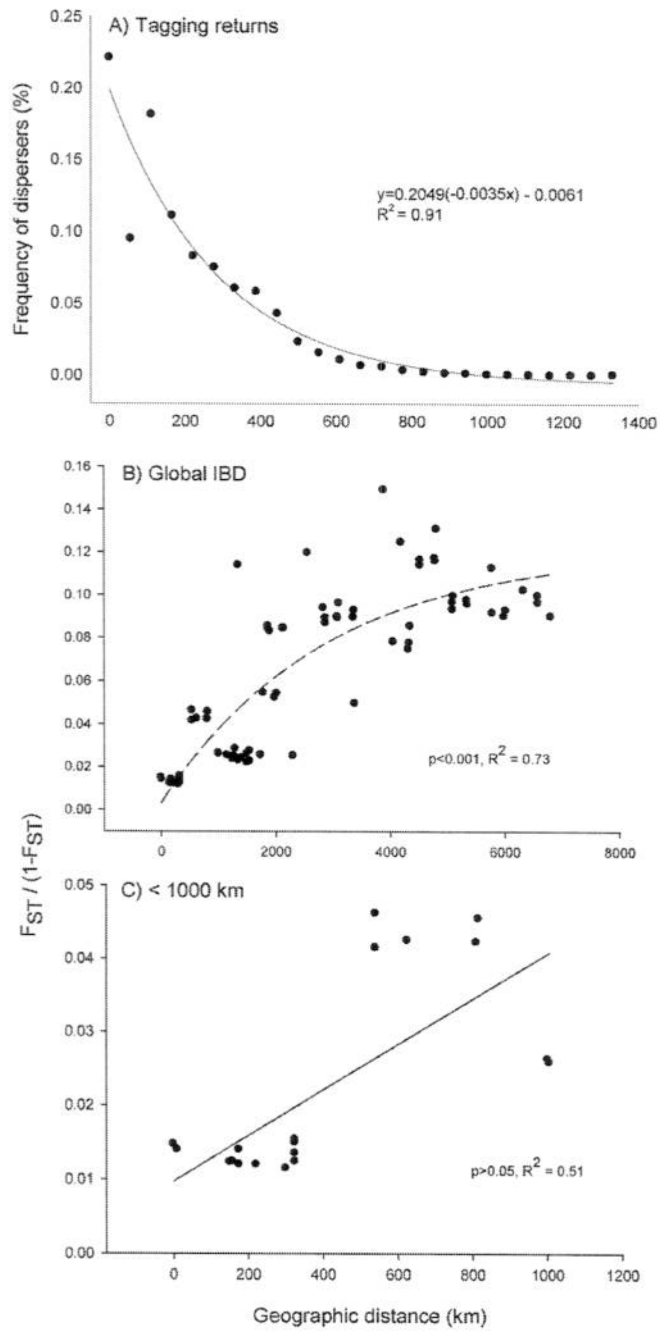


Figure 4. (A) Relationship between frequency of tag returns and geographic distance for cod tagged in Newfoundland waters 1954 to 1993 and genetic isolation by distance for both large (B) and small (C) scales from an analysis of 1405 single nucleotide polymorphisms (Bradbury *et al.* submitted).

Tagging studies can be used to examine straying rates across proposed DU boundaries and corroborate estimates of gene flow based on molecular markers. Brattey *et al.* (2008a) and Lawson and Rose (2000) document movements of 3Ps fish northward along the Avalon Peninsula rarely farther than Conception Bay. The Laurentian Channel, which is likely the main topographic barrier in Canada waters, separates the Laurentian North and Laurentian South DUs. Templeman (1962) reported "there do not appear to be any migration tracks or any considerable intermingling across channel and stocks on each side of the channel are thus separate." Estimates of trans-channel movements suggests crossing rates of <3% (Thompson 1943; McKenzie 1956; McCracken 1959; Martin and Jean 1964). Recent estimates using otolith elemental tags (Campana *et al.* 1999) or vertebral counts (see below, Swain *et al.* 2001) support the earlier conclusions of a low rate of cross channel mixing.

Summary of the evidence for trans-Laurentian Channel movements based on tagging studies from Templeman (1962).

Total Recoveries	Trans-Laurentian Channel Recoveries	%	Reference in Templeman (1962)
984	2	0.20	Thompson (1943)
670	2	0.30	Templeman and Fleming (1962)
2200	33	1.50	McKenzie (1957)
277	3	1.08	McCracken (1957)
215	0	0.00	McCracken (1957)
1022	18	1.76	McCracken (1959)
185	5	2.70	Martin (1959)

Wthin DUs, tagging studies suggest large spatial overlap, often associated with season migrations. Analysis of overwintering distributions along the slope of the Laurentian Channel suggest significant overlap among cod from 4T, 4Vn, and 4VsW along the southern slope, and 4PnRS and 3Ps along the northern slope consistent with their separation into the Laurentian North and Laurentian South DUs (Campana *et al.* 1999; Swain *et al.* 2001). Moreover, in contrast to the Laurentian Channel, straying rates across the Fundian Channel, which separates NAFO 4X and 5Z suggest that it is not a large impediment to movement (5-15% straying, e.g., Hunt *et al.* 1999) and support the formation of a Southern DU.

Genetic differentiation at selectively neutral loci

There is strong evidence of significant genetic differentiation at selectively neutral loci among the DUs (Table 1). In light of large populations, and likely post-glacial range expansions, it is not surprising that spatial differentiation in cod is often low, as is typical of marine fishes. Nonetheless, significant structuring has been observed in multiple studies, usually associated with physical isolation or barriers to gene flow. Bentzen *et al.* (1996) using microsatellite loci, observed significant structuring among Newfoundland, the Flemish Cap, and cod from the Scotian Shelf (Table 1). Similarly, Ruzzante *et al.* (1998) documented significant structuring at the bank scale, again suggesting significant differentiation across the Laurentian Channel (Table 1). Pogson *et al.*'s (2001) analysis of 10 nuclear restriction-fragment-length-polymorphism (RFLP) loci also revealed significant genetic differences among cod sampled from the DUs, particularly between the Newfoundland and Laurentian South DUs. Strong signatures of genetic isolation have also been observed associated with Gilbert Bay Labrador (Ruzzante *et al.* 2001; Beacham *et al.* 2002) and several Arctic lakes (Hardie *et al.* 2006) both of which are characterized by restricted access to the coastal ocean (Table 1). In the absence of obvious barriers to gene flow, evidence of the limits of dispersal are still observed through the presence of genetic isolation by distance. Pogson *et al.* (2001) reported a highly significant negative association between gene flow and geographic distance among cod sampled in Canadian waters from the Newfoundland & Labrador and mainland stocks. A similar association was also reported by Beacham *et al.* (2002) from their analysis of 7 microsatellite loci and the Pantophysin (*PanI*) locus (Table 1). Recently, Bradbury *et al.* (unpublished data) observed strong isolation by distance both range-wide and at small spatial scales (Figure 4B,C, see below for further details). These negative associations at spatial scales often less than 700 km imply that the greater the geographical separation of cod, the lower their genetic affinity. Moreover, significant isolation by distance at spatial scales <700 km corroborates both the declines in straying observed with tagging returns and the scale of differentiation observed in life history traits and demographic data (see above).

Microsatellite differentiation can further provide insight into gene flow associated with DU boundaries. Ruzzante *et al.* (1998) and Beacham *et al.* (2002) observed significant differentiation between Laurentian North and Newfoundland and Labrador cod supporting the separation of these DUs. Furthermore, significant differentiation was observed (Ruzzante *et al.* 1998, 2000) both across the Laurentian Channel, and between the Southern and the Laurentian South DUs supporting the designation of these boundaries and the formation of the Laurentian South DU. Within DUs at smaller spatial scales, spatial structure is generally absent (Bentzen 1996; Ruzzante *et al.* 1998; Beacham *et al.* 2002) with the exception of the above-noted instances of strong geographic isolation (e.g., Gilbert Bay). Evidence for genetic differentiation among the DUs at selectively neutral loci is summarized in Table 1. It is worth noting that many of the studies which reveal significant structuring included a specific microsatellite locus (Gmo132, Table 1), which has been identified as potentially under natural selection (Nielsen *et al.* 2006). This trend towards the reliance on non-neutral loci or traits for the resolution of isolation and adaptive significance in marine fishes is continuing with work using expressed DNA sequences (Bradbury *et al.* submitted) and common garden experiments (e.g., Hutchings *et al.* 2007), both of which are revealing evidence of fine scale (<500 km) adaptation in cod (see below).

Table 1. Summary of genetic estimates of differentiation from published literature.

Reference	Areas Compared		Marker Type	# Loci	Average Sample Size	Significant	F_{ST}
Bentzen *et al.* 1996	2J	3K	microsatellite	6	60	yes	0.007
Ruzzante *et al.* 1998	2J3KL	2J3KL	microsatellite	5	93	yes	0.001
Bentzen *et al.* 1996	2J3KL	4VSW	microsatellite	6	60	yes	0.003
Bentzen *et al.* 1996	2J3KL	4VSW	Gmo132	1	60	yes	0.021
Pogson *et al.* 1995	2J3KL	4X	RFLP	17	95	yes	Not given
Ruzzante *et al.* 1997	2J3KL (inshore)	2J3KL (offshore)	microsatellite	5	60	yes	0.0014
Ruzzante *et al.* 1997	2J3KL (inshore)	2J3KL (offshore)	microsatellite	5	60	yes	0.0015
Ruzzante *et al.* 2000	3K	3NO	microsatellite (with Gmo132)	5	148	yes	0.005
Hardie *et al.* 2006	3PS	4T	microsatellite	7	84	No	-0.0008
Pepin & Carr 1993	3O	3L	mtDNA	1		No	-0.0122
Carr *et al.* 1995	3L	3L	mtDNA	1	47	No	0.00
Hardie *et al.* 2006	3PS	4W	microsatellite	7	84	No	0.0025
Hardie *et al.* 2006	3PS	4X	microsatellite	7	84	No	-0.0008
Ruzzante *et al.* 2000	4RS	2J3KL	microsatellite (with Gmo132)	4	148	yes	0.025
Ruzzante *et al.* 1998	4RS	4T	microsatellite	5	93	yes	0.008
Hardie *et al.* 2006	4T	4W	microsatellite	7	84	No	0.0026
Hardie *et al.* 2006	4T	4X	microsatellite	7	84	No	0.0004
Hardie *et al.* 2006	4W	4X	microsatellite	7	84	No	-0.0005
Ruzzante *et al.* 1998	4W (Offshore)	4X (Offshore)	microsatellite	5	93	yes	0.004
Ruzzante *et al.* 2000	4X	$5Z_{jm}$	microsatellite (with Gmo132)	5	148	yes	0.007
Pogson *et al.* 2001	4XVsXw	4XVsXw (~600km)	RFLP	10	95	yes	not given, strong IBD
Lage *et al.* 2004	5Z	4X and Nantucket Shoals	pan	1	68	No	-0.0052
Lage *et al.* 2004	5Z	4X(Browns Bank)	microsatellite	5	68	No	0.0012
Lage *et al.* 2004	5Z	4X(Browns Bank)	Gmo132	1	68	No	0.0124
Ruzzante *et al.* 1998	5Z and 4X (Bay of Fundy)	4VSW	microsatellite	5	93	yes	0.011
Hardie *et al.* 2006	Gilbert Bay	3PS	microsatellite	7	84	yes	0.0576
Hardie *et al.* 2006	Gilbert Bay	4T	microsatellite	7	84	yes	0.0558
Hardie *et al.* 2006	Gilbert Bay	4W	microsatellite	7	84	yes	0.0526
Hardie *et al.* 2006	Gilbert Bay	4X	microsatellite	7	84	yes	0.051
Beacham *et al.* 2002	Newfoundland locations		micro (and Pan)	7	275	yes	0.008
Hardie *et al.* 2006	Ogac Lake	3PS	microsatellite	7	84	yes	0.1407
Hardie *et al.* 2006	Ogac Lake	4T	microsatellite	7	84	yes	0.1291
Hardie *et al.* 2006	Ogac Lake	4W	microsatellite	7	84	yes	0.1359
Hardie *et al.* 2006	Ogac Lake	4X	microsatellite	7	84	yes	0.1299

Reference	Areas Compared		Marker Type	# Loci	Average Sample Size	Significant	F_{ST}
Hardie *et al.* 2006	Ogac Lake	Gilbert Bay	microsatellite	7	84	yes	0.1966
Hardie *et al.* 2006	Ogac Lake	Qasigialiminiq Lake	microsatellite	7	84	yes	0.1952
Hardie *et al.* 2006	Ogac Lake	Tariujarusiq Lake	microsatellite	7	84	yes	0.2381
Hardie *et al.* 2006	Qasigialiminiq Lake	3PS	microsatellite	7	84	yes	0.0934
Hardie *et al.* 2006	Qasigialiminiq Lake	4T	microsatellite	7	84	yes	0.0913
Hardie *et al.* 2006	Qasigialiminiq Lake	4W	microsatellite	7	84	yes	0.0806
Hardie *et al.* 2006	Qasigialiminiq Lake	4X	microsatellite	7	84	yes	0.0834
Hardie *et al.* 2006	Qasigialiminiq Lake	Gilbert Bay	microsatellite	7	84	yes	0.1563
Hardie *et al.* 2006	Qasigialiminiq Lake	Tariujarusiq Lake	microsatellite	7	84	yes	0.2234
Hardie *et al.* 2006	Tariujarusiq Lake	3PS	microsatellite	7	84	yes	0.1432
Hardie *et al.* 2006	Tariujarusiq Lake	4T	microsatellite	7	84	yes	0.1295
Hardie *et al.* 2006	Tariujarusiq Lake	4W	microsatellite	7	84	yes	0.1456
Hardie *et al.* 2006	Tariujarusiq Lake	4X	microsatellite	7	84	yes	0.1324
Hardie *et al.* 2006	Tariujarusiq Lake	Gilbert Bay	microsatellite	7	84	yes	0.2141

In contrast to the studies noted above, studies of mtDNA variation indicate that "essentially none of the genetic variance in the Northwest Atlantic is attributable to subdivision among samples" (Carr and Crutcher 1998). See also Carr *et al.* (1995); and Carr and Marshall (2008).

Genetic differentiation among selectively important traits

In addition to differences at selectively neutral loci, there is increasing evidence that cod in the Northwest Atlantic differ from one another at loci or traits that are under selection reflecting local adaptation. This inference is drawn both from the examination of non-neutral molecular loci exhibiting elevated differentiation and from experiments in which differences among cod populations have been documented after the effects of the environment have been removed from the analysis.

Molecular loci may reflect selection and adaptive divergences if they are linked to expressed sequences under selection, as may be the case for microsatellite loci, or if they are expressed themselves and directly experience selection. Both Bentzen *et al.* (1996) and Ruzzante *et al.* (1998) reported significant structure among the DUs which was largely driven by a single locus, Gmo132. The locus has since been shown (Nielsen *et al.* 2006) to be experiencing elevated divergence associated with hitch-hiking selection (i.e. linkage to a gene under selection). Similar observations of elevated divergence associated with the Pantophysin locus have been made in Canadian waters, though the structure is much lower than observed in the eastern Atlantic (Beacham *et al.* 2002). Bradbury *et al.* (submitted) have examined 1641 expressed single nucleotide polymorphisms (SNPs) in cod from 19 locations throughout Canadian and adjacent waters (Fig. 4 & 5). Principal Component Analysis (PCA) and Bayesian clustering indicated the presence of six significant groups (Figure 5a). Twenty-five SNPs displayed clear trends in allele frequency (Figure 5b), elevated divergence, and are highly correlated with ambient temperature (r=0.93) suggesting local adaptation associated with ocean climate. The major transition in allele frequencies at these temperature-associated SNPs occurs between the Laurentian South and the Southern DUs (Figure 5b) consistent with large adaptive differences.

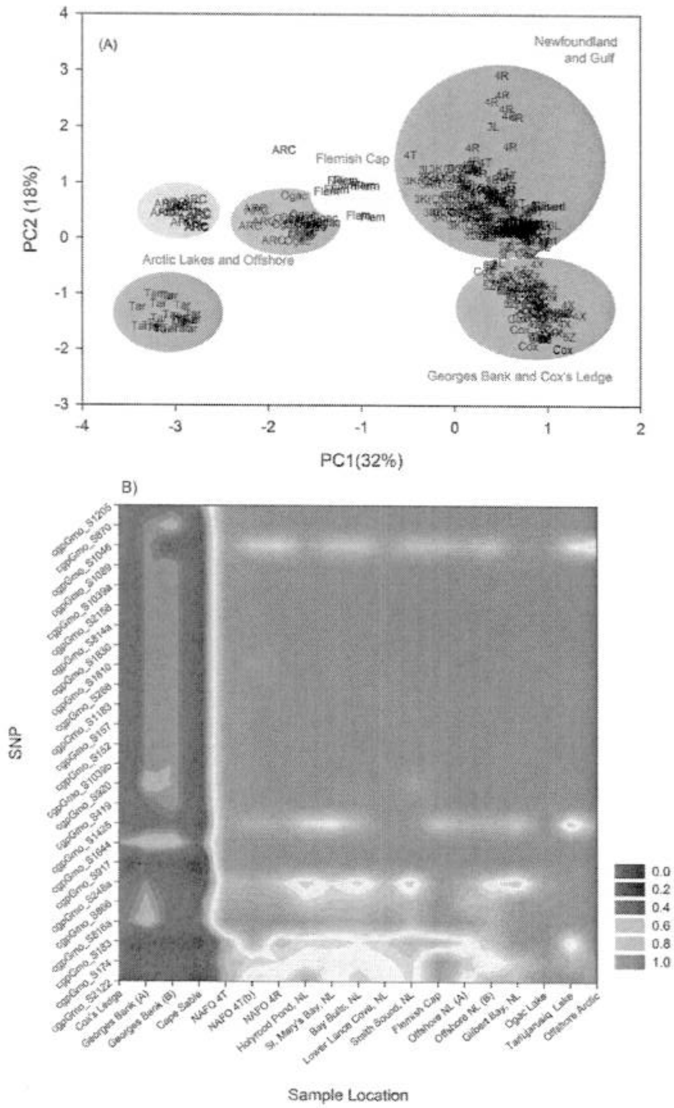


Figure 5. (A)Principal Components Analysis of 1405 single nucleotide polymorphisms (SNP) for 19 samples of Atlantic Cod from throughout Canadian and adjacent waters. Coloured ellipses represent genetic clusters identified using a Bayesian Clustering analysis. (B) Average allele frequencies at 25 SNPs associated with ocean temperature (R^2=0.88, Bradbury *et al.* submitted). Sites identified by NAFO region except, Cox= Cox's Ledge; Ogac = Ogac Lake; ARC = Arctic marine; 3K(OS)=offshore 3K; TAR= Tariujarusiq Lake; Flem=Flemish Cap).

Experimental studies often employing common rearing environments to remove environmental effects, suggest large adaptive differences among many populations. Initial work comparing cod from the Southern and Laurentian South DUs with those from the Newfoundland & Labrador documented genetic differences in juvenile growth rate (Purchase and Brown 2000), food conversion efficiency (Gulf of Maine, Purchase and Brown 2001), and in the influence of light intensity on survival and growth in early life (Laurentian South DU, Puvanendran and Brown 1998). This has been expanded in a series of common garden experiments (Marcil *et al.* 2006a,b, Hutchings *et al.* 2007) which documented clear genetic differences among traits of importance to fitness between cod from the Laurentian North and Southern DUs, the Laurentian South and Newfoundland and Labrador DUs, the Laurentian North and Newfoundland and Labrador DUs, and the Laurentian South and Southern DUs (Hutchings *et al.* 2007). Morphological variation associated with these experiments further indicate differences between all compared DUs (Marcil *et al.* 2006a,b). Overall, these experiments revealed significant main and interaction effects of temperature, food, and population on larval growth, survival, and morphological variation consistent with genetically based differences and the presence of locally adapted populations.

In summary, it seems likely based on the best current information that cod in Canadian waters represent six DUs using the criteria of isolation (as identified using tagging returns or neutral molecular markers) and evolutionary significance (expressed or non-neutral genetic markers; common garden experiments; life history traits; population growth rates). For details regarding population comparisons see table below. These six DUs display significant genetic differences, observed either with microsatellites and/or expressed single nucleotide polymorphisms consistent with significant isolation. Observed adaptive differences are strongest between DUs inhabiting water masses of contrasting water temperatures such as between the Southern DU and populations to the north or between the Northern Gulf DU and Newfoundland and Labrador DU. However, significance is also present through clear habitat discontinuities such as across the Laurentian Channel, or associated with the Arctic Lakes. Although data on the significance of the Arctic Marine DU is lacking, this DU displays the highest expressed genetic differentiation of any other marine Canadian cod population, and given its extreme habitat and evidence of genetic affinities of fish from NAFO 0A to the eastern Atlantic, the evidence for significance seems strong. It should also be noted that the coastal population of cod inhabiting Gilbert Bay, Labrador also displays excessively high genetic differentiation consistent with strong isolation. However, at present, data on the significance of this population are lacking, and as these coastal populations are found elsewhere (e.g., Holyrood Pond, NL), it seems at present it does not fit the DU criteria. Admittedly, the visible isolation presents a clear conservation priority and its DU status may change with additional life history information.

Summary of the evidence for genetic differentiation among the Newfoundland & Labrador, Laurentian North, Laurentian South and Southern DUs based on studies of selectively neutral loci and selectively important traits.

Designatable Unit	Laurentian North	Laurentian South	Southern
Newfoundland & Labrador	1. Seven microsatellite loci and pantophysin locus (Beacham *et al.* 2002) 2. Five microsatellite loci (Ruzzante *et al.* 1998) 3. Six microsatellite loci (Ruzzante *et al.* 2000) 4. Larval growth and survival (Hutchings *et al.* 2007) **5.** Morphological divergence (Marcil *et al.* 2006a)	1. Larval growth and survival (Hutchings *et al.* 2007) 2. Morphological divergence (Marcil *et al.* 2006a) 3. Six microsatellite loci (Bentzen *et al.* 1996) 4. Seventeen nuclear restriction-fragment-length-polymorphism (RFLP) loci (Pogson *et al.* 1995) 5. Ten nuclear restriction-fragment-length-polymorphism (RFLP) loci (Pogson *et al.* 2001) 6. Six microsatellite loci (Ruzzante *et al.* 2000) 7. Influence of light on survival and growth (Puvanendran and Brown 1998).	1. Five microsatellite loci (Ruzzante *et al.* 1998) 2. Morphological divergence (Marcil *et al.* 2006a,b) 3. Single nucleotide polymorphisms (n=1641) Bradbury *et al.* submitted.
Laurentian North	NA	1. Five microsatellite loci (Ruzzante *et al.* 1998) 2. Morphological divergence (Marcil *et al.* 2006a)	1. Six microsatellite loci (Ruzzante *et al.* 2000) 2. Five microsatellite loci (Ruzzante *et al.* 1998) 3. Larval growth and survival (Hutchings *et al.* 2007) 4. Morphological divergence (Marcil *et al.* 2006a) 5. Single nucleotide polymorphisms (n=1641) Bradbury *et al.* submitted. 6. Larval growth rate (Purchase and Brown 2000) and juvenile food conversion efficiency (Purchase and Brown 2001)
Laurentian South	NA	NA	1. Five microsatellite loci (Ruzzante *et al.* 1998) 2. Larval growth and survival (Hutchings *et al.* 2007) 3. Morphological divergence (Marcil *et al.* 2006a) 4. Single nucleotide polymorphisms (n=1641) Bradbury *et al.* submitted.

DISTRIBUTION

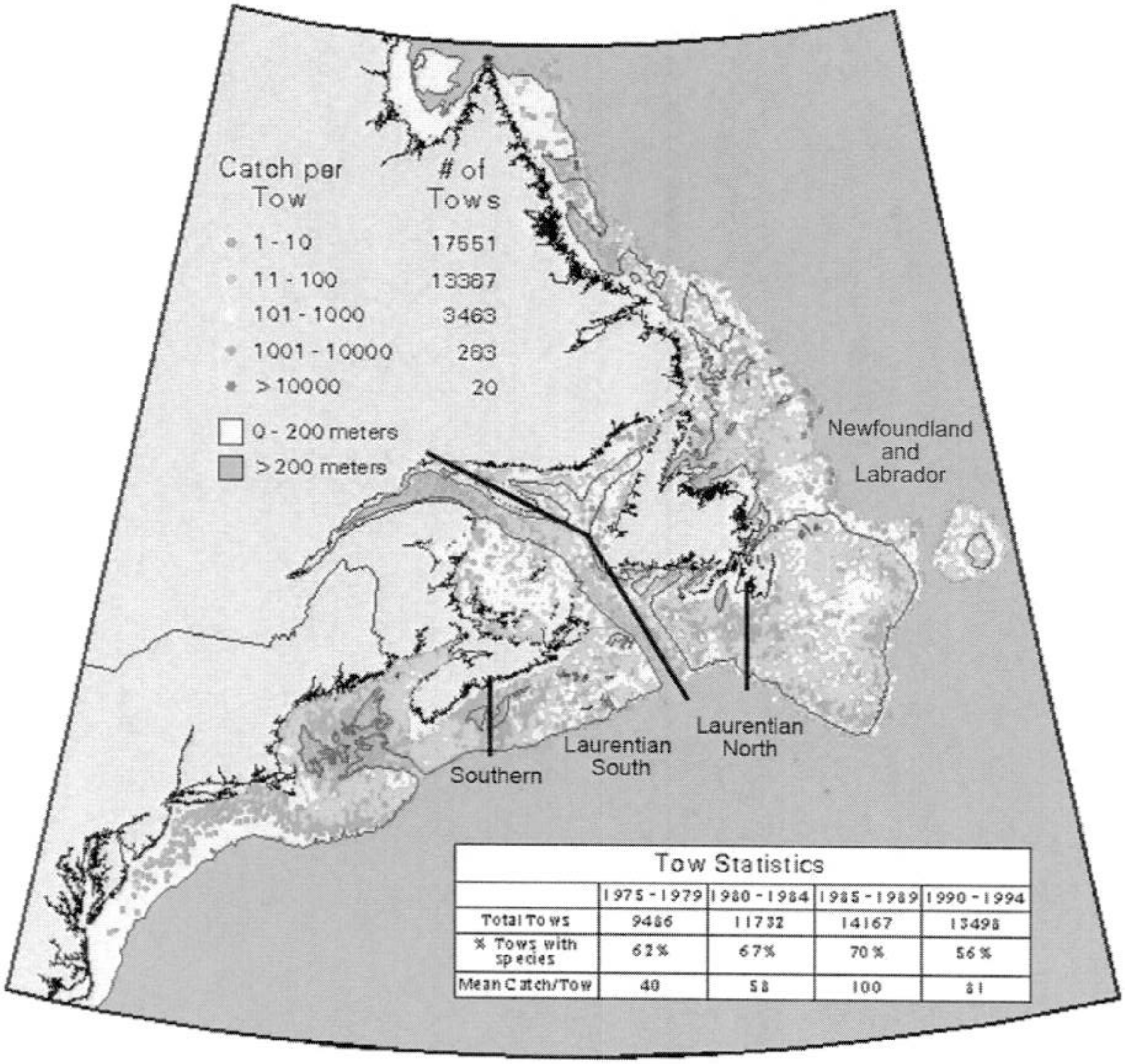
Global range

Atlantic Cod inhabit all waters overlying the continental shelves of the Northwest and the Northeast Atlantic Ocean. In the west, cod extend from waters just south of Georges Bank northward to Baffin Island, Nunavut, Canada (Figure 2). In the Northeast Atlantic, cod range from the North Sea northward through the Norwegian Sea to the Barents Sea off Norway and northern Russia. Cod are also found in abundance in the Skaggerak and Kattegat, the strait separating Norway and Sweden from Denmark, and in the southern parts of the Baltic Sea. On a global scale, the historical distribution of cod probably differs relatively little from that of its present distribution (Bigg *et al.* 2007).

Canadian range

In Canadian waters, Atlantic Cod are found contiguously along the east coast from Georges Bank and the Bay of Fundy in the south, northward along the Scotian Shelf, throughout the Gulf of St. Lawrence, around the island of Newfoundland, and finally along the east coasts of Labrador and Baffin Island, Nunavut (Figures 2, 6, 7). There are also three landlocked populations of Atlantic Cod on Baffin Island (McLaren 1967; Patriquin 1967; Hardie *et al.* 2006, 2008). Outside Canadian waters, cod can be found on the northeast and southeast tips of Grand Bank and on Flemish Cap, lying immediately northeast of Grand Bank.

In addition to these offshore waters (typically at depths less than 500 metres), cod can also be found throughout the coastal, inshore waters of Atlantic Canada. The best-studied of these is probably the small, resident Gilbert Bay population in southern Labrador (Green and Wroblewski 2000; Morris and Green 2002), a population that is geographically and genetically distinct from cod inhabiting the offshore waters in this area (Ruzzante *et al.* 2000; Beacham *et al.* 2002). A similar scenario of isolation has been noted in Holyrood Pond, Newfoundland (Bradbury *et al.* 2009). Local ecological knowledge, based on interviews with fishermen conducted by the Fisheries and Oceans Canada in concert with the Fishermen and Scientists Research Society in the Maritimes, suggests that local, inshore spawning aggregations of cod along coastal Nova Scotia were fewer in number in the late 1990s compared to earlier years.



	1975 - 1979	1980 - 1984	1985 - 1989	1990 - 1994
Total Tows	9486	11732	14167	13498
% Tows with species	62%	67%	70 %	56 %
Mean Catch/Tow	40	58	100	81

Figure 6. Distribution of Atlantic Cod in North America from the southern extreme of the species' range to northern Labrador, as determined from fisheries-independent surveys conducted by the Canadian Department of Fisheries and Oceans and the National Marine Fisheries Service in the United States. Dots represent survey catch rate data from 1975 to 1994. Solid lines mark DU boundaries. Arctic DUs not shown.

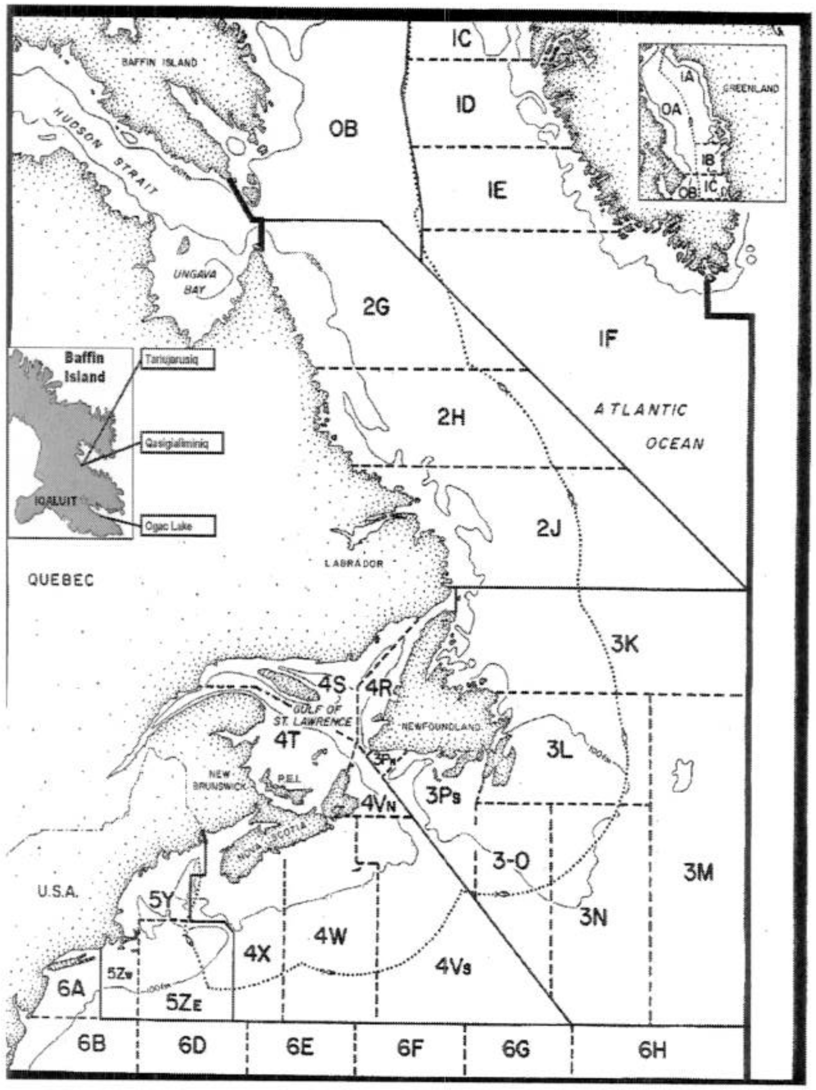


Figure 7. Map showing the NAFO (Northwest Atlantic Fisheries Organization) Divisions used to identify stocks of Atlantic Cod managed by NAFO and Fisheries and Oceans Canada. The insert on the left side of the map shows the location of the three Arctic lakes that constitute the Arctic Lakes DU. The Arctic Marine DU includes NAFO 0A and 0B. The Newfoundland and Labrador DU includes NAFO 2GHJ and 3KLNO. The Laurentian North DU includes NAFO 3P and 4RS. The Laurentian South DU includes NAFO 4TVW. The Southern DU includes NAFO 4X and the Canadian portions of Divisions NAFO 5Y and 5Z.

The extent of occurrence of Atlantic Cod in Canadian waters is probably on the order of 1.1 million square kilometres, an area larger than that of Ontario, and an area slightly smaller than to that of Quebec. The extent of occurrence has either remained stable over the past four decades (and earlier) or it has declined. Estimates of the extent of occurrence of the individual DUs are provided in the following sections.

HABITAT

Habitat requirements

Knowledge of the habitat requirements of Atlantic Cod is rather poor. Despite the paucity of data, it is reasonable to predict that habitat requirements change significantly with age in this species. With the exception of the few cod that have been observed in situ, the following information is based on the sampling of cod at various life stages from different depths and different areas of the ocean. Also the broad-scale habitat requirements may change with specific migratory life history which seems to correlate with abundance (Robichaud and Rose 2004). Small resident non-migratory populations may exist in inshore bays and likely complete their life cycle in a restricted geographic area (Bradbury *et al.* 2008) and hence have very different habitat requirements in comparison to migratory populations.

During the first few weeks of life, cod exist as eggs, and then as larvae, in the upper 10 to 50 metres of the ocean. The primary factors affecting habitat suitability for cod during these early stages of life are probably food availability and temperature (the lower the temperature, the longer the development time, and the longer the period of time during which cod are at sizes that make them highly vulnerable to predation and advection). As such, oceanographic features which retain and concentrate cod eggs and larvae as well as potential prey are likely important to early life history survival (e.g., Bradbury *et al.* 2000, 2002, 2008).

The most essential physical habitat characteristics for Atlantic Cod may be those required during the juvenile stage when cod have settled to the bottom for the first 1 to 4 years of their lives. Several studies suggest that a heterogeneous habitat, notably in the form of vertical structures, such as Eelgrass, *Zostera marina*, in nearshore waters, is favoured by juvenile cod (e.g., Gotceitas *et al.* 1995, 1997; Tupper and Boutilier 1995; Gregory and Anderson 1997; Laurel *et al.* 2003a,b, 2004). Based on observational studies (Tupper and Boutilier 1995) and on experimental manipulations (Gotceitas *et al.* 1995; Linehan *et al.* 2001; Laurel *et al.* 2003a, b), physically heterogeneous habitat appears advantageous to juvenile cod because it reduces the risk of predation and may allow for increased growth. As such, other habitats such as macroalgae (Keats 1990), obble (Gotceitas *et al.* 1995; Tupper and Boutilier 1995) and deep-water emergent structures (Lindholm *et al.* 2007) may also be important.

Offshore, it is logical to assume that physical structure would also reduce predator-induced mortality of juvenile cod. For example, video recorded on a submersible during an August 2001, survey of deep, continental-slope waters off southwestern Nova Scotia revealed juvenile cod amongst the extensive growths of deep-sea corals (Anna Metaxas, pers. comm., Department of Oceanography, Dalhousie University, Halifax, Nova Scotia).

As cod grow older, it appears as though their habitat requirements become increasingly diverse. Indeed, it is not clear that older cod have particular depth or bottom-substrate requirements. The primary factors affecting the distribution and habitat of older cod are probably temperature and food supply. In a general sense, it appears that cod tend to avoid cold temperatures. But what is cold for cod in one area is evidently not cold for cod in other areas. For example, it is widely believed that cod migrate out of the southern Gulf of St. Lawrence in autumn to avoid the cold water temperatures in the Gulf during winter (Campana *et al.* 1999). However, cod off eastern Newfoundland, notably those that overwinter in inshore waters, exist at temperatures below 0°C (Goddard *et al.* 1999). Perhaps the most reasonable explanation for these apparent differences in water temperature tolerance is that cod in different areas are adapted to their local environments. This conclusion is supported by the finding that cod in different areas of coastal Newfoundland possess different levels of antifreeze protein (see Physiology section below), a physiological adaptation that would influence the tolerance of cod to low water temperatures.

From a spawning perspective, it is not known if cod have specific habitat requirements. Cod spawn in waters ranging from tens (Smedbol and Wroblewski 1997, Morris and Green 2002) to hundreds of metres in depth (Hutchings *et al.* 1993; Bradbury *et al.* 2000; 2008). Atlantic Cod in Canadian waters are known to spawn extensively throughout the inshore, nearshore, and offshore waters (McKenzie 1940; Scott and Scott 1988; Hutchings *et al.* 1993; Morgan and Trippel 1996), a conclusion also supported by fishermen (Neis *et al.* 1999). Although cod spawning appears to be associated with the bottom (Morgan and Trippel 1996; Hutchings *et al.* 1999), this may have more to do with the cod mating system (a lek mating system has been hypothesized; Hutchings *et al.* 1999; Nordeide and Folstad 2000; Windle and Rose 2007) rather than any physical requirements for the offspring, given that cod neither build egg nests nor provide parental care. Perhaps the factor most beneficial to the survival of their offspring is the presence of physical oceanographic features (e.g., water currents) that would serve to entrain the buoyant eggs and prevent them from being dispersed to waters poorly suited to larval cod, e.g., waters off the continental shelf. It is highly unlikely that spawning habitat is limiting for Atlantic Cod.

Thus, the habitat most likely to be potentially limiting for Atlantic Cod may well be the vertical, "three-dimensional" structures provided by plants, rocks, physical relief, and corals. In addition to providing protection from predators, such physical heterogeneity would almost certainly provide habitat for small fish and invertebrates, organisms upon which juvenile cod could feed.

Trends

If physical structure is critically important to the survival of juvenile cod, notably in the form of plants, bottom physical relief, and corals, there may be less habitat available today than decades ago in some parts of the range of this species. Repeated trawling in a given area tends to "smooth" and flatten the bottom, reducing vertical and physical heterogeneity (Collie *et al.* 1997, 2000; Kaiser and de Groot 2000). Any reduction in physical heterogeneity on the bottom since the 1960s if present may be attributed to the increased use of bottom-trawling gear to catch groundfish such as cod, Haddock, Pollock, and several species of flatfish. The destruction of deep-dwelling corals off Nova Scotia—first reported and well-documented by fishermen—is another product of bottom-trawling and, to a considerably lesser degree, long-lining (Mortensen *et al.* 2005). Although physically heterogeneous areas frequented by juvenile cod may not have been heavily trawled where gear damage or loss was likely, no studies have been undertaken to evaluate the effects of trawling on the quantity and quality of juvenile cod habitat. Trawling in many areas has been substantially reduced following the ground fish collapse of the early 1990s. In addition to trawling effects, the recent discovery of Green Crab (*Carcinus maenas*) in Placentia Bay, Newfoundland, and their well documented negative impact on eelgrass beds (e.g., Davis *et al.* 2002), may present a significant threat to juvenile cod habitat and survival. The magnitude of the threat of Green Crab to juvenile cod habitat remains unknown and requires further evaluation.

BIOLOGY

General

Despite having been fished for more than 500 years in Canadian waters, there remain large gaps in our knowledge of many of the most basic elements of the biology and ecology of this species. Nonetheless, it is known that after hatching, a period of time that takes approximately 60 degree-days, the larvae obtain nourishment from a yolk sac for a few days. During the larval stage, the young feed on phytoplankton and small zooplankton in the upper 10 to 50 metres of the water column. After a few weeks, the larvae swim, or "settle", to the bottom, where they appear to remain for a period of 1 to 4 years throughout most of the species' Canadian range. These settlement areas are known to range from very shallow (< 10 m to 30 m) coastal waters to moderately deep (50 to 150 m) waters on offshore banks and almost certainly provide larval and juvenile cod protection from predators as well as potential prey. After this settlement period, it is believed that the fish begin to undertake the often-seasonal movements (apparently undirected swimming in coastal waters) and migrations (directed movements to and from specific, highly predictable locations) characteristic of adults (e.g., Cote *et al.* 2001; 2004).

Reproduction: Life history variation

The life history of cod varies a great deal (Myers *et al.* 1996; McIntyre and Hutchings 2003, Olsen *et al.* 2005, 2008). Most life history traits, such as age and size at maturity, longevity, and size-specific fecundity differ greatly among populations, while some, such as egg size, appear to be similar throughout the species' range. As with most indeterminately growing organisms (those that continue to increase in size after maturity), fecundity (the number of eggs per female per breeding season) increases with body size. In cod, as with most fish, the number of eggs per female generally increases with body mass as a power function. Body size at a given age is a function of growth rate, a parameter that varies greatly among cod populations, being relatively