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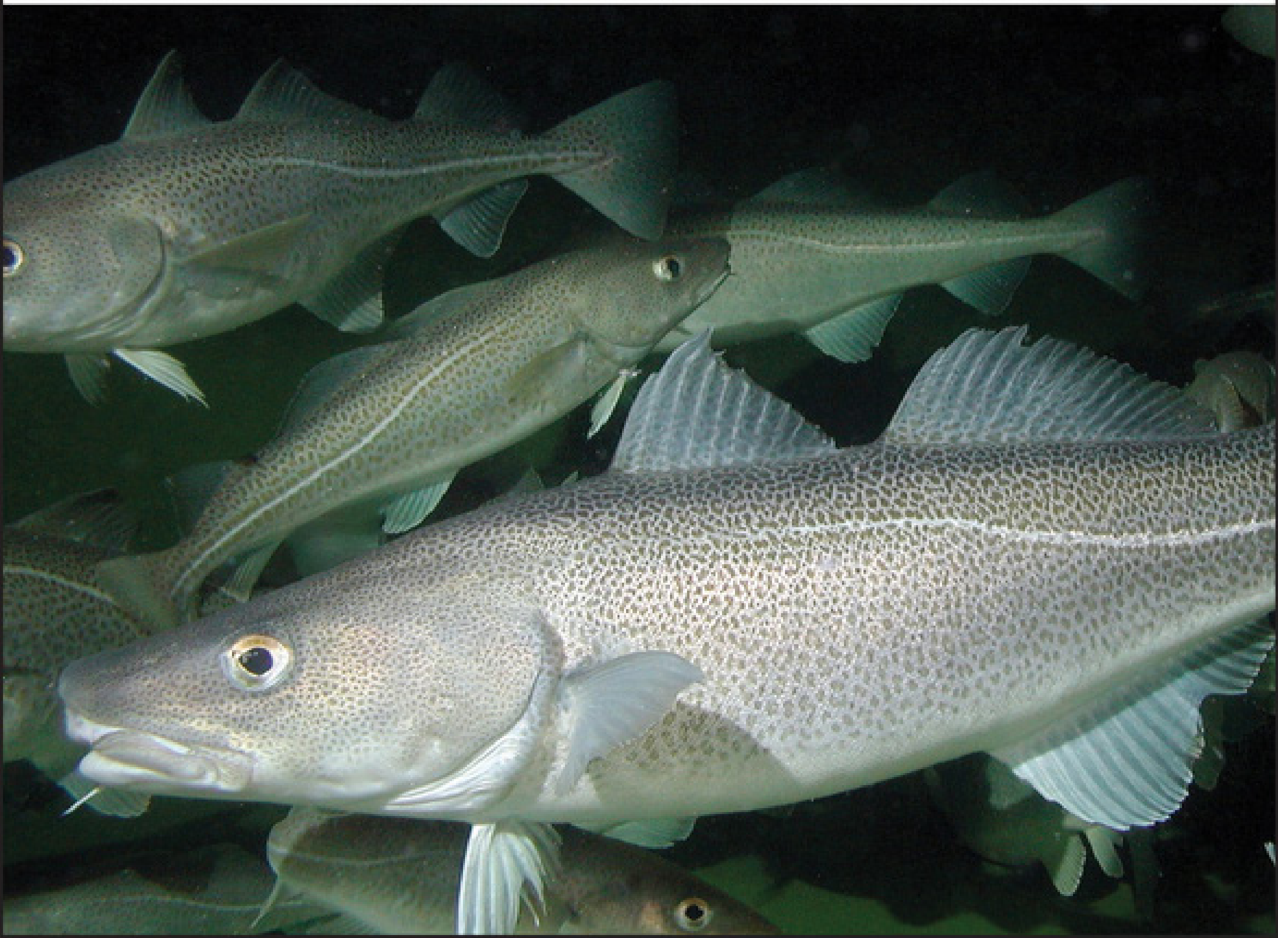
Atlantic Cod

A Bio-Ecology



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A Bio-Ecology

Edited by

George A. Rose
Institute for the Oceans and Fisheries, University of British Columbia,
Vancouver, Canada

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Preface

I met George Rose more than 20 years ago. At the time I was researching my book on cod. The Northern stock off Newfoundland and Labrador, the greatest commercial fish stock in human history, had just collapsed. I was turning to scientists for insights. I got quite a few from my meeting with George. But I also came away with this very important insight – not nearly enough was known about cod. Certainly not enough to save it.

But that was about to change. Now everyone wanted to know about cod and funding and support to research it were becoming available. This book is a by-product of this growth of research.

I think that the theme song for marine biology should be the Joni Mitchell song 'Big Yellow Taxi':

> Don't it always seem to go
> That you don't know what you've got till it's gone

At the time we were all focused on a cultural tragedy. The culture of Newfoundland was crushed. How sad today to watch the Canadian government try to replace the culture of commercial fishing with the culture of tourism. Today there are cod souvenirs of all kinds for purchase everywhere in Newfoundland – cod hats, cod tee-shirts, cod stuffed animals, I even got a ceramic cod stand for my business cards. In the old days Newfoundland was a fishing community. It did not sell tchotchke.

But it was not only Newfoundland and Labrador or even just much of Atlantic Canada that was at risk. What would become of my native New England? What was the future of Gloucester, New Bedford and Point Judith? What was the future of Newlyn on the Cornish coast and Grimsby on the North Sea and all the other cod ports in Iceland, the Faroe Islands, Norway and Denmark?

Is there anything more important than saving all the cultures of the northern world? But there is the problem of Darwin. Darwin had it right. And in *On the origins of species* he explains two natural laws that marine biologists cannot ignore. The first is that a species needs a large population in order to survive. How large that is hard to say but certainly the Northern cod stock and several others were driven well past the tipping point. The other is that all species are dependent on many other species to assure the survival of the natural order. If a species is lost, especially one as important as cod, others will be affected. We are already beginning to see this in the disappearance, despite tightly regulated fisheries, of other fish stocks and the disappearance of sea birds.

Yes, the earth could completely unravel. People want their cultures back, fishermen want to get to work. Governments want to say that their programmes have been a success, but natural laws, as Gandhi once said about the law of love and the law of gravity, will work, whether we believe in them or not.

Is there an answer to all this? While cod and other fish are faced with many challenges such as pollution and climate change, for the moment fishery management seems the problem with the best chance of being resolved. In fact, with the help of better science, it is steadily improving and showing results. Cod fisheries that have abandoned the wasteful practices of the past and become based on well-thought-out science and an accounting of the full ecosystem are doing well. Others not so. Highlighting that science is essential. And that is the purpose of this book.

Mark Kurlansky

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Atlantic Cod: A Bio-Ecology

Introduction

Atlantic cod (*Gadus morhua*) has been called *fish* for centuries in the many languages of fishing cultures across the North Atlantic. There was no need to say more, it was just *fish*. Cod was fish, and fish was cod. In Norway, Scotland, the Faroes, Iceland and Newfoundland, if *fish* was for dinner there was no doubt that it was cod. It could be nothing else. As with deities, it was considered inappropriate to refer directly to something held in such esteem. And rightly so, because for coastal communities around the North Atlantic, life or death depended on the cod. If fish failed to appear during their annual migrations, starvation, or severe economic depression was a likely outcome. All other species were referred to with common names, without reverence. In New England, despite the rapid advancement of industry and commerce that soon subsumed the cod fishery in the nineteenth century, the 'sacred cod' still hangs in the Massachusetts State House, bearing tribute since 1798 to a fish that gave life, and some say freedom, to a fledgling nation (Figure I.1).

The association of cod with the North Atlantic is more than a human construction. Gadoids, the classification group that includes the Atlantic cod, are one of the few families of fishes endemic to the North Atlantic, many others having made their way to these waters from the Pacific or southern waters (Chapter 1). Gadoids began, as have other key groups, as rather small and inconspicuous species, but once gaining a foothold in the expanding waters of the North Atlantic, over the past five million years have evolved to become dominant components of these ecosystems. The gadoid family came to occupy most all of the continental shelf regions of the North Atlantic, and even expanded to the North Pacific (see Chapter 1). The Atlantic cod became the most dominant of all. The main stocks – this is a human construction – are given in Table I.1, along with their commonly used names, with their geographic range shown in Figure I.2.

A highly adaptable physiology has enabled cod to inhabit a wide variety of habitats from coastal bays to large offshore banks across its range (Chapter 2). Cod exist over a wide range of sea temperatures, salinities, and feeding opportunities, with large and small populations adapting to local conditions. There is literally a cod for every continental shelf habitat.

Cod are highly fecund, as are most gadoids. Large females can produce tens of millions of very small eggs, and being a broadcast spawner, offer no parental care (Chapter 3). Cod rely on numbers and egg release in the right place at the right time. Thousands of

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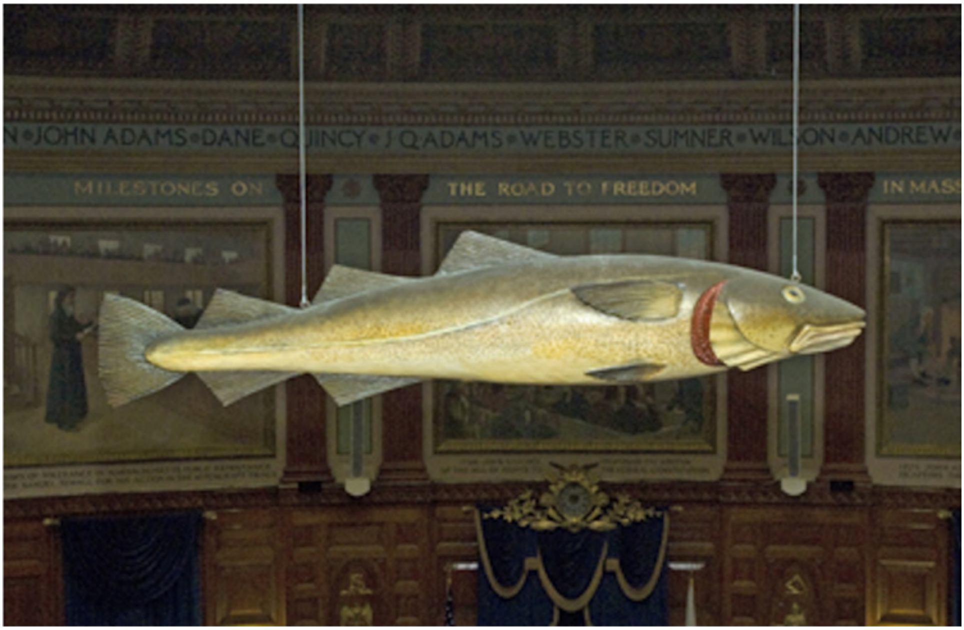

Figure I.1 The 'Sacred cod', in the State House of the Commonwealth of Massachusetts. On 17th March 1784, Mr John Rowe of Boston arose from his seat in the Hall of Representatives at the Old State House, and offered the following motion: 'That leave might be given to hang up the representation of a cod fish in the room where the House sit[s], as a memorial of the importance of the Cod-Fishery to the welfare of the Commonwealth…'. A symbolic cod was placed in the hall, and was later moved to the new State House building in 1798. A wooden 'Sacred cod' has remained there ever since – the current carving is the third since 1784. From Celebrate Boston and Ecology and Evolutionary Ethology of Fishes websites.

years of behavioural conditioning and selection have resulted in spawning locations that result in sustainable if imperfect and variable survival. Only a tiny fraction of released eggs will ever grow to adulthood, most dying, or being consumed by predators. The act of spawning is far from a mundane occupation. The cod is above all a social species, with complex behaviours occurring both before and during courtship and spawning, involving soundings, spatially-specific and pelagic behaviours whose functions are only partially understood.

Cod begin life as a drifting egg, completely at the mercy of the prevailing near-surface currents (Chapter 4). If their release timing and location leads to drift to waters with favourable environmental and feeding conditions after their on-board food supply (the yolk sac) is depleted, there is a small chance they may survive through the larval stage and settle to near bottom in a liveable location. If not, they cannot survive. It is perilous journey – many factors must work in their favour for survival. Predicting survival of young cod to adulthood or to a fishery, one of the holy grails of cod science, has proven to be an elusive goal.

The biggest cod stocks, those in the Barents Sea (Northeast Arctic cod), Icelandic waters and off the Northeast coast of Newfoundland and Labrador (Northern cod), are

Table I.1 Atlantic cod stocks, their management, statistical areas, geographic areas, and commonly used names (most stocks are referred to by their geographic location).

Management	Statistical area(s)	Name of area	Common names
ICES	NAFO 1 inshore	West Greenland inshore	
ICES	NAFO 1 A-E offshore	West Greenland offshore	
ICES	ICES 14b and NAFO 1F	East and South Greenland	
ICES	ICES 1 and 2	Barents Sea-Norway	Northeast Arctic cod, Arcto-Norwegian cod, Barents Sea cod
ICES	ICES 1, 2, 4a	Norwegian coastal	Norwegian Coastal cod
ICES	ICES 3a	Kattegat	
ICES	ICES 3b, c	Western Baltic	
ICES	ICES 3d	Eastern Baltic	
ICES	ICES 4, 7d, 3a	North Sea, Eastern English Channel, Skagerrak	
ICES	ICES 5a	Iceland	Icelandic cod
ICES	ICES 5b	Faroe Plateau	Faroe Island cod
ICES	ICES 6a	West Scotland	
ICES	ICES 6b	Rockall	
ICES	ICES 7a	Irish Sea	
ICES	ICES 7e-k	Eastern English Channel and Southern Celtic Sea	
NAFO	NAFO 3M	Flemish Cap	
NAFO	NAFO 3NO	Southern Grand Bank	Grand Bank cod
Canada	NAFO 2JH	Labrador	
Canada	NAFO 2J3KL	Northeast Newfoundland-Labrador	Northern cod
Canada	NAFO 3Ps	Southern Newfoundland	3Ps cod
Canada	NAFO 4RS (3Pn-4RS)	Northern Gulf of St. Lawrence	
Canada	NAFO 4T (4TvN)	Southern Gulf of St. Lawrence	
Canada	NAFO 4Vs	Northern Scotian Shelf	
Canada	NAFO 4W	Southern Scotian Shelf	
Canada	NAFO 4X	Bay of Fundy	
USA	NAFO 5Y	Gulf of Maine	
USA-Canada	NAFO 5Z	New England offshore-Georges Bank	Georges Bank cod

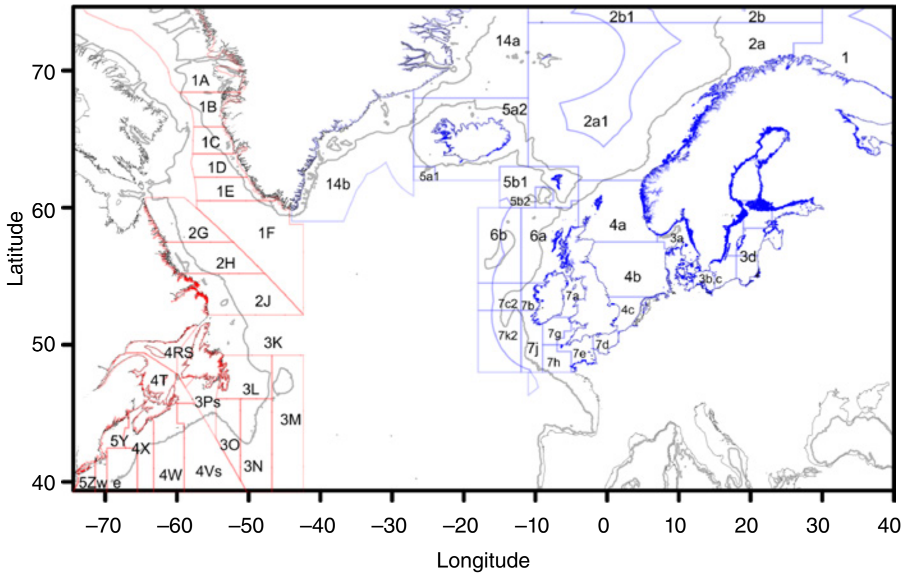

Figure I.2 The statistical regions assigned to the Atlantic cod stocks (red are the NAFO zones and blue those of ICES). The 500 m bathymetric contour which encompasses most but not all of the cod range appears as grey line.

all highly migratory. Other stocks are less so and many are sedentary (Chapter 5). Nonetheless, most stocks move to some extent over the North Atlantic seasons, even if within small coastal regions. Many groups exhibit what can be very exact homing behaviour between spawning and feeding areas, repeating patterns that largely determine stock structures. Fisheries have been dependent on this regularity for hundreds of years (Chapter 7).

Cod can and will consume most anything (Chapter 6). No doubt, their success as a species partly depends on being a 'generalist' predator – feeding on a wide range of prey across their range – and often focussing on prey that are both abundant and available. Nonetheless, they appear to have developed a preference for and dependence on certain types of prey with high energy content. The strongest association of cod with a singular prey occurs in the most northerly groups, the Northeast Arctic, Icelandic and Northern cod off Newfoundland and Labrador, that depend heavily on capelin (*Mallotus villosus*) and appear to have developed a preference for this prey. Cod appear to know what is good for them, and will pursue choice prey when available, for some stocks basing their entire annual cycle on intercepting this prey. Growth rates vary greatly among cod groups, dependent mostly on sea temperatures and the availability of high value prey. Cod are a key if not dominant component of the energy transfer up the food web in many North Atlantic ecosystems.

A thousand years ago, cod fisheries off present day Norway began as seasonal food gathering activities of peoples who farmed and fished for subsistence (Chapter 7). The advent of drying and salting of cod enabled not only the preservation of a high protein food for consumption year-around at home but enabled the Viking voyages of discovery and commerce. As the large stocks off Iceland and then Newfoundland and the New

Table I.2 Important Abbreviations

Acronym or short form	Definition
NAFO	Northwest Atlantic Fisheries Organization
ICES	International Council for the Exploration of the Sea
ICNAF	International Commission for the Northwest Atlantic Fisheries
PNAS	Proceedings of the National Academy of Science, USA
F	Instantaneous rate of fishing mortality
M	Instantaneous rate of natural mortality
Z	Instantaneous rate of total mortality ($F+M$)

World became accessible to European interests, cod became one of the dominant trade items of the eighteenth and ninetieth centuries. Whole economies became dependent on fish. In the twentieth century, major increases in technology and unrestrained harvests led to decimation of many stocks. Science-based management in the twenty-first century has led to increases in some stocks, and rebuilding in others, but some groups have yet to recover from the major declines that occurred in the last half of the twentieth century.

Although cod occur over a relatively wide range of sea temperatures, they are fundamentally a species of the cool waters of the North Atlantic. But climates change, and at present the North Atlantic is experiencing relatively rapid changes in sea temperatures that will influence cod distribution and abundance (Chapter 8). Northern areas have in the past benefitted from warming periods, and are likely to see increased cod abundance in coming years, but others near the southern limits of distribution are likely to see contraction.

So what of the future for this iconic species? Will cod's long history as a key component of the continental shelf ecosystems of the North Atlantic and as a human food source continue? The answer must be a qualified yes (Chapter 9). Despite the massive overfishing that depleted most stocks in the twentieth century, some stocks have regained their abundance (they have literally retaken their place in the ecosystem) or are increasing. For all stocks, the key to continuance or resurgence remains uncompromising scientific management. Failures of the past all stem from one mistake: harvesting more than a stock can produce. Much of the knowledge needed to prevent this from reoccurring is contained in the extensive information given in the following chapters. Some commonly used acronyms and short forms used are given in Table I.2.

This book has been a work dictated not only by science but by a love for *the fish* and its fisheries by all of its authors. It has taken many years to complete. Moreover, the knowledge contained in these chapters rests on the shoulders of many who came before us and the work of many contemporary scientists whose work is cited here. We hope that this accumulated knowledge will lead to wisdom about how to sustainably manage the Atlantic cod and its fisheries. This is the goal we aspire to. In short, may cod prosper long into the future – may it always be *fish*….

January 31, 2018. *George A. Rose*

1

Atlantic Cod: Origin and Evolution

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> *Gadidae proper is virtually unique among fishes in having its headquarters on the continental shelf of the temperate North Atlantic … a region with a fish fauna comprised chiefly of the tag ends of groups having their main centers of diversity farther to the south or in the temperate North Pacific*
>
> Marshall and Cohen, 1973

> *The hero, Gadus morhua … is built to survive. Fecund, impervious to disease and cold … it was the perfect commercial fish*
>
> Mark Kurlansky, 1997

1.1 Introduction

The Atlantic cod (*Gadus morhua*) is one of the best-known fishes of the world. It has none of the cachet of the Atlantic salmon (*Salmo salar*), nor the pure majesty of the Bluefin Tuna (*Thunnus thynnus*), nor the terrifying awe of the Great White Shark (*Carcharodon carcharias*), but alone among fishes, cod did indeed 'change the world' (Kurlansky 1997). It is a fish for all seasons and all people. Over the past millennium, the humble cod has fuelled economies and exploration, been fought over in a multitude of wars, changed history, and fed millions. No other fish, or indeed, any animal, can claim this. And despite 100 years of scientific research, the biology and behaviour of this species continues to surprise researchers and amaze human observers.

The Atlantic cod fisheries in Norway and the North and Baltic Seas have long and well-known histories, and the role of the cod in the settlement and development of Iceland and Newfoundland is also well established, the latter having been described as a 'great ship moored near the fishing banks' (Harris et al. 1990). Less well known is how the cod fishery jump-started the economy of Massachusetts and much of the New England colonies, now one of the most prosperous regions of the world. To this day, centre stage in the Massachusetts State House, still hangs the 'sacred cod.'

Atlantic Cod: A Bio-Ecology, First Edition. Edited by George A. Rose.

The Atlantic cod is indeed a sacred fish over much of its range in the North Atlantic (Rose 2007). It has many names, in many languages and dialects, but almost everywhere, as with deities, it is seldom referred to directly. Most often it is simply fish, or *fiskr*, or variations of that ancient name.[1]

Cod is not just a fish, it is *the* fish (Figure 1.1).

Figure 1.1 The *fish* – the Atlantic cod – here the yellow-dark with white belly colour phase.

Figure 1.2 Cod aggregation at a spawning location in Þistilfjörður, North of Iceland. Spawning at this location often takes place at low temperatures (<3 °C; Thorsteinsson, personal communication). Photo Erlendur Bogason.

1 The modern English fish etymology: 'from Old English *fisc*, from Proto-Germanic **fiskaz* (compare West Frisian/Swedish *fisk*, Dutch *vis*, German *Fisch*), from Proto-Indo-European **pik̂sk̂os* (compare Irish *iasc*, Latin *piscis*, Russian пискарь (*piskárĭ*) "groundling", Sanskrit *picchā* "calf (leg)", *picchila, picchala* "slimy, slippery)". A connection with Sanskrit indicates an ancient origin.' Quote from Wiktionary.

1.2 Taxonomy and Morphology

The Atlantic cod takes its scientific name, *Gadus morhua*, from the Greek *gados*, meaning fish, and the Latin *morua*, for cod. The species is a member of the family Gadidae of the order Gadiformes and superorder Paracanthopterygii. The Gadidae family includes 13 genera and 24 species, of which the genus *Gadus* contains only three (maybe four) species, the Atlantic cod, Pacific walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) (Coulson et al. 2006).[2] It is still uncertain if the Greenland or Rock cod (*Gadus ogac*) is the same species as Pacific cod, or a very close relative. In coastal waters of Newfoundland and Labrador and Greenland, Atlantic and Greenland cod live in close proximity (Knickle and Rose 2014a,b). Other close-living relatives in the Gadidae family include pouts, poutings and poor cod (*Trisopterus* species), saffron cod (*Microgadus* species and *Eleginus navaga*), haddock (*Melanogrammus aeglefinus*), Atlantic pollock or saithe (*Pollachius virens*), whiting (*Merlangius merlangus*) and the sister species the polar cod (*Boreogadus*) and Arctic cod (*Arctogadus*) that are endemic to the Arctic (Carr et al. 1999; Coulson et al. 2006).

Atlantic cod and its relatives are distinguished by the presence of three dorsal fins on the back, two anal fins on the lower side and anteriorly located pelvic fins positioned slightly in front of the pectorals. The pelvic fins stand high on the body, a characteristic of all Paracanthopterygii. A distinguishing feature of the cod and some relatives is a barbel positioned at the end of the chin. Cod vary in colour depending on location, diet and immediate environment (Gosse and Wroblewski 2004; Sherwood and Grabowski 2010). The two main phases of coloration vary from grey-green-yellow to red-brown, but other variations also occur.

1.3 Origin and Evolution

Atlantic cod adapted to occupy most all of the continental shelves that circumscribe the North Atlantic boreal region. These extensive continental shelves resulted from plate tectonics and the formation of the Atlantic Ocean that began some 150–200 million years ago (MYA) with a rift separating what would become the American and Eurasian landmasses (Rose 2007). To the north, North America and Greenland moved north-westward from Eurasia, opening the Norwegian Sea about 60–55 MYA. The stretching of the edges of the continental landmasses led to the formation of massive shallow shelf regions that became drowned with seawater. Most notable are the Barents Sea and the Grand Bank, the later which has waters only 50m deep 400km from land. The trailing edge of the western-moving North America became the Flemish Cap, a part of the

2 The genus *Gadus* has commonly been thought to contain three species: Atlantic cod (*Gadus morhua*), Pacific cod (*Gadus macrocephalus*) and Greenland cod (*Gadus ogac*). However, recent studies by Coulson et al. (2006) have demonstrated that the endemic pacific species, walleye pollock (*Theragra chalcogramma*) is more closely related to the endemic Atlantic cod than is the Pacific cod (*Gadus macrocephalus*). Coulson et al. (2006), have therefore suggested that the walleye pollock should be of the genus *Gadus* as originally described (*Gadus chalcogrammus* Pallas 1811). They also found that the Arcto-Atlantic Greenland cod previously regarded as a distinct species (*G. ogac*) should be more correctly classified as subspecies within the pan-Pacific *G. macrocephalus*.

continental shelf off Newfoundland that lies over 500 km from land but lies less than 150 m in depth, and which became the grounds for the most easterly of the northwest Atlantic cod stocks.

Several major tectonic events over the past 100 million years have had large influences on the formation of the cod grounds as well as the species compositions and resultant ecology of the North Atlantic. The first event occurred about 80 MYA, as the westward-moving North America shunted towards Siberia. Gradually, the circulation of warmer Pacific waters to the Arctic slowed. Eventually the flows would stop, as a land bridge from Alaska to Asia emerged which spanned the Bering Sea and blocked the passage of waters from the Pacific to the Arctic North Atlantic. These regions remained biologically isolated for over 50 million years, until warming conditions about 6–12 MYA led to sea level rises and the reopening of the northwest Arctic passage (Briggs 2003). As sea levels rose, the passage of species and genera through the Bering Strait to the Arctic and North Atlantic increased, and by about 3.5 MYA movements of molluscs and other fauna appear to have been unrestricted.

The passage of species from the North Pacific to the Arctic and North Atlantic 3–6 MYA has been called the Great Trans-Arctic Biotic Interchange (Briggs 1995, 2003). Its importance to the ecology and fisheries of all regions can hardly be overemphasized. It was a time of warming, with the Arctic becoming ice-free and boreal (Golikov and Scarlato 1989; Raymo et al. 1990). Most importantly, the opening of the Northwest Passage led to movements of the much richer Pacific marine fauna to the relatively impoverished North Atlantic, with a few movements the other way. This interchange would have great importance to the developing gadoid stocks of the North Atlantic, providing them with whole new sources of prey and creating opportunities for larger stocks and greater ranges, and, in a stark reversal of the general Pacific-to-Atlantic pattern, resulted in a migration of gadoids from the Atlantic to the North Pacific (Rose 2007).

A second key factor in the formation of the Atlantic cod stocks occurred between 3 and 4 MYA, with the rise of the Panama Isthmus, which blocked the westward tropical ocean flows from the Atlantic to Pacific. This blockage reinforced the turning of the westward-flowing currents northward along the coast of North America, which drive the Gulf Stream and North Atlantic Drift (Barry 1989; Raymo 1994). The Gulf Stream carries immense amounts of tropical waters northward, some 19 million cubic metres per second, more than 25 times the combined flows of all the world's rivers (Gaskell 1972). These currents would ultimately lead to the formation of much additional and productive habitat for cod and other North Atlantic species. The most productive of the cod stocks would form in the direct path of these currents.

A third major tectonic influence on the cod stocks of the North Atlantic was the emergence of the mid-Atlantic Ridge, the spreading line of the widening North Atlantic. From this ridge emerged the island of Iceland and its continental shelf, which would form one of the greatest cod grounds.

After the biotic exchange of prey from the Pacific, with the Gulf Stream and North Atlantic Drift bringing warming waters northward and the emergence of entirely new continental shelf regions, the stage was set for massive expansion and adaptation by the Atlantic cod. It would end with cod as the dominant predator over most of the shelf regions of the entire North Atlantic (Figure 1.3).

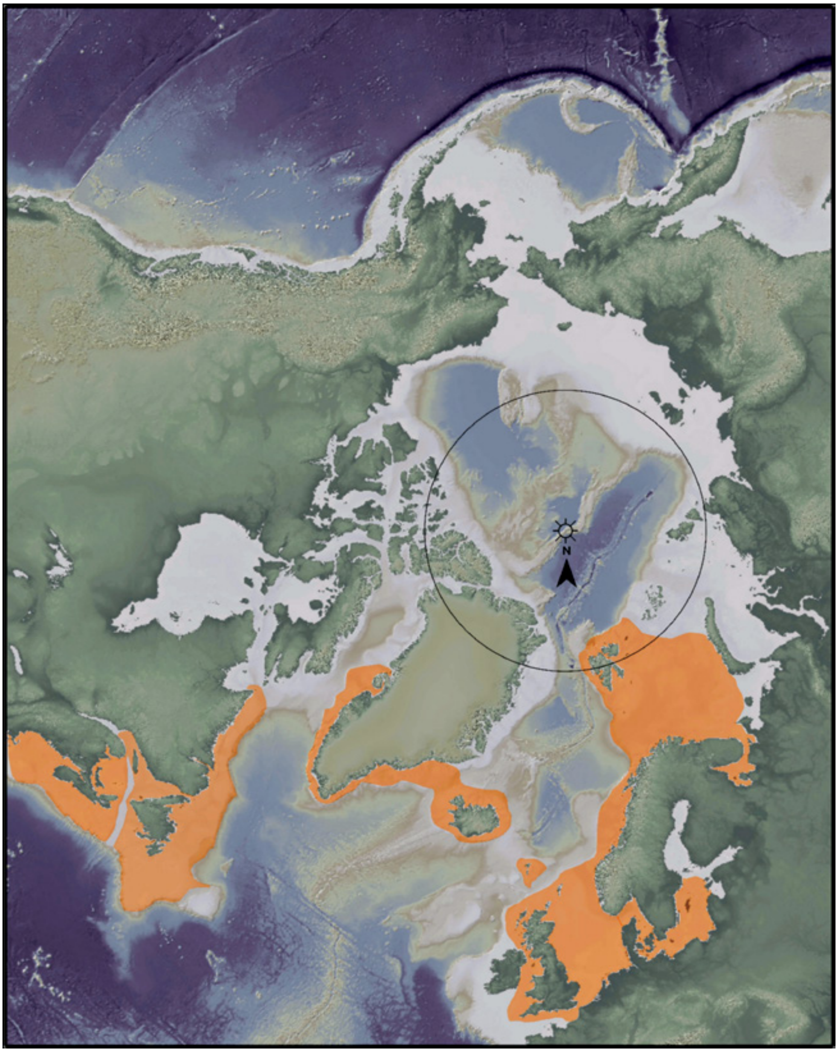

Figure 1.3 Geographical distribution of Atlantic cod.

1.4 Cod: One of Few Endemic Atlantic Species

The modern gadoids are among the few fishes endemic to the continental shelves of the North Atlantic (Ekman 1953). The North Atlantic is a young ocean relative to the Pacific and Indian Oceans. The gadoids are young species. Svetovidov (1948) suggested that gadoids originated in the eastern North Atlantic in the early Tertiary (50–65 MYA). This notion has been supported by the finding of a fossil gadoid in Greenland (Fedotov and Bannikov 1989 and references therein) and the discovery of fossil gadoid otoliths from the North Atlantic (Nolf and Steurbaut 1989). Additional supporting evidence based on genetic analysis has been provided by Carr et al. (1999) and

Coulson et al. (2006), demonstrating that the basal gadoid genera is endemic to the Northeast Atlantic. By about 5 MYA, Atlantic cod and two closely related gadoids, haddock (*Melanogrammus aeglefinus*) and pollock (*Pollachius virens*, also known as saithe) had evolved as separate species, likely from a common ancestor of the basic gadoid lineage. Counter to the general movement of Pacific marine fauna to the North Atlantic during the Great Trans-Arctic Biotic Interchange (including some key species such as capelin (*Mallotus villosus*), snow crab (*Chionocetes opilio*) and the pandalid shrimps, the progenitors of modern Atlantic cod moved westward from the North Atlantic to the Pacific (Raymo et al. 1990; Coulson et al. 2006; Bigg et al. 2008; Carr and Marshall 2008).[3] At least 3.5 MYA, Atlantic cod made it to the Pacific and evolved to become Pacific cod (*Gadus macrocephalus*). About 2 MYA, Atlantic cod made another excursion to the Pacific, and these fish evolved to become the Pacific walleye pollock (*Theragra chalcogramma*), which really is a cod (Coulson et al. 2006)! It is thought that much more recently, perhaps around a hundred thousand years ago (TYA), the Pacific cod came back to the Atlantic and now exists as the Greenland or Rock cod (*Gadus ogac*).

1.5 The Ancient North Atlantic: Dispersal and Early Population Structure

The phylogeography of Atlantic cod indicates that the ancestor of modern-day *Gadus morhua* dispersed from the northeastern Atlantic westward via Iceland and Greenland to the western Atlantic and the banks of Newfoundland and continental North America (Carr and Marshall 2008). It is likely that cod were widely distributed across much of the North Atlantic by 3.5 MYA. During this period, nonetheless, major climactic shifts have occurred which almost certainly impacted cod distribution (also see Chapter 8).

During the past million years, the North Atlantic has been subject to a series of Ice Ages interspersed with warmer periods. These climatic events resulted in a dynamic environment, with sequential latitudinal shifts in suitable cod habitats over much of the potential cod range on the continental shelves. The result was a varied and dynamic North Atlantic ecological seascape with many evolutionary opportunities and niches for a generalist species such as cod (Rose 2007). In this way, the vicariant events of glacial periods enhanced opportunities for local adaptation among fragmented portions of cod populations separated by lowered sea levels and loss of shelf habitats during glacial maximums. It is likely that the spatial variations in the environment and habitat spurred the diverse life histories of modern cod populations, despite their common ancestry.

3 There is general agreement on the origin of the *Gadus* species, i.e. that they have all originated from an Arcto-Atlantic gadine lineage. However, there are several hypotheses revolving around the invasion of the Gadus species into the Pacific. As pointed out by Coulson et al. (2000), it is clear that the timing of the formation of the Panamanian Isthmus is critical due to its effects on oceanic circulation in the northern hemisphere, i.e. resulting in redirection of flow through the Bering Strait from a southward to a northward direction (Marincovich and Gladenkov 1999). For a different hypothesis see Grant and Ståhl (1988); Pogson and Mesa (2004) and Coulson et al. (2006).

The most recent wave of cod evolution occurred quite recently in geological time. The modern 'cod Eve' (most recent common mitochondrial ancestor), from which it has been purported that all modern cod descended, was present in the North Atlantic about 162 TYA (Carr and Marshall 2008), or perhaps up to 250 TYA ago, most likely in the northeast Atlantic (Lait et al. 2018). This means that diverse lines of modern cod across the North Atlantic have survived several subsequent Ice Ages. Modelling exercises have suggested the persistence of suitable habitats and the survival of cod on both sides of the Atlantic, and possibly also in Iceland, since the glacial maximum that occurred 100–150 TYA (Bigg et al. 2008; Carr and Marshall 2008). These studies suggest that cod in the northeast and northwest Atlantic have been isolated for 80–150 thousand years. Based on a review of existing genetic data, Bigg et al. (2008) indicated that the divergence between Icelandic and Canadian cod occurred more recently but prior to the last glacial maximum (LGM) about 21 TYA, while the divergence between Greenland, Iceland and Europe was even more recent as a consequence of colonization since the LGM (see Chapters 5 and 8).

1.6 Rise of Cod and Current Population Structure

Gadoid evolution in the North Atlantic filled many habitats and ecological niches. The Atlantic cod became a generalist and the most widespread, abundant and adaptable of the gadoids. Different cod populations would eventually range from thousands to billions of fish and occupy almost every possible habitat of the continental shelves across the North Atlantic (Robichaud and Rose 2004). Across its expanding range, in both small and large populations, the Atlantic cod became the dominant large predatory fish of the continental shelves of the North Sea, the Baltic, the Barents Sea, the Faroe Islands shelf, the Celtic Sea, the Iceland shelf, the Greenland shelf, the northeast Labrador and Newfoundland shelves, the Grand Banks, the Gulf of St Lawrence, the Scotian Shelf and all waters south to Cape Cod. The species remained a true gadoid, retaining the high reproductive rates of most of its gadoid cousins, such as the more specialized haddock, which became oriented towards slightly warmer benthic habitats, and the Atlantic Pollock, which became more pelagic. But the Atlantic cod's generally unspecialized behaviour and wide physiological tolerances led to broader distributions and a more lasting dominance of the North Atlantic ecosystems than can be claimed by any other species (Rose 2007, see also Chapters 2, 5, and 8).

Today, 26 stocks (management units) of Atlantic cod have been recognized (see Table 1.1). Historically, these stocks have been identified based on geographical distribution and dispersal based on information from tagging experiments, variation in quantitative and meristic (morphology) traits as well as genetic properties (ICES 2005). There are likely many more partially isolated reproductive units that are pooled to form these management units. For example, the Northern cod has long been recognized as a stock complex, and recent studies support the notion that these form a metapopulation that at times exchanges numbers of individuals (e.g. Smedbol and Wroblewski 2002; Rose et al. 2011). In addition to those listed in Table 1.1, five other fishing stocks have been historically recognized. These include: Coastal cod, Norway; East Greenland; and Bay of Fundy–Scotian Shelf.

Table 1.1 Years assessed, and ranges of maximum and minimum landings, total and spawning stock biomass (SSB) (1000 tonnes) of the major cod stocks in the North Atlantic.

Stock	Years	Landings	Biomass	SSB	References
Georges Bank	1978–2005	4.5–57	25–135	17–92	O'Brien et al. 2006
Gulf of Maine	1982–2005	1.6–18	15–42	11–24	Mayo and Col 2006
N Scotian Shelf	1970–2003	0.01–61	5–171		Clark and Hinze 2003; Fanning et al. 2003
S Gulf St. Lawrence	1971–2003	1–69	92–473	63–354	Chouinard et al. 2003
N Gulf St. Lawrence	1974–2003	0.1–106	36–603	13–379	Fréchet et al. 2003
St. Pierre Bank	1959–2003	0.6–80	5–250	45–125	Brattey et al. 2003
Grand Bank	1959–2007	0.2–227	6–395	4–125	Morgan et al. 2007
Flemish Cap	1972–2001	3–57	2–113	2–40	Cervino and Vázquez 2004
NE Newfoundland-S Labrador (Northern)	1962–1993	0.3–810	100–3000	22–1552	Lilly et al. 1998; Smedbol et al. 2002
W Greenland (inshore and offshore)	1924–2003	0.7–478	0.2–4129	0.1–3200	Wieland and Storr-Paulsen 2004; Buch et al. 1994; ICES 2004
Iceland	1955–2012	146–545	550–2359	122–940	ICES NWWG 2012a
Faroes	1961–2010	6–40	29–161	18–123	ICES NWWG 2012a
NE Arctic	1946–2012	212–1343	736–4168	102–1165	ICES AFWG 2012b
E Baltic Sea	1966–2011	45–392	131–1057	65–697	ICES WGBFAS 2012c
W Baltic Sea	1965–2011	14–54	27–116	9–57	ICES WGBFAS 2012c
Kattegat	1971–2011	0.1–22	1.6–43	1.21–34	ICES WGBFAS 2012d
North Sea	1963–2011	34–589	144–1460	29–276	ICES WGNSSK 2012d
W Scotland	1978–2003	1.3–28	9–54	6–40	ICES 2005
Irish Sea	1968–2003	1.8–15	6–30	2–21	ICES 2005
Celtic Sea	1971–2003	3–19	9–34	6–24	ICES 2005

Assessment information on stock size and age structure from various population models is available dating back to 1946 for the Northeast Arctic, 1950 for the Icelandic cod stock, and the 1960s–1970s for most other stocks (Table 1.1). These stocks differ greatly with respect to size, ranging in biomass over at least three orders of magnitude,

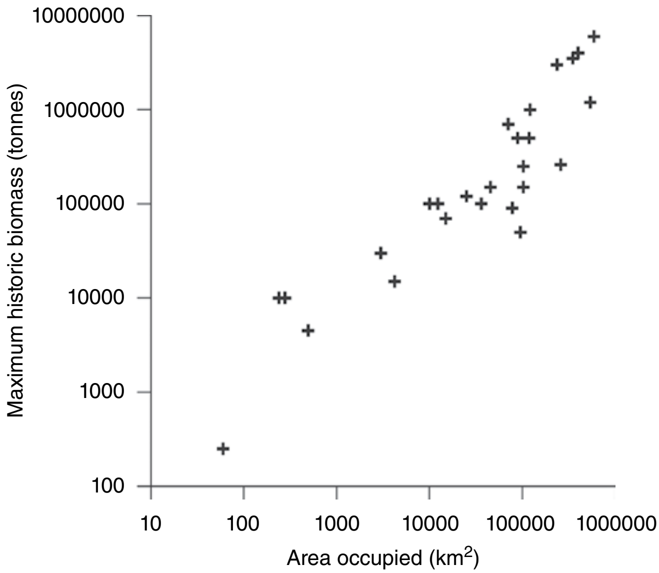

Figure 1.4 Maximum historic biomass and area occupied by the major Atlantic cod stocks (redrawn and updated from Robichaud and Rose 2004).

from thousands to millions of tonnes, as well as in range and migration characteristics (Robichaud and Rose 2004; Marteinsdóttir et al. 2005, Chapters 5 and 7), age structure, growth and life history characteristics (ICES 2005; see other chapters in this book). The many small stocks almost always occupy small ranges, with the large and more migratory stocks occupying much wider ranges, such that maximum biomass correlates strongly with range (Figure 1.4) (Robichaud and Rose 2004).

Only a relatively few stocks are large. During the recent assessment periods, only five stocks, Northeast Arctic, North Sea, East Baltic, Icelandic and Northern cod, have attained a biomass exceeding 1 million tonnes. Most stocks have been considerably smaller, i.e. having biomasses less than 150 thousand tonnes on the average, including the Irish Sea, Celtic Sea, West of Scotland, West Baltic, Faroe Plateau, Georges Bank, and the Grand Bank. In terms of spawning stock biomass (SSB), only the three largest stocks, Northeast Arctic cod, Icelandic cod, and Northern cod off Newfoundland and Labrador, have sustained spawning biomasses exceeding 1 million tonnes for any length of time. Most stocks (Celtic, Irish Sea, West of Scotland, Faroe and West Baltic, Grand Bank and Georges Bank) have experienced considerably smaller spawning biomasses (<100 thousand tonnes on average) while the size of the East Baltic and North Sea spawning stocks have been at intermediate levels ranging from 130 to 300 thousand tonnes on average with a maximum biomass of 250 thousand tonnes (North Sea) and 700 thousand tonnes (East Baltic). It is noteworthy that some of these stocks may have had considerably higher biomasses prior to the overfishing that became the dominant influence on stock size in the 1960s, and before systematic stock assessments were conducted.

Although these stocks form the basis of most cod management, it has long been recognized that many more locally adapted populations occur within many of these management units. Perhaps the best example is the Northern cod stock off the northeast coast of Labrador and Newfoundland, which has been regarded as a stock complex since the imposition of stock range limits in the late 1940s and early 1950s (Templeman 1966). Since then, many studies based on tagging, meristics, fishing ranges and more recently genetics have confirmed that the Northern cod is made up of at least several sub-stock components which, while not totally isolated from each other, do exhibit identifiable migration patterns and some degree of range and reproductive isolation (e.g. Lear 1984; deYoung and Rose 1993; Ruzzante et al. 1999). Some components, such as the well-studied group in Gilbert Bay, Labrador, may be highly isolated and of very small population size, numbering only in the tens of thousands of fish (Morris et al. 2003, 2010). Others may be much larger and not so isolated. For example, it has been proposed that various cod groups, some spawning inshore in Smith Sound (Rose 2003) and to the south in Placentia Bay (Lawson and Rose 2000a,b), are loosely linked with the larger spawning groups on the offshore banks. Together, these spawning groups may form integrated meta-populations (Smedbol and Wroblewski 2002; Rose et al. 2011; Rose and Rowe 2018). A similar situation, with multiple inshore and offshore spawning groups, has also been recognized on the Scotian Shelf for many years (McKenzie 1956). In the Gulf of Maine, the former existence of many small sub-stock coastal spawning groups has also been hypothesized (Ames 2004).[4] As noted, some of these may have been extirpated by the time formal stock assessments were carried out. The productive diversity resulting from the existence of many small and spatially (potentially genetically) diverse spawning and feeding groups may have played an important role in the productive capacity of broader management units, the stocks. Indeed, Robichaud and Rose (2004) speculated that most of the genetic variability in the species would reside within these diverse small groups.

1.7 Is Diversity a Key to Cod's Success?

It is difficult to narrowly define the parameters of a cod spawning group, in particular in terms of its size and life history, although all do express some common features and behaviour (see Chapter 3). But as discussed above, the size of the groups ranges over several orders of magnitude (Table 1.1), and the migration and range patterns mirror that (Chapter 5). This diversity characterizes cod. Moreover, the evolution of such a diverse population size and life history panorama, combined with the relative rarity of very large populations (the Northeast Arctic cod, the Icelandic cod, and Northern cod are the three ultra-large groups), suggests that the prototype cod is a fish of small and relatively sedentary groups. It also suggests that its adaptability is such that given opportunity, the species can expand its range and develop very large populations. That opportunity may have come after the Great Trans-Arctic Biotic Interchange brought entirely

4 Ames (2004) reported that 'This study clarifies the structure of the Gulf of Maine cod grouping by deriving the distribution, movements, and behaviour of population components from 1920s data and surveys of retired fishermen. These derivations are consistent with current cod populations and with the existence of localized spawning components. Nearly half the coastal spawning grounds of 50–70 years ago are abandoned today and their spawning components have disappeared, suggesting depletion, undetected by system-wide assessments, may have been well advanced by the 1980s.'

new food sources over wide expanses of the continental shelves of the North Atlantic (Briggs 1995; Rose 2007). It is thought that pandalid shrimp arrived in the North Atlantic some 10–20 MYA from the older Pacific Ocean, and likely influenced the widespread distribution of cod, but the arrival of capelin much more recently within the past few million years had the biggest impact. For an adaptable predator such as the cod, these were unparalleled opportunities. Moreover, it is difficult to conceive how the three large stocks could exist in their recent forms, with biomasses and ranges as known, without these food sources, especially capelin. All of the three mega-stocks, the Northeast Arctic, Icelandic and Northern cod, are essentially dependent on capelin for their distribution and abundance.

An important question is whether the success of the cod in the North Atlantic, assessed by its distribution into almost every conceivable habitat, both coastal and offshore, and its exploitation of a variety of potential prey and thermal conditions, is simply a result of such diversity, or, more importantly, is dependent on it. The notion of cod groups forming meta-populations suggests the later, and the extirpation of small groups of spawning fish, once thought irrelevant to larger scale production, may have reduced both the resiliency of the stock units and their productive capacity. The potential value of such a metapopulation structure is demonstrated by the Icelandic cod stock where the contribution of the smaller spawning sites buffers recruitment failures at the main spawning sites (Marteinsdóttir et al. 2000; Begg and Marteinsdóttir 2002; see also Figure 1.2). As a result, variation in recruitment is less in Icelandic cod than any other cod stock. As another example, the rebuilding Northern cod may have depended on a coastal aggregation to kick-start more widespread distribution across the range (Rose and Rowe 2015, 2018). Correspondingly, a relatively unexplored facet of cod population structure and dynamics is the possibility that a form of 'portfolio effect'[5] has existed with cod, as shown for Alaskan sockeye salmon (*Onchorynchus nerka*) (Schindler et al. 2010) in that pulses of spatially dynamic small-scale productivity sustained the larger scale biomass over time (Rose et al. 2011).

1.8 The Genetic Seascape

Few marine species have received as much attention from population geneticists as the Atlantic cod. Since the early days of gel electrophoresis and its application in comparing allelic frequencies between a-priori known aggregations of cod in the 1960s–1980s (i.e. Sick 1965; Frydenberg et al. 1965; Mork et al. 1985; Smith et al. 1989; Carr and Marshall 1991; Arnason and Rand 1992), development of new genetic technologies has enabled direct studies of the DNA itself, which in turn have revealed genetic differences

5 The 'portfolio effect' (or the 'statistical averaging effect'), is the name given to the phenomenon whereby stability in aggregate community properties, for instance biomass productivity, tends to rise with species diversity, owing to the statistical averaging of fluctuations in species' properties. Schindler et al. (2010) stated that biodiversity arguments 'have not considered the importance of biologically relevant diversity within individual species. Current rates of population extirpation are probably at least three orders of magnitude higher than species extinction rates, so there is a pressing need to clarify how population and life history diversity affect the performance of individual species.'

between stocks residing on the large cod grounds as well as within smaller geographical areas (Bentzen et al. 1996; Ruzzante et al. 2000a,b; Nielsen et al. 2006; Bradbury et al. 2010). The genetic differentiation between the northeast and northwest Atlantic cod populations is well established in terms of differences in allelic frequencies at the RFLP loci pantophysin (*Pan* I; Pogson et al. 1995; Pogson 2001) and several microsatellite loci (Bentzen et al. 1996; Hutchinson et al. 2001; Nielsen et al. 2006; Bradbury et al. 2010) as well as at the genomic level (Bradbury et al. 2013; Lait et al. 2018).

Like many other marine species with a wide geographical distribution, the population structure of cod is shaped by high levels of gene flow and large effective population sizes (Hemmer-Hansen et al. 2013 and references therein). Regardless, ever-increasing numbers of studies have demonstrated not only substantial genetic differences among stocks whose ranges do not overlap, but also between cod populations that coexist within regions. Differences may occur at relatively small scales of distances, from hundreds of kilometres to only few tens of kilometres. In Canadian waters, genetic differentiation has been observed between most of the major population complexes: northeast Newfoundland and Labrador Shelf, Grand Banks, Flemish Cap, Scotian Shelf (Bentzen et al. 1996; Ruzzante et al. 1996, 1998, 2000a,b). Within the large Northern cod stock complex on the Newfoundland and Labrador shelf, differences between historic northern and southern groups, albeit small, have consistently been shown (Ruzzante et al. 2000a,b; Rose et al. 2011), although more recent genomic studies support a more panmyctic distribution (Lait et al. 2018). At least one of the coastal groups, in Gilberts Bay, Labrador, appears to be well differentiated genetically from the cod offshore (Ruzzante et al. 2000a,b). These genetic patterns are in general agreement with nearly 100 years of tagging in these same waters (Robichaud and Rose 2004). During rebuilding of stock areas that became highly depleted in the 1990s, however, a recent genomic investigation suggests that redistributions of expanding groups of Northern cod may ameliorate historic differences (G. Puncher, University of New Brunswick, Canada, personal communication). In USA waters, three genetically distinct groups have been identified: the Georges Bank populations, the northern spring spawning coastal complex in the Gulf of Maine and a southern winter spawning in the Gulf of Maine together with the cod spawning south of Cape Cod (Kovach et al. 2010; Wirgin et al. 2007). In some cases, cod of the different genetic complexes have been shown to spawn in the same bays but in different seasons.

In the Northeast Atlantic, genetic differences have been established for all the major cod stocks, i.e. Northeast Arctic, North Sea, and Baltic Sea (Nielsen et al. 2001). In Norway, genetic differences between the Northeast Arctic cod and the Norwegian coastal cod have been demonstrated (Fevolden and Pogson 1997; Sarvas and Fevolden 2005). In addition, genetic differences exist among cod groups within the coastal zone at scales of less than 30 km (Dahle et al. 2006; Knutsen et al. 2003, 2007; Jorde et al. 2007; Skarstein et al. 2007). In the North Sea, Hutchinson et al. (2001) described genetic differences between the Bergen, Moray Firth, Flamborough Head, and the Southern Bight populations. These differences were supported by tagging studies that demonstrated limited migration between these populations (Neat et al. 2006; Wright et al. 2006). In the mid-Atlantic, weak differences were detected between cod sampled south and north of Iceland as well as between South Iceland and the Faroe Islands (Pampoulie et al. 2006, 2008). However, no differences were detected between the

Faroes and cod at spawning locations on the East coast of Iceland (Pampoulie et al. 2008).

Despite much genetic research on cod, unexpected results are still emerging involving loci that are under selection. In this regard the different ecotypes, the migratory and stationary cod have received deserved attention. Stationary and migratory cod are found on both sides of the Atlantic (Robichaud and Rose 2004; Nordeide et al. 2011). In the eastern Atlantic, cod that migrate and forage in deep waters are found in both Icelandic and Norwegian waters (Palsson and Thorsteinsson 2003; Nordeide et al. 2011; Grabowski et al. 2011). In both areas, the different ecotypes have been associated with variation at the non-neutral *Pan* I loci. In Norway, the coastal cod (stationary) was shown to exhibit very high frequencies of the *Pan* I^{A} allele while the Arcto-Norwegian cod (migratory) expressed high frequencies of the *Pan* I^{B} allele (Fevolden and Pogson 1997; Sarvas and Fevolden 2005). Similarly, in Iceland the deep migrating frontal cod were more likely to be *Pan* I^{BB} than the more stationary coastal cod that had higher frequencies of Pan I^{A} alleles (Pampoulie et al. 2008). These differences have been supported by observations obtained from data storage tags showing that the different ecotypes occupied distinct seasonal thermal and bathymetric niches both during feeding and spawning (Grabowski et al. 2011; Thorsteinsson et al. 2012). At the same time, cod of the different *Pan* genotypes were also shown to differ with respect to morphology and life history where *Pan* I^{AA} cod were characterized by shorter gaps between the fins, grew faster and matured at an earlier age than the *Pan*-I^{BB} cod (Jakobsdóttir et al. 2011; McAdams et al. 2012).

Variation at the Pan I loci has been correlated with behaviour and habitat selection linked with differences in depth and temperature in other cod stocks as well (review in Case et al. 2005 and references therein). However, it is not clear if the patterns of differentiation are due to disruptive selection in current time or a result of historical selection. For example, the *Pan* I^{BB} genotype appears to be found only in areas with access to deep waters such as the Icelandic and Barents Sea regions while being more or less absent from the shallower areas, the North Sea, Irish and Celtic Seas and the Baltic (Figure 1 in Case et al. 2005). This by itself may indicate that the different *Pan* I genotypes of cod represent genomes that have gone through vicariant periods of high and low sea levels during which different genotypes have been favoured. Findings by Hemmer-Hansen et al. (2013) support this hypothesis. In a study on the cod genome they demonstrated that few though large regions could be affected by selection even if the corresponding populations were influenced by gene flow. They also postulated that following colonization such as the settlement of cod in the Baltic, genomic differentiation can occur over a much shorter time period than previously thought to be possible, i.e. <8000 years.

In summary, the Atlantic cod is an endemic species of the North Atlantic that inhabits almost all of its continental shelves, and in many of these regions has become the dominant large fish predator. The evolution of the species and its varied life histories were moulded by the varied oceanic regimes, environments and prey fields across the North Atlantic, and in particular by the arrival of pandalid shrimps and capelin from the Pacific over past millennia. The life histories, behaviours, production and exploitation histories and future all depend on these basic relationships, which will be addressed in the following chapters.

Bibliography

Ames, E. P. (2004). Atlantic cod stock structure in the Gulf of Maine. *Fisheries* 29: 10–28.

Árnason, E. and Rand, D. M. (1992). Heteroplasmy of short tandem repeats in mitochondrial DNA of Atlantic cod, *Gadus morhua*. *Genetics* 132: 211–220.

Barry, R. G. (1989). The present climate of the Arctic Ocean and possible past and future states. In: *The Arctic Seas: Climatology, Oceanography, Geology and Biology* (ed. Y. Herman). New York: Van Nostrand Reinhold.

Begg, G. A. and Marteinsdóttir, G. (2002). Environmental and stock effects on spawning origins and recruitment of cod *Gadus morhua*. *Marine Ecology Progress Series* 229: 245–262.

Bentzen, P., Taggart, C. T., Ruzzante, D. E. et al. (1996). Microsatellite polymorphism and the population structure of Atlantic cod (*Gadus morhua*) in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 2706–2721.

Bigg, G. R., Cunningham, C. W., Ottersen, G. et al. (2008). Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. *Proceedings of the Royal Society of London* 275: 163–172.

Bradbury, I. R., Hubert, S., Higgins, B. et al. (2010). Parallel adaptive evolution of Atlantic cod on both sides of the Atlantic Ocean in response to temperature. *Proceedings of the Royal Society of London B* 277: 3725–3734.

Bradbury, I. R., Hubert, S., Higgins, B. et al. (2013). Genomic islands of divergence and their consequences for the resolution of spatial structure in an exploited marine fish. *Evolutionary Applications* 6 (3): 450–461.

Brattey, J., Cadigan, N. G., Healey, B. P. et al. (2003). An assessment of the cod (*Gadus morhua*) stock in NAFO subdivision 3Ps in October 2003. *Canadian Stock Assessment Secretariat Research Document* 2003(092).

Briggs, J. C. (1995). *Global Biogeography*. Netherlands: Elsevier.

Briggs, J. C. (2003). Marine centers of origin as evolutionary engines. *Journal of Biogeography* 30: 1–18.

Buch, E., Horsted, S. A., and Hovgård. (1994). Fluctuations in the occurrence of cod in Greenland waters and their possible causes. *ICES Marine Science Symposia* 198: 158–174.

Carr, S. M. and Marshall, H. D. (1991). Detection of intraspecific DNA sequence variation in the mitochondrial cytochrome b gene of Atlantic cod (*Gadus morhua*) by the polymerase chain reaction. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 48–52.

Carr, S. M. and Marshall, H. D. (2008). Intraspecific phylogeographic genomics from multiple complete mtDNA genomes in Atlantic cod (*Gadus morhua*): origins of the "Codmother" transatlantic vicariance and midglacial population expansion. *Genetics* 180: 381–389.

Carr, S. M., Kivlichan, D. S., Pepin, P. et al. (1999). Molecular systematics of gadid fishes: implications for the biogeographic origins of Pacific species. *Canadian Journal of Zoology* 77: 19–26.

Case, R. A. J., Hutchinson, W. F., Hauser, L. et al. (2005). Macro- and micro-geographic variation in pantophysin (pan I) allele frequencies in NE Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* 301: 267–278.

Cervino, S. and Vásquez, A. (2004). A survey based assessment of cod in division 3M. *NAFO SCR Document* 04 (53).

Coulson, M. W., Marshall, H. D., Pepin, P. et al. (2006). Mitochondrial genomics of gadine fishes: implications for taxonomy and biogeographic origins from whole-genome data sets. *Genome* 49: 1115–1130.

Chouinard, G. A., Swain, D. P., Currie, L. et al. (2003). Assessment of the cod in the southern Gulf of St. Lawrence, February 2003. *Canadian Stock Assessment Secretariat Research Document* 2003(015).

Clark, D.S. and Hinze, J. (2003). Assessment of cod in division 4X in 2004. *Canadian Stock Assessment Secretariat Research Document* 2004(100).

Dahle, G., Jørstad, K. E., Rusaas, H. E. et al. (2006). Genetic characterisation of broodstock collected from four Norwegian coastal cod (*Gadus morhua*) populations. *ICES Journal of Marine Science* 63: 209–215.

Ekman, S. (1953). *Zoogeography of the Sea*. London: Sidgwick and Jackson.

Fanning, L. P., Mohn, R. K., and MacEachern, W. J. (2003). Assessment of 4VsW cod to 2002. *Canadian Stock Assessment Secretariat Research Document* 2003(027).

Fedotov, F. and Bannikov, A. F. (1989). On phylogenetic relationships of fossil Gadidae. In: *Papers on the Systematics of Gadiform Fishes*, Natural History Museum of Los Angeles City Science Serial 32 (ed. D.M. Cohen), 187–196. Los Angeles: NHM.

Fevolden, S. E. and Pogson, G. H. (1997). Genetic divergence at the synaptophysin (Syp I) locus among Norwegian coastal and north-East Arctic populations of Atlantic cod. *Journal of Fish Biology* 51: 895–908.

Fréchet, A., Gauthier, J., Schwab, P. et al. (2003). The status of cod in the Northern Gulf of St. Lawrence (3Pn, 4RS) in 2002. *Canadian Stock Assessment Secretariat Research Document* 2003(065).

Frydenberg, O., Möller, D., Nævdal, G. et al. (1965). Haemoglobin polymorphism in Norwegian cod populations. *Hereditas* 53: 257–271.

Gaskell, T. E. (1972). *The Gulf Stream*. London: Camelot Press.

Golikov, A. N. and Scarlato, O. A. (1989). Evolution of Arctic ecosystems during the Neogene period. In: *The Arctic Seas: Climatology, Oceanography, Geology and Biology* (ed. Y. Herman). New York: Van Nostrand Reinhold.

Gosse, K. R. and Wroblewski, J. S. (2004). Variant colourations of Atlantic cod (*Gadus morhua*) in Newfoundland and Labrador nearshore waters. *ICES Journal of Marine Science* 61 (5): 752–759.

Grabowski, T., Thorsteinsson, V., McAdam, B. J. et al. (2011). Evidence of segregated spawning in a single marine fish stock: sympatric divergence of ecotypes in Icelandic cod? *PLOS ONE* 6 (3): 1–9.

Grant, W. S. and Stahl, G. (1988). Evolution of Atlantic and Pacific cod: loss of genetic variation and gene expression in Pacific cod. *Evolution* 42: 138–146.

Harris, L. (1990). *Independent Review of the State of the Northern Cod Stock*. Ottawa: Department of Fisheries and Oceans Canada.

Hemmer-Hansen, J., Nielsen, E. E., Therkildsen, N. O. et al. (2013). A genomic island linked to ecotype divergence in Atlantic cod. *Molecular Ecology* 22 (10): 2653–2667.

Hutchinson, W. F., Carvalho, G. R., and Rogers, S. I. (2001). Marked genetic structuring in localised spawning populations of cod (*Gadus morhua*) within the North Sea and adjoining waters as revealed by microsatellites. *Marine Ecology Progress Series* 223: 251–260.

ICES. (2004). Report of the Northwestern working group. *ICES CM 2004/ACFM*:25
ICES (2005). *Spawning and Life History Information for North Atlantic Cod Stocks*, ICES Cooperative Research Report, no. 274. Copenhagen: ICES.
ICES. (2012a). Report of the North-Western Working Group. ICES CM 2012/ACOM:07, Copenhagen: ICES.
ICES. (2012b). Report of the Arctic Fisheries Working Group. ICES CM 2012/ACOM:05, Copenhagen: ICES.
ICES. (2012c). Report of the Baltic Fisheries Assessment Working Group. ICES CM 2012/ACOM:10, Copenhagen: ICES.
ICES. (2012d). Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak. ICES CM 2012/ACOM:13, Copenhagen: ICES.
Jorde, P. E., Knutsen, H., Espeland, S. H. et al. (2007). Spatial scale of genetic structuring in coastal cod *Gadus morhua* and geographic extent of local populations. *Marine Ecology Progress Series* 343: 229–237.
Jakobsdóttir, K. B. (2011). Changes in genotypic frequencies at the Pantophysin locus in Atlantic cod (*Gadus morhua*) in Icelandic waters: evidence of fisheries-induced selection? *Evolutionary Applications* 4 (4): 562–573.
Knickle, D. C. and Rose, G. A. (2014a). Microhabitat use and vertical habitat partitioning of juvenile Atlantic (*Gadus morhua*) and Greenland (*Gadus ogac*) cod in coastal Newfoundland. *Open Fish Science Journal* 7: 32–41.
Knickle, D. C. and Rose, G. A. (2014b). Examination of fine-scale spatial-temporal overlap and segregation between two closely related congeners *Gadus morhua* and *Gadus ogac* in coastal Newfoundland. *Journal of Fish Biology* 85 (3): 713–735. doi: 10.1111/jfb.12454.
Knutsen, H., Jorde, P. E., André, C. et al. (2003). Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. *Molecular Ecology* 12: 385–394.
Knutsen, H., Olsen, E. M., Ciannelli, L. et al. (2007). Egg distribution, bottom topography and small-scale population structure in a coastal marine system. *Marine Ecology Progress Series* 333: 249–255.
Kovach, A. I., Breton, T. S., Berlinsky, D. L. et al. (2010). Fine-scale and temporal genetic structure of cod off the Atlantic coast of the USA. *Marine Ecology Progress Series* 410: 177–195.
Kurlansky, M. (1997). *Cod: The Biography of the Fish that Changed the World*. New York: Penguin.
Lait, L. A., Marshall, H. D., and Carr, S. M. (2018). Phylogeographic mitogenomics of Atlantic cod *Gadus morhua:* Variation in and among trans-Atlantic, trans-Laurentian, Northern cod, and landlocked fjord populations. *Ecology and Evolution* 8: 6420–6437. doi.org/10.1002/ece3.3873.
Lawson, G. L. and Rose, G. A. (2000a). Seasonal distribution and movement patterns of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. *Fisheries Research* 49: 61–75.
Lawson, G. L. and Rose, G. A. (2000b). Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1011–1024.
Lear, W. H. (1984). Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. *Journal of Northwest Atlantic Fishery Science* 5 (2): 143–159.

Lilly, G. R., Shelton, P. A., Brattey, J. et al. (1998). An assessment of the cod stock in NAFO divisions 2J+3KL. *Canadian Stock Assessment Secretariat Research Document* 98 (15).

Marincovich, L. and Gladenkov, A. Y. (1999). Evidence for an early opening of the Bering Strait. *Nature* 397: 149–151.

Marshall, N. B. and Cohen, D. M. (1973). Order Anacanthini (Gadiformes), characters and synopsis of families. *Memoirs of the Sears Foundation for Marine Research* 1: 479–495.

Marteinsdóttir, G., Gunnarsson, B., and Suthers, I. M. (2000). Spatial variation in hatch date distributions and origin of pelagic juvenile cod in Icelandic waters. *ICES Journal of Marine Science* 57: 1184–1197.

Marteinsdóttir, G., Ruzzante, D., and Nielsen, E.E. (2005). History of the North Atlantic cod stocks. *ICES CM* 2005/AA:19, http://www.hafro.is/Bokasafn/Greinar/ices_2005_AA19.pdf.

Mayo, R. K. and Col, L. A. (2006). *The 2005 Assessment of the Gulf of Maine Atlantic Cod Stock. U.S. Department of Commerce, Northeast Fiseries Science Center Research Document* 06-02. Woods Hole, MA: National Marine Fisheries Service.

McAdam, B. J., Grabowski, T. B., and Marteinsdóttir, G. (2012). Identification of stock components using morphological markers. *Journal of Fish Biology* 81 (5): 1447–1462.

McKenzie, R. A. (1956). *Atlantic Cod Tagging off the Southern Canadian Mainland.* Bulletin of the Fisheries Research Board of Canada, no. 105.

Morgan, M.J., Murphy, E.F., and Brattey, J. (2007). An Assessment of the Cod Stock in NAFO Divisions 3NO. *NAFO Science Council Research Document* no. 07/40.

Mork, J., Ryman, N., Stahl, G. et al. (1985). Genetic variation in Atlantic cod (*Gadus morhua*) throughout its range. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1580–1587.

Morris, C.J., Green, J.M., and Simms, J.A. (2003). Abundance of resident Atlantic cod in Gilbert Bay, Labrador, based on mark recapture, sampling catch per unit effort and commercial tag return data collected from 1998 to 2002. Department of Fisheries and Oceans Canada Scientific Advisory Research Document 2003/039.

Morris, C., Green, J.M., and Simms, J.A. (2010). Fish movements in a small, Atlantic cod population in Labrador and their management implications for an MPA. In: *Ecosystem Based Management: Beyond Boundaries.* Proceedings of the Sixth International Conference of Science and the Management of Protected Areas (ed. S. Bondrup-Nielsen, K. Beazley, G. Bissix et al.). Wolfville, Nova Scotia: Acadia University, Science and Management of Protected Areas Association.

Neat, F. C., Wright, P. J., Zuur, A. F. et al. (2006). Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). *Marine Biology* 148: 643–654.

Nielsen, E. E., Hansen, M. M., Schmidt, C. et al. (2001). Determining the population of origin of individual cod in the Northeast Atlantic. *Nature* 413: 272.

Nielsen, E. E., Hansen, M. M., and Meldurp, D. (2006). Evidence of microsatellite hitch-hiking selection in Atlantic cod (*Gadus morhua* L.): implications for inferring population structure in nonmodel organisms. *Molecular Ecology* 15: 3219–3229.

Nolf, D. and Steurbaut, E. (1989). Evidence from otoliths for establishing relationships within Gadoformes. In: *Papers of the Systematics of Gadiform Fishes*, Natural History Museum Los Angeles City Science Series 32 (ed. D.M. Cohen). Los Angeles: NHM.

Nordeide, J. T., Johansen, S. D., Jorgensen, T. E. et al. (2011). Population connectivity among migratory and stationary cod *Gadus morhua* in the Northeast Atlantic-A review of 80 years of study. *Marine Ecology Progress Series* 435: 269–283.

O'Brien, L., Shepherd, N., and Col, L. (2006). *Assessment of the Georges Bank Atlantic Cod Stock for 2005*. U.S. Department of Commerce Northeast Fisheries Science Center Reference Document 06-10;. Woods Hole, MA: National Marine Fisheries Service.

Pálsson, Ó. K. and Thorsteinsson, V. (2003). Migration patterns, ambient temperature, and growth of Icelandic cod (*Gadus morhua*): evidence from storage tag data. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1409–1423.

Pampoulie, C., Ruzzante, D. E., Chosson, V. et al. (2006). The genetic structure of Atlantic cod (*Gadus morhua*) around Iceland: insight from microsatellites, the *Pan* I locus, and tagging experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 2660–2674.

Pampoulie, C., Steingrund, P., Stefánsson, M. Ö. et al. (2008). Genetic divergence among east Icelandic and Faroese populations of Atlantic cod provides evidence for historical imprints at neutral and non-neutral markers. *ICES Journal of Marine Science* 65: 65–71.

Pogson, G. H. (2001). Nucleotide polymorphism and natural selection at the pantophysin (PanI) locus in the Atlantic cod, *Gadus morhua* (L.). *Genetics* 157: 317–330.

Pogson, G. H. and Mesa, K. A. (2004). Positive Darwinian selection at the pantophysin (pan I) locus in marine gadidfishes. *Molecular Biology and Evolution* 21: 65–75.

Pogson, G. H., Mesa, K. A., and Boutilier, R. G. (1995). Genetic population structure and gene flow in the Atlantic cod, *Gadus morhu*a: a comparison of allozyme and nuclear RFLP loci. *Genetics* 139: 375–385.

Raymo, M. E. (1994). The initiation of northen hemisphere glaciation. *Annual Review of Earth and Planetary Sciences* 22: 353–383.

Raymo, M. E., Ruddiman, W. F., Shackleton, N. J. et al. (1990). Evolution of Atlantic–Pacific $\delta^{13}C$ gradients over the last 2.5 m.Y. *Earth and Planetary Science Letters* 97: 353–368.

Robichaud, D. and Rose, G. A. (2004). Stock structure and range in Atlantic cod (*Gadus morhua*): inference from 100 years of tagging. *Fish and Fisheries* 5: 1–31.

Rose, G. A. (2003). Monitoring coastal northern cod: towards and optimal survey of smith sound, Newfoundland. *ICES Journal of Marine Science* 60: 453–462.

Rose, G. A. (2007). *Cod: An Ecological History of the North Atlantic Fisheries*. St. John's, Canada: Breakwater Books.

Rose, G. A. and Rowe, S. (2015). Northern cod comeback. *Canadian Journal of Fisheries and Aquatic Sciences* 72: 1789–1798.

Rose, G. A. and Rowe, S. (2018). Does redistribution or local growth underpin rebuilding of Canada's Northern cod? *Canadian Journal of Fisheries and Aquatic Sciences* 75: 825–835.

Rose, G. A., Nelson, J., and Mello, L. G. S. (2011). Isolation or metapopulation: whence and whither the smith sound cod. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 152–169.

Ruzzante, D. E., Taggart, C. T., Cook, D. et al. (1996). Genetic divergence between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 634–645.

Ruzzante, D. E., Taggart, C. T., and Cook, D. (1998). A nuclear basis for shelf- and bank-scale population structure in Northwest Atlantic cod (*Gadus morhua*): Labrador to Georges Bank. *Molecular Ecology* 7: 1663–1668.

Ruzzante, D. E., Taggart, C. T., and Cook, D. (1999). A review of the evidence for genetic structure of cod (*Gadus morhua*) populations in the NW Atlantic and population affinities of larval cod off Newfoundland and the Gulf of St. Lawrence. *Fisheries Research* 43: 79–97.

Ruzzante, D. E., Wroblewski, J. S., Taggart, C. T. et al. (2000a). Bay-scale population structure in coastal Atlantic cod in Labrador and Newfoundland, Canada. *Journal of Fish Biology* 56: 431–447.

Ruzzante, D. E., Taggart, C. T., Cook, D. et al. (2000b). Mixed-stock analysis of Atlantic cod near the Gulf of St. Lawrence based on microsatellite DNA. *Ecological Applications* 10 (4): 1090–1109.

Sarvas, T. H. and Fevolden, S. E. (2005). The scnDNA locus pan I reveals concurrent presence of different populations of Atlantic cod (*Gadus morhua* L.) within a single fjord. *Fisheries Research* 76: 307–316.

Schindler, D. E., Hilborn, R., Chasco, B. et al. (2010). Population diversity and the portfolio effect in an exploited species. *Nature* 465: 609–613.

Sherwood, G. D. and Grabowski, J. H. (2010). Exploring the life-history implications of colour variation in offshore gulf of Maine cod (*Gadus morhua*). *ICES Journal of Marine Science* 67 (8): 1640–1649.

Sick, K. (1965). Haemoglobin polymorphism of cod in the Baltic and the Danish Belt Sea. *Hereditas* 54: 19–48.

Skarstein, T. H., Westgaard, J. I., and Fevolden, S. E. (2007). Comparing microsatellite variation in north-East Atlantic cod (*Gadus morhua* L.) to genetic structuring as revealed by the pantophysin (PanI) locus. *Journal of Fish Biology* 70: 271–290.

Smedbol, R. K. and Wroblewski, J. S. (2002). Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population. *Fisheries Research* 55: 161–174.

Smith, P. J., Birley, A. J., Jamieson, A. et al. (1989). Mitochondrial DNA in the Atlantic cod, *Gadus morhua*: lack of genetic divergence between eastern and western populations. *Journal of Fish Biology* 34: 369–373.

Sveditovidov, A. N. (1948). *Gadiformes. Israel Program of Scientific Translations*, vol. IX, no. 4. S. (from the Russian). Jerusalem: Monson.

Templeman, W. (1966). Marine resource of Newfoundland. *Bulletin of the Fisheries Research Board of Canada* 154: 1–170.

Thorsteinsson, V., Pálsson, Ó. K., Tómasson, G. G. et al. (2012). Consistency in the behavior types of the Atlantic cod (*Gadus morhua* L.): repeatability, timing of migration and geo-location. *Marine Ecology Progress Series* 462: 251–260.

Wieland, K. and Storr-Paulsen, M. (2005). East and West Greenland. *ICES Cooperative Research Report* 274.

Wirgin, I., Kovach, A. I., Maceda, L. et al. (2007). Stock identification of Atlantic cod in U.S. waters using microsatellite and single nucleotide polymorphism DNA analyses. *Transactions of the American Fisheries Society* 136: 375–391.

Wright, P. J., Neat, F. C., Gibb, F. M. et al. (2006). Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *Journal of Fish Biology* 69 (Supplement C): 181–199.

deYoung, B. and Rose, G. A. (1993). On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2729–2741.