Population Genetics, Life History, and Ecology of Arctic Marine Fishes

by David Cameron Hardie

INTRODUCTION

DESPITE PERENNIALLY FRIGID WATER TEMPERATURES and extended periods of ice cover, which limit productivity for much of the year, Canadian Arctic waters are home to approximately one-quarter of this country's freshwater (23%) and marine (27%) fish species (Reist, 1997). Despite this richness, very little is known about cold-water fishes of polar waters. My research uses a comparative approach to reveal genetic, ecological, and life-history adaptations of Arctic fish species to the unique challenges of their environment at the northern extreme of their ranges.

This paper highlights recent developments in my doctoral research, which can be separated into two general areas. The first is directed towards advancing knowledge of the evolutionary ecology and biodiversity of noncommercial Arctic marine fishes. The second concerns landlocked populations of Atlantic cod (*Gadus morhua*) persisting as marine relicts in saline coastal lakes on Baffin Island, at the northern extreme of the species' range in Canada.

COMPARATIVE BIOLOGY OF NONCOMMERCIAL ARCTIC MARINE FISHES

Because many Arctic fish species' ranges extend broadly across longitude and latitude, different populations can experience vastly divergent conditions. This diversity provides a good opportunity for comparative research on the life-history traits of Arctic fishes to evaluate whether they differ fundamentally from related taxa in more temperate climes, with a view towards advancing knowledge about the evolution and ecology of fishes in cold-water settings.

The study of life history is based on the fundamental premise that trait combinations are constrained by trade-offs among traits (Roff, 2002). The primary life-history traits—size at birth; growth pattern; age and size at maturity; number, size, and sex ratio of offspring; age and size specific mortality schedules; and length of life—are important determinants of population dynamics, and as such provide useful information for resource management. Although very few Arctic marine species are of commercial significance at this time, their populations may be impacted by, or otherwise linked to, ongoing fisheries for shrimp, scallops, turbot, and Arctic charr in the Canadian North. Furthermore, since an organism's fitness is so tightly linked to life-history parameters, variability in these traits is among the most fundamental ways in which organisms adapt to environmental pressures (Schaffer and Elson, 1975). This research will help to assess the potential sensitivities of these species, and the biological communities within which they are intertwined, to the various natural and anthropological changes that are ongoing or imminent in the Arctic. Lastly, these data will address some of the many gaps in our knowledge concerning Arctic fishes by exploring several fundamental biological questions. How old are they, and how fast do they grow? At what age do they mature, and how frequently do they reproduce throughout their lifetime? Do they produce many small offspring, or a few larger ones, and do they provide care for them?

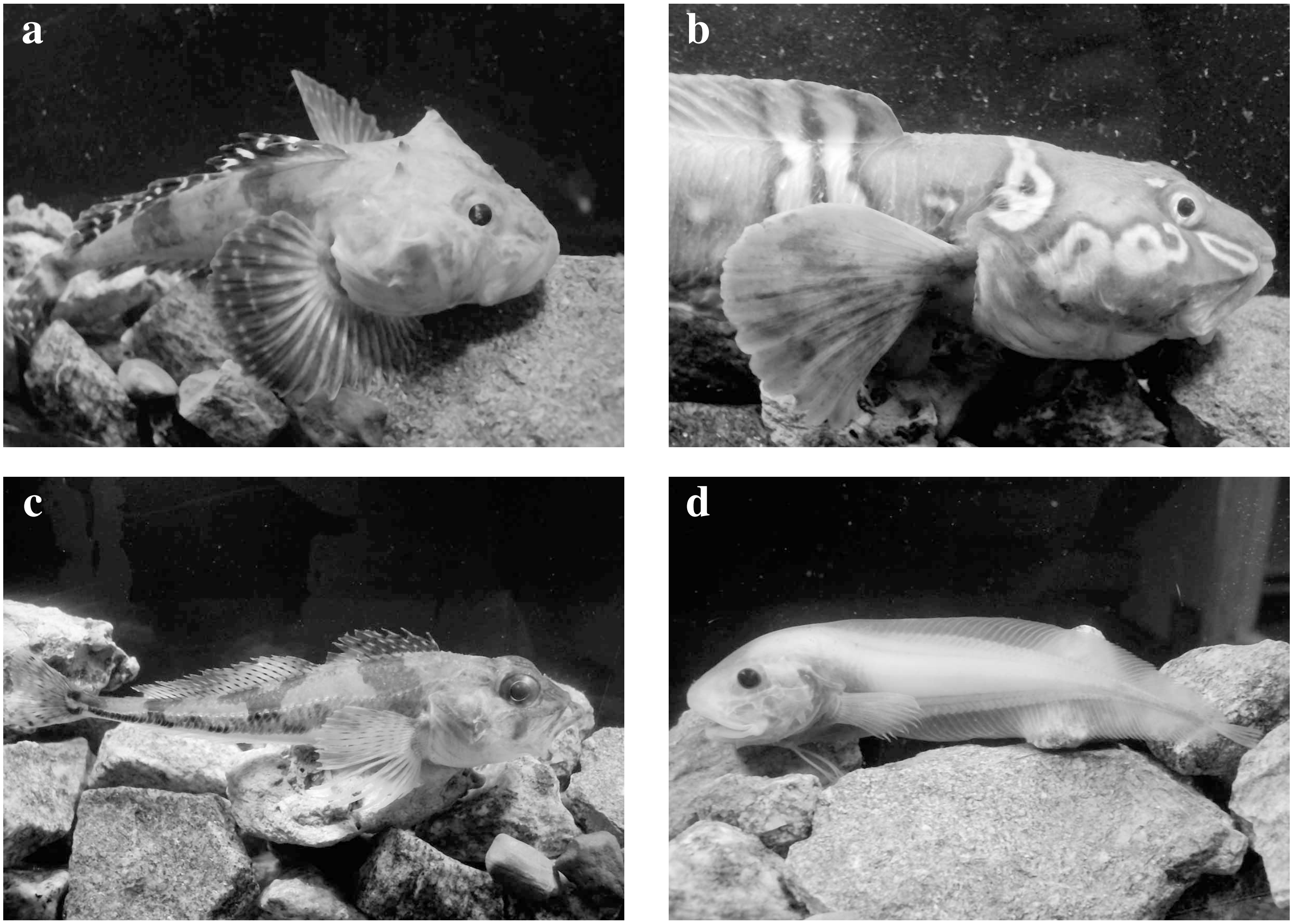
Methods

Noncommercial fishes were sampled from bycatch taken during Fisheries and Oceans Canada's turbot surveys in Baffin Bay and Davis Strait in September and October 2004. Trawling occurred at randomized stations in depth strata ranging from 400 to 1500 m in depth in Baffin Bay and Davis Strait, in the Northwest Atlantic Fisheries Organization (NAFO) area 0A. My goal was to obtain approximately 100 specimens of species for which we had already obtained large samples of conspecifics or closely related taxa from temperate Atlantic waters.

Preliminary Results

Although I was unable to obtain very many High Arctic specimens of species for which we already have samples from temperate Atlantic populations, I did collect large samples of several closely related taxa. Because the samples of Arctic fishes are most difficult to obtain, we will now endeavour to obtain temperate samples of these species from ongoing Atlantic Ocean surveys. As conspecific samples are obtained, we will collect basic biological data, such as distribution, length, weight, sex, age, growth rate, fecundity, and age and size at maturity, to compare these features between high Arctic and temperate Atlantic populations.

The most notable trend in the bycatch obtained during the fall 2004 surveys of NAFO area 0A was the paucity of species occurring to the north of Lancaster Sound. In these extreme northern latitudes of Baffin Bay, bycatch consisted primarily of gelatinous snailfish (*Liparis fabricii*), Arctic skate (*Raja hyperborea*), and four-beard rockling (*Gaidropsarus ensis*). Some eelpouts (*Lycodes* spp.), sculpins (*Cottunculus* spp.) and other snailfish species (*Paraliparis bathybius*, *Rhodichthys regina*, and *Careproctus* spp.) were also taken, but in very low abundance. Species diversity was slightly higher in the southern part of 0A, off northeastern Baffin Island, where



Representative benthic Arctic marine fishes from Baffin Bay, collected from depths of 400 to 1500 m. a) Atlantic hookear sculpin, Artediellus atlanticus; b) Arctic eelpout, Lycodes reticulatus; c) ribbed sculpin, Triglops pingeli; d) threadfin snailfish, Rhodichthys regina. (Photos: D. Hardie.)

redfishes (*Sebastes* spp.), more Lycodes species (*L. mcallisteri*, *L. paamiuti*, *L. eudipleurostictus*), Arctic cod (*Boreogadus saida*), American plaice (*Hippoglossoides platessoides*), tapirfish (*Notacanthus chemnitzi*), and ribbon barracudina (*Arctozenus risso*) were also observed.

LANDLOCKED POPULATIONS OF ATLANTIC COD (Gadus morhua) IN CANADIAN ARCTIC LAKES

An Atlantic cod (*Gadus morhua*) population in Ogac Lake, on the south shore of Frobisher Bay, has been known to science for quite some time (Patriquin, 1967) and to local Inuit for even longer. In 2002, the Pangnirtung Hunters and Trappers' Organization identified two lakes containing large gadids at the southwestern end of Cumberland Sound, locally known as Qasigialiminiq and Tariujarusiq. Our fieldwork in 2003 confirmed that the large cod in these lakes were *Gadus morhua*, and not the more frequently landlocked Greenland cod, *Gadus ogac*, and that the lakes were saline meromictic lakes akin to Ogac Lake.

Although exploitation of these populations has been low historically, harvest by subsistence and recreational fishers may be intensifying. Current knowledge suggests potential sensitivity to exploitation (Patriquin, 1967; Lewis, 1989; Hardie, 2003), which is particularly significant given that most marine stocks of this species have been depleted or extirpated. The objectives of this part of my research include (i) basic physical, chemical, and biotic characterization of Arctic lakes in which Atlantic cod occur, and (ii) the study of aspects of their population biology, life history, and genetics.

As discussed in a previous report (Hardie, 2003), Ogac Lake was intensely studied during the 1950s and 1960s by Dr. I.A. McLaren (1961, 1967a, b, 1969a, b). This work characterized Ogac Lake as meromictic, having a freshwater layer at its surface, with a deeper saline layer of almost full-strength seawater extending from approximately 3 to 30 m, and a hypersaline anoxic layer at its bottom. The lake contains a simple community of marine organisms, either persisting as truly landlocked forms or carried into the lake during tidal inflows, which occur in series each month during the open-water season. This work also provided the samples and data for the only peer-reviewed study of the cod in Ogac Lake, which found that this population was small, consisting of a breeding population on the order of only 500 individuals (Patriquin, 1967). The cod were found to exhibit a high degree of cannibalism, to vary considerably in growth rate, and to mature at a remarkably large size and advanced age. In fact, the size and age at maturity reported for Ogac Lake cod were the highest that had ever been recorded for the species. Some genetic information was provided in an M.Sc. thesis from Dalhousie University (Brooker, 1994), and an internal report of the Iqaluit office of Fisheries and Oceans Canada provided population age and size structure data for Atlantic cod from Qasigialiminiq (Lewis, 1989). Several popular accounts of the "cannibal cod" of Ogac Lake have also been published (Kennedy, 1953; Bruemmer, 1966). Tariujarusiq Lake, however, had never been studied prior to my fieldwork in 2003.

Methods

Field camps were established at Ogac Lake, Qasigialiminiq, and Tariujarusiq during July and August 2003. Cod were collected by hook and line, and as a result, consisted mostly of subadult and adult cod. A small number of juvenile cod were collected using minnow traps. In 2004, 100 juvenile cod were collected using small-mesh gill nets and a battery of 20 minnow traps set at various depths around Ogac Lake, but logistical constraints precluded visits to Qasigialiminiq and Tariujarusiq. As a result, we have collected data on the length, weight, sex, maturity, liver weight, gonad weight, and stomach contents from 100 subadult and adult cod from each lake, and from a further 100 juvenile cod from Ogac Lake. Tissue samples and otoliths were also collected, for genetic and age/growth analysis, respectively. Underwater video was used to qualify benthic macrofauna and to observe cod behaviour in all three lakes. Plankton tows were made as described by McLaren (1969a) to compare micro-invertebrate populations among lakes, as well as in Ogac Lake over the four decades since McLaren's studies. Bathymetric measurements were taken using sonar across a number of transects in both Qasigialiminiq and Tariujarusiq to compare them to Ogac Lake, where the bathymetry is known from McLaren (1967b). Salinity, temperature, and dissolved oxygen strata were measured in each basin of each lake, again to compare abiotic limnology across lakes and over time at Ogac Lake. Plankton samples and temperature/salinity/dissolved oxygen measurements were repeated in 2004 to provide two years of data for Ogac Lake. Temperature data loggers were deployed near the outflow of each lake to record the timing and frequency of tidal inflows. The temperature logger deployed in Ogac Lake in 2003 was not recoverable, so a new logger was deployed with more robust equipment for recovery in 2005, when we also aim to recover the 2003 loggers from Qasigialiminiq and Tariujarusiq.

Field assistant Michael Mipeegaq prepares to release a large cod back into Ogac Lake.

During the series of high spring tides that entered Ogac Lake in early July 2004, we collected samples of marine biota flowing into the lake, using 12×15 cm rectangular hand nets held in the inflowing current for 60-second intervals at several stations across the river joining the lake to Ney Harbour. These samples consisted primarily of marine fish larvae and amphipods, although a high biomass of jelly-plankton, ranging from small ctenophores to jellyfish more than 1 m in diameter, was also observed entering the lake. A similar event was observed during the series of tides that entered in early August, although samples were not collected. The current speed and cross-sectional area of the river during tidal inflows were also recorded to enable approximation of total tidal volume of seawater and biomass entering the lake during these events.

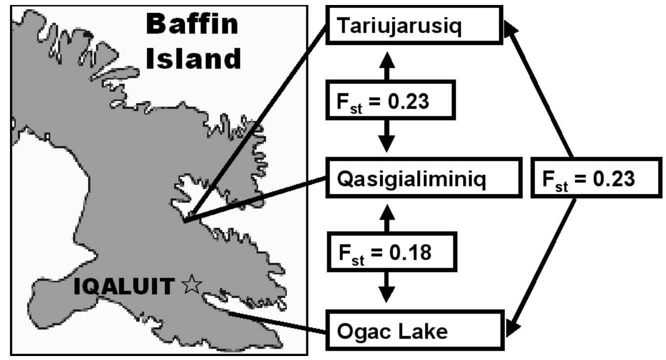
In 2004 a temperature challenge was carried out with cod from Ogac Lake. Sixteen cod between 30 and 45 cm were angled from 5 m depth using barbless hooks. They were allowed to acclimate for a period of eight hours in large coolers of water at the same temperature and salinity as the waters from which they were collected (5˚C, 28‰). To begin the challenge, eight cod were transferred to identical coolers of 18˚C water at the same salinity. Four cod from each cooler were removed and sacrificed after one hour and again at the end of the experiment after eight hours. Blood, white muscle, spleen, and liver tissues were collected from each individual and stored in RNAlater™. This experiment will be repeated with cod from temperate Atlantic waters to compare the expression of heat-shock protein between Arctic landlocked and temperate Atlantic marine populations of the species. If Arctic landlocked cod differ physiologically from marine stocks, then we should observe a difference in the expression of heat-shock protein between these populations. This work is being undertaken in collaboration with Dr. Dan Heath, at the University of Windsor, Ontario.

Preliminary Results

Although Qasigialiminiq and Tariujarusiq are salt meromictic lakes, similar to Ogac Lake, both are warmer at all depths, and surface salinity is higher at Tariujarusiq (7‰) than at the other two lakes (< 1‰). Curiously, sea urchins are absent from Qasigialiminiq, although they predominate in the benthos (and cod stomach contents) in Tariujarusiq. Cannibalism appears to be less frequent among adult and subadult cod in the Cumberland Sound lakes (~14%) compared to Ogac Lake (~35%).

Our calculations of total fish larva and amphipod biomass entering the lake during tidal inflows in early July 2004 yielded a surprising result, and provided an important clue as to how these cod populations have persisted under such harsh conditions. Our observations of large cod aggregations around the river mouth during tidal inflows at Ogac Lake led us to explore what kind of biota, and in what quantities, enter the lake during these events, since this is the only supplement to these cod's normal diet of resident sea-urchins, bivalves, pectinarid (ice-cream cone) worms, and each other. Remarkably, our most conservative estimate of fish and amphipod biomass entering the lake during a 55-minute tidal inflow is 238 kg. There were five such events at Ogac Lake during the tidal series in early July of 2004, and a further six in early August 2004. Our calculations from tide predictions suggest that between 35 and 45 tides enter the lake during the open-water season each year. Although not all of these events would contribute the same type or amount of marine biota, what is clear is that tidal inflows are crucial not only to replenish lake salinity, but also as a vital source of nutritive biomass to support these populations.

The results of our genetic studies revealed remarkably low allelic variation at seven polymorphic microsatellite loci, providing evidence that these are small, inbred, and isolated marine relict populations. Furthermore, F_{st} values for these populations were two orders of magnitude higher than have previously been reported for this species. These data confirm Patriquin's (1967) estimate that the population of cod in Ogac Lake is small, probably on the order of only hundreds of adult individuals, and suggest that this is true of Qasigialiminiq and Tariujarusiq as well.



F_{st} values among landlocked populations of Atlantic cod (Gadus morhua) from Canadian Arctic lakes. F_{st} values among these populations, as well as between these Arctic lacustrine and temperate Atlantic oceanic populations, are two orders of magnitude greater than has previously been reported for the species.

The fact that all three cod lakes occur in areas that were glaciated during the last ice age, and that the contemporary range of Atlantic cod in Canadian waters is constrained to the northern tip of Labrador, suggests that Atlantic cod probably extended their range northward during a post-glacial period of ameliorated Arctic Ocean conditions, and colonized these coastal lakes, which would have been in the process of formation by glacioisostatic rebound during that period. In fact, several lines of evidence support the theory that the Arctic Ocean was warmer and more ice-free between 4000 and 6000 years ago, which may have allowed Atlantic cod to extend their range northward. For example, several sub-Arctic marine molluscs expanded their range northward during the late and middle Holocene, arriving in Cumberland Sound around 8700 years ago, during a period of milder marine conditions associated with the collapse of the Laurentide Ice Sheet. This expansion was followed by a southward retreat of some species as ocean conditions cooled over the last 3000 years (Aitken and Gilbert, 1989). Carbon dating of driftwood on raised beaches supports this scenario, suggesting that more ice-free conditions prevailed during this same period (Stewart and England, 1983). This timeline is consistent with the low allelic diversity and strong population genetic structure of these landlocked cod populations, which suggest that these populations have been isolated from each other, and from marine stocks, for several thousand years. Overall this is consistent with the hypothesis that Atlantic cod may have extended their range northward during a warmer period between 8000 and 4000 years ago, when they could have colonized the recently formed lakes, and persisted in this warmer environment when cooling ocean temperatures returned the species' range southward over the last 3000 years. To further explore this hypothesis, we have sequenced a segment of the cytochrome b gene of the mitochondrial genome from all three Arctic populations and compared these sequences to sequences from oceanic stocks of the species (Carr et al., 1995). Cod in all three lakes derive from the most common western Atlantic mitochondrial haplotype.

Future Work

The recovery of our temperature loggers will reveal the frequency of tidal inflows, which, coupled with estimates of rates of isostatic rebound, will allow us to project expected rates of change in these lakes. Plankton abundance and species composition, as well as temperature, oxygen, and salinity profiles, will be compared among lakes as well as to these same data from McLaren's initial studies.

We are currently working to obtain age and growth data from otolith analysis. These data will be compared to existing data for temperate marine stocks, and we will work towards relating variability in these features within and among the populations to biotic and abiotic differences among lacustrine and oceanic populations. For example, cannibalism may be the only way for cod in these lakes to attain high growth rates or maturity, or both. How do growth rates and age/size at maturity compare to differences in the degree of cannibalism among lakes?

Once we have completed the temperature manipulation experiment with cod from a temperate oceanic stock, we will compare the expression of heat-shock protein of these cod to that of cod from Ogac Lake. As its name implies, the sample storage medium 'RNAlater™' will allow us to extract RNA from our samples. This will be transcribed into cDNA, which allows us to employ quantitative PCR techniques to measure the amount of heat-shock protein RNA expressed. This project represents the first such work on cod at the northern extremity of its range.

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