Calanus finmarchicus in Icelandic waters: population genetics and ecology at the Norwegian Sea / N. Atlantic Ocean boundary

Ann Bucklin, Olafur S. Astthorsson, Astthor Gislason, and Peter H. Wiebe

Abstract

Large-scale circulation patterns in the N. Atlantic may partition the ocean basin into three semi-distinct gyre systems: the Norwegian Sea, the northern N. Atlantic, and the western N. Atlantic Ocean. Zooplankton species living throughout these gyres may be ecologically, reproductively, and (perhaps) genetically distinct due to geographic isolation in different circulation systems and/or to isolation by distance. We hypothesize that genetic differentiation among populations of ecologically important and numerically predominant species may serve as indicators to delimit and distinguish functionally distinct ocean ecosystems. We are now testing this hypothesis for Icelandic waters. Iceland is a surface manifestation of the Greenland-Iceland-Scotland ridge, which separates the warm waters of the N. Atlantic Ocean from the cold Arctic deepwater of the Norwegian Sea, between which flow is restricted. We first examine evidence of different functional dynamics of ecosystems to the north and south of Iceland, in terms of zooplankton species abundances, fish stocks, and temporal and spatial linkages between zooplankton and fish stocks in the two water masses. With this context, we examine growing evidence of the ecological and genetic distinctiveness of *Calanus finmarchicus* populations in these two domains. Our goal is to place the distribution, abundance, and genetic variation of C. *finmarchicus* in a realistic ocean setting, including water mass structure and ocean circulation patterns, in order to understand the interaction between ocean circulation and structure, zooplankton stocks, secondary production, and fish stocks.

Keywords: N. Atlantic, ocean gyres, Iceland, water mass, population genetics, *Calanus finmarchicus*

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Introduction

Understanding the dynamics of marine ecosystems, including linkages between zooplankton and fish stocks and their production, will require analysis across all temporal and spatial scales. Analysis at the largest, ocean-basin scales will require conceptual models to focus field efforts and allow synthesis of the results of multi-disciplinary and regional studies.

A conceptual model for large-scale circulation patterns in the N. Atlantic Ocean partitions the ocean basin into three semi-distinct gyre systems: the Norwegian Sea, the northern N. Atlantic, and the western N. Atlantic (Bucklin et al., 2000; Wiebe, 2000; Figure 1). The gyres also define and delimit ocean ecosystems, which - although connected - may be functionally distinct. Most southerly is a small gyre in the western N. Atlantic defined by the Scotian Current and Gulf Stream. The largest gyre encompasses the northern N. Atlantic and comprises the N. Atlantic Current, Labrador Current. Most northerly is the Norwegian Sea gyre, including the N. Atlantic Current, East Greenland Current, and East Iceland Current. Zooplankton entrained in these gyres may be ecologically, reproductively, and (perhaps) genetically distinct due to geographic isolation in different circulation systems and/or to isolation by distance. Our goal is to examine the degree to which N. Atlantic gyres define functionally distinct ecosystems and contain ecologically and genetically distinct species populations. We have selected for study the boundary region between the Norwegian Sea and northern N. Atlantic gyres because of the logistical advantage for field work, the detailed understanding of this region by Icelandic oceanographers and fisheries scientists, and the extensive field programs of the Icelandic Marine Research Institute.

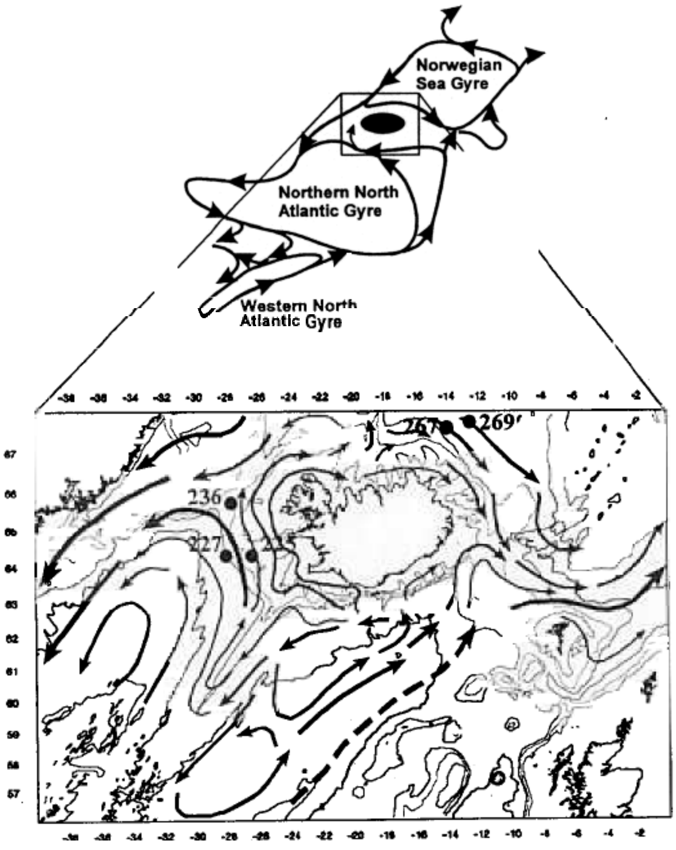


Figure 1. Climatological patterns of current flow surrounding Iceland, in the context of the three-gyre system in the N. Atlantic. Southward-flowing Arctic Water (darker gray arrows) is carried in the East Greenland and East Iceland Currents; northeast-ward flowing Atlantic Water (lighter gray arrows) is carried in the Irminger and North Iceland Irminger Currents. Inset figure modified from Valdimarsson and Malmberg (1999); figure reproduced from Bucklin et al. (2000).

The northern N. Atlantic - Norwegian Sea boundary region

Iceland lies between the two largest N. Atlantic gyre systems: the northern N. Atlantic gyre and the Norwegian Sea gyre. The warm waters of the N. Atlantic Ocean are separated from the cold Arctic waters of the Iceland and Norwegian Seas by the Greenland-Iceland-Scotland ridge, of which Iceland is a surface manifestation. Icelandic waters reflect the complex and dynamic water mass structure of the boundary region. Although ocean ecosystems to the north and south of Iceland may appear contiguous, in fact exchange between them is likely to be restricted (Aksnes and Blindheim, 1996). Flow from the N. Atlantic into the Norwegian Sea is largely restricted to the Faeroes-Shetland Channel, although overflows to the south may carry overwintering ***Calanus*** into the **N.** Atlantic basin (Heath et al., 1999). Flow in the reverse direction is largely through the Denmark Strait (Figure **1),** although coastal currents near Iceland may carry Atlantic water and **copepods** to the north of Iceland..

Calanus finmarchicus *as an indicator species*

The calanoid **copepod,** *C.* ***finmarchicus,*** occurs across the northern N. Atlantic, and is an important member of the zooplankton assemblage in all three gyre systems (Aksnes and Blindheim, 1996; Planque *et al.,* 1997). ***Calanus finmarchicus*** can dominate the zooplankton assemblage in both abundance and biomass throughout much of the northern N. Atlantic (Planque and Ibanez, 1997; Planque *et al.,* 1997) and may typically account for 50 to 80% of the numbers of zooplankton (Astthorsson and Gislason, 1995; Heath et al., 1999).

Year-to-year variation in the standing stock of *C. jinmarchicus* may play an important role in determining the success or failure of larval fish development, and ultimately recruitment into the fish stock. In Icelandic waters, the strength of the O-group cod has been associated with the abundance of zooplankton (Astthorsson and Gislason, 1995). The close association between ***Calanus*** abundance and production rates has also been documented for capelin and haddock (Jakobsson and **Stefánsson,** 1998). ,

Population genetic analysis

Patterns of dispersal, reproduction, and mortality of plankton are reflected in the spatial and temporal patterns of genetic variation of the species. Population genetic structure (i.e., genetic differences between geographic populations) may be used as a measure of the transport and mixing of plankton across the species' range. Many marine species, including zooplankton, meroplankton, and fish, exhibit significant population genetic structuring at large oceanographic scales, either because the geographic separation exceeds the dispersal capability of the species (see Palumbi, 1992) or because large-scale ocean structure and circulation patterns represent geographic boundaries to dispersal (Bucklin *et al.,* **1996a,** 1996b).

Population- and community-level differences may be reflected in different patterns of recruitment to commercial fish stocks. The functional nature of the relationship between zooplankton and fish stocks and their production requires additional study. We will focus here on examining the degree of concordance between spatial patterns of population genetic structure of a key zooplankton species, *C. finmarchicus*, and community dynamics related to fish production. An additional goal is to provide a unique means to understand how population dynamics of zooplankton are linked to fish production and stock structure.

Technical approach

Collection and preservation of samples: Zooplankton samples and hydrographic data were collected as part of the Spring Survey Cruises of the Icelandic Marine Research Institute in 1999 (Cruise No. B07-99; Figure *2)* and *2000 (Cruise No.* B06-2000) on the *R/V Bjarni Saemundsson.* The cruises circumnavigated Iceland with nine cross-shelf transects, allowing sampling from Atlantic, Arctic, and Polar Waters surrounding Iceland. A primary cruise objective was synoptic mapping of hydrographic variability. The hydrographic data are used to describe water mass structure and circulation patterns (e.g., Valdimarsson and Malmberg, 1999). The integrated biological / physical analyses allow placement of each zooplankton sample in the complex and dynamic water mass structure of the boundary waters between the two gyres.

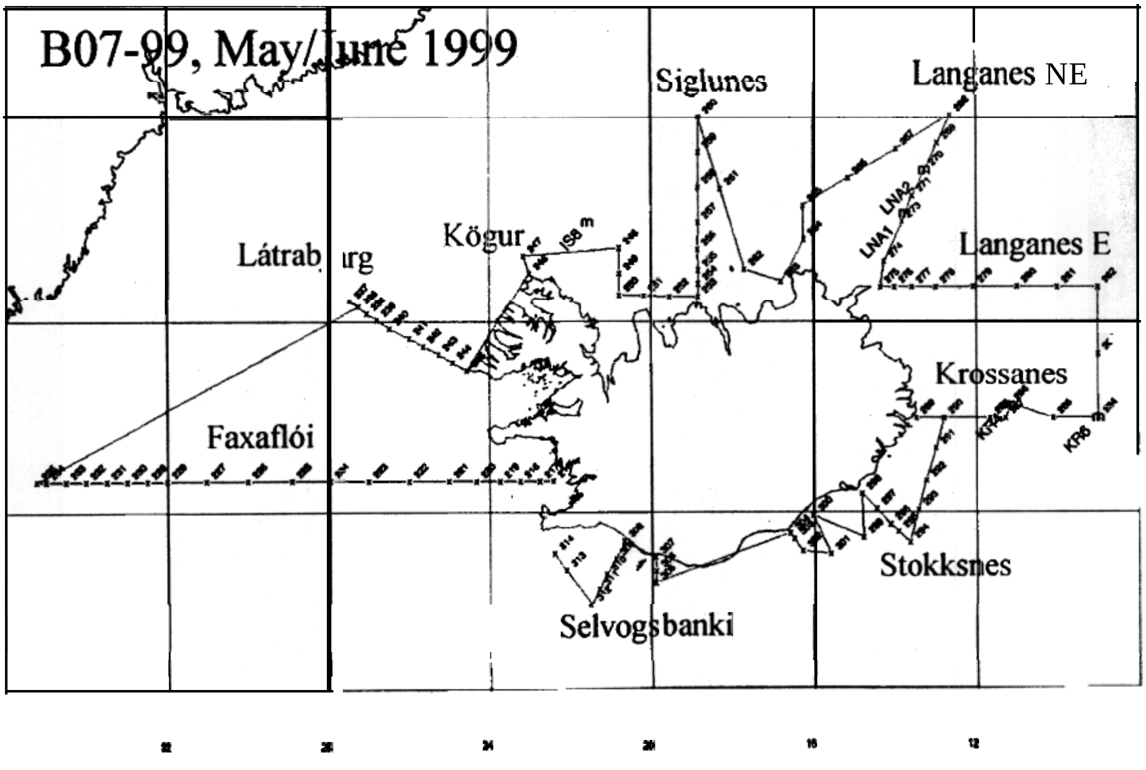
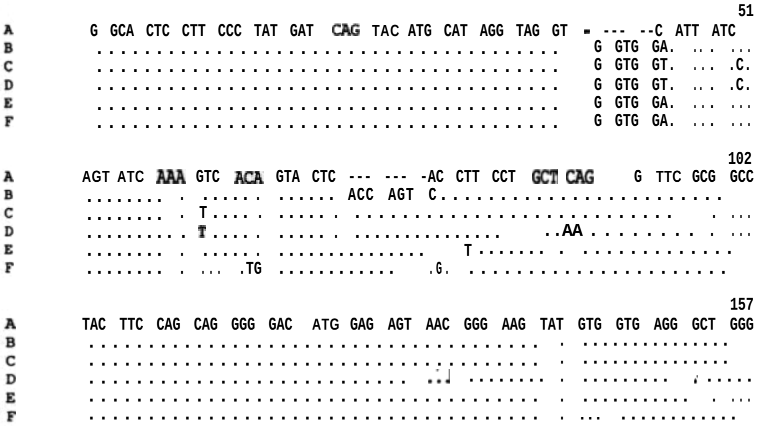


Figure 2. Cruise track with locations of hydrographic stations and zooplankton collections during the 1999 MRI Spring Survey Cruise. The 2000 Survey was very similar.

During the 1999 Spring Survey, 98 stations were occupied and 65 zooplankton samples were collected and preserved in alcohol for this study; in 2000, 118 stations were occupied and 92 samples were collected. The alcohol-preserved samples were returned to the University of New Hampshire for molecular analysis. Two additional zooplankton samples were collected at most stations: a live tow for biomass and biochemical analysis and a quantitative tow for species composition and abundance.

Population genetic analysis: DNA sequence variation of three genes was evaluated for C. *finmarchicus*, including: mitochondrial cytochrome oxidase I (COI), the nuclear gene encoding phosphoglucose isomerase (PGI), and a putative nuclear pseudogene of COI. Patterns of DNA sequence variation - including the number of sequence variants (i.e., alleles) and the differences between them - indicated that PGI was the best gene for population genetic analysis of C. *finmarchicus*. Since PGI is a nuclear gene, the gene exists in two copies and direct sequencing of PCR products yields an ambiguous combination of both sequences, which we termed the “diploid phenotype”. The initial study included determination of the diplioid phenotype of PGI for 76 individuals (Bucklin et al., 2000), but allelic variation could not be determined from this study.

Figure 3. Partial DNA sequences of six alleles of phosphoglucose isomerase (PGI) for four individuals of *Calanus finmarchicus* collected in Icelandic waters. An intervening sequence (i.e., non-transcribed or intron), including two polymorphic insertion-deletions, is indicated by shading.



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                                                                         51
A     G GCA CTC CTT CCC TAT GAT CAG TAC ATG CAT AGG TAG GT - --- --C ATT ATC
B      .......................................    G GTG GA. ... ...
C      .......................................    G GTG GT. ... .C.
D      .......................................    G GTG GT. ... .C.
E      .......................................    G GTG GA. ... ...
F      .......................................    G GTG GA. ... ...

                                                                        102
A    AGT ATC AAA GTC ACA GTA CTC --- --- -AC CTT CCT GCT CAG   G TTC GCG GCC
B    ........ . ...... ...... ACC AGT C.........................
C    ........ . T..... ...... ...........................     . ...
D    ......... . T..... ...... ...............  ..AA........ . ...
E    ........ . ...... ...............  T....... . .............
F    ........ . ... .TG ............   .G. ......................

                                                                        157
A    TAC TTC CAG CAG GGG GAC ATG GAG AGT AAC GGG AAG TAT GTG GTG AGG GCT GGG
B     ................................... . ..............
C     ................................... . ..............
D     ............................ ... ........ . .........  ......
E     ................................... . ..........   . ...
F     ................................... . ...  ...........
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In recent studies, we have begun to characterize allelic variation of PGI by cloning a 390 base-pair region using the Topo TA Cloning Kit (Invitrogen, Inc., Carlsbad, CA) and sequencing the cloned insert. We report here our study of patterns of DNA sequence variation based on 32 sequences: eight clones for each of four individuals of C. *finmarchicus*. This initial survey is intended to give some idea of the level of variation of the selected gene, PGI; it is not intended to estimate variation across the species as a whole.

Common substitutions in PGI coding regions and introns for the four individuals were considered to represent allelic variation; sequence variation defined six alleles (A - F; Figure 3). Two intervening sequences (introns) were identified within the 390 base-pair region of PGI for one of the individuals sequenced. The first intron contained two insertion-deletion polymorphisms, of six- and seven base-pairs, resulting in intron lengths ranging from 38 to 51 base-pairs (Figure 3). This length polymorphism was also observed at relatively high frequency in genomic sequencing of numerous individuals (Bucklin et al., 2000).

Hydrographic analysis of water mass structure: The analysis of population genetic structure is being carried out in parallel with the hydrographic analysis of water mass structure and source in Icelandic waters. The goal is to place the population genetic *structure* of C. *finmarchicus* surrounding Iceland in a realistic ocean setting, including current flow, in order to examine probable source regions for the copepods.

Results and conclusions

Population genetic analysis: Based on our preliminary survey of DNA sequence variation of PGI, the selected gene portion is highly variable, with patterns of variation that indicate that PGI is an excellent gene for population genetic examination of C. *finmarchicus* (Bucklin et al., 2000; unpublished data). There were six different alleles (A - F) for four individuals cloned and sequenced (Figure 3), with large sequence differences between them (1 to 6% of the nucleotides). The genotypes of the four individuals were AE and FF (collected at Station 225, in Atlantic Water west of Iceland) and BC and CD (collected at Station 267, in Polar Water northeast of Iceland).

The pattern of DNA sequence variation revealed by these preliminary studies suggest that design of rapid protocols for discrimination of allelic variation will be feasible. Our intention is to semi-automate the population genetic analysis, in order to allow assay of sample sizes on the order of hundreds. Large sample sizes are essential to adequately resolve population genetic and water mass structure in Icelandic waters.

Source regions for C. finmarchicus in Icelandic waters: Patterns of current flow around Iceland indicate that *C. finmarchicus* may be transported via the Labrador Current, N. Atlantic Current, and Irminger Current to the shelf area south of Iceland (Figure 1). Regions to the north and east of Iceland may be populated by copepods originating in the Norwegian Sea. Thus, the sea areas around Iceland may contain two distinct populations of *C. finmarchicus*, which originate from distinctive oceanographic domains, but are juxtaposed in waters surrounding Iceland.

Based on water mass analysis of hydrographic data collected during the 1999 cruise, we hypothesized that copepods collected in the Irminger Sea (at Stns 225 and 227; Figure 2) may have originated in the Labrador Sea/Irminger Sea gyre, which is thought to be a major center of distribution for *C. finmarchicus* (Gislason and Astthorsson, 2000). However, the inference of sources of water and copepods was not as straightforward in other water masses surrounding Iceland. For example, in the western part of the Denmark Strait (Stn 236), the East Greenland Current carried Arctic Water southward, while in the eastern part the Irminger Current carried Atlantic Water northward. *Thus, the C. finmarchicus* sample at this station may have represented a mixture of animals from both of these sources (Astthorsson *et al.*, 1995). Similarly, the East Icelandic Current (Stns 267 and 269), which intermixes Atlantic Water from the North Icelandic Irminger Current and Norwegian Sea, and Polar Water from the East Greenland Current, may have carried copepods originating from any or all of these regions.

*From **zooplankton population** genetics **to fish stocks:** The* population genetic structure of ecologically important and numerically predominant species can also help to delimit the boundaries and determine the functional linkage between ocean ecosystems. The accumulation of significant genetic differentiation necessitates biological (e.g., timing of reproduction) and / or physical (e.g., entrainment in different current patterns, differences in vertical distribution) barriers between the populations, Population genetic differentiation of an important species in the planktonic assemblage can thus suggest functional differences in the respective ecosystems, because of distinct seasonal patterns in abundance of key species or altered trophic relationships - to name a couple of examples.

Calanus normally makes up about 80% of the zooplankton biomass in Icelandic waters during Spring (Astthorsson and Gislason, 1995) and up to 70 % in the eastern N. Atlantic during Summer (Heath et al., 1999). Fish species dependent upon *Calanus as* a food resource at some stage in their life history include: capelin, cod, haddock, salmon, redfish, herring, and mackerel. Jakobsson and Stefánsson (1998) documented a significant correlation - on decadal time scales - between stock size of capelin and zooplankton biomass in the waters to the north of Iceland. And further, when capelin stocks were low, the weight at age of cod (which feed predominately on capelin) was also very low. Astthorsson and Gislason (1995) related the abundance of O-group cod to the zooplankton abundance. It appears that recruitment of many commercial fish species may depend upon *Calanus* abundance, which in turn exhibits complex spatial patterns in relation to ocean structure and circulation. This spatial structure may be delimited and described by population genetic analysis.

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