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Published in:
ICES Journal of Marine Science

Link to article, DOI:
10.1093/icesjms/fsac076

Publication date:
2022

Document Version
Publisher's PDF, also known as Version of record

Citation (APA):
Christensen, H. T., Rigét, F., Retzel, A., Nielsen, E. H., Nielsen, E. E., & Hedeholm, R. B. (2022). Year-round genetic monitoring of mixed-stock fishery of Atlantic cod (*Gadus morhua*); implications for management. *ICES Journal of Marine Science*, *79*(5), 1515-1529. Article fsac076. https://doi.org/10.1093/icesjms/fsac076

ICES Journal of Marine Science, 2022, **79**, 1515–1529
DOI: 10.1093/icesjms/fsac076
Advance access publication date: 6 May 2022
Original Article

Year-round genetic monitoring of mixed-stock fishery of Atlantic cod (*Gadus morhua*); implications for management

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Mixed-stock fisheries pose a challenge for fisheries management recommendations and management, as mixed stocks can lead to unintentional over- or under-exploitation of stocks, with both short- and long-term biological and economic consequences. This study demonstrates practical application and implementation of year-round high-resolution genetic stock monitoring in management of mixed Atlantic cod (*Gadus morhua*) stocks in western Greenland. Using a panel of 96 high resolution gene-associated SNPs, we identified the stock of origin for four cod stocks in the two major inshore mixed-stock fisheries. Contribution of individual stocks was quantified to identify if fjord sections, times of year, and fish size, would allow a "clean fishery" with a minimal contribution of the depleted West Greenland Offshore (WGO) population. High level of mixing was identified with 50% of inshore catches originating from the inshore stock, 20% from the East Greenland/Iceland offshore stock, and 30% from the WGO stock. Although some spatiotemporal variation of stock proportions was identified, a practice allowing exclusively fishing a specific stock was not possible. Accordingly, we demonstrate the need to allocate catches at the biological stock level and show that application of high-resolution genetics is a reliable and necessary tool.

Keywords: DNA, fisheries management, fishery, migration, mixed stocks.

Introduction

Temporal and spatial mixing of species unit with distinct demographic dynamics, i.e. stocks (Secor, 2014), has long been recognized for fish species inhabiting the North Atlantic (Heincke, 1898) and documented in ecologically different species such as herring (*Clupea harengus*; Gröhsler *et al.*, 2013), Atlantic cod (*Gadus morhua*; Michalsen *et al.*, 2014), beaked redfish (*Sebastes mentella*; Saha *et al.*, 2017), and salmon (*Salmo salar*; Gilbey *et al.*, 2017). In general, stocks encountered in mixed-stock fisheries lack easily discernable morphological traits (e.g. Cadrin *et al.*, 2010; Hedeholm *et al.*, 2016), and, accordingly, the proportional contribution of different stocks cannot be assessed in real time using a simple visual approach for stock identification.

In mixed-stock fisheries, if stock tolerance to fishing intensities differs, that can lead to unintentional over- or under-exploitation or even stock collapse, which can affect short term gain (Heath *et al.*, 2014; Jardim *et al.*, 2018; Cadrin, 2020). This can have long-term consequences for genetic diversity and evolutionary potential (Allendorf *et al.*, 2008). With a substantial part of the world fisheries being overexploited, depleted, or recovering (FAO, 2018), there is a need to manage stocks according to their inherent demographic dynamics, and amongst other things, this requires knowledge of stock-specific catches and management set-ups that incorporate such knowledge (Hemmer-Hansen *et al.*, 2019; Cadrin, 2020). Thus, methods that can discern between different stock units are in high demand (Cadrin *et al.*, 2014). Initially, the mixed units were often demonstrated using external tags (Hovgård and Christensen, 1990; Hall, 2014) and meristic/morphometric traits (Chase, 2014; Stransky, 2014), while otolith morphology and chemistry (Campana and Casselman, 1993; Campana, 1999) was later added to the toolbox and are still extensively applied (ICES, 2017, 2019a).

Genetic methods for quantifying stock mixtures have been applied for more than 50 years (Sick, 1965). In recent times, fisheries management has increasingly employed genetic methods to elucidate population structure, provide evidence for stock mixing on fishing grounds (or migratory grounds), and to estimate the relative proportions of stocks encountered in mixed-stock fisheries (Reiss *et al.*, 2009; Ovenden *et al.*, 2015). The reason for this genetic progression is the "genomic revolution," which has allowed the development of high-resolution genetic markers even for non-model organisms (Helyar *et al.*, 2011; Nielsen *et al.*, 2013). Genetic methods can only be applied if the "stocks" represents at least semi-isolated reproductive units (Waples and Gaggiotti, 2006) and genetic differentiation in marine fish is generally low (Ward *et al.*, 1994). Nevertheless, genetic analyses are now so powerful, that even the relatively small overall genomic differences among marine fish populations can be used to identify and to discern population mixing with high resolution (Nielsen *et al.*, 2009; Ovenden *et al.*, 2015; Bernatchez *et al.*, 2017). The high resolution for individual identification of population of origin

Received: August 30, 2021. **Revised:** January 28, 2022. **Accepted:** March 10, 2022

either relies on using a high number of genetic markers, combining the power of many gene loci each with small differences (Nielsen, 2016) or using panels of “minimum markers with maximum power” (Nielsen *et al.*, 2012). The latter relies on the concept of choosing genetic markers involved in or linked to genes subject to local adaptation, i.e. genetic adaptation to the local environment experienced by semi-isolated populations, which displays highly divergent allele frequencies among populations of marine fish (Nielsen *et al.*, 2009, 2012; Lamichhaney *et al.*, 2012). Even single gene approaches can be applied in simple cases where alternate alleles are almost fixed in different stocks (populations), such as with the Pantophysin gene, which allows almost unambiguous identification of Northeast Arctic/Norwegian coastal cod in the mixed-stock fishery in the Lofoten area (Dahle *et al.*, 2018).

In the Lofoten area, the aim has been to protect the relatively small Norwegian coastal cod population from overfishing by directing fisheries efforts towards areas with a relatively high proportion of the much more abundant Northeast Arctic cod. In this case, more than 18 000 fish were analyzed between 2007 and 2017. To our knowledge, this is the only published non-salmonid example of continuous fisheries monitoring using genetic tools. Most often studies of marine fish stock mixtures represent snapshot of samples for proof-of-concept studies, more focused on the molecular methods than directly providing biological information to inform management and policy (Casey *et al.*, 2016). To some extent this may reflect a literature bias since genetic tool development is likely to be more commonly published than practical application studies. Moreover, genetic methods are often (mis)conceived as expensive, although it is generally recognized that genotyping an appropriate proportion of the surveys and commercial catch used for mixture assessment purposes would be the ideal approach (Martinsohn *et al.*, 2018). Finally, the lack of appropriate frameworks and models for incorporating genetics into widely used stock assessment and management approaches may also be hampering the methodical uptake of genetics.

With focus on the well-documented mixed-stock fishery for Atlantic cod in West Greenland, our aims with this study were to provide an example of practical implementation of genetics in fishery management of mixed stocks with relatively small levels of genetic differentiation. Focus is particular on a holistic integration of genetics in the total stock assessment and advice giving for the spatial and temporal management of co-occurring stocks with different management objectives.

Historically, the large cod fishery in Greenland in the middle of the 20th century included several stocks (Therkildsen *et al.*, 2013). However, mixed stock considerations were not an issue at that time, as this was before exclusive economic zones (EEZ’s), stock assessments, and total allowable catch (TAC) limitations, although the general pattern of stock delineation were known at the time (Hansen, 1949). Hence, the less resilient West Greenland offshore (WGO) stock collapsed during the years of very high catches (> 400 000 t), while other stocks present in the same area kept catches high for decades (Bonanomi *et al.*, 2015). When the fishery collapsed around 1990, the WGOstock was left highly depleted, and remains so three decades later (ICES, 2019b).

As indicated above, the “Greenland cod complex” is a mixture of several stocks, each with distinct spawning grounds (Therkildsen *et al.*, 2013; Bonanomi *et al.*, 2016). The stocks are the West Greenland Inshore stock (WGI), the West Greenland Offshore stock (WGO), the East Greenland/Iceland offshore stock (EGI), and the Iceland inshore stock (IIS; Figure 1). Drift events from EGI passively supply the WGI area with eggs and larvae (Ribergaard, 2004) and the juveniles use the area as nursery and feeding grounds (Storr-Paulsen *et al.*, 2004) before actively homing to their spawning grounds when reaching maturity (Bonanomi *et al.*, 2016). In the past, the inflow of cohorts from EGI has occasionally been very large and given rise to large, but short-lived, catches in West Greenland. The last major occurrence was the 1984 cohort that over a 3-year period (1988–1990) resulted in catches over 200 000 t in West Greenland (ICES, 2019b). Currently, the stocks are in different states. The WGO stock is considered depleted and has been for decades, the EGI stock in the East Greenland part of the stock distribution grew considerably between 2000 and 2014, but it is now on a downwards trend. In contrast, the EGI in the Icelandic part of the stock distribution has been on an upward trend since 2000. The WGI stock is at a high level but on a downwards trend since 2016 (ICES, 2019b).

Over the past decade, the WGO fishery has on average been 10 times lower than the WGI fishery. Hence, the mixed inshore fishery determines the overall outtake from the WGO stock. The fishery in East Greenland catches almost exclusively the EGI stock, as the WGI and WGO stocks do not migrate east to any significant degree (Bonanomi *et al.*, 2016). Therefore, the area of most interest when addressing mixed stocks from a quantitative perspective is the WGI area, where recent catches have increased from around 10 000 to between 20 000 and 30 000 t in the last 10 years (ICES, 2019b). Quantification of the different stocks present in the catches here would provide stock specific estimates of the total outtake of all stocks in all of Greenland improving assessment and informing managers on TAC implications. All three cod stocks in Greenland are managed by a TAC limitation, and in the offshore area also a combination of area and periodical closures during spawning. To some extent the WGI and EGI stocks are both assessed taking cod migration into account, but none of the assessments incorporates mixed stocks in catches. However, all assessment (including WGO) explicitly state, that more knowledge is needed on mixed stock to improve the assessments (ICES, 2019b).

Attempts have been made to separate the different Greenland cod stocks based on simple, easily applicable visual methods, such as morphology (Hedeholm *et al.*, 2016) and otolith shape (Glindtvad, 2017). These have been unsuccessful, and the only applicable method to stock assignment is a genetic Single Nucleotide Polymorphism (SNP) panel developed specifically for the Greenland cod stock complex (Therkildsen *et al.*, 2013). However, until now only qualitative and proof of concept studies on stock delineation (Therkildsen *et al.*, 2013) and mixed stocks (Henriksen, 2015) are available.

Hence, in this study we use genetic assignment to quantify the proportional contribution of the three different Greenlandic cod stocks to commercial landings throughout the year 2017 in the WGI area. Specifically, to answer if the fishery can be managed so that it targets a specific cod stock, we investigate how the catch proportions change dependent on catch location (“Inner,” “Mid,” or “Outer” fjord; Figure 1), season (“Summer” or “Winter”), and size (“Large” or “Small”). The stock proportions in the catch are related to the total catch of cod to provide stock specific catches and the results are discussed from a managerial perspective.

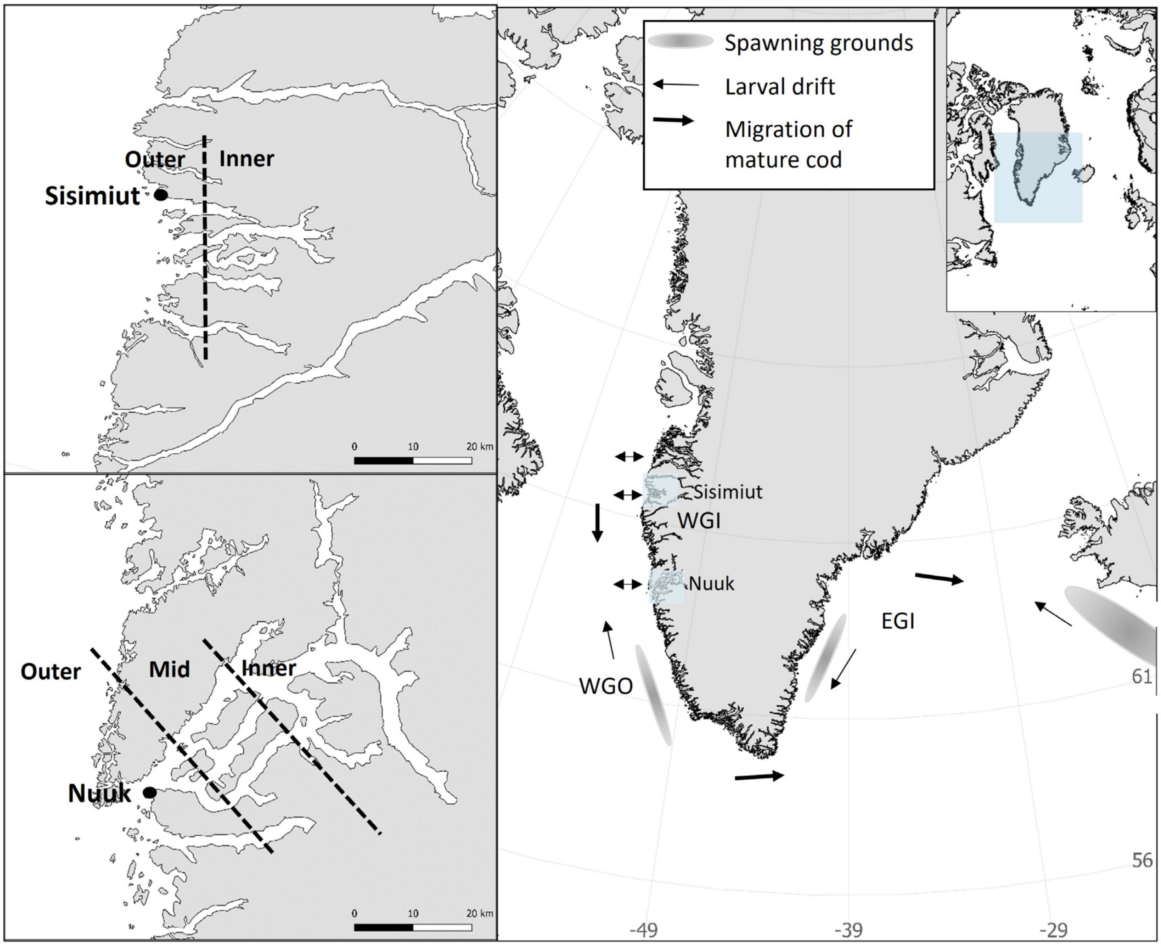

Figure 1. Map of study sites in Nuuk and Sisimiut including a general map of offshore spawning locations (WGO, WGI, and EGI), larval drift and migration routes of Atlantic cod (*G. morhua*) in Greenland.

Methods

Study area

Samples were collected in two West Greenland fjord systems: Sisimiut (NAFO area 1B) and Nuuk (NAFO area 1D; Figure 1). Both fjord systems have relatively shallow entrance sills, are large (60 km and 100 km long, respectively) and consists of multiple sections and shallow inlets separated by areas with depths of 400–500 m. The cod fishery extends both North and South of Nuuk and Sisimiut (see Figure 1), but the two areas are traditionally the most important cod fishing regions, currently accounting for approximately 30% of total cod landings in the WGI region (ICES, 2019b). Furthermore, the two largest inshore spawning grounds are found in Nuuk and Sisimiut (Storr-Paulsen *et al.*, 2004). Pound nets anchored to the shore dominate the fishery (~70%), but gill nets and jigs are also used, while bottom trawling is disallowed in the inshore area. The fishery takes place throughout the year, however, catches peak in the summer months when cod migrate to shallow areas, probably following capelin, their key prey species (Nielsen and Andersen, 2001; Grønkjær *et al.*, 2020). Besides a TAC, the only other regulation of the fishery includes a valid commercial fishery license and a minimum landing size (40 cm). Currently, around 1640 people are licensed to fish for cod inshore in Greenland.

Sampling

DNA samples were collected every week during 2017 at fish factories in Nuuk and Sisimiut. The number of samples collected per week was adjusted to the intensity of the fishery. On each sampling date, cod were randomly chosen from one or several landings. Samples were taken from as many different landings as possible (Table 1). Hence, no specific number of cod were sampled from each catch, but sample size typically ranged from 10 to 15 cod. The samples consisted of fin clips preserved in 96% ethanol. For each sample, information on fish length, fish state (with/without head), catch position given as field code, and date of catch was registered. Total lengths in cm were recorded when possible. Most fish were landed without head and lengths of these fish were converted to total length using a conversion factor of 1.23.

Fjord section and season

Both Nuuk and Sisimiut fjord systems are geographically extensive and allow for analyses of local spatial differences in catch composition during the year. Accordingly, both fjords were divided into sections, with designated “Inner,” “Mid,” and “Outer” fjord sections for Nuuk and “Inner” and “Outer” sections for Sisimiut (Figure 1). The sections were defined to follow changes in fjord bathymetry and both “Inner” sections

Table 1. Total number of cod samples collected per week in Nuuk and Sisimiut during 2017. WGI cod, WGO cod, and EGI cod.

Week	Nuuk *N*	Sisimiut *N*
1	8	0
2	11	0
3	0	0
4	39	0
5	35	0
6	34	0
7	28	0
8	0	0
9	10	0
10	10	0
11	9	0
12	0	50
13	27	79
14	16	20
15	16	60
16	33	10
17	31	10
18	20	20
19	40	100
20	0	60
21	69	0
22	30	50
23	49	60
24	86	50
25	99	60
26	30	70
27	54	40
28	51	50
29	20	50
30	55	50
31	20	50
32	14	0
33	14	0
34	40	10
35	0	20
36	11	30
37	12	30
38	41	10
39	32	2
40	0	11
41	0	29
42	0	20
43	55	10
44	59	30
45	61	30
46	0	60
47	40	30
48	20	0
49	20	10
50	19	30
51	59	0
52	0	10

included known spawning grounds for the WGI stock in both areas.

Samples were also grouped by season where April–September was defined as "Summer" and October–March as "Winter." The change from "Winter" to "Summer," was defined based on the known spawning migration of capelin from offshore to the inshore area in the beginning of April (Friis-Rødel and Kanneworff, 2002). Due to ice cover, there was no fishery, and therefore, no samples from Sisimiut in January and February (Table 2).

Size category

Based on the maturity function for Nuuk and Sisimiut (2007–2016; Tomkiewicz *et al.*, 2002), > 90% of the sampled cod were categorized as mature. Thus, maturity stage was not considered relevant in further analyses. Instead, we categorized cod in both Nuuk and Sisimiut as either "Large" (> 57 cm) or "Small" (≤ 57 cm) based on the median length of all sampled fish. There were 236 cod without length information because the fish was partly processed before arriving at the factory, and the total length measurement could not be obtained (Table 3).

Stock assignment to Greenland cod baseline

We used a slightly modified SNP panel and assignment approach from the procedure described for the same populations in Bonanomi *et al.* (2015, 2016). Briefly, DNA was extracted from fin-clips using the Chelex resin (Estoup *et al.*, 1996) and used for genotyping a panel of 96 gene-associated SNPs specifically selected as the most informative for population assignment for cod in Greenland waters (see also Therkildsen *et al.*, 2013; Hedeholm *et al.*, 2016). Samples were genotyped on a Fluidigms 96.96 Dynamic Array™ IFC. Individuals genotyped at less than 50 SNPs were discarded from further analysis. The GENECLASS2 program (Piry *et al.*, 2004), using the Bayesian probability approach (Rannala and Mountain, 1997), to assign individual cod genotypes back to baseline cod samples originating from the four known stocks in the Greenland stock complex: WGI stock, the WGO stock, the EGI stock, and the IIS. The baseline genetic samples originated from the overarching SNP based study of population structure in Greenlandic waters (Therkildsen *et al.*, 2013), where 847 contemporary and historical cod tissue samples were analyzed with 935 previously validated transcriptomic SNP's. Individual genotypes were subsequently clustered with DAPC (Jombart *et al.*, 2010) into the four stocks, which was the model that showed the highest likelihood given the data (see Therkildsen *et al.*, 2013 for details). From this pool of high-resolution genotypes, more than 400 individuals from the four populations were selected for the genetic baseline based on their genetic population affinity and subsequently genotyped with the informative 96 SNPs panel. All individuals genotyped for less than 90 SNPs were discarded, providing a final genetic baseline consisting of 386 individuals with close to complete genotypes (WGI: 78, WGO: 157, EGI: 89, and IIS: 62, individuals, respectively). Due to the combined stock assessment of the EGI and the IIS stock in Icelandic waters (ICES, 2021a), the two stocks were also combined in our analyses, using the "EGI" notation. Accordingly, all fish were included in the downstream analysis based on their most likely stock of origin.

Statistical analyses

In each area, the proportions of cod belonging to each stock (WGO, WGI, and EGI) were calculated and 95% confidence limits were estimated by bootstrapping using 1000 random sampling with replacement. The proportions were arcsine square root transformed prior to the statistical analyses to approximate normal distribution as recommended by Zar (1974, 1999) and Snedecor and Cochran (1967). Chi-squared tests were applied to test for differences in stock proportions between Nuuk and Sisimiut and monthly pairs of stock proportions in each area were compared by correlation analyses.

The proportions of cod belonging to the WGO, WGI, and EGI stocks were calculated in each of the combinations of

Table 2. Number of cod samples, mean cod size (±CI), and cod stock proportions in each area and month in 2017. WGI cod, WGO cod, and EGI cod.

	Nuuk					Sisimiut				
		Size (cm)		Proportions by stock			Size (cm)		Proportions by stock	
Month	*N*	Mean [95% *CI*]	WGI	WGO	EGI	*N*	Mean [95% *CI*]	WGI	WGO	EGI
January	93	55.6 [54.2–57.0]	0.61	0.27	0.12	NA	NA	NA	NA	NA
February	72	53.9 [52.5–55.3]	0.57	0.35	0.08	NA	NA	NA	NA	NA
March	46	55.8 [53.8–57.9]	0.30	0.43	0.26	129	63.5 [62.3–64.6]	0.51	0.31	0.18
April	96	53.3 [51.9–54.8]	0.59	0.23	0.18	100	62.0 [60.8–63.3]	0.57	0.25	0.18
May	149	55.4 [53.9–56.8]	0.39	0.38	0.23	190	59.2 [57.9–60.4]	0.39	0.36	0.25
June	264	54.6 [53.6–55.5]	0.44	0.33	0.23	280	58.2 [57.2–59.3]	0.39	0.29	0.32
July	180	52.9 [52.1–53.8]	0.46	0.33	0.21	200	57.9 [56.8–59.0]	0.38	0.30	0.32
August	68	53.8 [52.2–55.3]	0.50	0.29	0.21	50	57.4 [55.7–59.1]	0.54	0.18	0.28
September	96	55.8 [54.4–57.2]	0.45	0.42	0.14	92	60.6 [59.3–62.0]	0.37	0.35	0.28
October	55	53.8 [52.2–55.4]	0.51	0.20	0.29	81	61.8 [60.1–63.4]	0.47	0.25	0.28
November	180	55.3 [54.0–56.7]	0.54	0.27	0.19	140	59.0 [57.3–60.7]	0.64	0.18	0.19
December	98	60.9 [59.4–62.4]	0.66	0.26	0.08	50	67.4 [65.5–69.3]	0.62	0.18	0.20
Total	1397	54.9 [54.5–55.3]	0.50	0.31	0.19	1312	59.9 [59.5–60.4]	0.46	0.28	0.26

Table 3. Number of collected cod samples in each area, fjord section, and size category in 2017. WGI cod, WGO cod, and EGI cod.

	Nuuk, Fjord section				Sisimiut, Fjord section		
Size category	Inner	Mid	Outer	Total	Inner	Outer	Total
Small	168	215	399	782	373	139	512
Large	81	103	195	379	566	233	799
No length	45	62	129	236	1	–	1
Total	294	380	723	1 397	940	372	1 312

fjord section ("Inner," "Mid," and "Outer"), season ("Summer" and "Winter"), and size category ("Small" and "Large"). A linear model including fjord section, season, size, and first order interaction effects was applied to the arcsine transformed data to test for differences between proportions. The tests of the explanatory variables were based on Type III Sum of Squares, where every term in the model is tested considering every other term in the model ("partial"). Only results from the first order interaction effects including the stock proportions are relevant for this study. The results of the main effects are not relevant for this study as we focus on differences in stock proportions and the main model effects express results across the stock proportions. All statistical tests were done using R (R Core Team, 2018).

Spatio-temporal harvest and catch composition

To estimate the annual stock specific catch, we initially calculated the stock proportions in each area, fjord section, and month (Tables 2 and 3). In some cases, there were no samples for combinations of month and fjord section (e.g. "Inner" in November in Nuuk). In these cases, the average stock proportions for that fjord section in either winter or summer were used. Generally, this had negligible effect on the estimates of catch composition, as samples were only absent when the fishery was very close to zero in specific areas. These time–area specific stock proportions were combined with similar specific catches to provide time–area specific catches for each stock. These were then added across area–time to provide as detailed catch proportions as possible.

To evaluate if future studies and monitoring can apply a simpler and more cost-effective sampling approach, the "Detailed" approach was compared to a "Simple" approach, were the overall mean proportions in each area for the whole year were simply multiplied with the catch in the area to provide stock specific catches (Table 2).

Results

Samling

A total of 2709 DNA samples from Nuuk ($N = 1397$) and Sisimiut ($N = 1312$) were analyzed (Table 2). The mean length of cod sampled in Nuuk for the present study was comparable to the mean length of cod documented from the commercial fishery in the area in general. The mean length of cod sampled in Sisimiut was approximately 4 cm larger than in Nuuk (Table 2).

Stock assignment to Greenland cod baseline

Genetically based self-assignment of baseline samples showed very high power, with overall 97% of individual cod correctly assigned (WGI: 96%, WGO: 94%, EGI: 100%, and IIS: 100%). Individual membership probability was high, with a mean individual score of 98% and only nine individuals with a score < 75% (WGI: 1, WGO: 6, EGI: 1, and IIS: 1 individual, respectively) (Supplementary Figure S1). The same high membership probability was reflected in the cod samples of unknown origin, with only 259 of 2709 samples assigned with a membership probability < 75% (mean 93%) including multilocus SNP genotypes with some missing loci (mean number of scored SNP loci per multilocus genotype = 88).

The overall stock proportions (95% Cl) in 2017 in Nuuk were 50% (47–52) WGI, 31% (29–33) WGO, and 19% (17–

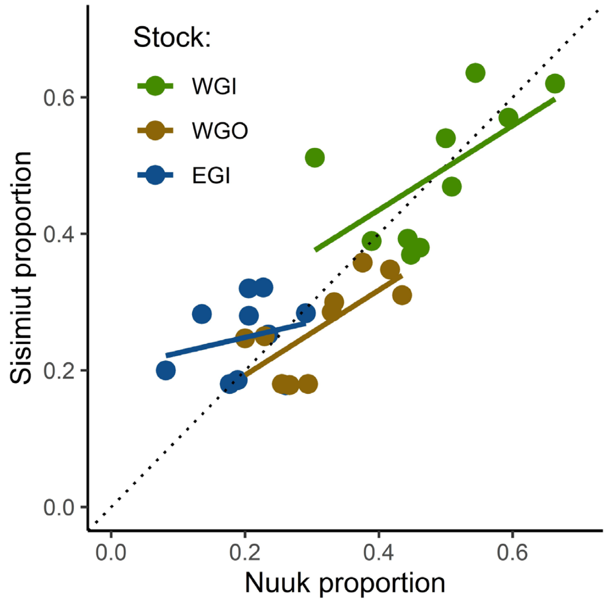

Figure 2. Correlation between stock proportions in Nuuk and Sisimiut in 2017. Monthly pairs of proportions for the three stocks are plotted (WGO $r = 0.72$, $p = 0.02$, WGI $r = 0.62$, $p = 0.06$, and EGI $r = 0.24$, p = 0.51).

Table 4. Results of ANOVA (type III test) in Nuuk.

	Sum Sq	Df	F value	Pr(> F)
Intercept	0.0118	1	14.61	0.001***
Fjord section	0.0058	2	3.58	0.046*
Stock	< 0.00001	2	0.01	0.993
Size	0.0014	1	1.75	0.200
Season	0.0061	1	7.50	0.012*
Fjord section: stock	0.0058	4	1.79	0.169
Stock: season	0.0005	2	0.28	0.757
Stock: size	0.0053	2	3.28	0.058.
Residuals	0.0170	21		

Signif. codes: 0 "***", 0.001 "**", 0.01 "*", 0.05 ".", and 0.1 " " 1.

21) EGI, while the Sisimiut proportions were 46% (44–49) WGI, 28% (26–30) WGO, and 26% (23–28) EGI (Table 2). The stock proportions differed between Sisimiut and Nuuk ($\chi2 = 19.147$, $p < 0.001$). Although the differences were small, the proportions of WGI and WGO were significantly higher in Nuuk while the EGI proportion was highest in Sisimiut. Between fisheries areas, monthly pairs of stock proportions showed that the EGI stock proportion was highest in Sisimiut, and conversely, the WGO stock proportion was highest in Nuuk (Figure 2, above and below unity line, respectively). There was a positive correlation in monthly pairs of stock proportions between areas, albeit only significantly for WGO ($p = 0.02$), and marginally insignificant for WGI ($p = 0.06$).

Fjord section and season

Stock proportions between fjord sections were not significantly different in Nuuk (ANOVA $p = 0.169$, Table 4), but significantly different in Sisimiut (ANOVA $p = 0.056$, Table 5; Figure 3). In Nuuk, the proportions of the three stocks were more equally distributed in the "Inner" part of the fjord than in the "Outer" part of the fjord, with the WGI proportion being especially higher in the "Outer" part of the fjord (Figure 3; Supplementary Figure S2). In Sisimiut, the WGO proportion was similar in both fjord sections, while the EGI proportion increased from the "Inner" to the "Outer" part of the fjord. In Sisimiut, WGI was the prevalent stock in both fjord sections, but the proportion was lower in the "Outer" section of the fjord (Figure 3; Supplementary Figure S3). The stock proportions were similar between "Summer" and "Winter" in both Nuuk and Sisimiut (ANOVA $p = 0.757$; Nuuk, Table 4, $p = 0.482$; Sisimiut, Table 5). WGI was the most prevalent stock in both "Summer" and "Winter" in both areas, but during "Winter" the proportion of WGI increased while the proportion of EGI and WGO decreased in both areas (Figure 4; Supplementary Figure S2).

Table 5. Results of ANOVA (type III test) in Sisimiut.

	Sum Sq	Df	F value	Pr(> F)
Intercept	0.0462	1	45.28	< 0.001***
Fjord section	0.0044	1	4.36	0.059.
Stock	0.0208	2	10.18	0.002**
Size	0.0003	1	0.27	0.614
Season	0.0188	1	18.44	0.001**
Fjord section:Stock	0.0075	2	3.70	0.056.
Stock:Season	0.0016	2	0.78	0.482
Stock:Size	0.0057	2	2.78	0.102
Residuals	0.0122	12		

Signif. codes: 0 "***", 0.001 "**", 0.01 "*", 0.05 ".", 0.1 " " 1.

Size category

In Nuuk, there was a small difference between stock proportions in the different size categories (ANOVA $p = 0.058$, Table 4), while there were no significant differences in Sisimiut (ANOVA $p = 0.102$, Table 5; Figure 5; Supplementary Figure S5).

Spatio-temporal harvest and catch composition

In Nuuk, the majority of the catch was taken during spring and summer (Figure 6). In general, the fishery commenced in March/April but with spatial displacements. In the inner fjord section, the fishery started in late winter and in April the fishery moved to the mid and outer fjord sections. In the outer fjord section, the fishery was approximately 1 month delayed compared to the inner fjord section. In July, the intensity of the fishery declined and remained stable for the remainder of the year, except for the inner fjord section where the intensity increased again in winter (Figure 6). In Sisimiut, most of the catch was taken in the outer fjord section. Opposite to Nuuk, the fishery accelerated in April in the outer part while the inner part was 1 month delayed (Figure 7). The annual catch of each stock in both areas was estimated by integrating the stock proportions in each area, fjord section and month. In Nuuk, the total catch of cod was 3312 t with 1537 t from the WGI stock, 1090 t cod from the WGO stock, and 685 t from the EGI stock (Table 6). In Sisimiut, the total catch of cod was 4742 t with 1961 t cod from the WGI stock, 1257 t cod from the WGO stock, and 1524 t cod from the EGI stock (Table 6).

The simpler approach of integrating overall annual stock proportions and total catch per area (Nuuk and Sisimiut) was also applied (Table 6). In Nuuk, the total catch changed to WGI: 1656 t (+8%), WGO: 1027 t (−6%), and EGI: 629 t (−8%) and in Sisimiut they changed to WGI: 2181 t (+11%), WGO: 1328 t (+6%), and EGI: 1233 t (−19%; Table 6).

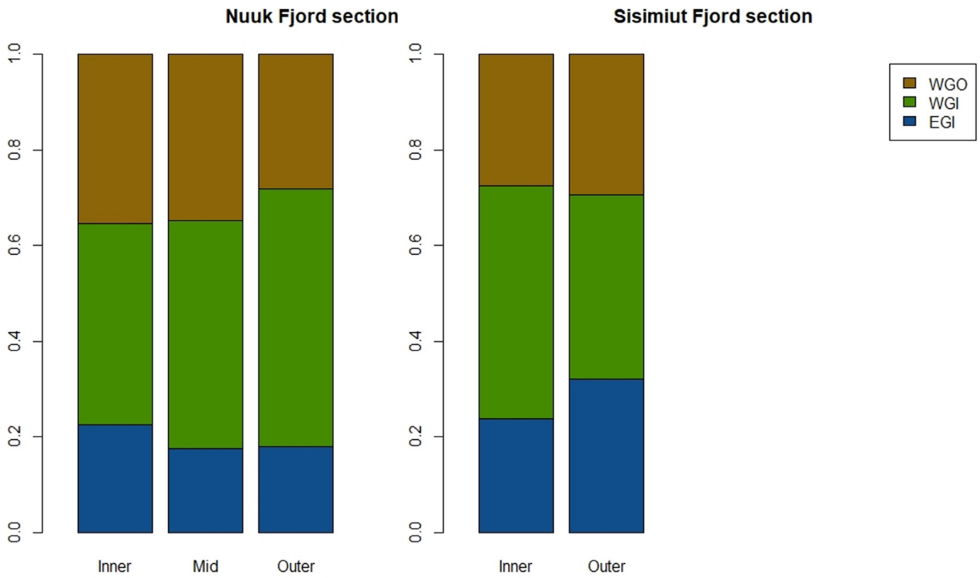

Figure 3. Proportions of cod stocks from WGO, WGI, and EGI in the different fjord sections in Nuuk and Sisimiut in 2017.

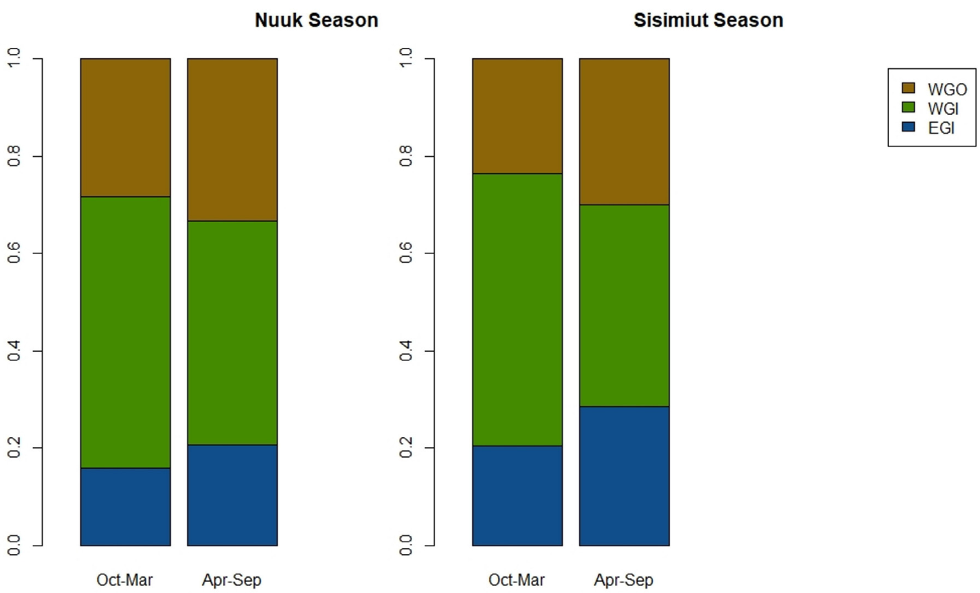

Figure 4. Proportions of cod stocks from WGO, WGI, and EGI in different seasons in Nuuk and Sisimiut in 2017. "Winter" includes October–March; "Summer" includes April–September.

Discussion

Genetic studies (Therkildsen *et al.*, 2013; Bonanomi *et al.*, 2016) are consistent with previous observations made from tagging data and knowledge of larval drift (Ribergaard, 2004; Storr-Paulsen *et al.*, 2004), which confirms distinct, stock-specific behaviours and reproductive isolation of populations. The knowledge of at least four well-differentiated genetic stocks has previously been used for genetically based stock assignment of individual cod for assessing the causes of collapse of the historical West-Greenland fishery (Bonanomi *et al.*, 2015), the stock specific homing between West-Greenland and Iceland (Bonanomi *et al.*, 2016) and for evaluating the fisher's ability to visually differentiate between cod from the different stocks (Hedeholm *et al.*, 2016). However, the present study is the first to quantify the actual year-round contribution from each stock to the inshore fishery.

We quantified the proportion of Atlantic cod from the different stocks present in Greenland waters (but pooling EGI and the IIS as EGI), caught in the mixed-stock inshore fishery in West Greenland. Individual cod generally assigned with a very high probability to one of the stocks, as also shown in previous studies using the same or a very similar SNP panel and statistical approach (Bonanomi *et al.*, 2016; Hedeholm *et al.*, 2016). Thus, we consider the sampled proportions to be robust towards any potential methodological bias. Further, the intense sampling effort across a full year and including cod from many different catches, also ensured robust estimates of catch composition. In Sisimiut, stock proportions were simi-

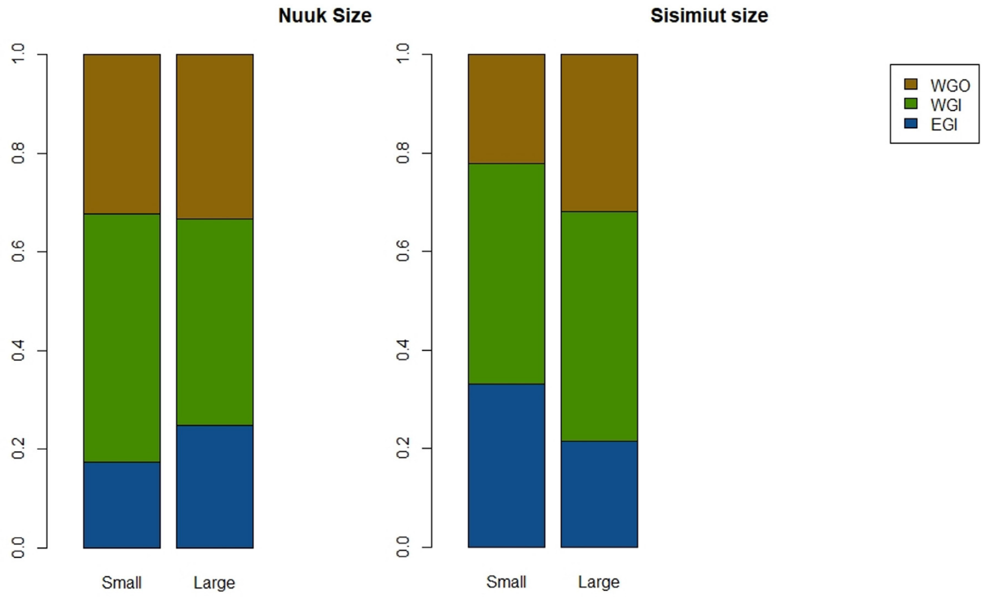

Figure 5. Proportions of cod stocks from WGO, WGI, and EGI in different size categories in Nuuk and Sisimiut in 2017. Based on medial length, with "Small" defined as cod < 57 cm.

larly distributed in both space and time, and while stock proportions in Nuuk did differ significantly between fjord sections and with fish size, the differences were relatively small. Hence, in general, distinct spatiotemporal patterns of stock distribution were missing in the year-round catches for both regions. All three stocks were mixing on both a temporal and spatial scale and all sampled catches contained cod from all three stocks also illustrating a high degree of mixing. It is simply not possible to exclusively fish a specific stock at any site or time of year, and mixed-stock catches seems a fixed premise for this fishery.

In general, 50% of the cod caught in the inshore fishery originated from the inshore stock (WGI), 30% from the WGO stock, and 20% from the EGI offshore stock (EGI). We found some regional differences in stock proportions between Nuuk and Sisimiut. However, stock dynamics through the year in the two areas were correlated and, therefore, appeared to be linked. Accordingly, given the current fishery pattern, we find it reasonable to assume the simultaneous findings for the two regions are representative for the majority of the inshore fishery, although the marginal regions should be further investigated as stock proportions may wary here.

Temporal and spatial change

From other regions of the distribution of Atlantic cod, feeding and spawning related to mixing events of cod stocks are well-known and documented. Along the Norwegian coast, the Northeast Atlantic cod migrate back from their feeding grounds in the Barents Sea to spawn along the Norwegian coast, where they overlap in distribution with the coastal cod (Bergstad *et al.*, 1987). In the Baltic Sea, cod from the eastern and western Baltic Sea overlap in distribution in the Arkona Basin (Hüssy *et al.*, 2015; Weist *et al.*, 2019), while North Sea and local Kattegat cod mix in the transition area between the North Sea and the Baltic Sea (Hemmer-Hansen *et al.*, 2019). Challenges due to stock and species mixing is also known from other species such as herring in the Baltic Sea (Gröhsler *et al.*, 2013; Bekkevold *et al.*, 2016), Atlantic Salmon in Greenland waters (Bradbury *et al.*, 2016) and redfish in East Greenland and Iceland waters (Saha *et al.*, 2017). Stock proportions in the overlapping areas can change for different reasons e.g. feeding, or spawning migrations (Bergstad *et al.*, 1987; Dahle *et al.*, 2018), variation in stock size (Hüssy *et al.*, 2015), change in climatic conditions (Stein and Borovkov, 2004), or variable fishing intensities in other regions (i.e. offshore waters). Historically, the abundance of Atlantic cod in the WGI area has varied greatly (ICES, 2019b). West Greenland includes the northern distribution limit for Atlantic cod, and the abundance is particularly influenced by climatic variations (Wieland and Hovgård, 2009), but other factors such as fishing intensity, and recruitment success both locally and in other regions have historically influenced both stock proportions and the fishery substantially (Buch *et al.*, 1994; Bonanomi *et al.*, 2015, 2016). Particularly, the inflow of large year classes from EGI have had a major impact on local cod abundance. Given the erratic and significance of such recruitment events and the homing behaviour associated with maturation and spawning in East-Greenland/Icelandic waters, the need for continued monitoring of spatio-temporal stock dynamics is highly relevant to ensure stock health and exploitation optimization. Furthermore, the knowledge of the changing stock composition needs to be implemented in the management procedures as highlighted by Reiss *et al.* (2009). They documented a mismatch between available knowledge of genetic population structures and the current management units for a range of highly commercial species (e.g. Haddock; *Melanogrammus aeglefinus*, whiting; *Merlangius merlangus*, and herring; *C. harengus*; Reiss *et. al.*, 2009). Such mismatches can lead to both under and over estimation of stock status, potentially effecting both fishery and fish populations, leading to unintentional or undesirable exploitation levels. The present findings were comparable to earlier studies on mixed stocks of Atlantic cod in the inshore area. Henriksen (2015) identified 46% of cod collected in the inshore area as cod belonging to the inshore stock (WGI) and unpublished results based on

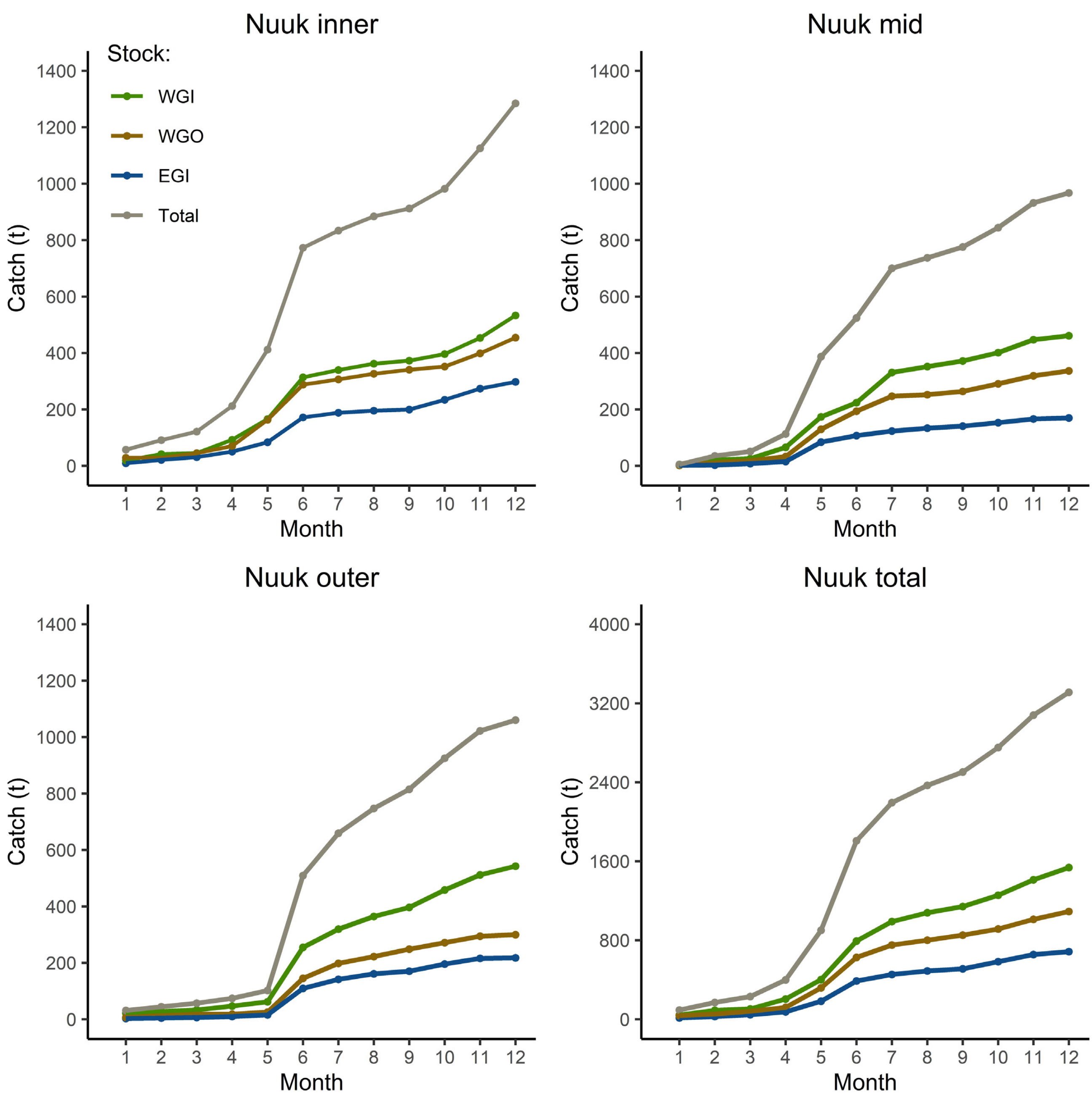

Figure 6. Cumulative catch composition of total and stock specific catches of cod stocks from WGO, WGI, and EGI through 2017 in Nuuk.

samples taken from landings in 2018 also find proportions close to 50% WGI, 30% WGO, and 20% EGI. Hence, the stock proportions appear to be relatively stable, at least in the short term and with the current stock status. However, as long as the inflow of juveniles from EGI and the WGO area is unpredictable there will be a need for continues monitoring. Such inflow events can be substantial (Stein and Borovkov, 2004) and monitoring should include juvenile stages caught in surveys to allow for time to adjust management before the year–classes recruit to the fishery. The narrow length range of the samples (Table 2) clearly shows that the landings consist of very few year classes, i.e. mainly 5–6-year-old cod, which is typical for the fishery (ICES, 2019b). Therefore, updated knowledge on stock proportions in the upcoming year classes is crucial. Using a classical advisory approach, where biological advice is provided 1 year ahead based on data from preceding years, missing information on the origin of year–classes recruited to the fishery could lead to failed management by missing the opportunity to fish more if a strong cohort enters the inshore area from offshore stocks and *vice versa* if the recruitment fails. The current advice for the WGI fishery relies heavily on a recruitment survey, and a first step towards more robust advice would be to compare survey stock proportions to catch proportions. If these align, advice can be improved to be timelier and management more flexible to better reflect a dynamic system with spatiotemporal variability in stock contributions.

The current management regime for the WGO stock in offshore West Greenland aims at rebuilding the stock to previous levels, where the area supported annual mixed-stock catches

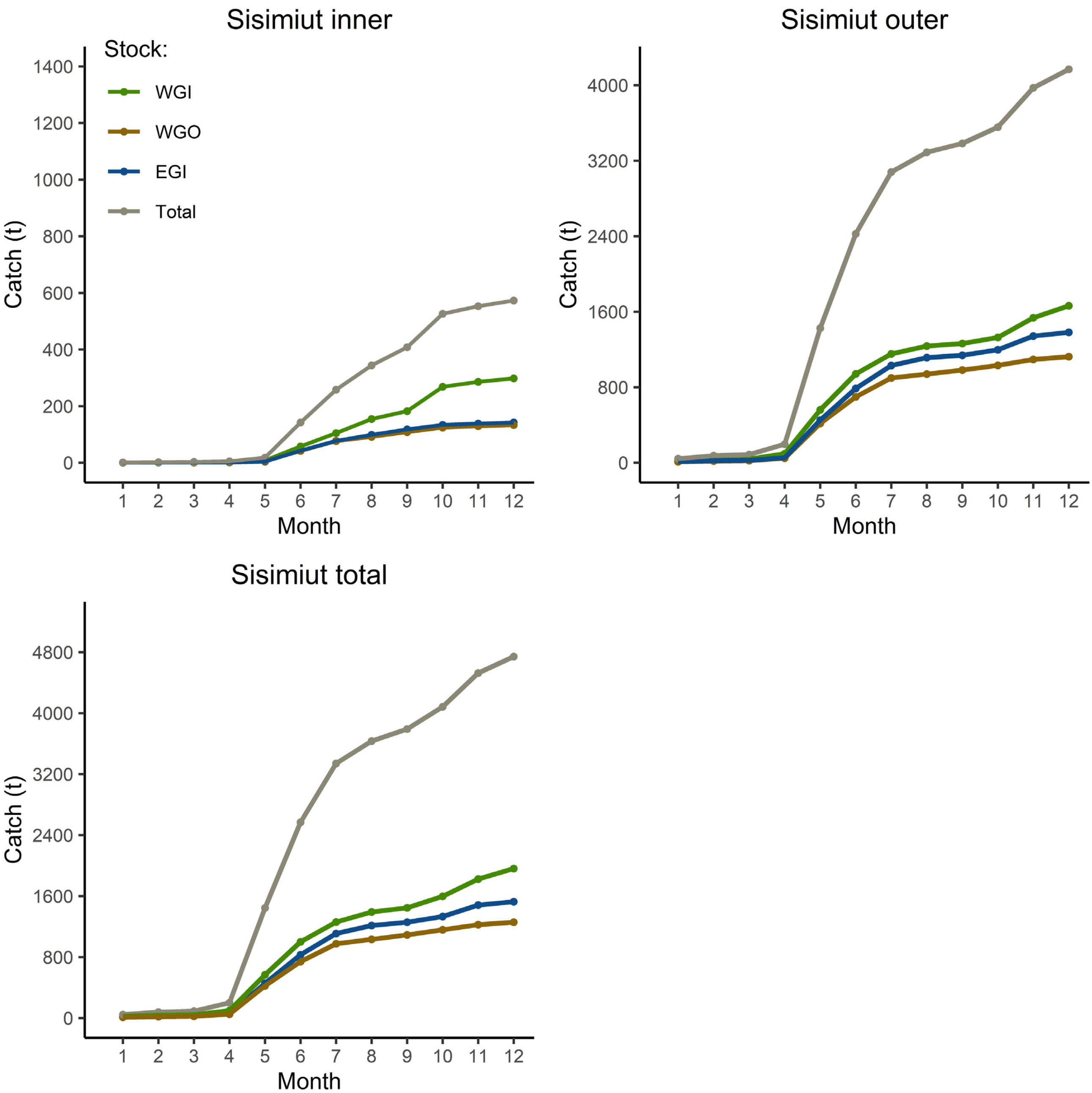

Figure 7. Cumulative catch composition of total and stock specific catches of cod stocks from WGO, WGI, and EGI through 2017 in Sisimiut.

Table 6. Catch allocated to each cod stock based on a detailed vs. a simple approach in Nuuk and Sisimiut in 2017. WGI cod, WGO cod, and EGI cod.

	Nuuk				Sisimiut			
	Detailed approach	Detailed approach	Simple approach	Simple approach	Detailed approach	Detailed approach	Simple approach	Simple approach
	tons	%	tons	%	tons	%	tons	%
EGI	685	21	629	19	1 524	32	1 233	26
WGI	1 537	46	1 656	50	1 961	41	2 181	46
WGO	1 090	33	1 027	31	1 257	27	1 328	28
Total	3 312		3 312		4 742		4 742	

of WGO and EGI as high as 400 000 t, and regularly more than 200 000 t over several decades (Bonanomi *et al.*, 2015; ICES, 2019b). A rebuilding strategy for the WGO stock appears to be incompatible with a maximum utilization of the WGI stock. Possibly, the current WGI exploitation pattern maintains the WGO stock at a relatively low level by continuing to target mature WGO individuals, thereby suppressing any positive development that would otherwise be expected given the current warm regime normally favourable for cod in Greenland (Stein and Borovkov, 2004). The inshore fishery has been a *de facto* unregulated fishery over the past decades since more quotas have been allocated when the TAC was exhausted. This, together with an experimental quota in the WGO area, could explain why the WGO stock remains at a low level, despite decades of near moratorium conditions in offshore sea areas of West Greenland (ICES, 2019b). In this context, it is also noteworthy that other North Atlantic cod stocks in Iceland and in the Barents Sea have seen a dramatic increase in recent decades, presumably partly as a result of favourable environmental conditions. In both cases, the estimated fishery induced mortality is approximately half of that estimated for the WGI area (ICES, 2019b).

Stock dynamics through the year

Fjord section

Because the most important inshore spawning ground in Nuuk and Sisimiut are found in the inner part of the fjord systems (Storr-Paulsen *et al.*, 2004), we *a priori* expected that the inner fjord sections, at least in the spawning period (April–May), would have a significantly higher proportion of WGI cod compared to mid and outer fjord sections. This was, however, not the case. In Nuuk, the proportions did not vary significantly, but the highest proportion of WGI was found in the outer part of the fjord system. In Sisimiut, there was a significant difference between fjord sections, with highest proportion of WGI in the inner part of the fjord. However, cod spawning grounds can be very local. Nordeide (1998) documented that Northeast Atlantic cod and Norwegian Coastal cod simultaneously stay at the same local spawning ground within an area of less than 0.012 km^2. The spawning grounds in the Nuuk fjord are indeed small. Swalethorp *et al.* (2016) showed that cod egg density declines rapidly moving out of the very inner creek of the fjord known as the most important spawning area (Storr-Paulsen *et al.*, 2004) and spawning is probably restricted to within this approximately 16 km^2 area compared to the entire Nuuk fjord of more than 2000 km^2. Furthermore, it has been documented that different stocks can be in the same spawning ground simultaneously, but with different depth preferences (Nordeide, 1998). Therkildsen *et al.* (2013) specifically targeted spawning cod in the Nuuk fjord system to establish a genetic baseline and found that cod from several samples were almost exclusively WGI cod. However, to specifically map more areas and times with clean WGI catch composition would require a high-resolution sampling design outside the scope of this study.

Season

We found no clear differences in stock proportions between "Summer" and "Winter." However, a higher proportion of WGI was found during winter in both Nuuk and Sisimiut (Figure 4). We expected to see a seasonal change in proportion since earlier studies have described a feeding migration from the offshore to the inshore area (Hedeholm *et al.*, 2017). The migration could, possibly, be linked to a capelin migration. In Western Greenland, capelin spawn in the inshore area from April/May to June/July and Atlantic cod is one of the dominating fish predators on capelin (Friis-Rødel and Kanneworff, 2002). Furthermore, fishermen describe a yearly cycle with cod moving out of reach for the inshore fishery into deeper water or more open coastal areas during autumn, and they do not return until spawning in March and April (Qualitative interview, unpublished data). Similar seasonal feeding migrations have also been documented for cod in the Gulf of Maine (Zemeckis *et al.*, 2017), the Baltic Sea (Nielsen *et al.*, 2013), Scotland (Neat *et al.*, 2006), and Norway (Godø, 1995). Accordingly, the link between migration and feeding for cod in West Greenland appears to be well-supported, but this is not significantly reflected in the fishery, at least with the sampling intensity used in the present study.

Size categories

The significant difference in stock proportions between "Small" and "Large" cod in Nuuk was mainly caused by the WGI stock being more prevalent in "Small" cod (60%) compared to "Large" cod (40%), with the reverse change in EGI and WGO. This shift was not seen in Sisimiut. One explanation is that the shift was simply caused by different year–class strengths of the different mixing stocks i.e. the higher proportion of small WGI was due to relatively stronger recent inshore year–classes. The change was consistent across the year and was not driven by an extreme value in a particular month/period. This suggested that it was unrelated to spawning of the WGI stock and support the hypothesis of difference in year class strength. Another explanation is that we based the maturity on a maturity function for East Greenland, and not direct observations of the samples fish, since the gonads were removed from the fish before landing. If EGI cod mature later when they are the slightly colder west Greenland water than they would otherwise, the reason behind the missing size related difference of proportion could be because the sampled fish has not yet reached maturity.

Alternatively, the differences could be caused by a size-related migration behaviour, where larger cod from EGI and WGO may have a higher propensity to migrate into the fjord with increasing size or somehow become relatively more susceptible to the fishery than the WGI. Since earlier studies of migration (Storr-Paulsen *et al.*, 2004; Bonanomi *et al.*, 2016) show that large cod are more inclined to initiate a spawning migration to their natal spawning area, and in this study the effect would be caused by larger fish from the northern part of West Greenland migrating to more southern (WGO) and Eastern (EGI) spawning grounds. A similar effect may not be seen in Sisimiut because it is located further north. To address this in detail, maturity data on the caught cod are needed, however, such data were not available for this study.

Spatio-temporal harvest and catch composition

The observed differences in the distribution of the catches among fjord sections was due to different fishing dynamics of the two systems. In Nuuk, the fishery typically starts in the inner part of the fjord, but as the season progresses and the weather conditions allow for smaller dinghies with a shorter operation radius to take part in the fishery, the fishing intensity moves outwards. In Sisimiut, most of the fishery takes place in the outer part of the fjord throughout the year and the distance between the fishing area and the factory is not as long as in Nuuk. Thus, the differences in location of the fishery in the two fjord areas can explain their differences in the development of the cumulative catches in different fjord sections.

Challenges for a single stock advice and effects of migration

Despite significant differences in proportions between fjord section and cod size in Nuuk, no pragmatic management approaches are likely to result in a clean single stock fishery in the inshore area as a whole. Hence, continuous monitoring of stock proportions is needed to provide detailed knowledge on stock specific catches. The monitoring can follow either a detailed or simple approach, depending on available resources, but due to the limited changes through the year, sampling should preferentially target months with the highest fishing intensity. Such a relatively simple genetic monitoring setup will significantly improve future advice by including stock proportions in the assessment and allowing for adaptive management. The assessment can, with relatively little effort, be even further improved by monitoring incoming cohorts based on genetic sampling from existing surveys. The importance of including knowledge of stock proportions in assessment and management of mixed stocks is also highlighted in other fisheries. The Baltic Sea cod stocks were until 2015 treated as separate stocks despite their overlapping distribution (Hüssy *et al.*, 2015), as it is the case for cod stocks in Greenland today. In recognition of this issue, a new assessment procedure that basically splits the catches into the different stocks was implemented, and the advice is adjusted for each stock accordingly (ICES, 2019a). The implementation of a similar approach for the WGI fishery is recommended. A similar scenario is seen in the western Baltic herring fishery, where challenges with stock splitting have led to uncertainties in the stock assessment and skewed stock perceptions (Gröhsler *et al.*, 2013; ICES, 2021b). Also, difficulties in splitting herring from sprat especially in the industrial fishery has been highlighted as a potential problem for the perception of the stocks and needs further investigation (ICES, 2021b). In Greenland and Iceland waters (ICES subareas 5 and 14) the fishery on golden redfish (*S. norvegicus*) is managed as a single population unit (ICES, 2016), even though the presence of cryptic species has been documented (Saha *et al.*, 2017). Valid for all examples is that different stocks can have different tolerance to fishing intensity, which potentially can lead to unintentionally over- or under-exploitation (Cadrin, 2020). With detailed knowledge of stock proportions, the risk can be reduced.

With this new information on the year-round stock proportions in the inshore fishery, management should not be focused solely on the inshore, WGI, stock. Half of the catch was comprised of cod from other stocks; thus, the inshore fishery is not only highly dependent on, but also significantly affecting, these stocks, particularly in relation to the vulnerable WGO stock. A failure to implement a more holistic approach to stock management increases the risk of sequentially fishing down stocks, if the mixed stock proportions change with changing stock abundance. If the WGO stock is significantly reduced due to poor recruitment, then continuous inshore catches at the same magnitude can severely deplete the local WGI stock as it will constitute a larger part of the catch. This can lead to a detrimental overexploitation of the WGI stock, which is the most likely explanation of the very rapid declines in the inshore stock biomass documented in the late 1970s and 1980s (ICES, 2019b). We reiterate that it is essential for managers to consider the effects of the mixed-stock fishery by applying a more holistic perspective. Similarly, scientific advisors must be more specific when formulating advice for mixed stock fisheries i.e. the advice must be defined such that it is clear whether it regards a specific biological stock (population) or an area defined stock, and what the effect of a certain catch level will be on both the targeted (inshore) stock and on other "bycatch" stocks.

The current scientific advice for the WGO stock is zero catch. If managers were to follow this advice, the inshore fishery would be severely limited by the WGO stock occurrence. The same situation is relevant for the EGI stock. Tagging studies have repeatedly shown, that the onset of maturity triggers a unidirectional migration from West to East Greenland of the EGI stock (e.g. Hovgård and Christensen, 1990; Storr-Paulsen *et al.*, 2004; Bonanomi *et al.*, 2016). Hence, the current decline in the EGI stock in Greenland waters (ICES, 2019b) should take into consideration that a considerable amount (i.e. approximately 6240 t in 2017) of the spawning stock is caught in WGI waters prior to the spawning migration to East Greenland and Iceland. In comparison, the advised catch in East Greenland was 7930 t in the same year (ICES, 2019b). Thus, the bycatch of the EGI in West Greenland is comparable to the advised fishery in East Greenland.

Conclusion

We demonstrate by using Greenland cod reference populations and fishery samples the need to allocate catches at the biological stock level and show that the application of high-resolution genetics is the only reliable, and therefore, necessary tool. A future genetic monitoring set-up including both the fishery and survey samples would make it possible to conduct a stock-based assessment, considering both fishing pressure on the specific stock and variation between years. This approach will allow for annual advice that include stock dynamics that were earlier masked in the indiscriminate overall assessment of stocks and increase the probability of the Greenland cod fishery returning to a more profitable state. Despite some significant difference in stock proportions in Nuuk, no specific fjord section or season in either area could even remotely be defined as single stock fishery. Hence, with the current knowledge it is not possible to significantly optimize the catch of a specific stock in the fishery, which further highlights the need for continuous monitoring that should include a historical perspective to provide stock specific time series data for assessment purposes.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Authors' contributions

HTC, FR, and RBH contributed to the conception of the paper and designed and conducted the data analysis. EEN was responsible for the genetic analysis and interpretation of results. EHN was responsible for the coordination and collection of data. AR contributed to the interpretation of results. HTC led the writing of the manuscript and all authors contributed to writing and editing the manuscript and approved the final draft.

Data availability

Part of the data is owned by a third party. The data underlying this article were partly provided by the Greenland Fisheries License Control Authority (GFLK) by permission. Data can be shared on request to the corresponding author with permission of GFLK.

Acknowledgements

We are grateful for the collaboration with the Royal Greenland factories in Nuuk and Sisimiut, and to the fishermen and their big effort in collecting samples. Also, the contributions by technicians at the Greenland Institute of Natural Resources and DTU Aqua is greatly appreciated. Lastly, we want to thank the editor and two anonymous reviews for their valuable input to the manuscript. The project was funded by the Greenland Institute of Natural Resources.

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Handling Editor: Daniel Gomez-Uchida